

This is the peer reviewed version of the following article: Pellegrini, A. F. A., Anderegg, W. R. L., Paine, C. E. T., Hoffmann, W. A., Kartzinel, T., Rabin, S. S., Sheil, D., Franco, A. C. and Pacala, S. W. (2017), Convergence of bark investment according to fire and climate structures ecosystem vulnerability to future change. *Ecol Lett*, 20: 307–316, which has been published in final form at <https://doi.org/10.1111/ele.12725>. This article may be used for non-commercial purposes in accordance With Wiley Terms and Conditions for self-archiving.

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

Adam F. A. Pellegrini^{1*+}, William R. L. Anderegg^{1,2}, C. E. Timothy Paine³, William A. Hoffmann⁴, Tyler Kartzinel^{1,5}, Sam S. Rabin¹, Douglas Sheil⁶, Augusto C. Franco⁷, & Stephen W. Pacala¹

1) Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA

2) Department of Biology, University of Utah, Salt Lake City, UT, USA

3) Biological and Environmental Sciences, University of Stirling, Stirling, UK

4) Department of Plant and Microbial Biology, North Carolina State University, Raleigh, NC, USA

5) The Nature Conservancy, Arlington, VA, USA

6) Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway

7) Department of Botany, Universidade de Brasília, DF, Brazil

+ current address: Department of Earth System Science, Stanford University, Stanford, CA, USA

*correspondence to afapelle@stanford.edu, 6126695952

Running title: Fire tolerance in savanna and forest biomes

Keywords: fire ecology, functional traits, bark thickness, global change, savanna, forest

Data accessibility: Unpublished trait data will be made available in Dryad.

Type of article: Letter

Statement of 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, ACF contributed data. AFAP wrote the first draft of the paper and all authors contributed comments.

Words/Figures: Main text: 5,473; Abstract: 150; 4 figures; 0 tables; 50 references

Accepted for publication in *Ecology Letters*, published by Wiley-Blackwell.

1 Abstract

2 Fire regimes in savannas and forests are changing over much of the world. Anticipating the
3 impact of these changes requires understanding how plants are adapted to fire. Here we test
4 whether fire imposes a broad selective force on a key fire-tolerance trait, bark thickness, across
5 572 tree species distributed worldwide. We show that investment in thick bark is a pervasive
6 adaptation in frequently burned areas across savannas and forests in both temperate and tropical
7 regions where surface fires occur. Geographic variability in bark thickness is largely explained
8 by annual burned area and precipitation seasonality. Combining environmental and species
9 distribution data allowed us to assess the vulnerability to future climate and fire conditions:
10 tropical rainforests are especially vulnerable, whereas seasonal forests and savannas are more
11 robust. The strong link between fire and bark thickness provides an avenue for assessing the
12 vulnerability of tree communities to fire and demands inclusion in global models.

13 **Introduction**

14 How plant communities respond to perturbations imposed by novel fire regimes is an
15 important uncertainty in predicting the reaction of ecosystems to future global change (Cochrane
16 *et al.* 1999; Westerling *et al.* 2006). Increased burning in ecosystems that rarely experienced fire
17 historically, such as moist tropical forests (Nepstad *et al.* 1999), can result in rapid ecosystem
18 degradation due to the lack of woody plant species with fire-tolerance traits (Uhl & Kauffman
19 1990; Cochrane *et al.* 1999). The loss of woody plant biomass during fires produces substantial
20 carbon emissions (van der Werf *et al.* 2010), and may act to accelerate climate change, which is
21 critical given projections of increasing fire occurrence in future climates (Moritz *et al.* 2012) .
22 Consequently, predicting the future of the terrestrial carbon sink depends on the ability of
23 ecosystem models to accurately capture the fire tolerance of woody plants to future fire regimes
24 (Huntingford *et al.* 2008).

25 Fire can be a strong selective force, and many tree species have evolved traits to better
26 tolerate frequent burning and intense fires (Simon *et al.* 2009; Rosell *et al.* 2014). Variability in
27 plant traits related to fire tolerance can determine the response of ecosystems to fire (Rogers *et*
28 *al.* 2015), thus requiring a need to understand both the current distribution of traits as well as the
29 mechanisms that generate their variability. The evolution of fire tolerance traits within numerous
30 and widely distributed plant species and clades may allow communities containing those taxa to
31 be more robust to increasing fire frequency (Pellegrini *et al.* 2016). Alternatively, if the global
32 distribution of taxa that have evolved fire tolerance traits is limited to specific biomes or plant
33 lineages, then some communities may be especially vulnerable. Consequently, understanding the
34 mechanisms leading to the evolution of fire tolerance traits will give insight into potential
35 constraints on the capacity of ecosystems to respond to changes in fire regimes.

36 In addition to the vulnerability of individual plant species, the distribution of fire
37 tolerance traits in a community is important for determining vulnerability of an ecosystem to
38 increased burning. On short timescales (i.e., years to decades), the potential for loss of woody
39 plant biomass and carbon storage is determined largely by the vulnerability of individuals
40 present in a community (Uhl & Kauffman 1990). Variability in the distribution of fire tolerance
41 traits within a plant community is important, however, as it determines the overall proportion of
42 plant species vulnerable to intensifying fire regimes as well as the potential for fire-tolerant
43 species to replace fire-sensitive ones (i.e., ecological filtering; (Cavender-Bares & Reich 2012)).
44 Moreover, trait-environment relationships can reveal how environmental conditions may filter
45 species according to their traits, providing insight into the vulnerability of communities to
46 change (Diaz *et al.* 1998). Consequently, we can estimate the ability of plant communities to
47 tolerate increased burning by combining knowledge on the present-day distribution of fire-
48 tolerance traits with projections of future fire regimes.

49 Here we examine global patterns of a key woody plant trait, bark thickness, which
50 confers fire tolerance for trees in ecosystems with surface fire regimes such as xeric pine and oak
51 forests (Harmon 1984); rainforests (Brando *et al.* 2012); savannas (Hoffmann *et al.* 2009; Lawes
52 *et al.* 2011)). Bark is important because it helps protect the stem from overheating during a
53 surface fire, conferring resistance to losses of aboveground biomass through either complete
54 mortality or topkill. Although other traits can also influence whether fire actually kills a tree,
55 such as the ability to resprout and location of buds inside the stem (Clarke *et al.* 2010; Pausas *et*
56 *al.* 2016), bark thickness has been shown in numerous studies across multiple ecosystems
57 (Harmon 1984; Van Nieuwstadt & Sheil 2005; Hoffmann *et al.* 2009; Brando *et al.* 2012;
58 Pellegrini *et al.* 2016) to be a critical trait for the vulnerability of plant bole biomass – the largest

59 carbon storage pool in trees – to fire (explaining the majority of the variability in biomass losses
60 with $r^2 \geq 0.80$). Crown fire regimes are also important for a number of ecosystems, where plants
61 contain a suite of other adaptations to either resist crown char (by growing tall and dropping
62 branches) or quickly re-grow after a stand-replacing fire (through adaptations like serotinous
63 cones, e.g., (Rogers *et al.* 2015)). However, here we focus on ecosystems with surface fire
64 regimes.

65 We examine patterns of bark thickness to better understand ecosystem vulnerability to
66 fire by addressing three questions: (i) how does bark thickness differ across species in different
67 biomes and regions? (ii) to what degree do differences in fire frequency and fire-climate
68 interactions filter species' relative bark thickness? and (iii) based on current bark thickness
69 distributions and projected changes in climate and fire, how does the vulnerability to future fire
70 regimes differ across savannas and forests worldwide? Although absolute bark thickness
71 generally increases with stem size, plant species differ in their relative investment in bark.
72 Consequently, we quantify bark investment as the thickness of bark at a standardized stem
73 diameter (i.e., relative bark thickness).

74

75 **Methods**

76 *Dataset compilation*

77 We compiled a dataset of bark thickness investment across 572 abundant woody plant
78 species distributed across biomes worldwide from published and unpublished sources (Table S1).
79 To account for the influence of stem size and allometric equations reported (which varied from
80 linear to saturating), we calculated bark thickness at three stem diameters —10cm, 20cm, and
81 30cm—which spanned the critical range of stem size over which trees are most vulnerable to

82 topkill and comprise a large proportion of tree biomass in savannas and forests (Uhl & Kauffman
83 1990). We also verified that our results were robust to alternative calculations of bark thickness
84 (*Supplementary Information, SI*).

85

86 *Comparison among biomes and continents*

87 We classified species as being associated with savanna vs. forest biomes because these
88 biomes have different fire regimes and woody plant species tend to specialize in either savanna
89 or forest biomes, but not both (Hoffmann *et al.* 2012). Savannas are defined as ecosystems with
90 intermediate tree cover (20-80%) and a continuous grassy layer while forests have complete
91 woody cover and grasses are minimal to absent (Staver *et al.* 2011). Species were grouped as
92 specializing on savanna or forest biomes based on how they were categorized by the paper
93 authors. In all cases where we compare bark thickness between savanna and forest biomes, we
94 are referring to the comparison of species classified as specializing on either biome.

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

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

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

113

114 *Establishing environmental conditions for each species*

115 We determined the spatial distribution of species using field georeferenced locations
116 from the Global Biodiversity Information Facility (GBIF) to obtain global occurrence data (Fig.
117 S1). These distribution data were combined with burned area estimates and climate data to obtain
118 the average environmental conditions over the distribution of each species. In all cases, the
119 distribution of the mapped areas cover the complete ranges of all the included species. For fire,
120 we analyzed two burned area datasets spanning 10 and 19 years, which are currently the longest
121 available datasets on global fire patterns. This assumes that relatively recent spatial patterns of
122 fire frequency structure patterns in bark thickness. The first fire dataset is the annual burned area
123 product from the Global Fire Emissions Database 3 with small fires (spanning 2001-2010)
124 (hereafter referred to as GFED3s), which aims to account for detection of fires in closed-canopy
125 forests (Randerson *et al.* 2012; Giglio *et al.* 2013). The second is the annual burned area product
126 from GFED4, which spans 1997-2015, but does not yet have the correction for small fires. We

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

131 Here we were concerned with the climate factors that have the potential to influence fire
132 behavior. Consequently, we focused on precipitation partitioned into the driest and wettest
133 quarter obtained via WorldClim (Hijmans *et al.* 2005). Higher precipitation in the driest quarter
134 can increase fuel moisture and thus reduce burned area and intensity. On the other hand, higher
135 precipitation in the wettest quarter can increase fire intensity in biomes with grasses (which grow
136 but then dry out, becoming highly flammable in the dry season (Govender *et al.* 2006)).

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

144

145 *Comparison across taxonomic groups*

146 We used linear mixed-effects models to compare the bark thickness of savanna and forest
147 species nested within their corresponding genera and families, using either family or genus as
148 random effects. Consequently, this analysis is only performed on the species where both savanna
149 and forest species are present in the same genus or family. We also performed a regression

150 between the mean bark thickness of savanna species and forest species grouped within each
151 genus and family. This was used to determine whether the bark thickness of savanna species was
152 correlated with the bark thickness in forest species.

153

154 *Vulnerability to future changes*

155 To estimate the vulnerability of plant communities to future changes in climate and fire,
156 we aggregated individuals into 1°x1° gridcells across the globe using the GBIF distribution data
157 to calculate mean bark thickness values for each gridcell (incorporating the abundance of
158 individuals within a species and the bark thickness for that species). We performed this
159 aggregation process separately for savanna and forest species because of the potential biome-by-
160 climate interaction. We refer to these spatially aggregated values as the “community” bark
161 thickness. Climate and burned area data were also calculated for each gridcell. We fit a
162 generalized additive model between bark thickness and environmental data across all gridcells
163 for both savanna and forest communities (statistical fits and a verification that our results are
164 robust to spatial autocorrelation are in the *SI*).

165 We then used the regressions between climate, fire, and community bark thickness to
166 project the future expected distribution of bark thickness according to future fire and climate
167 conditions. Future climate conditions were determined from five climatic models obtained via
168 CMIP5 outputs for 2070 RCP8.5 scenario (*SI*). Future fire conditions come from a recent output
169 of annual burned area from LPJ-GUESS-SIMFIRE (Knorr *et al.* 2015), which incorporates
170 future climates, human populations, and fuel loads (*SI*), for 2071-2100 RCP8.5 scenario. We
171 chose the high emissions scenario to quantify an upper bound on potential changes in fire
172 regimes. We averaged forecasted values across all models within each grid cell. To evaluate

173 climate uncertainty, we used the standard deviation among climate model precipitation
174 projections to calculate “wet” and “dry” (+1 vs. -1 standard deviation precipitation, respectively)
175 future scenarios. The potential role of uncertainties in fire projections are presented in the
176 discussion.

177 The robustness of communities to change was then quantified by comparing the current
178 distribution of bark thickness within gridcells with the expected future distribution. Specifically,
179 we used the log-transformed community means and variances to generate a normal distribution
180 of bark thicknesses for each gridcell. Next, we used the projected community mean bark
181 thicknesses to generate a normal distribution curve of future bark thickness for each gridcell,
182 assuming that present day variances remained unchanged. The ability of a particular community
183 to achieve the future expected bark thickness was quantified as the area under the two probability
184 densities (Fig. S2), which is known as the overlapping coefficient (OVL, (Inman & Bradley
185 1989)). Here we interpret the OVL to be a measure of robustness because it estimates the
186 fraction of individuals with bark thicknesses compatible with future conditions. Consequently,
187 the OVL estimates the potential for an ecosystem to adjust to more extreme conditions through
188 shifts in the abundance of its current species pool. Importantly, this metric estimates only the
189 relative robustness of gridcells, it does not predict the percent of individual trees that will be lost.

