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 Paine[3], William A. Hoffmann[4], Tyler Kartzinel[1,5], Sam S. Rabin[1], Douglas Sheil[6], Augusto C. Franco[7], & Stephen W. Pacala[1]

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

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 reseeding 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 reseeding 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

Variables included	Dev	AIC
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 ($F_{4,562}=15.6$, $p<0.0001$).

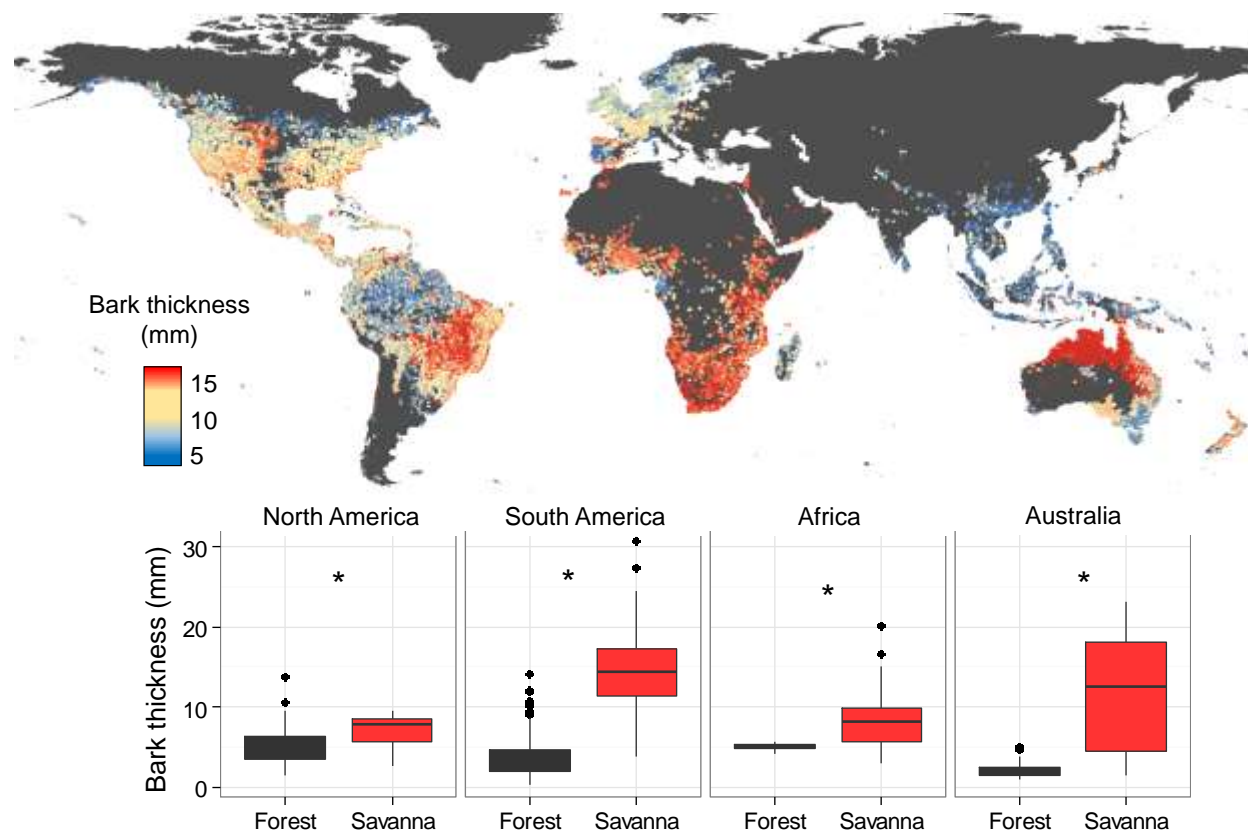572   For specific comparison among continents, see Table S4.

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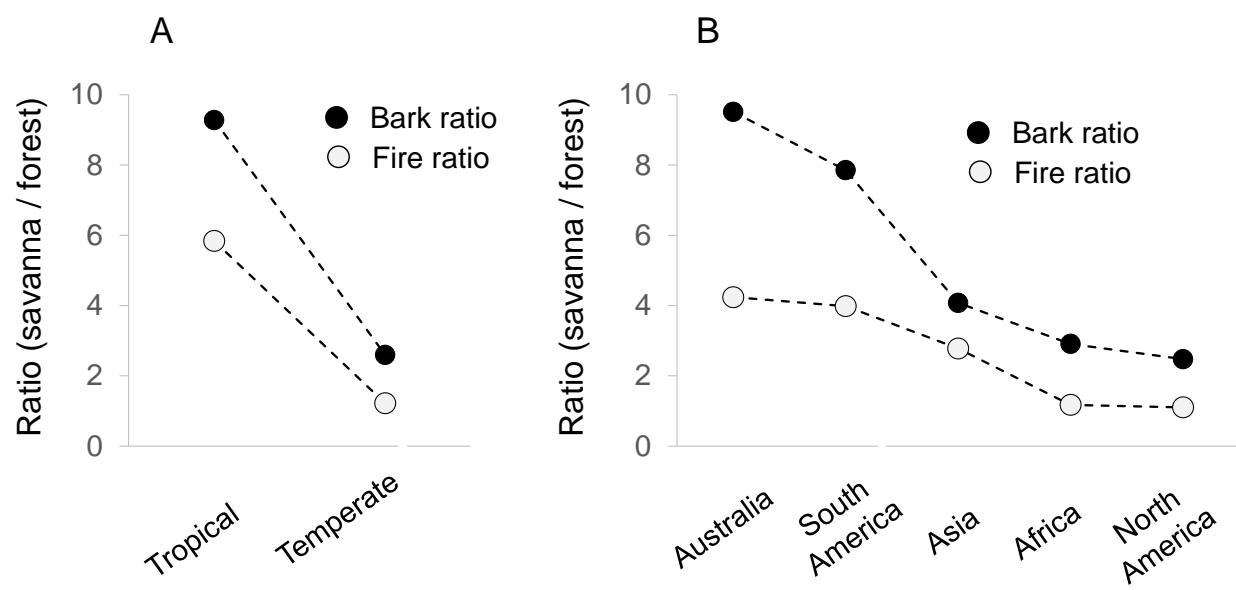
583   **Figure 4: Savanna species have consistently thicker bark than their congeners.** A)