190

191 **Results**

192 Across the globe, investment in thick bark is a consistent adaptation to fire-prone
193 environments. At the biome scale, bark was three-fold thicker in tree species specialized in fire-
194 frequent savannas vs. fire-infrequent forests (Fig. 1, Tables 1,S2). This pattern was observed
195 across Africa, Australia and the Americas, each of which contain extensive savanna-forest

196 boundaries (Fig. 1, Tables 1,S3), and was robust to variation in stem size and alternative
197 calculations of relative bark thickness (Fig. S3, Table S3). We confirmed that savanna species
198 differed broadly from forest species in their characteristic fire regimes using remotely sensed
199 estimates of annual burned area from both the long time series ($F_{1,569}=154.8$, $p<0.0001$) as well
200 as the shorter time series that corrects for small fires ($F_{1,570}=187$, $p<0.0001$).

201 Within the broad global pattern, the differences in bark thickness between species
202 specialized in savanna vs. forest differed in magnitude across regions and continents (Figs.
203 2,S4,S5, Tables S2-S4). In the tropics, savanna species had 3.3-fold thicker bark than forest
204 species, while in temperate regions this difference was only 1.4-fold (Table S2), consistent with
205 the greater between-biome differences in the fire frequency characterizing species' distributions
206 in the tropics (Fig. 2).

207 Among continents, there was substantial variability in the bark thickness of species both
208 in the savanna and forest biomes (continent-by-biome interaction: $F_{4,562}=15.6$, $p<0.0001$, Figs.
209 1,S5, Tables S2,S4). As a result, Australia and South America had the starkest contrast between
210 biomes, with savanna species having 5.3- and 3.8-fold thicker bark than forest species,
211 respectively (Figs. 1,2,S5, Tables S2,S4). On the other hand, North American and African
212 savanna species were only 1.4- and 1.8-fold thicker than forest species (Figs. 1,2,S5, Table S4).
213 Only in Asia did we not find a significant difference between biomes (Table S3), although there
214 were data on only a few savanna species ($n=5$). Consistent with the continent-by-biome
215 interaction for bark thickness, we also found a significant interaction for fire frequency
216 ($F_{4,562}=4.54$, $p=0.0013$). Subsequently, the contrast in bark thickness between savanna and forest
217 species was largely consistent with the contrast in fire frequencies that characterized their
218 distributions (Fig. 2); we quantitatively test for the relationship between bark and fire below.

219 A more detailed evaluation of the habitat preferences of species in North America
220 revealed qualitatively similar results: species that that predominantly occurred in savanna
221 habitats experienced a higher frequency of burning than those found only in forests (GFED3s:
222 $F_{2,74}=9.15$, $p=0.0002$, GFED4: $F_{2,74}=10.75$, $p<0.0001$); correspondingly, species that
223 predominantly occurred in savannas tended to have 1.4-fold thicker bark than those found only
224 in forests ($F_{2,74}=4.1$, $p=0.020$), in spite of North American forest species experiencing relatively
225 frequent burning (*SI*, Fig. S6).

226 Globally, variation in bark thickness across species could be explained by the fire regime,
227 climate, and the interaction between climate and fire that characterized a species' distribution.
228 First, annual burned area alone explained 20% of the global variation in bark thickness, with
229 bark thickness increasing as a nonlinear function of the annual burned area that characterized a
230 species' distribution (Fig. 3A, Table 1). Second, species found in areas with lower dry season
231 rainfall tended to have thicker bark in both savannas and forests (Fig. 3B, Table 1), likely a
232 result of the negative relationships between dry season moisture and annual burned area ($t= -$
233 3.726 , $p<0.001$) and fire intensity (Govender *et al.* 2006). Third, there was a significant
234 interaction between precipitation in the wet season and the biome a species specialized on; bark
235 thickness of savanna species increased with wet-season precipitation whereas that of forest
236 species decreased (Fig. 3C, Table 1). This climate-biome interaction likely reflects adaption to
237 the higher fuel loads and more intense fires in the more productive wetter savannas, which our
238 remote sensing fire metric cannot capture but has been well established across savannas
239 (Williams *et al.* 1999; Govender *et al.* 2006). All conclusions were robust to variation in stem
240 diameter (Table S5) and the different burned area products (Fig. S7, Table S6,S7). AIC-based
241 model selection illustrated that the most parsimonious model included annual burned area and

242 biome-precipitation interactions and explained 50% of the deviance in bark thickness across all
243 572 woody plant species (Table 1).

244 The potential for crown fire regimes to influence our results was explored by evaluating
245 bark-fire relationships across plant communities in North America, under the assumption that
246 gymnosperm forests have a higher probability of experiencing crown fires and may invest less in
247 bark. Across all species, fire frequency appears to be a less powerful, but still significant,
248 predictor of bark thickness (explaining 7.6% of deviance across species, Table S8). Comparisons
249 between gymnosperm and angiosperm species illustrated no significance difference in bark
250 thickness between groups when we considered either all species or only forest species (*SI*).
251 However, when gymnosperms were analyzed alone, we found that the significant relationship
252 between bark and fire frequency depended on the habitat of a species ($F_{1,24}=5.16$, $p=0.032$), with
253 no relationship between fire and bark in species that occurred only in forests. Consequently, the
254 relationship between fire frequency and bark becomes less significant in habitats prone to crown
255 fires.

256 Comparisons among congeneric species and species within the same family illustrated
257 that bark thickness is well matched to the environment across diverse plant lineages. At the
258 genus level, species associated with the savanna biome had 2.07-fold thicker bark than their
259 congeneric forest species ($n=32$ genera, 156 species, $t=8.46$, $p<0.0001$; Fig. 4A). At the family
260 level, savanna-associated species had on average 2.59-fold thicker bark than forest-associated
261 species in the same family ($n=36$ families, 377 species, $t=20.52$, $p<0.0001$; Fig. S8). Moreover,
262 there was no significant relationship between the bark thicknesses of forest species and the
263 savanna species within either shared genera or shared families ($r^2<0.01$, $p=0.29$ and $r^2<0.01$,
264 $p>0.5$ respectively; Fig. 4B,C), illustrating that the investment in bark of a savanna species is

265 independent from the investment in bark of a forest species within shared clades (i.e., thicker
266 barked savanna species are not significantly more likely to come from thicker barked forest
267 species and vice versa).

268 Fire frequency is expected to increase in many areas that currently contain savanna and
269 forest species. Specifically, 61% and 63% of savanna- and forest-containing grid cells are
270 expected to experience increases in the proportion of area burned each year, respectively, in a
271 high emissions climate scenario (Fig. 5A). However, the robustness of plant communities is
272 forecasted to vary widely among biomes. Communities of savanna species have higher
273 robustness than forest communities, on average, despite having higher fire frequencies and
274 experiencing equivalent relative gains in annual burned area (Figs. 5,S9). Accordingly, the
275 distribution of robustness across grid cells reveals that 93% of savanna gridcells had >50% of
276 individuals with traits consistent with future fire conditions whereas only 62% of forest gridcells
277 exceeded the threshold of 50% (Fig. S9C). The qualitative trends were consistent regardless of
278 different precipitation scenarios, although on average forest communities tended to be less robust
279 under the “dry” scenario (only 55% of cells exceeded the threshold of 50%) and more robust
280 under the “wet” scenario (63% of cells exceeded the threshold of 50%), while savanna
281 community showed little change (both scenarios ~93% of cells above the threshold).

282 Variability in the potential robustness across regions identified sensitive areas, such as
283 moist tropical forests and temperate forests in western North America, which have the lowest
284 forecasted robustness. However, some areas of forest in western North America and transitional
285 tropical forest at savanna-forest ecotones in South America have relatively high robustness (Fig.
286 5C,D), perhaps due to the historical presence of fire in these contrasting forests having selected
287 for thicker barked species (Harmon 1984; Paine *et al.* 2010). Importantly, this analysis of

288 vulnerability is to surface fire regimes, and further analysis of the western North American
289 forests that can experience crown fires in addition to surface fires is warranted. Tree
290 communities in savannas tend to be robust because of the presence of thick-barked species that
291 can persist even with increased annual burned area.

292

293 **Discussion**

294 Convergence of thick bark as a fire tolerance trait reflects consistent filtering of species
295 with thin bark from areas prone to surface fires. The physics that govern how fire kills a tree are
296 consistent across biomes: the insulation provided by bark protects the tissue inside the stem from
297 overheating. As a result, the negative relationship between bark thickness and the loss of
298 aboveground stem biomass in a fire is remarkably similar across ecosystems (Uhl & Kauffman
299 1990; Lawes *et al.* 2011) and is even present in forests that can also experience crown fires such
300 as those in western North America (Harmon 1984). Consequently, plant lineages distributed
301 across the seed plants contain a broad range of bark thicknesses, and species that occur in
302 historically fire-prone environments consistently exhibit high bark thickness, a pattern consistent
303 with the convergent evolution of bark as a fire-tolerance adaptation.

304 The general relationship between frequent fire and investment in bark identified here is a
305 substantial step forward, given that a recent review concluded the paucity of data on bark
306 investment across species limits generalizability (Pausas 2015). Indeed there has been debate on
307 the role of fire and potential climate-fire interactions in determining species' investment in bark
308 (Hoffmann *et al.* 2012; Poorter *et al.* 2014; Rosell 2016). We help resolve this debate by
309 illustrating the substantial role of fire and fire-climate interactions in determining global patterns
310 of bark investment (Figs. 1-3). Additional explanations for variability in bark investment such as

311 defense against pathogens and mechanical stability are likely to contribute to the variability in
312 the relationship between bark investment and fire (Paine *et al.* 2010; Rosell *et al.* 2014). These
313 alternative factors may explain the result in Asia, where we did we not find a significant
314 difference in bark thickness between savanna and forest species. Nonetheless, our relatively
315 simple model predicts 50% of the variance in bark thickness, illustrating the predominant role of
316 fire in structuring the distribution of bark and presenting a framework to gain inference into how
317 certain ecosystems differ in their vulnerability to future fire regimes.

318 Our approach to characterize the climate and fire niches of species using available
319 distribution data allowed us to complement our between-biome analysis with continuous
320 estimates of fire regimes. The consideration of continuous variability in climate and fire
321 illustrated that a substantial amount of the variance among regions within biomes is due to their
322 different fire and climate conditions. The variability in fire frequency and climates that exists
323 across savanna and forest biomes (Lehmann *et al.* 2014) may explain why studies find
324 inconsistent evidence on the degree to which thick bark is an adaptation to frequent fire
325 (Hoffmann *et al.* 2009; Pausas 2015; Rosell 2016). For instance, even within savannas, species'
326 investment in bark increased in areas with more frequent fire and higher wet quarter rainfall (Fig.
327 3B,C). This climate-fire interaction provides one explanation for the relatively greater
328 investment in bark found in the wet South American savannas relative to the drier African
329 savannas (Dantas & Pausas 2013).

330 North America presents a number of interesting contrasts to observations from the
331 tropical savanna-forest ecotones. Many forest species in North America experience relatively
332 frequent fires (Fig. S6), likely leading to their higher investment in bark relative to forest species
333 in tropical forests in Australia and South America (Fig. S4). The comparable fire frequencies in

334 savannas and forests in North America is likely to contribute to the small differences in bark
335 thickness between savanna vs. forest congeners in *Pinus* and *Quercus* (Fig. 4A,S8). Moreover,
336 although we found that the bark-fire relationships were robust in North America where many
337 species experience mixed fire regimes, gymnosperm tree species, which occur in habitats more
338 likely to experience crown fires had a weaker relationship between bark and fire. Specifically,
339 the bark thickness of gymnosperm forest species was not significantly related to fire frequency,
340 which supports the hypothesis that other traits such as reseeded and resprouting are critical in
341 crown fire ecosystems (Keeley *et al.* 2011). Consequently, consideration of other traits will be
342 important for predicting the vulnerability to crown fires and presents a useful expansion to our
343 current study that focused on surface fires.

344 We predict striking differences in robustness across biomes and regions, identifying
345 especially sensitive areas in carbon-dense forests of the wet tropics where increases in fire
346 activity are forecasted to occur throughout a large area where trees invest relatively little in bark
347 (Fig. 5). In contrast, trees in drier tropical forests and the ecotonal areas between savannas and
348 forests invest more in bark (Fig. 3B,C) and are better suited to tolerate the intensifying fire
349 regimes (Fig. 5). Consequently, important heterogeneity exists across forests in different climates
350 not just due to projections in fire activity, but the distribution of species with fire tolerance traits.

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

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

367 The ability to simulate the effects of fire on ecosystem carbon pools will depend on
368 accurately capturing the distribution of traits within and across communities. Many Dynamic
369 Global Vegetation Models, which are commonly used to forecast change in the global carbon
370 cycle, use fire modules that represent fire tolerance traits as static properties of plant functional
371 types, fixed within broad vegetation classifications (Thonicke *et al.* 2010; Li *et al.* 2012). We
372 suggest that using a single bark thickness value per plant functional type fails to capture
373 important heterogeneity in fire tolerance that exist within geographies and ecosystems and may
374 allow for ecological filtering. Consequently, the use of fixed trait means, rather than
375 distributions, may underestimate robustness to fire and lead to large error in estimates of carbon
376 emissions.

377 We show that the widespread convergence of a fire tolerance trait, bark thickness,
378 underpins a striking range of robustness exhibited by vegetation communities to future fire
379 regimes. Estimates of ecosystem robustness can be further improved by considering additional

380 traits of the plant community, variation in the rates and mechanisms of trait evolution, other
381 important disturbances such as drought. Nonetheless, trait-based approaches to assessing
382 robustness to fire have the potential to be powerful predictors of the future response of
383 ecosystems to fire.

384

385

386 **References**

387 1.

388 Barlow, J., Lagan, B.O. & Peres, C.A. (2003). Morphological correlates of fire-induced tree
389 mortality in a central Amazonian forest. *Journal of Tropical Ecology*, 19, 291-299.

390 2.

391 Bond, W.J. & Midgley, J.J. (2001). Ecology of sprouting in woody plants: the persistence niche.
392 *Trends in ecology & evolution*, 16, 45-51.

393 3.

394 Brando, P.M., Nepstad, D.C., Balch, J.K., Bolker, B., Christman, M.C., Coe, M. *et al.* (2012).

395 Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood
396 density and fire behavior. *Global Change Biology*, 18, 630-641.

397 4.

398 Cavender-Bares, J. & Reich, P.B. (2012). Shocks to the system: community assembly of the oak
399 savanna in a 40-year fire frequency experiment. *Ecology*, 93, S52-S69.

400 5.

- 401 Clarke, P.J., Lawes, M.J. & Midgley, J.J. (2010). Resprouting as a key functional trait in woody
402 plants—challenges to developing new organizing principles. *New Phytologist*, 188, 651-
403 654.
- 404 6.
- 405 Cochrane, M.A., Alencar, A., Schulze, M.D., Souza Jr, C.M., Nepstad, D.C., Lefebvre, P. *et al.*
406 (1999). Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science*,
407 284, 1832-1835.
- 408 7.
- 409 Dantas, V.d.L. & Pausas, J.G. (2013). The lanky and the corky: fire-escape strategies in savanna
410 woody species. *Journal of Ecology*, 101, 1265-1272.
- 411 8.
- 412 Diaz, S., Cabido, M. & Casanoves, F. (1998). Plant functional traits and environmental filters at
413 a regional scale. *J Veg Sci*, 9, 113-122.
- 414 9.
- 415 Giglio, L., Randerson, J.T. & Werf, G.R. (2013). Analysis of daily, monthly, and annual burned
416 area using the fourth-generation global fire emissions database (GFED4). *Journal of*
417 *Geophysical Research: Biogeosciences*, 118, 317-328.
- 418 10.
- 419 Govender, N., Trollope, W.S.W. & Van Wilgen, B.W. (2006). The effect of fire season, fire
420 frequency, rainfall and management on fire intensity in savanna vegetation in South
421 Africa. *Journal of Applied Ecology*, 43, 748-758.
- 422 11.

- 423 Harmon, M.E. (1984). Survival of trees after low-intensity surface fires in Great Smoky
424 Mountains National Park. *Ecology*, 65, 796-802.
- 425 12.
- 426 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution
427 interpolated climate surfaces for global land areas. *International journal of climatology*,
428 25, 1965-1978.
- 429 13.
- 430 Hoffmann, W.A., Adasme, R., Haridasan, M., T. de Carvalho, M., Geiger, E.L., Pereira, M.A.B.
431 *et al.* (2009). Tree topkill, not mortality, governs the dynamics of savanna-forest
432 boundaries under frequent fire in central Brazil. *Ecology*, 90, 1326-1337.
- 433 14.
- 434 Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L. *et al.*
435 (2012). Ecological thresholds at the savanna-forest boundary: how plant traits, resources
436 and fire govern the distribution of tropical biomes. *Ecology letters*, 15, 759-768.
- 437 15.
- 438 Huntingford, C., Fisher, R.A., Mercado, L., Booth, B.B., Sitch, S., Harris, P.P. *et al.* (2008).
439 Towards quantifying uncertainty in predictions of Amazon 'dieback'. *Philosophical*
440 *Transactions of the Royal Society B: Biological Sciences*, 363, 1857-1864.
- 441 16.
- 442 Inman, H.F. & Bradley, E.L. (1989). The overlapping coefficient as a measure of agreement
443 between probability distributions and point estimation of the overlap of two normal
444 densities. *Communications in Statistics - Theory and Methods*, 18, 3851-3874.

445 17.

446 Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J. & Bradstock, R.A. (2011). Fire as an
447 evolutionary pressure shaping plant traits. *Trends in Plant Science*, 16, 406-411.

448 18.

449 Knorr, W., Arneth, A. & Jiang, L. (2016). Demographic controls of future global fire risk.
450 *Nature Clim. Change*, advance online publication.

451 19.

452 Knorr, W., Jiang, L. & Arneth, A. (2015). Climate, CO₂, and demographic impacts on global
453 wildfire emissions. *Biogeosciences Discussions*, 12.

454 20.

455 Lawes, M.J., Adie, H., Russell-Smith, J., Murphy, B. & Midgley, J.J. (2011). How do small
456 savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark
457 thickness. *Ecosphere*, 2, art42.

458 21.

459 Lehmann, C.E., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A. *et*
460 *al.* (2014). Savanna vegetation-fire-climate relationships differ among continents.
461 *Science*, 343, 548-552.

462 22.

463 Li, F., Zeng, X.D. & Levis, S. (2012). A process-based fire parameterization of intermediate
464 complexity in a Dynamic Global Vegetation Model. *Biogeosciences*, 9, 2761-2780.

465 23.

- 466 Midgley, J.J. & Lawes, M.J. (2016). Relative bark thickness: towards standardised measurement
467 and analysis. *Plant Ecol*, 217, 677-681.
- 468 24.
- 469 Moritz, M.A., Parisien, M.-A., Batllori, E., Krawchuk, M.A., Van Dorn, J., Ganz, D.J. *et al.*
470 (2012). Climate change and disruptions to global fire activity. *Ecosphere*, 3, 1-22.
- 471 25.
- 472 Nepstad, D.C., Verssimo, A., Alencar, A., Nobre, C., Lima, E., Lefebvre, P. *et al.* (1999). Large-
473 scale impoverishment of Amazonian forests by logging and fire. *Nature*, 398, 505-508.
- 474 26.
- 475 Ondei, S., Prior, L.D., Vigilante, T. & Bowman, D.M. (2015). Post-fire resprouting strategies of
476 rainforest and savanna saplings along the rainforest–savanna boundary in the Australian
477 monsoon tropics. *Plant Ecol*, 1-14.
- 478 27.
- 479 Paine, C.E.T., Stahl, C., Courtois, E.A., Patino, S., Sarmiento, C. & Baraloto, C. (2010).
480 Functional explanations for variation in bark thickness in tropical rain forest trees. *Funct*
481 *Ecol*, 24, 1202-1210.
- 482 28.
- 483 Pausas, J.G. (2015). Bark thickness and fire regime. *Funct Ecol*, 29, 317-327.
- 484 29.
- 485 Pausas, J.G., Pratt, R.B., Keeley, J.E., Jacobsen, A.L., Ramirez, A.R., Vilagrosa, A. *et al.* (2016).
486 Towards understanding resprouting at the global scale. *New Phytologist*, 209, 945-954.
- 487 30.

- 488 Pellegrini, A.F.A., Franco, A.C. & Hoffmann, W.A. (2016). Shifts in functional traits elevate
489 risk of fire-driven tree dieback in tropical savanna and forest biomes. *Global Change*
490 *Biology*, 22, 1235–1243.
- 491 31.
- 492 Poorter, L., McNeil, A., Hurtado, V.-H., Prins, H.H.T. & Putz, F.E. (2014). Bark traits and life-
493 history strategies of tropical dry- and moist forest trees. *Funct Ecol*, 28, 232-242.
- 494 32.
- 495 Randerson, J., Chen, Y., Werf, G., Rogers, B. & Morton, D. (2012). Global burned area and
496 biomass burning emissions from small fires. *Journal of Geophysical Research:*
497 *Biogeosciences*, 117.
- 498 33.
- 499 Rogers, B.M., Soja, A.J., Goulden, M.L. & Randerson, J.T. (2015). Influence of tree species on
500 continental differences in boreal fires and climate feedbacks. *Nature Geoscience*, 8, 228-
501 234.
- 502 34.
- 503 Rosell, J.A. (2016). Bark thickness across the angiosperms: more than just fire. *New Phytologist*,
504 211, 90–102.
- 505 35.
- 506 Rosell, J.A., Gleason, S., Méndez-Alonzo, R., Chang, Y. & Westoby, M. (2014). Bark functional
507 ecology: evidence for tradeoffs, functional coordination, and environment producing bark
508 diversity. *New Phytologist*, 201, 486-497.
- 509 36.

- 510 Scheiter, S. & Higgins, S.I. (2009). Impacts of climate change on the vegetation of Africa: an
511 adaptive dynamic vegetation modelling approach. *Global Change Biology*, 15, 2224-
512 2246.
513 37.
- 514 Simon, M.F., Grether, R., de Queiroz, L.P., Skema, C., Pennington, R.T. & Hughes, C.E. (2009).
515 Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution
516 of adaptations to fire. *Proceedings of the National Academy of Sciences*, 106, 20359-
517 20364.
518 38.
- 519 Staver, A.C., Archibald, S. & Levin, S.A. (2011). The global extent and determinants of savanna
520 and forest as alternative biome states. *Science*, 334, 230-232.
521 39.
- 522 Thonicke, K., Spessa, A., Prentice, I., Harrison, S.P., Dong, L. & Carmona-Moreno, C. (2010).
523 The influence of vegetation, fire spread and fire behaviour on biomass burning and trace
524 gas emissions: results from a process-based model. *Biogeosciences*, 7, 1991-2011.
525 40.
- 526 Uhl, C. & Kauffman, J.B. (1990). Deforestation, fire susceptibility, and potential tree responses
527 to fire in the eastern Amazon. *Ecology*, 71, 437-449.
528 41.
- 529 van der Werf, G.R., Randerson, J.T., Giglio, L., Collatz, G., Mu, M., Kasibhatla, P.S. *et al.*
530 (2010). Global fire emissions and the contribution of deforestation, savanna, forest,
531 agricultural, and peat fires (1997–2009). *Atmos. Chem. Phys*, 10, 11707-11735.

532 42.

533 Van Nieuwstadt, M.G. & Sheil, D. (2005). Drought, fire and tree survival in a Borneo rain forest,
534 East Kalimantan, Indonesia. *Journal of Ecology*, 93, 191-201.

535 43.

536 Westerling, A.L., Hidalgo, H.G., Cayan, D.R. & Swetnam, T.W. (2006). Warming and earlier
537 spring increase western US forest wildfire activity. *Science*, 313, 940-943.

538 44.

539 Williams, R.J., Cook, G.D., Gill, A.M. & Moore, P.H.R. (1999). Fire regime, fire intensity and
540 tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology*,
541 24, 50-59.

542

543

544 **Table 1:** Statistical results from generalized additive models between log bark thickness (for
 545 stems 10cm in size), fire, climate, and biome using model selection. Dev refers to deviance
 546 explained. Mean_fire = annual burned area, Precip_Wetq = precipitation in the wettest quarter,
 547 Precip_Dryq = precipitation in the driest quarter, Biome = biome a species specialized in (either
 548 savanna or forest). The best fit models are highlighted in bold, we utilized the more
 549 parsimonious of the two.

550
 551

<u>Variables included</u>	<u>Dev</u>	<u>AIC</u>
Mean_fire+Precip_Wetq*Biome+Precip_Dryq*Biome	50.20%	930
Mean_fire+Precip_Wetq*Biome+Precip_Dryq	49.90%	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%	1049
Biome	35.50%	1066
Mean_fire+Precip_Wetq+Precip_Dryq	30.20%	1065
Mean_fire	21.60%	1180

552

553

554

555

556

557 **Figure 1: Broad evidence for high bark investment in savanna environments.** Comparison
558 of bark thickness, normalized to a 10 cm stem size, in plant species across the globe. Map was
559 generated using an inverse distance weighted approach to create spatial averages of trait values
560 from GBIF occurrence data within distances of 0.5° around each observation point. Dark grey
561 areas indicate locations that do not contain species distribution/bark thickness data. Color ramp is
562 pivoted on the median of bark thickness to illustrate relative variability across the globe. The
563 box-plot comparisons between savanna and forest species are across four continents that contain
564 extensive savanna-forest ecotones. Statistics and sample sizes are in Table S2.

565 **Figure 2: Difference between savanna and forest species across regions and continents.**
566 Comparison of the ratio of the mean bark investment and fire frequency of savanna vs. forest
567 species between regions (A) and among continents (B). In all cases the ratio is calculated by
568 dividing the savanna value (averaged within either the region or continent) by the forest value.
569 Significance of the interactions were determined by ANOVAs. A) Region-by-biome interaction
570 for fire ($F_{1,568}=26.4$, $p<0.0001$) and bark thickness ($F_{1,568}=26.0$, $p<0.0001$). B) Continent-by-
571 biome interaction for fire ($F_{4,562}=4.54$, $p=0.0013$) and bark thickness ($F_{4,562}=15.6$, $p<0.0001$).
572 For specific comparison among continents, see Table S4.