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 ±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

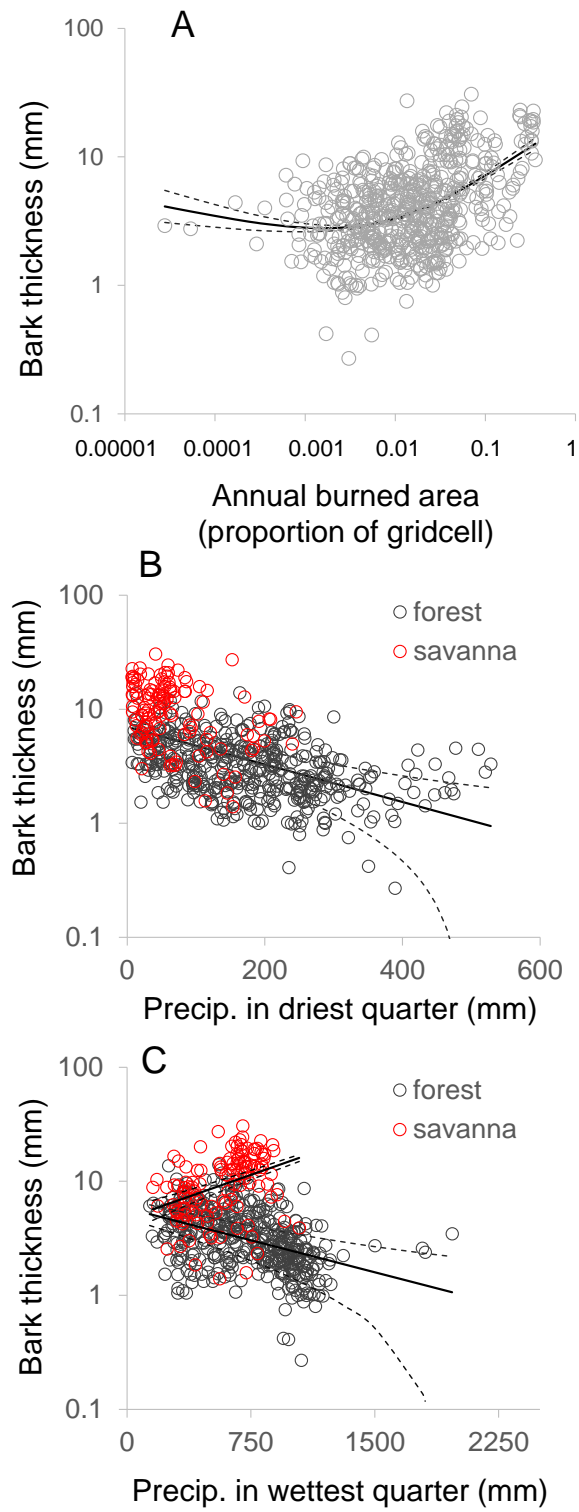596   projected to experience gains in fire frequency are mapped in panels C and D.