573 **Figure 3: Key role of environment in determining the relative bark thickness of plant**
574 **species.** A) Relative bark thickness of a species vs. the mean annual burned area of a species'
575 distribution across all species on log-transformed annual burned area and bark thickness data.
576 Solid line represents model fit. Appropriate nonlinear fit determined using model selection
577 (nonlinear fit AIC=1180, linear fit AIC=1209). Bark thickness of savanna and forest species vs.
578 mean climate of a species' distribution for precipitation in the driest quarter (B) and wettest
579 quarter (C), solid line indicates fitted model relationship with the dashed lines indicating 95%

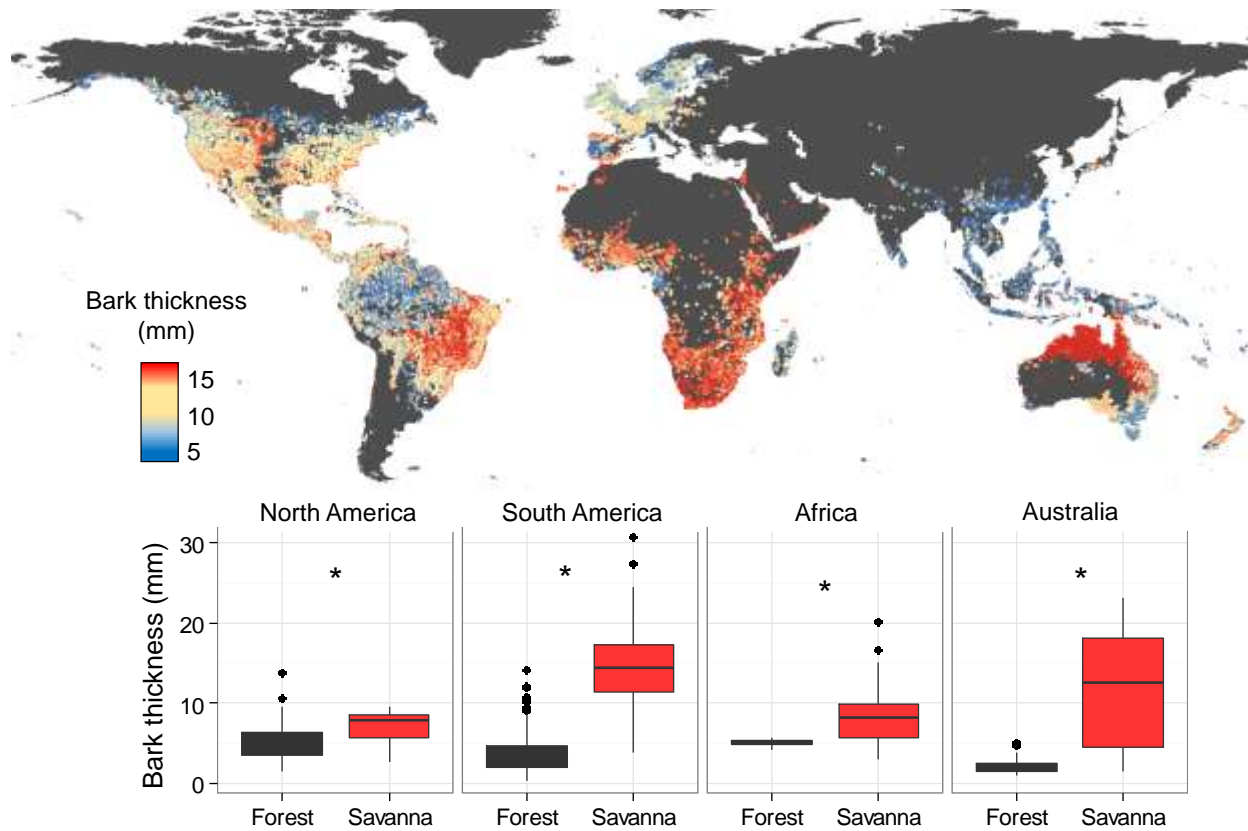
580 confidence intervals. Separate lines were fitted in (C) because of the significant climate-biome
581 interaction. The complete model of annual burned area, precipitation, and biome explained 50%
582 of variation in bark thickness.

583 **Figure 4: Savanna species have consistently thicker bark than their congeners. A)**

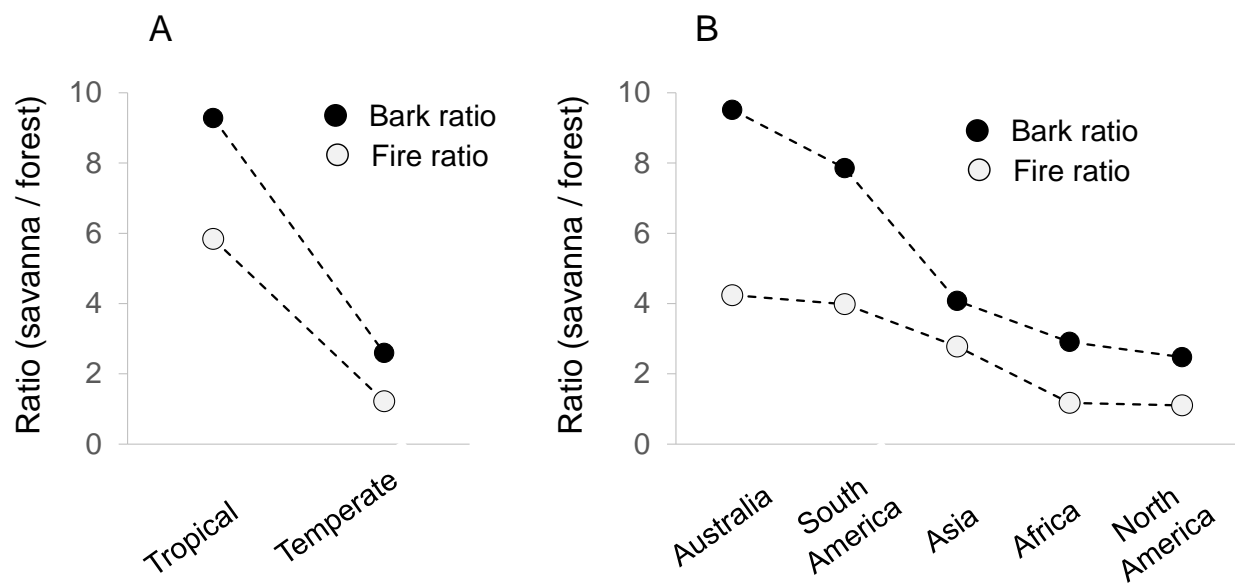
584 Comparison of bark thickness in species specializing in savannas vs. forests in the same genus
585 across 32 genera containing 156 species. Scatter plots comparing the bark thicknesses of savanna
586 vs. forest species within each genus (B) and family (C). Error bars are $\pm 95\%$ confidence
587 intervals. The dashed line illustrates a 1-to-1 line.

588 **Figure 5: Heterogeneity in robustness.** Global distribution of future fire regimes and the
589 overlapping coefficient (OVL) comparing the difference in probability distributions of bark
590 thicknesses between present day and future conditions. A) relative change in annual burned area,
591 expressed as the % of a gridcell burned, between the present day (based on 2001-2010
592 observations) and the future (projections to 2070-2100). B) forecasted annual burned area for
593 year the 2070-2100 period. C-D) OVL between present day and future trait distributions for
594 forest (C) and savanna (D) communities. The spatial overlap of colored points in panels C and D
595 results from the spatial proximity of savanna and forest biomes in those gridcells. Only gridcells
596 projected to experience gains in fire frequency are mapped in panels C and D.

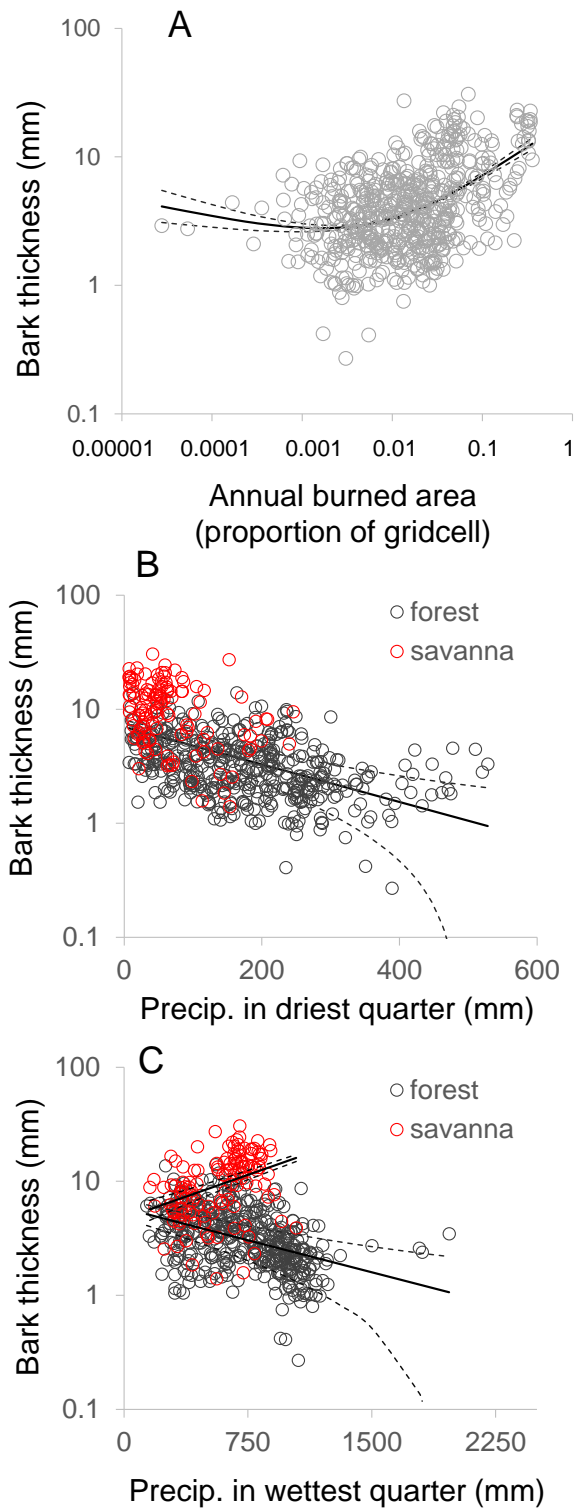
597 **Figure 1:**



598
599
600

601 **Figure 2:**

602

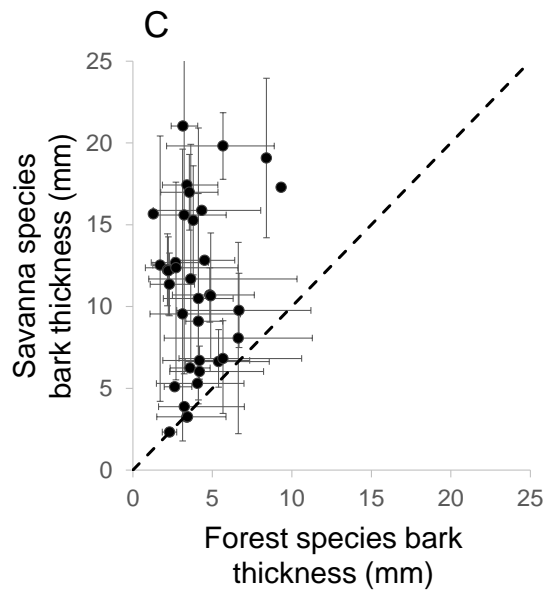
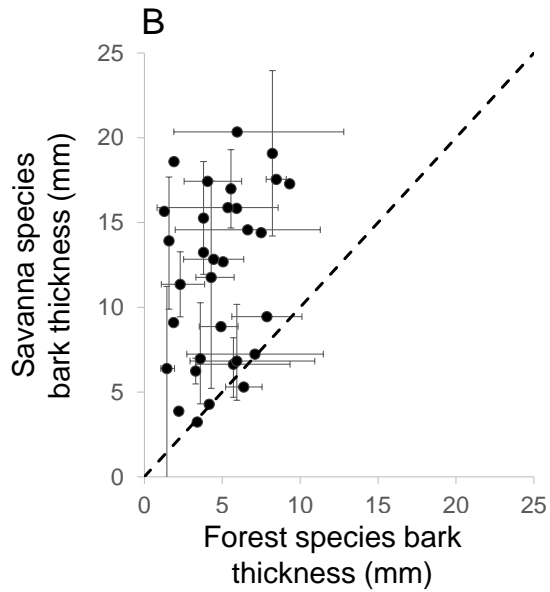
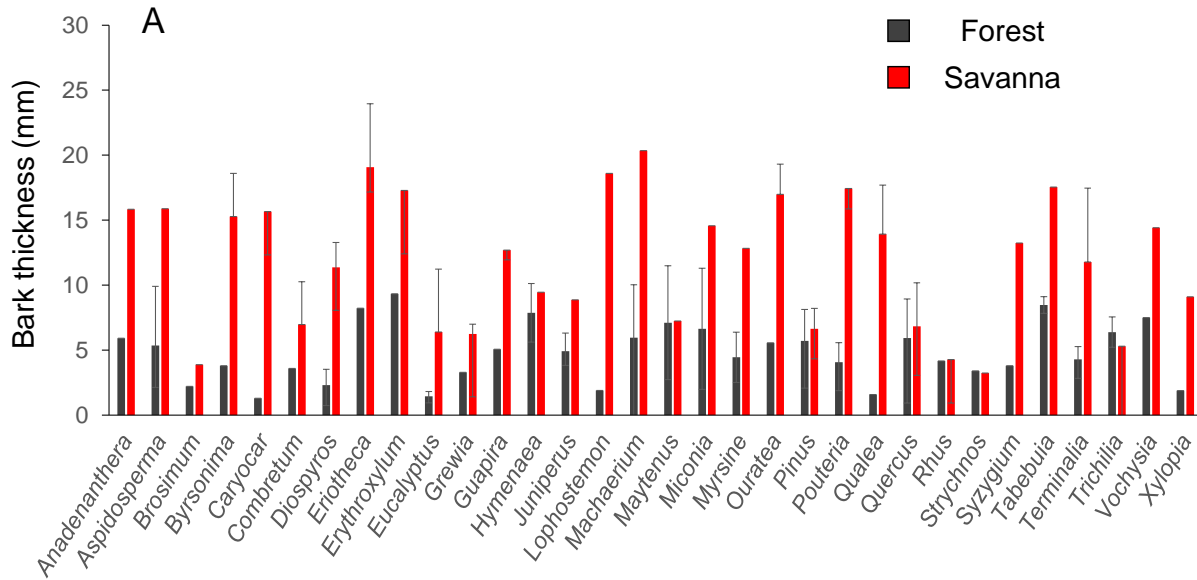
603 **Figure 3:**

604

605

606 **Figure 4:**

607

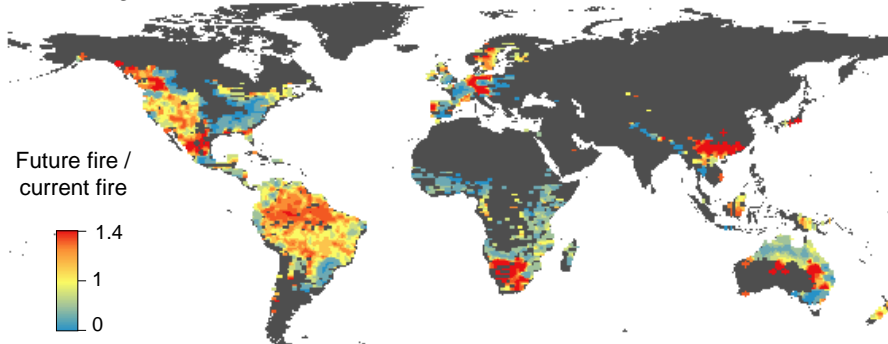


608

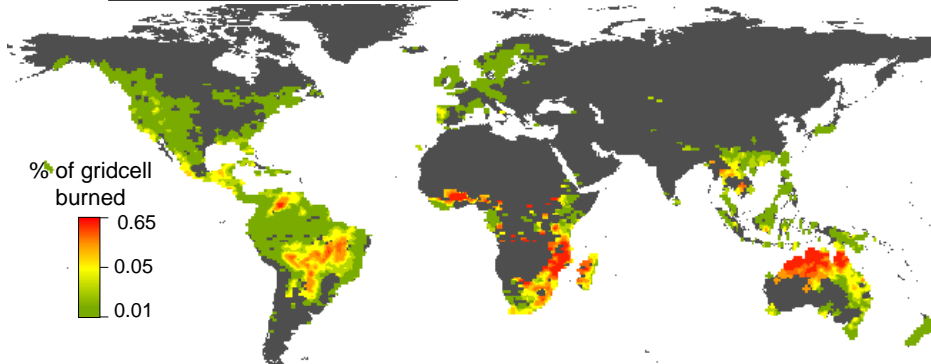
609

610 **Figure 5:**

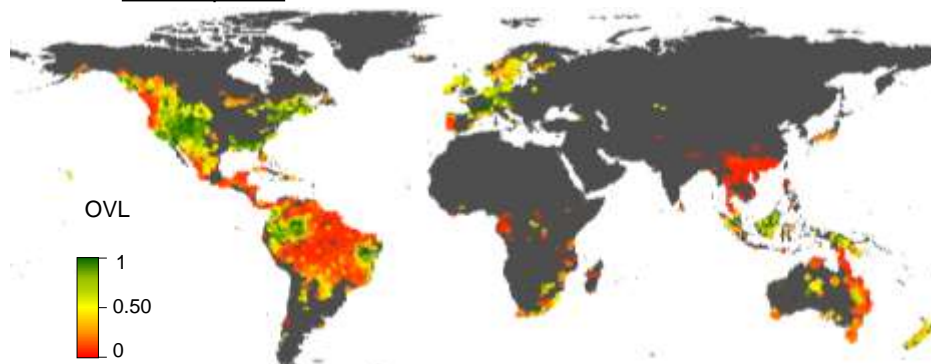
A Change in annual burned area



B Forecasted annual burned area



C Forest species



D Savanna species



611
612
613

Supplemental Information

614

615

616 Different stem allometries and calculations

617 Because absolute bark thickness is positively associated with stem diameter, and
618 published studies have used different allometric equations to relate stem diameter with bark
619 thickness, we calculated bark thickness for identically sized trees to allow for comparability. We
620 calculated bark thickness at three stem diameters—10cm, 20cm, and 30cm. These diameters
621 span the critical range of stem size over which trees are most vulnerable to topkill and comprise
622 a large proportion of tree biomass in savannas and forests (Uhl & Kauffman 1990; Barlow *et al.*
623 2003; Pellegrini *et al.* 2016). The consistency of our results across these stem diameters
624 illustrates our results are robust to the number of different allometric relationships (power, linear,
625 logarithmic, etc.) both across and within studies.

626 Here, we calculate bark thickness based off of relationships determined between bark
627 thickness and the stem diameter measured on the outside of the bark. One alternative way to
628 calculate relative bark thickness is to relate bark thickness with the bole diameter of a stem (the
629 diameter inside of the bark) (Midgley & Lawes 2016). We verified our results were robust to
630 consideration of the ratio between bark and bole diameter by back calculating the bole diameter
631 and calculating bark thickness on stems that were 10cm in bole diameter (we chose 10cm,
632 because that is the primary size of our analysis). We found that in general bark thickness
633 estimated from bole diameter was higher than from the outer bark, which tended to increase in
634 thicker barked species (Fig. S3). However, the majority of our points have litter residual error
635 and a partial re-analysis of the data illustrate that our qualitative results are not sensitive to
636 whether bark thickness is calculated by outer stem size or bole stem size (Fig. S3).

637 Establishing differences in fire frequencies between biomes

638 Using data on fire from a longer time-series (GFED4, 1997-2015), we found that savanna
639 species experienced a 9.2-fold higher frequency of burning than forest species, expressed as the
640 average proportion of a grid-cell that burns each year ($F_{1,569} = 154.8$, $p < 0.0001$). The shorter fire
641 time-series (2001-2010) corroborated these results as savanna species experienced a 5.4-fold
642 higher frequency of burning than forest species ($F_{1,570} = 187$, $p < 0.0001$) but also illustrated the
643 potential that the longer fire product is biased against detecting fires in forests relative to
644 savannas (inter-biome differences were twice as high when there were no corrections for small
645 fires). Moreover, using GFED4, one species was categorized as experiencing no fire, likely due
646 to the lack of small fire correction. Consequently we utilize the shorter time series to avoid
647 detection bias in forests.

648

649 Analyses in North America

650 We complemented our analysis with a more detailed dataset specific to North America
651 from the Fire Effects Information System (USDA, <http://www.feis-crs.org/feis>) that classifies
652 species into multiple habitat types based on a synthesis of existing distribution data and
653 knowledge. The FEIS is a searchable database of fire regime characteristics and habitat
654 associations for plant species that occur in North America. Because habitat categorizations were
655 descriptive (and not quantitative), we developed our own classification scheme to best determine
656 savanna vs. forest species. This involved categorizing species as associating with (i) only forest
657 habitats, (ii) >90% forest habitats, (iii) mixed between forest and woodlands/grasslands/
658 prairie/savanna, (iv) predominantly in woodlands/grassland/prairie/savanna. We then repeated
659 our analyses comparing the two disparate categories as forest vs. savanna as well as the “mixed”

660 species. This allowed us to further test whether our assumption that species associate with more
661 open vegetation (savannas and woodlands) experience fires more frequently than those with
662 closed vegetation (mixed woodlands and forests).

663 Incorporating newly classified species as savanna vs. forest specialists using the detailed
664 habitat dataset yielded quantitatively similar results in our comparison between savannas and
665 forests in North America (savannas species had 1.31-fold thicker bark in original classification
666 vs. 1.37-fold thicker bark in detailed classification).

667 We also used comparisons within North America to estimate potential effects of crown
668 fire regimes influencing our results. Under the assumption that other traits such as reseeded,
669 resprouting, and/or height allometry are more important than bark thickness, we would expect
670 the relationship between fire and bark to be weak. Although we found that fire frequency was
671 still a significant predictor of bark investment, fire only explained 7.6% of the deviance across
672 species (Table S8), which is ~1/3 of its explanatory power in the global analysis (21.6%). Model
673 selection illustrated two models that were within 2 AIC of one another. The model that explained
674 the most deviance included fire frequency, precipitation in the driest quarter, and habitat (19.7%
675 of variance explained). Consequently, fire frequency appears to be a less powerful, but still
676 significant, predictor of bark thickness.

677 Gymnosperm dominated forests in North America tend to be the forest types most prone
678 to crown fires. Consequently, we compared the relative bark thickness of gymnosperm vs.
679 angiosperm plant species as another indirect test of how crown fire regimes may be influencing
680 the selection for bark thickness. We found no significant difference in relative bark thickness
681 between gymnosperm vs. angiosperm tree species either across the entire dataset
682 ($F_{1,59}=1.8, p=0.184$) or within the subset of species that occurred primarily in forests ($F_{1,39}=1.0,$

683 $p=0.32$), suggesting that different fire regimes may not influence the bark relationship heavily.
684 However, we found no significant relationship between bark and fire frequency when we
685 analyzed gymnosperms alone ($F_{1,26}=1.9, p=0.18$). Further analysis revealed that the lack of a
686 relationship between fire and bark thickness was dependent on the habitat of a species
687 (fire*habitat interaction, $F_{1,24}=5.16, p=0.032$); in other words, the relationship between fire and
688 bark was weak in species that occurred only in forests and stronger in species that occurred in
689 savannas. Consequently, species that occur in habitats more likely to experience crown fires have
690 a weaker relationship between bark and fire, under the assumption that gymnosperm forests are
691 more susceptible to crown fire than angiosperm forests or savannas.

692

693 Statistical relationship between bark thickness, climate, and fire frequency

694 Incorporation of GFED4 to determine the fire frequency of species' distributions resulted
695 in no significant qualitative changes to our model fit and selection analysis (Tables S6,S7).

696 In all cases, we performed model selection to determine the most parsimonious
697 combination of variables (using the lowest AIC with a threshold value of two). We tested for
698 potential non-linear relationships between variables by comparing the AIC of non-linear and
699 linear fits. Analyses were performed separately for bark thickness on standardized diameters of
700 10, 20 and 30 cm, all of which yielded qualitatively similar results. Bark thickness and annual
701 burned area were log-transformed prior to analysis to reduce heteroscedasticity.

702

703 Congener comparison

704 We removed the *Acacia* genus given the taxonomic issues as well as those with species
705 that occurred in fundamentally different habitats (e.g., *Melaleuca* forest trees specializing in
706 swamps).

707

708 Quantifying within-species variability in bark thickness allometries

709 To assess whether within-species variability in bark thickness could impact our
710 conclusions, we evaluated the error within bark thickness allometry relationships across the
711 studies that presented goodness of fit measures. An analysis of the goodness of fit between stem
712 diameter and bark thickness illustrated low error when assessing variability explained (mean:
713 $r^2=0.77$; median: $r^2=0.83$; $n=235$ species) and the ratio of the standard error vs. slope of bark
714 thickness ~ stem diameter relationship (ratio of SE/slope mean: 0.19; median: 0.16; $n=151$
715 species). These errors are relatively minor when compared to the differences across biomes
716 (Figure 1, Tables S2-S4).

717

718 Spatial analyses of grid cell bark thickness means

719 This involved summarizing traits, fire regimes, and climate conditions within $1^\circ \times 1^\circ$ grid
720 cells using the GBIF occurrence data. A model without considering different effects in biomes
721 explained less of the variance and had a higher AIC than when considering biome ($r^2=0.39$ vs.
722 $r^2=0.57$; AIC = 13038 vs. 10865). Consequently, we split the analysis into different biome
723 categories and analyzed savanna and forest species trait means separately to avoid inflating the
724 fire regime of forest species and deflating the fire regime of savanna species in ecotonal areas
725 with high co-occurrence of the two biomes in spatial proximity (e.g. Fig. 1, South America and
726 Australia).

727 Within biomes, a statistical model of the probability density of community as a function
728 of fire and wet and dry quarter precipitation explained 33% and 35% of deviance in forest and
729 savanna communities, respectively. There were significant non-linear relationships between bark
730 thickness and climate variables (savanna, non-linear AIC: 3023.91, linear AIC: 3584.998; forest,
731 non-linear AIC: 1702.902, linear AIC: 3160.667). These models were then used to project the
732 bark thickness distributions under future conditions.

733 We also evaluated the potential for spatial autocorrelation affecting the model fit and
734 results. To do so, we calculated the residuals from the model for each gridcell and performed a
735 Moran's I test. We found significant spatial autocorrelation for the savanna ($p < 0.0001$) and
736 forest ($p < 0.0001$) models. To verify our results were robust to potential spatial autocorrelation
737 we (i) compared our model with a model include latitude and longitude as an interactive effect
738 and (ii) used a correlogram to determine the minimum distance for independence and fit the
739 model on repeatedly resampled independent data. To evaluate the robustness of our model, we
740 compared our model's predictions with those of the resampled fittings.

741 Incorporating latitude and longitude as an interactive effect increased the explanatory
742 power of the model (deviance explained: 68% in savanna and 45% in forests) and produced
743 significantly similar predictions to the model without spatial effects (regression between
744 predicted bark thickness: slope=1.004, $r^2=0.35$, $p < 0.0001$ in savanna and slope=1.000, $r^2=0.43$,
745 $p < 0.0001$ in forests). Importantly, the predictions of the spatial distribution of bark thicknesses
746 were qualitatively the same (e.g., savanna fit in Fig. S10).