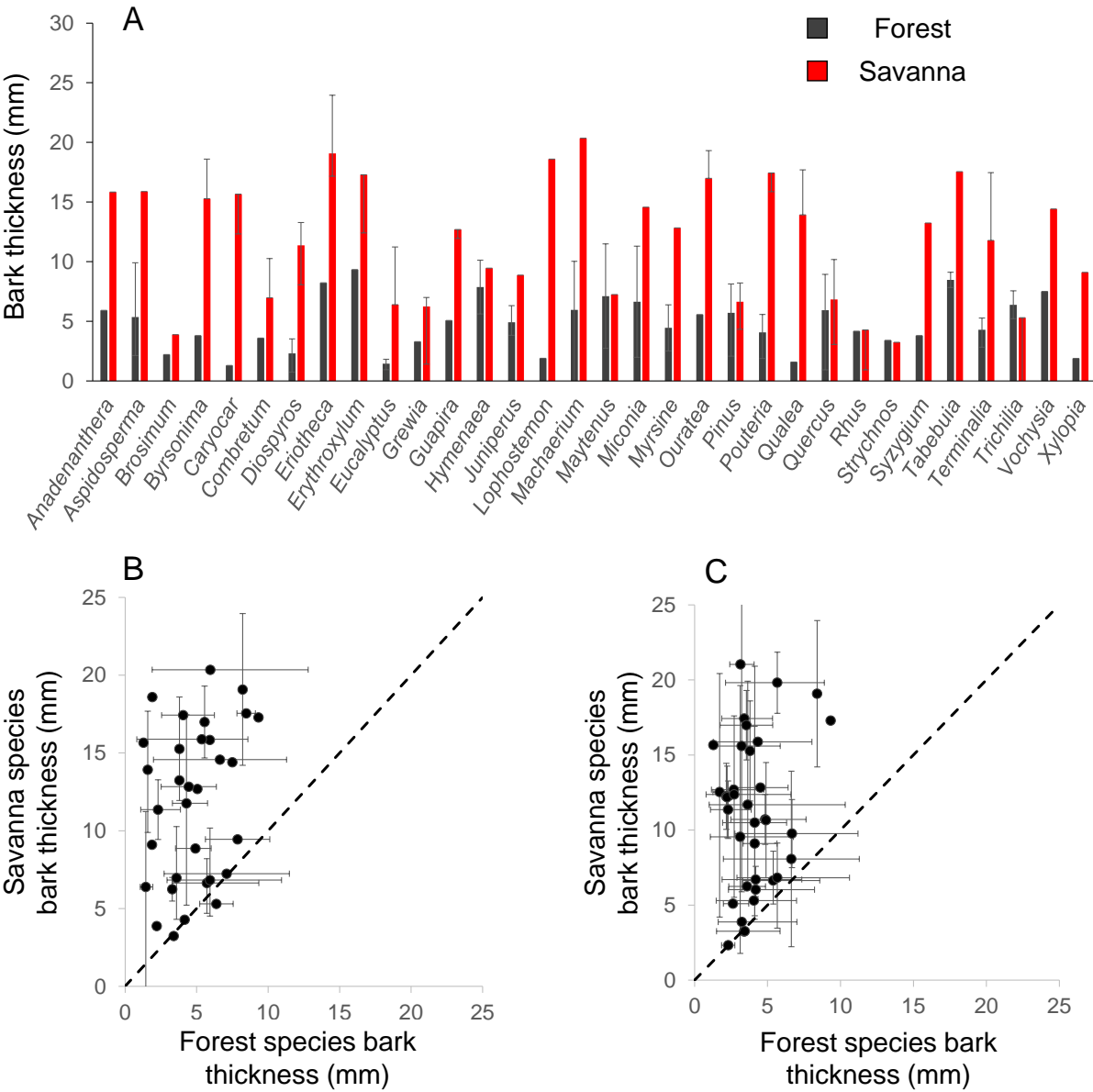597   **Figure 1:**

598
599
600

601 **Figure 2:**

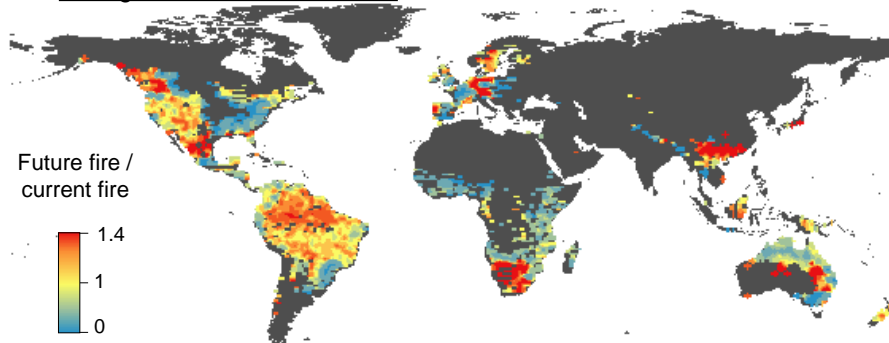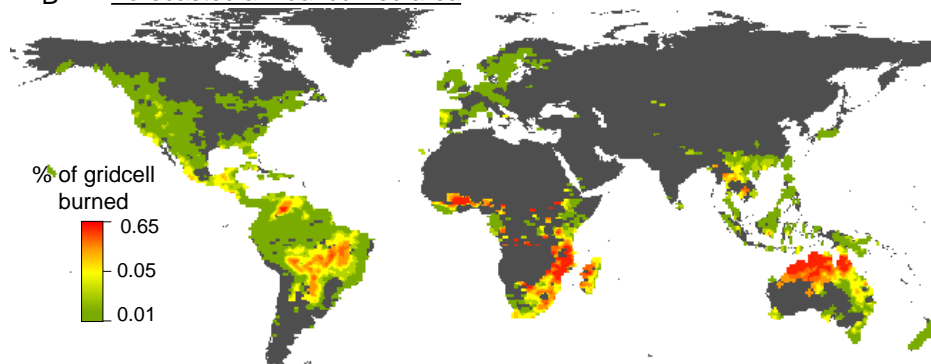

602

603   **Figure 3:**

606   **Figure 4:**

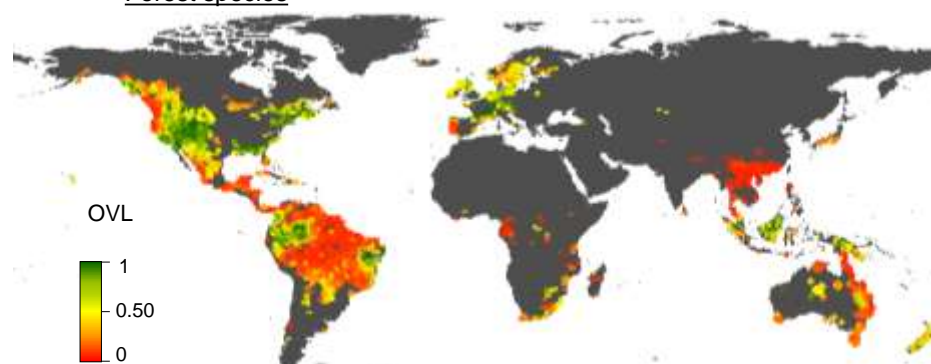607

608

609

610 **Figure 5:**

A <u>Change in annual burned area</u>

Future fire /
current fire

- 1.4
- 1
- 0

B <u>Forecasted annual burned area</u>

% of gridcell
burned

- 0.65
- 0.05
- 0.01

C <u>Forest species</u>

OVL

- 1
- 0.50
- 0

D <u>Savanna species</u>

OVL

- 1
- 0.50
- 0

611
612
613

614

615

616   <u>Different stem allometries and calculations</u>

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   <u>Establishing differences in fire frequencies between biomes</u>