747 Repeatedly fitting the model on resampled data sufficiently far apart to allow for
748 independence also reproduced our results. The fitted values from the different re-sampling
749 models ($n=500$ resample model fits) were significantly related to the global model fits for

750 savannas and forests: mixed effects model with iteration number as random effect, savannas:
751 $F_{1,4592}=1806$, $p<0.0001$; forests: $F_{1,5605}=13864$, $p<0.0001$.

752

753 Climate projections

754 Models included are: BCC-CSM1-1, GFDL-CM3, HadGEM2-ES, MIROC-ESM,
755 NorESM1-M. The model outputs are bias-corrected and calibrated using WorldClim 1.4 at 5-
756 minute resolution. We averaged forecasted values across all models within each grid cell. Future
757 fire projections come from a recent output of LPJ-GUESS-SIMFIRE (Knorr *et al.* 2015), which
758 incorporates future climates, human populations, and fuel loads. The model projects changes in
759 annual burned area to 2071-2100 assuming the RCP8.5 climate scenario. We chose this high
760 emissions scenario to quantify an upper bound on potential changes in fire regimes. Because
761 future fire projections rely on human factors (e.g. population growth, ignition sources,
762 suppression), climate factors (e.g. rainfall, temperature, vapor pressure deficit), and vegetation
763 itself, they inherently contain a large degree of uncertainty in the amount of annual burned area
764 and the areas where it may change the most. Thus, we consider the potential sensitivity of our
765 results to variation in projected climate conditions and examine qualitatively the potential
766 influence of uncertainties in human factors on our findings based on published patterns (Knorr *et*
767 *al.* 2015). To evaluate uncertainty across climate model projections, we used the standard
768 deviation among climate model precipitation projections (CMIP5 outputs for 2070 RCP8.5 from
769 BCC-CSM1-1, GFDL-CM3, HadGEM2-ES, MIROC-ESM, NorESM1-M.) to calculate “wet”
770 (+1 standard deviation) and “dry” (-1 standard deviation) future scenarios.

771

772 Uncertainties in future projections

773 The model forecasts used here focus on the upper bound scenarios for both changes in
774 climate (RCP8.5) as well as fire (incorporates a high RCP8.5 scenario as well as high population
775 growth).

776 Although evaluation of the full variability in future climate and fire projections are out of
777 the scope of this study, we evaluate uncertainties in our projections within gridcells. We evaluate
778 the uncertainty by considering uncertainty in the climate projections of wet and dry season
779 precipitation.

780 To evaluate uncertainty within the climate projections we used the standard deviation in
781 precipitation among the models (CMIP5 outputs for 2070 RCP8.5 from BCC-CSM1-1, GFDL-
782 CM3, HadGEM2-ES, MIROC-ESM, NorESM1-M.) to calculate a “wet” scenario by adding one
783 standard deviation to the mean to for wet and dry season precipitation . Similarly, we calculated
784 a “dry” scenario by subtracting one standard deviation from the mean.

785 Similarly, because future fire projections rely on human factors (e.g. population growth,
786 ignition sources, suppression), climate factors (e.g. rainfall, temperature, vapor pressure deficit),
787 and vegetation itself, they inherently contain a large degree of uncertainty in the amount of
788 annual burned area and the areas where it may change the most. Thus, we consider the potential
789 sensitivity of our results by discussing the potential influence that uncertainties in human factors
790 may have on our findings based on published patterns (Knorr *et al.* 2015).

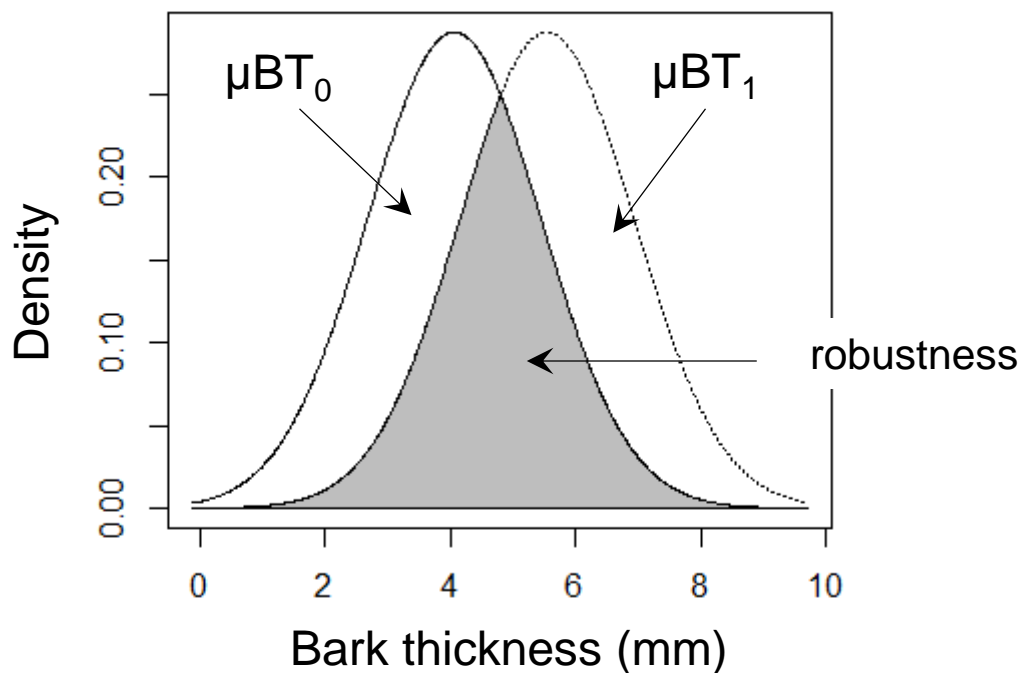
791

792 **Figure S1:** Distribution of plant species used in the analysis taken from GBIF and amounting to
793 578,071 observations. grey indicates areas where the species under consideration do not occur.



794
795

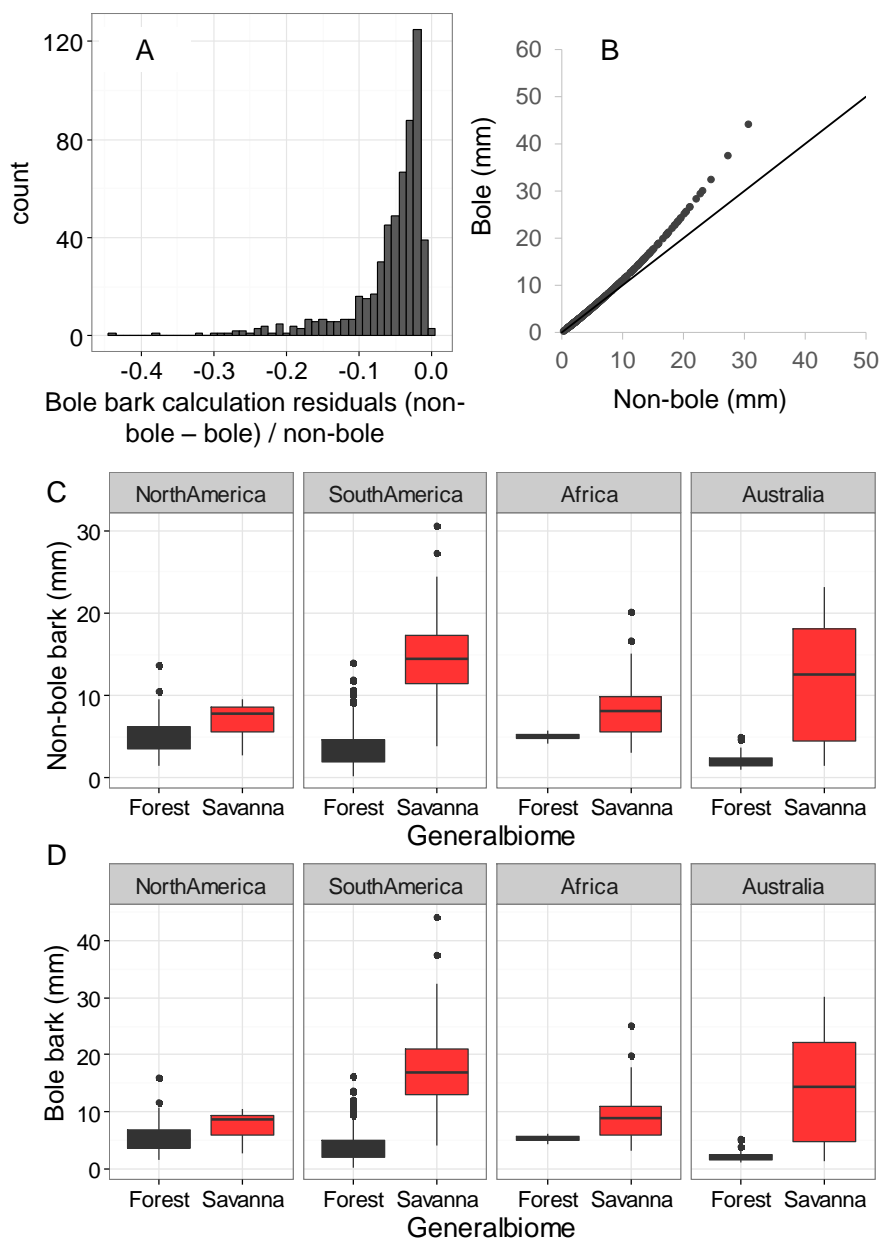
796 **Figure S2:** Schematic representing trait overlap to calculate robustness. Bark thickness
797 distributions within a location calculated using present-day means in a grid cell combined with
798 total variance in bark thickness. Future means are calculated by integrating projected fire and
799 climate into the bark thickness ~ environment model. Variance in bark thickness is assumed
800 constant. The integral under overlapping curves is the overlapping coefficient and we interpret it
801 here to quantify robustness. Present-day mean bark thickness indicated by μ_{BT_0} and future mean
802 bark thickness indicated by μ_{BT_1} .



803

804

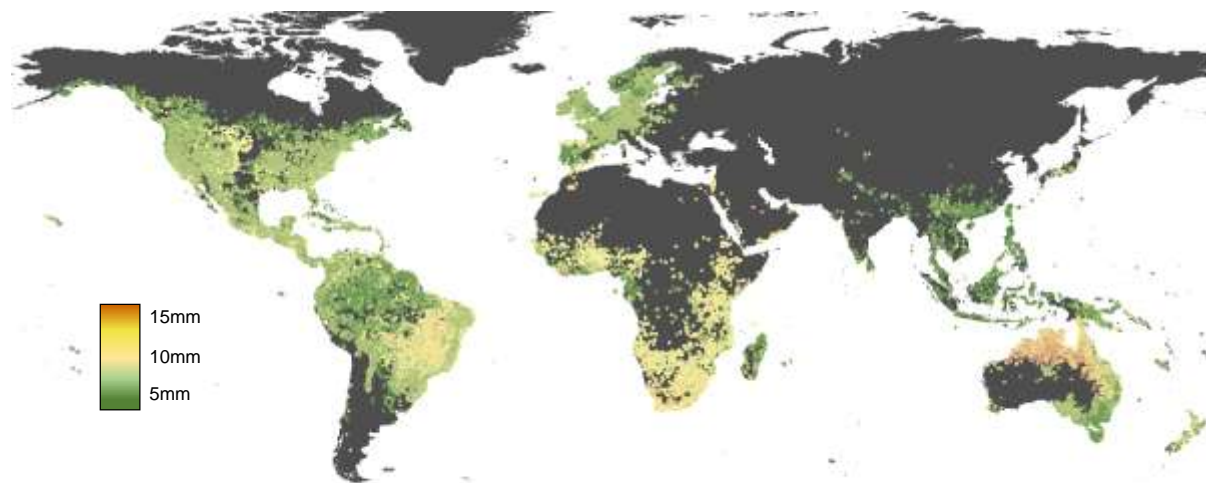
805 **Figure S3:** Sensitivity of our results to calculations of relative bark thickness based off of outer
 806 stem diameter from alternative calculations using the diameter from the stem bole (Midgley &
 807 Lawes 2016). All calculations were performed on stem diameters of 10cm. A) histogram of the
 808 residuals between the calculation of outer bark (non-bole) vs. bole. B) scatter plot of the two
 809 calculation methods with the solid line representing the 1:1 relationship. C and D) comparison
 810 between biomes across continents using the two different calculation methods of outer bark (C)
 811 and bole (D). Qualitative results using bole calculations were the same (NA: $F_{1,103}=6.57$,
 812 $p=0.0118$; SA: $F_{1,269}=217$, $p<0.0001$; AF: $F_{1,36}=5.15$, $p=0.0294$; AU: $F_{1,91}=144.6$, $p<0.0001$).
 813



814
 815
 816
 817

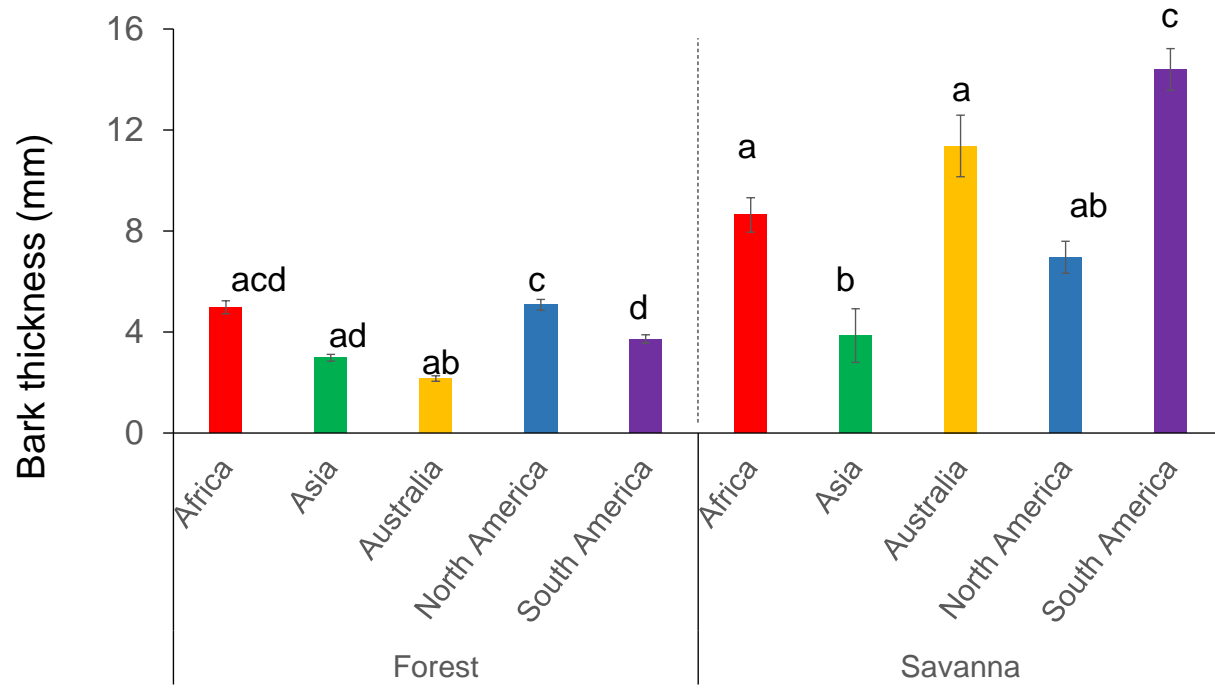
818 **Figure S4:** Global distribution of bark thickness across all species. Occurrence points were
819 inverse distance weighted to create spatial averages within distances of 0.5 degrees around each
820 observation point. Bark thicknesses correspond to trees with a reference stem diameter of 10 cm.
821 Grey areas are locations where we do not contain data.
822

Global distribution of bark thickness across biomes



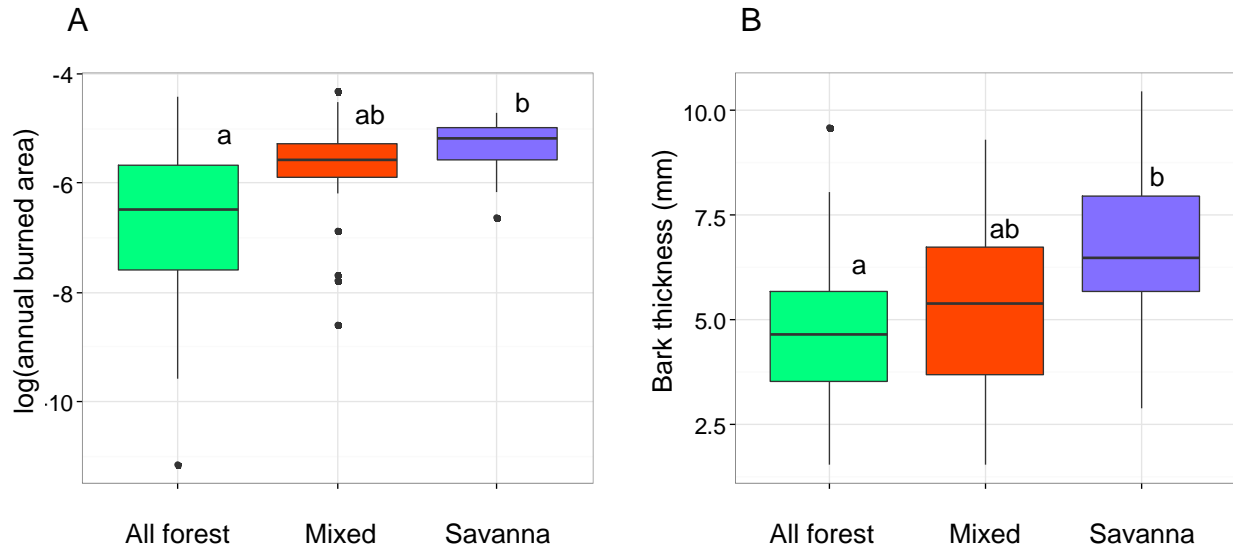
823
824

825 **Figure S5:** Bark thickness of 10cm diameter stems in savanna and forest biomes across
826 continents. Letters indicate significant differences determined via Tukey HSD with correction for
827 multiple comparisons (Table S4 for statistics).
828



829
830
831
832
833

834 **Figure S6:** Annual burned area and bark thickness across species specialized in different habitat
835 types in North America. Bark thickness is evaluated for a stem 10 cm in diameter. Letters
836 indicate significant differences among treatments evaluated using a Tukey HSD post-hoc at
837 $p < 0.05$.

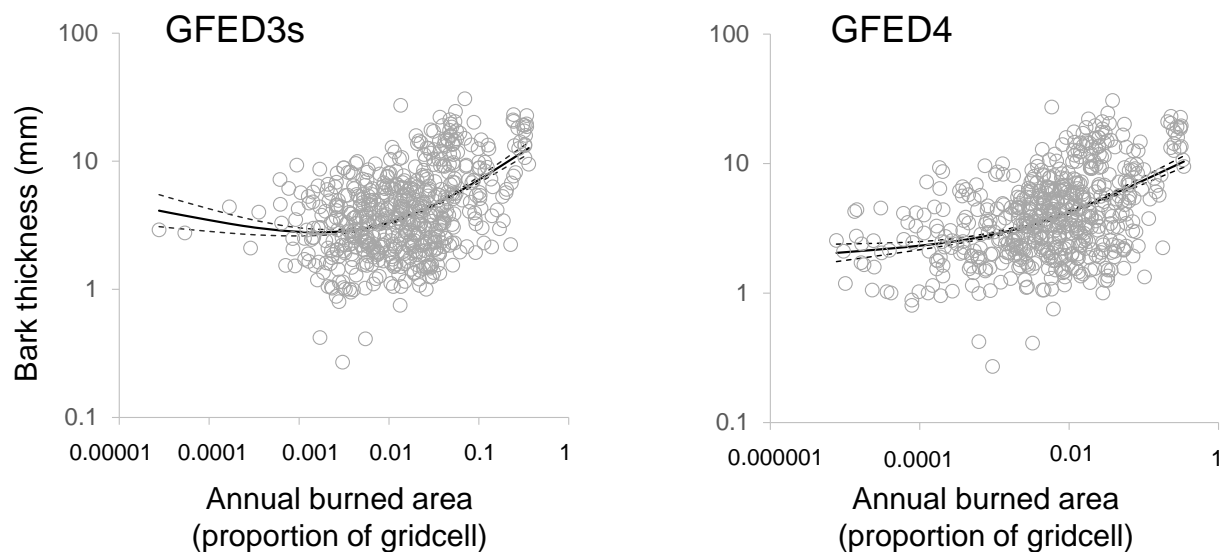


838

839

840 **Figure S7:** Comparison of the relationship between burned area and bark thickness using the two
841 different fire frequency datasets. GFED3s is based off of data from 2001-2010 and includes
842 correction for small fires (20% of deviance explained). GFED4 is based off of data from 1996-
843 2015 but does not include correction for small fires likely leading to the lower-bound x-axis
844 being smaller (20% of deviance explained).

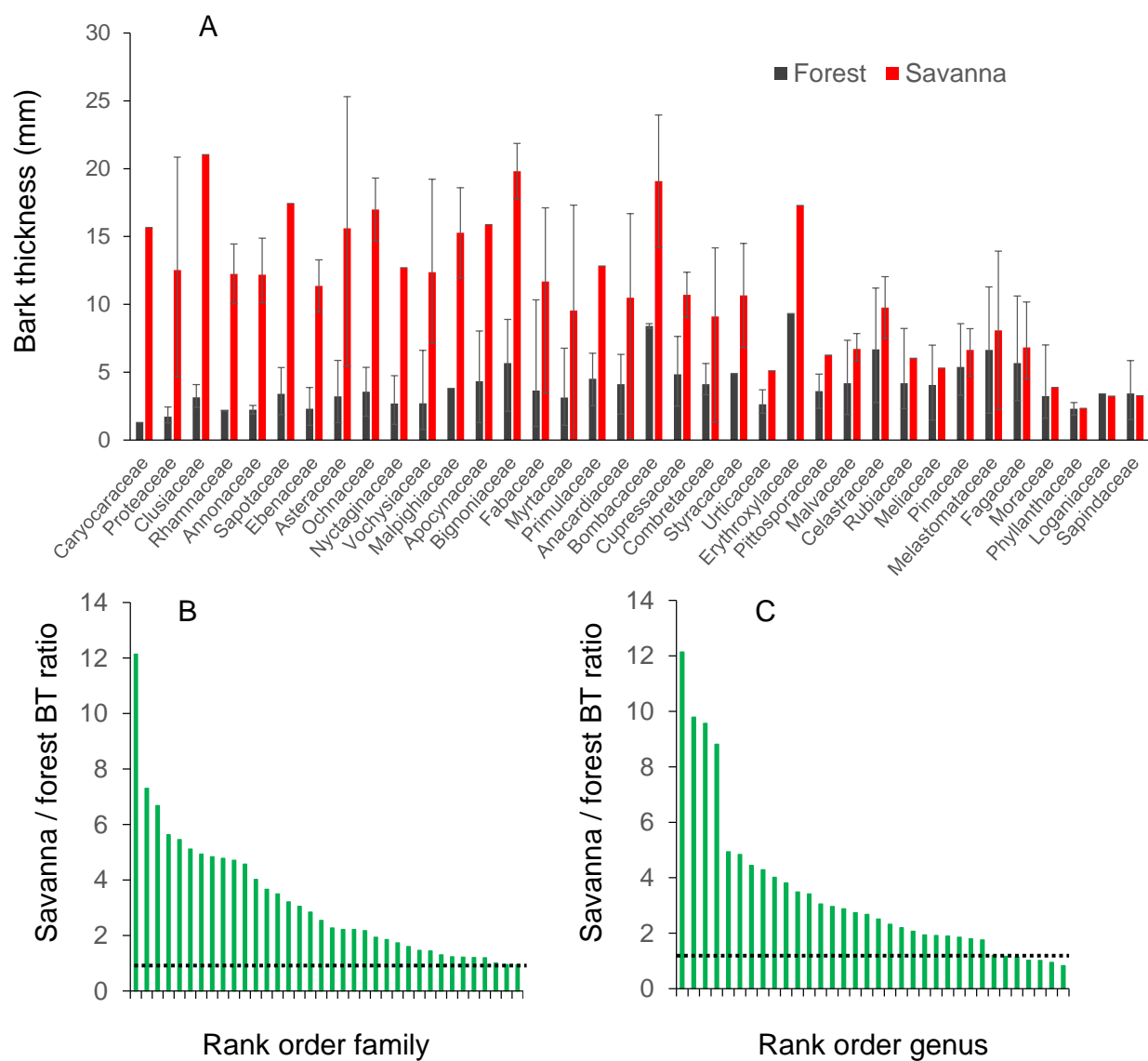
845



846

847 **Figure S8:** A) Comparison of bark thickness in species specializing in savannas vs. forests in the
 848 same family. Error bars are $\pm 95\%$ confidence intervals. Rank order figure illustrates the
 849 distribution of bark thickness ratios (savanna / forest) with individual families (B) and genera
 850 (C), with the dashed line indicating 1.