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   <u>Analyses in North America</u>

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 reseeding,

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   <u>Statistical relationship between bark thickness, climate, and fire frequency</u>

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   <u>Congener comparison</u>

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   <u>Quantifying within-species variability in bark thickness allometries</u>

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   <u>Spatial analyses of grid cell bark thickness means</u>

719   This involved summarizing traits, fire regimes, and climate conditions within 1°x1° 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 μBT_0 and future mean
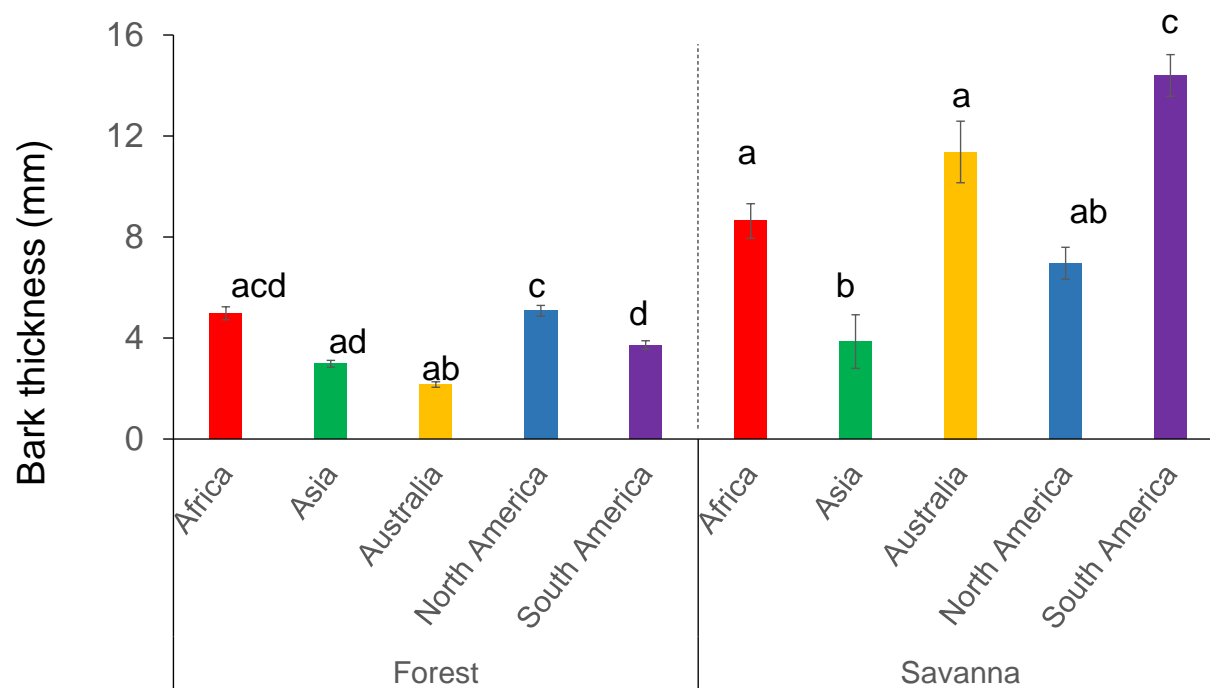802 bark thickness indicated by μBT_1.
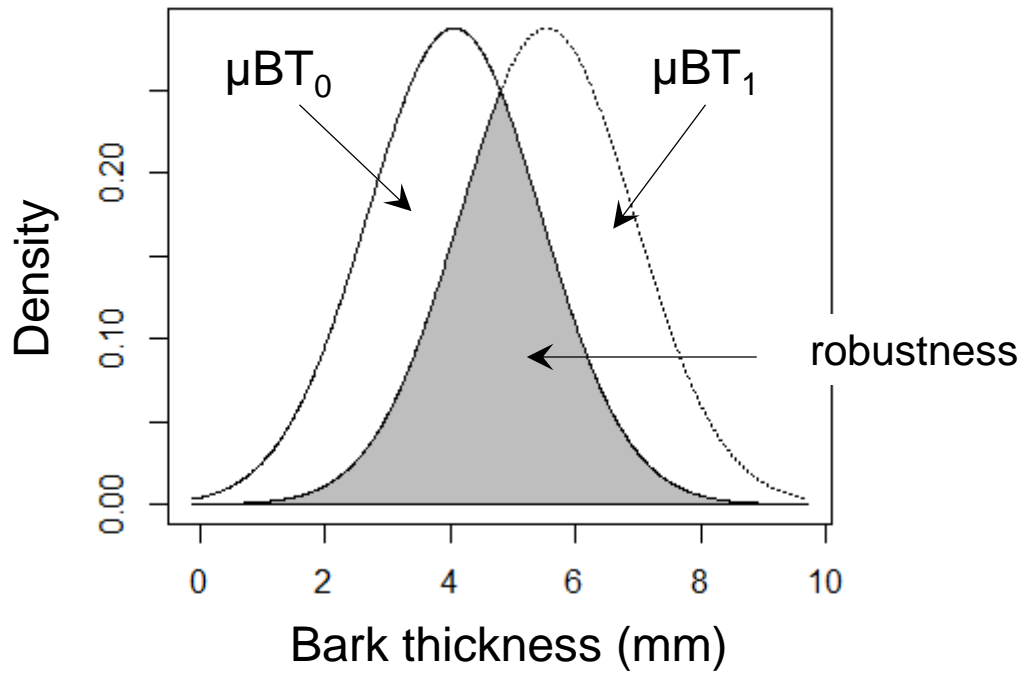
803

804

Figure S3: Sensitivity of our results to calculations of relative bark thickness based off of outer stem diameter from alternative calculations using the diameter from the stem bole (Midgley & Lawes 2016). All calculations were performed on stem diameters of 10cm. A) histogram of the residuals between the calculation of outer bark (non-bole) vs. bole. B) scatter plot of the two calculation methods with the solid line representing the 1:1 relationship. C and D) comparison between biomes across continents using the two different calculation methods of outer bark (C) and bole (D). Qualitative results using bole calculations were the same (NA: $F_{1,103}=6.57$, 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).
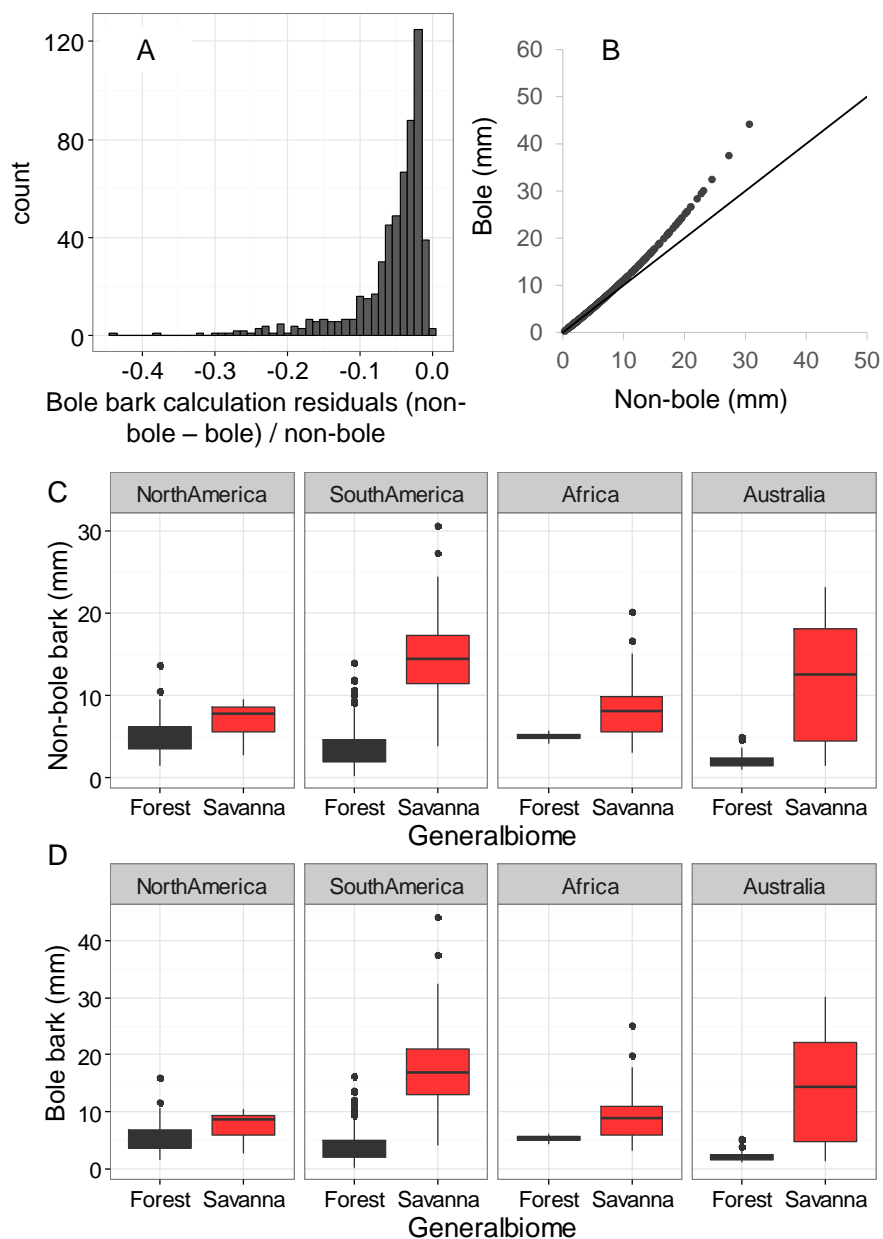
Figure S4: Global distribution of bark thickness across all species. Occurrence points were inverse distance weighted to create spatial averages within distances of 0.5 degrees around each observation point. Bark thicknesses correspond to trees with a reference stem diameter of 10 cm. Grey areas are locations where we do not contain data.