851

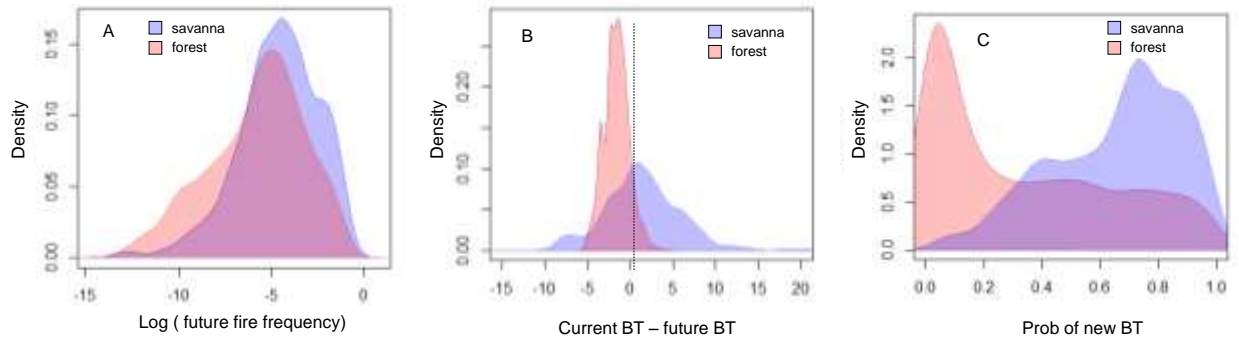


852

853

854

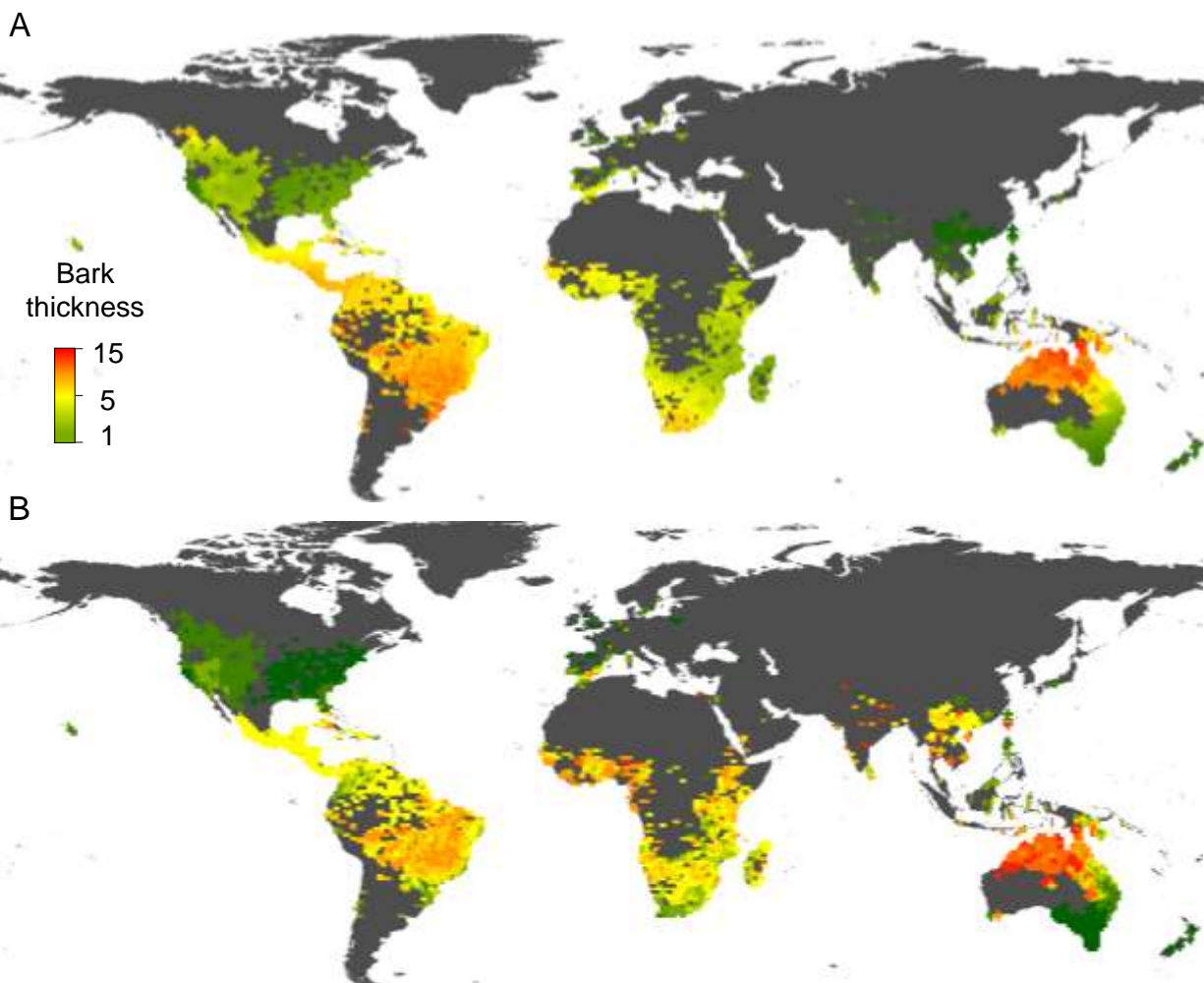
855 **Figure S9:** Future changes in fire and bark thicknesses from modelled projections. A) future
856 annual burned area for grid cells partitioned between savanna vs. forest species. B) absolute
857 changes in bark thickness assuming model projections expressed as probability distributions; C)
858 estimated proportion of individuals in an area containing the new bark thickness (only for cells
859 which are projected to experience increased annual burned area).
860



861
862

863

864 **Figure S10:** Fitted model output of bark thickness in savannas using a model that either (A)
865 includes latitude and longitude as model covariates or (B) only includes climate and fire.



866

867 **Table S1:** List of species, the studies that they were compiled from, their location, biome, and
 868 bark thicknesses. The bark thickness for a specific species in some cases came from multiple
 869 studies, which we averaged, but present the full dataset for the species available here. **Attached.**

870

871 **Table S2:** Means and standard errors of bark thicknesses at particular stem sizes (10, 20, and
 872 30cm) in savanna and forest biomes (both global and across continents). Biome refers to the
 873 general biome a species was categorized into and location refers to the geographical grouping.
 874 Sample size is given for the 10cm comparison.

875

876

Biome	Location	# species	10cm mean	SE	20cm mean	SE	30cm mean	SE
Forest	Global	445	3.71	0.11	6.94	0.20	10.34	0.33
	Tropical	329	3.42	0.12	6.46	0.24	9.43	0.36
	Temperate	116	4.52	0.21	8.29	0.35	13.09	0.74
Savanna	Global	127	11.10	0.54	21.56	1.11	33.50	1.74
	Tropical	110	11.80	0.58	23.20	1.20	34.53	1.83
	Temperate	17	6.22	0.51	10.95	0.88	26.44	5.29
Forest	Africa	5	4.98	0.26	7.49	0.45	10.01	0.81
	Asia	60	2.97	0.14	5.72	0.27	8.43	0.42
	Australia	60	2.16	0.11	4.31	0.22	6.47	0.33
	North America	94	5.08	0.22	9.23	0.36	14.78	0.83
	South America	226	3.72	0.17	6.99	0.33	10.18	0.49
Savanna	Africa	33	8.64	0.68	15.91	1.48	22.99	2.31
	Asia	5	3.85	1.06	7.71	2.12	11.56	3.19
	Australia	33	11.37	1.22	22.74	2.44	34.11	3.66
	North America	11	6.96	0.63	11.63	1.21	33.56	7.60
	South America	45	14.40	0.82	28.80	1.65	43.20	2.47

877

878

879

880 **Table S3:** Statistical analyses comparing the effect of biome both globally and within continents.
 881 All models have log transformed bark thicknesses. Significance of including continent into
 882 biome model indicated by the “+” inclusions.

	Df	<u>10cm</u>		<u>20cm</u>		<u>30cm</u>	
		F	p	F	p	F	p
Biome	1,570	313	<0.0001	321	<0.0001	322	<0.0001
+Continent	4,562	18.8	<0.0001	15.2	<0.0001	20	<0.0001
+Continent:Biome	4,562	15.6	<0.0001	17.3	<0.0001	9.7	<0.0001
Biome - Asia	1,63	1.03	0.31	1.5	0.22	1.71	0.19
Biome - Africa	1,36	5.22	0.028	6.21	0.017	5.8	0.021
Biome - Australia	1,92	149	<0.0001	149	<0.0001	149	<0.0001
Biome - North America	1,107	7.78	0.006	4.8	0.031	24.4	<0.0001
Biome - South America	1,287	194	<0.0001	211	<0.0001	215	<0.0001

883

884

885 **Table S4:** Bark thickness differences among continents. Comparison among biomes using Tukey
 886 HSD post-hoc test performed separately within each biome. Difference refers to the difference
 887 between means (statistics performed on log transformed bark thickness data for 10cm stems).
 888

Comparison	<u>Forest</u>		<u>Savanna</u>	
	<u>Diff</u>	<u>p value</u>	<u>Diff</u>	<u>p value</u>
Asia-Africa	-0.57	0.178	-0.86	0.014
Australia-Africa	-0.90	0.004	0.11	0.923
NorthAmerica-Africa	-0.06	0.999	-0.18	0.895
SouthAmerica-Africa	-0.50	0.270	0.53	<0.001
Australia-Asia	-0.34	0.008	0.97	0.004
NorthAmerica-Asia	0.50	<0.001	0.68	0.160
SouthAmerica-Asia	0.07	0.910	1.38	<0.001
NorthAmerica-Australia	0.84	<0.001	-0.29	0.574
SouthAmerica-Australia	0.41	<0.001	0.41	0.014
SouthAmerica-NorthAmerica	-0.44	<0.001	0.70	0.003

889
 890
 891
 892
 893
 894
 895
 896
 897
 898
 899

900 **Table S5:** Statistical results from generalized additive models between log bark thickness, fire,
 901 climate, and biome using model selection on stems 20cm and 30cm in size. Dev refers to percent
 902 deviance explained. The best fit models are highlighted in bold, we utilized the most
 903 parsimonious of the two.
 904

<u>Variables included</u>	AIC 20cm	Dev 20cm	AIC 30cm	Dev 30cm
Mean_fire+Precip_Wetq*Biome+Precip_Dryq*Biome	940	49.7%	993	48.0%
Mean_fire+Precip_Wetq*Biome+Precip_Dryq	941	49.4%	991	48.0%
Mean_fire+Precip_Wetq+Precip_Dryq*Biome	976	46.2%	1027	45.2%
Mean_fire+Precip_Wetq+Precip_Dryq+Biome	980	45.8%	1026	44.5%
Precip_Wetq+Precip_Dryq+Biome	980	45.5%	1024	44.4%
Mean_fire+Precip_Dryq+Biome	988	42.3%	1033	43.5%
Mean_fire+Precip_Wetq+Biome	1014	39.9%	1056	41.3%
Mean_fire+Biome	1053	38.1%	1091	37.4%
Biome	1068	36.0%	1096	36.5%
Mean_fire+Precip_Wetq+Precip_Dryq	1088	34.3%	1147	31.2%
Mean_fire	1189	21.1%	1240	18.1%

905
 906
 907
 908
 909

910 **Table S6: Using GFED4 to characterize environmental conditions that determine bark**
 911 **thickness.** Statistical results from generalized additive models between log bark thickness (for
 912 stems 10cm in size), fire, climate, and biome using model selection. Dev refers to deviance
 913 explained. Mean_fire = annual burned area, **Precip_Wetq** = precipitation in the wettest quarter,
 914 **Precip_Dryq** = precipitation in the driest quarter, Biome = biome a species specialized in (either
 915 savanna or forest). The best fit models are highlighted in bold, we utilized the more
 916 parsimonious of the two.
 917

<u>Variables included</u>	<u>Dev</u>	<u>AIC</u>
Mean_fire+Precip_Wetq*Biome+Precip_Dryq*Biome	49.8%	784.654
Mean_fire+Precip_Wetq*Biome+Precip_Dryq	49.6%	785.1415
Mean_fire+Precip_Wetq+Precip_Dryq*Biome	47.2%	807.0707
Mean_fire+Precip_Wetq+Precip_Dryq+Biome	46.6%	809.7317
Precip_Wetq+Precip_Dryq+Biome	46.6%	810.6547
Mean_fire+Precip_Dryq+Biome	45.1%	823.489
Mean_fire+Precip_Wetq+Biome	43.3%	838.3743
Mean_fire+Biome	39.2%	869.499
Biome	36.5%	888.4946
Mean_fire+Precip_Wetq+Precip_Dryq	33.0%	916.2993
Mean_fire	19.2%	1001.298

918
 919
 920

921 **Table S7: Using GFED4 to characterize environmental conditions that determine bark**
 922 **thickness.** Statistical results from generalized additive models between log bark thickness, fire,
 923 climate, and biome using model selection on stems 20cm and 30cm in size. Dev refers to percent
 924 deviance explained. The best fit models are highlighted in bold, we utilized the most
 925 parsimonious of the two.
 926

<u>Variables included</u>	AIC 20cm	Dev 20cm	AIC 30cm	Dev 30cm
Mean_fire+Precip_Wetq*Biome+Precip_Dryq*Biome	789.79	49.4%	997.90	47.5%
Mean_fire+Precip_Wetq*Biome+Precip_Dryq	790.30	49.2%	998.88	47.5%
Mean_fire+Precip_Wetq+Precip_Dryq*Biome	815.84	46.4%	1032.13	44.0%
Mean_fire+Precip_Wetq+Precip_Dryq+Biome	817.92	45.9%	1033.71	44.0%
Precip_Wetq+Precip_Dryq+Biome	819.6	45.8%	1035.67	43.9%
Mean_fire+Precip_Dryq+Biome	826.09	45.0%	1040.80	43.2%
Mean_fire+Precip_Wetq+Biome	849.79	42.1%	1060.54	41.2%
Mean_fire+Biome	870.78	39.3%	1082.00	38.8%
Biome	885.32	37.2%	1095.02	37.2%
Mean_fire+Precip_Wetq+Precip_Dryq	931.79	31.0%	1165.29	29.2%
Mean_fire	1007.84	18.4%	1253.13	17.0%

927
 928
 929
 930

931 **Table S8: Analysis within North America.** Statistical results from generalized additive models
 932 between log bark thickness (for stems 10cm in size), fire, climate, and biome using model
 933 selection. Dev refers to deviance explained. Mean_fire = annual burned area, Precip_Wetq =
 934 precipitation in the wettest quarter, Precip_Dryq = precipitation in the driest quarter, Biome =
 935 biome a species specialized in (either savanna or forest). The best fit models are highlighted in
 936 bold, we utilized the more parsimonious of the two.
 937

<u>Variables included</u>	<u>Dev</u>	<u>AIC</u>
Mean_fire+Precip_Wetq+Precip_Dryq	17.40%	110.6098
Mean_fire+Precip_Dryq+Biome	19.70%	111.6916
Mean_fire+Precip_Wetq+Precip_Dryq+Biome	20.30%	112.8949
Mean_fire+Precip_Wetq*Biome+Precip_Dryq	22.60%	115.8903
Mean_fire+Precip_Wetq+Precip_Dryq*Biome	21.20%	117.6691
Mean_fire	7.57%	118.1583
Mean_fire+Biome	11.20%	119.9901
Mean_fire+Precip_Wetq*Biome+Precip_Dryq*Biome	23.50%	120.6815
Mean_fire+Precip_Wetq+Biome	11.30%	121.9151
Biome	7.57%	122.1543
Precip_Wetq+Precip_Dryq+Biome	9.33%	124.1714

938