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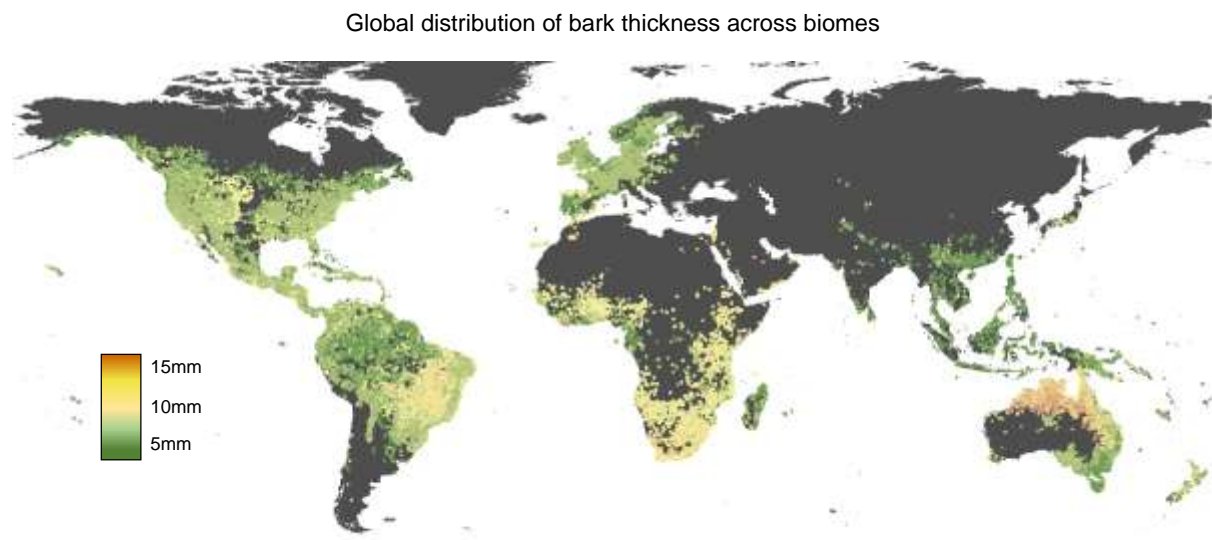
825 **Figure S5:** Bark thickness of 10cm diameter stems in savanna and forest biomes across
826 continents. Letters indicate significant differences determined via Tukey HSD with correction for
827 multiple comparisons (Table S4 for statistics).
828

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
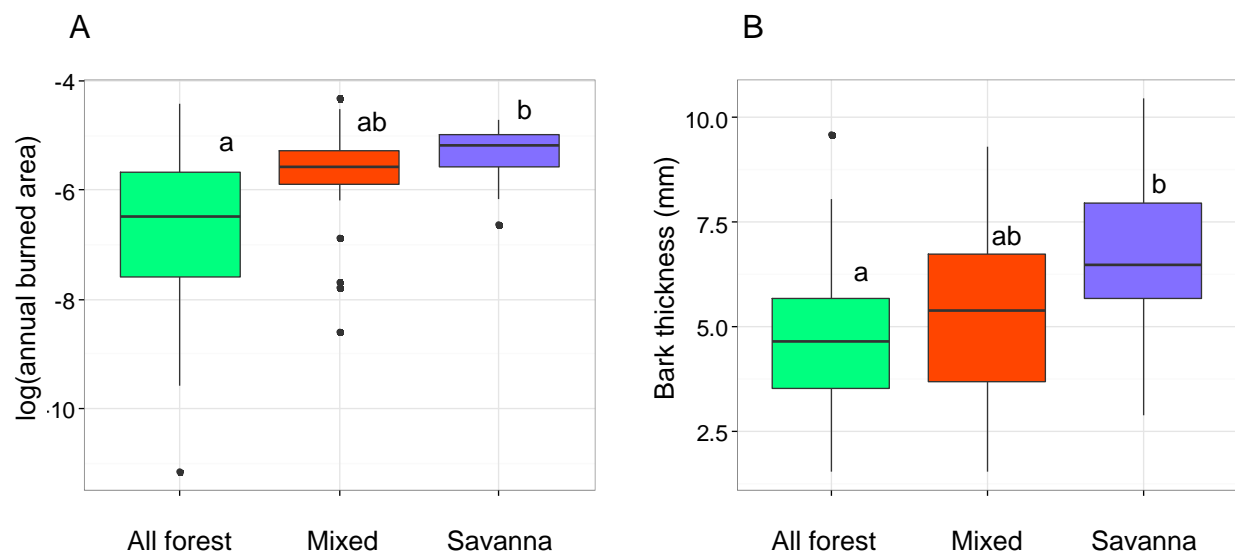
**Figure S7:** Comparison of the relationship between burned area and bark thickness using the two
different fire frequency datasets. GFED3s is based off of data from 2001-2010 and includes
correction for small fires (20% of deviance explained). GFED4 is based off of data from 1996-
2015 but does not include correction for small fires likely leading to the lower-bound x-axis
being smaller (20% of deviance explained).
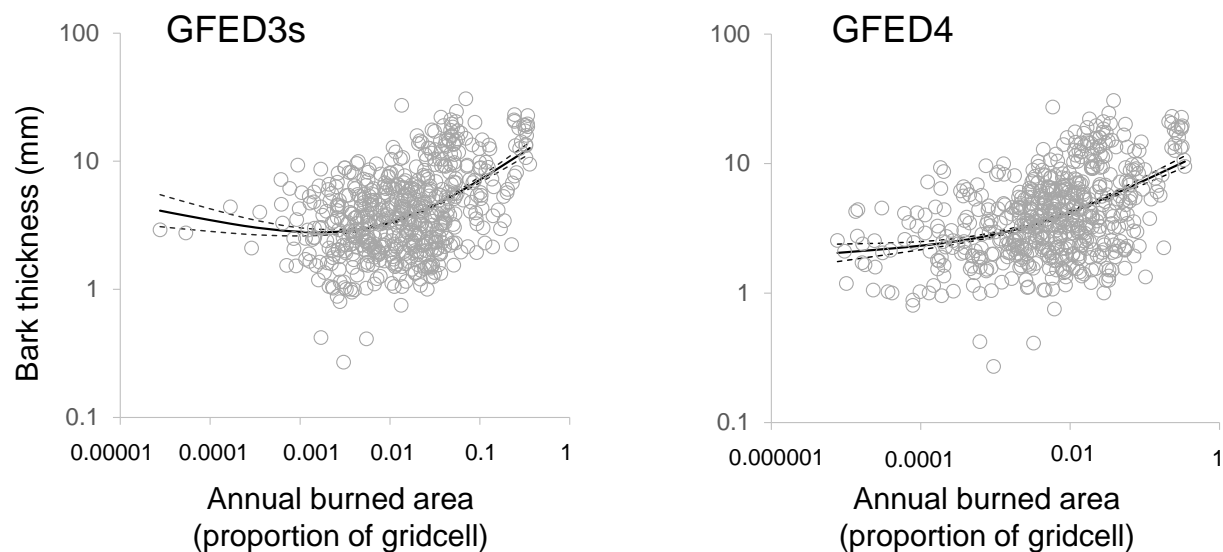
847 **Figure S8:** A) Comparison of bark thickness in species specializing in savannas vs. forests in the
848 same family. Error bars are ±95% confidence intervals. Rank order figure illustrates the
849 distribution of bark thickness ratios (savanna / forest) with individual families (B) and genera
850 (C), with the dashed line indicating 1.

851

852
853
854
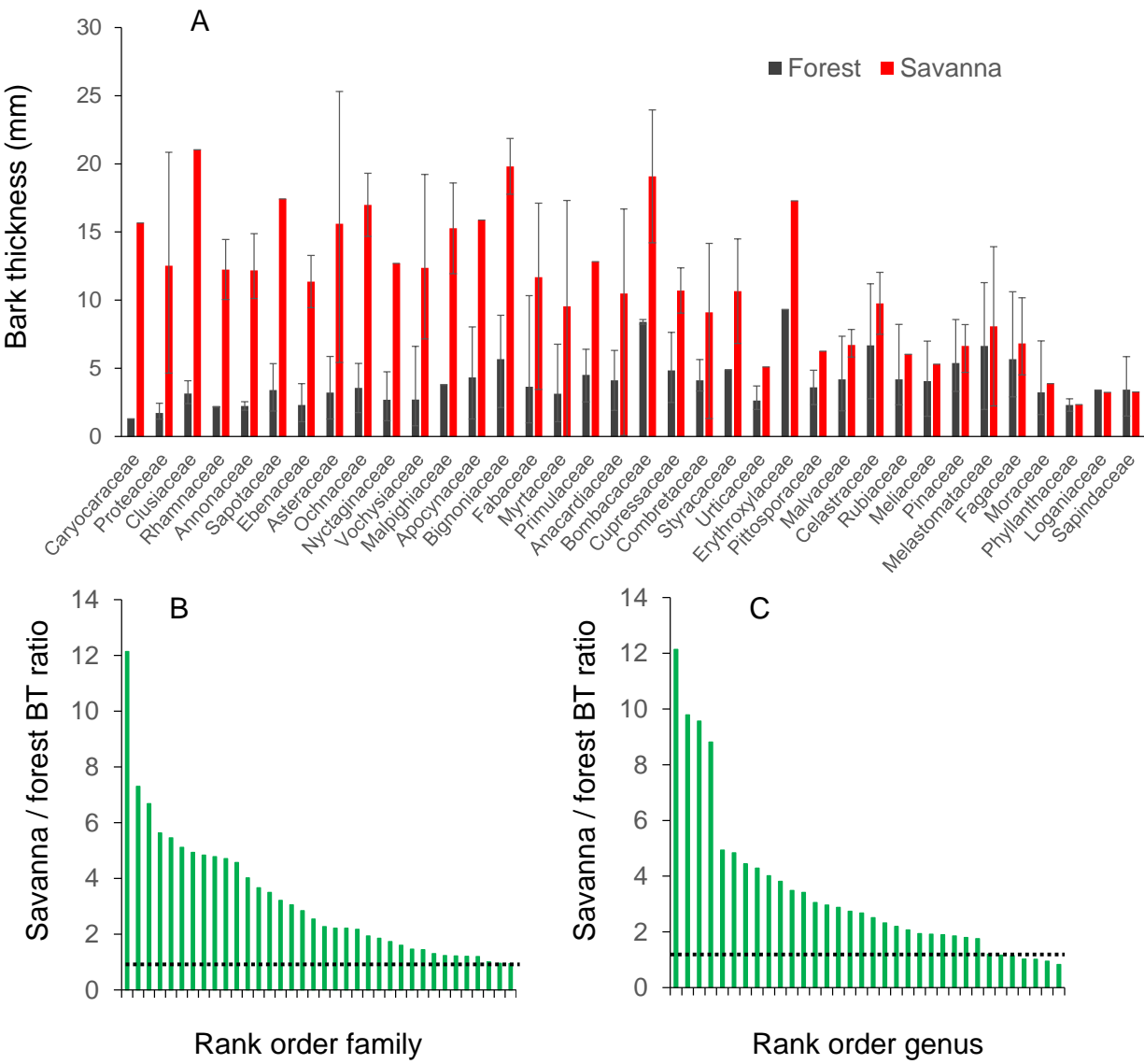
855 **Figure S9:** Future changes in fire and bark thicknesses from modelled projections. A) future
856 annual burned area for grid cells partitioned between savanna vs. forest species. B) absolute
857 changes in bark thickness assuming model projections expressed as probability distributions; C)
858 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
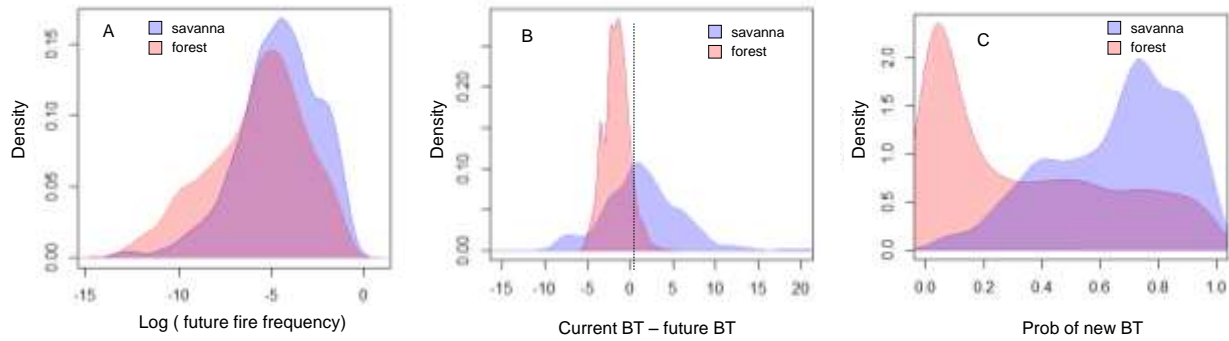
864 **Figure S10:** Fitted model output of bark thickness in savannas using a model that either (A)
865 includes latitude and longitude as model covariates or (B) only includes climate and fire.

A

B

866
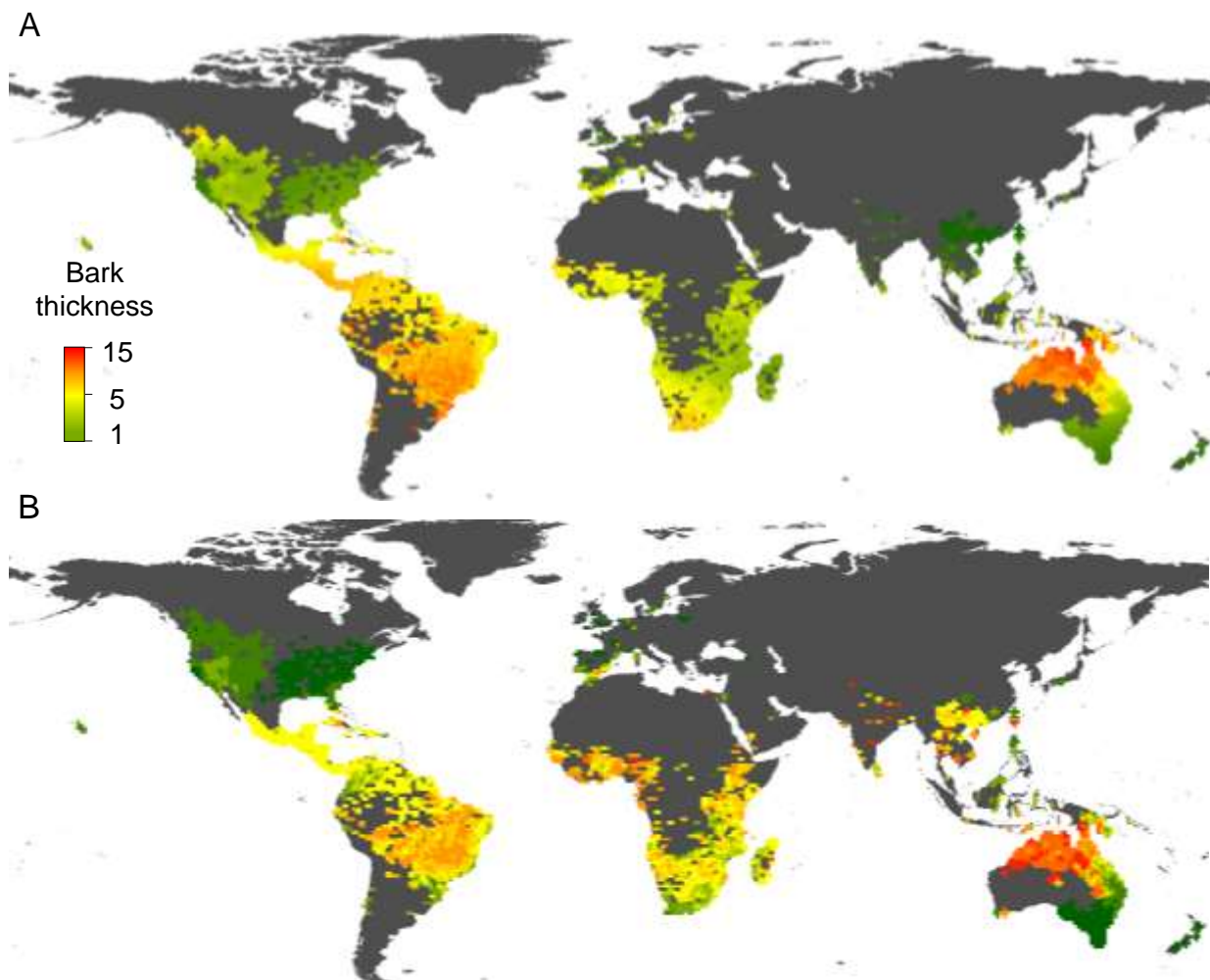
867 **Table S1:** List of species, the studies that they were compiled from, their location, biome, and
868 bark thicknesses. The bark thickness for a specific species in some cases came from multiple
869 studies, which we averaged, but present the full dataset for the species available here. **Attached.**
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	10cm		20cm		30cm	
		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

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

Comparison	Forest		Savanna	
	Diff	p value	Diff	p value
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

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

Variables included	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%

Table S6: Using GFED4 to characterize environmental conditions that determine bark thickness. Statistical results from generalized additive models between log bark thickness (for stems 10cm in size), fire, climate, and biome using model selection. 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 specialized in (either savanna or forest). The best fit models are highlighted in bold, we utilized the more parsimonious of the two.

Variables included	Dev	AIC
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

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

Variables included	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

Variables included	Dev	AIC
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