

Decadal changes in fire frequencies shift tree communities and functional traits

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1 Global change has resulted in chronic shifts in fire regimes, increasing fire frequency in
2 some regions and decreasing it in others. Predicting the response of ecosystems to changing
3 fire frequencies is challenging because of the multi-decadal timescales over which fire
4 effects emerge and the variability in environmental conditions, fire types, and plant
5 composition across biomes. Here, we address these challenges using surveys of tree
6 communities across 29 sites that experienced multi-decadal alterations in fire frequencies
7 spanning ecosystems and environmental conditions. Relative to unburned plots, more
8 frequently burned plots had lower tree basal area and stem densities that compounded
9 over multiple decades: average fire frequencies reduced basal area by only 4% after 16
10 years but 57% after 64 years, relative to unburned plots. Fire frequency had the largest
11 effects on basal area in savanna ecosystems and in sites with strong wet seasons. Analyses
12 of tree functional-trait data across North American sites revealed that frequently burned
13 plots had tree communities dominated by species with low biomass nitrogen and
14 phosphorus content and with more efficient nitrogen acquisition through ectomycorrhizal
15 symbioses (rising from 85% to nearly 100%). Our data elucidate the impact of long-term
16 fire regimes on tree community structure and composition, with the magnitude of change
17 depending on climate, vegetation type, and fire history. The effects of widespread changes
18 in fire regimes underway today will manifest in decades to come and have long-term
19 consequences for carbon storage and nutrient cycling.

20

21

22 Ecosystem resilience to changing fire regimes^{1–3} will be a key determinant of how terrestrial
23 biomes respond to global change^{3–5}. Fire is a pervasive disturbance, burning ~5% of global land
24 area each year and releasing carbon stored in plant biomass equivalent to 20% of anthropogenic
25 fossil fuel emissions^{6,7}. Historically, much of this carbon is re-sequestered through time as plants
26 recover and regrow, then lost again in the next fire. However, in many systems, changes in
27 climate and land use have shifted fire frequencies, potentially changing the ability of plants to
28 regrow between fires^{1,8–10}.

29 More frequent burning increases productivity, biodiversity, and plant biomass in some
30 ecosystems, whereas in other ecosystems, little change or even the opposite occurs^{11–15}. Our
31 ability to determine why these different responses occur across ecosystems remains limited. At
32 large biogeographic scales, many analyses rely on observational datasets comparing spatial
33 patterns in fire frequency with tree cover and biomass^{16,17}; although informative, this approach is
34 limited by the collinearity between variables that both determine fire frequency and tree cover,
35 such as rainfall. Furthermore, the effect of repeated burning on tree cover can take multiple
36 decades to become significant^{12,15,18–20}, emphasizing the need to account for the length of time
37 fire frequencies have differed and consider multi-decadal alterations in fire frequencies.

38 In addition to environmental factors and timescale, plant community composition and
39 species' functional traits may explain additional variability in responses to long-term changes in
40 fire frequency²¹. For example, traits related to physiological protection from heating during fire
41 and the capacity to colonize and regrow rapidly could help predict losses of trees due to frequent
42 burning^{15,22–24}. Additionally, nutrient acquisition and use traits can influence the future
43 productivity of plants and their ability to regrow after fire²⁵ and also have long-term implications
44 for carbon and nutrient cycling in soils²⁶. For example, plants that form symbioses with
45 ectomycorrhizal fungi, arbuscular mycorrhizal fungi, or nitrogen-fixing bacteria may be better
46 equipped to access limiting nutrients under frequent burning. The distinction between strategies
47 is important, however, because ectomycorrhizal plants tend to slow nutrient cycling and
48 productivity, while arbuscular and nitrogen-fixing species can accelerate cycling and increase
49 productivity^{25–28}.

50 The existence of experimental manipulations of fire frequencies across sites that span
51 large environmental and compositional gradients offers an opportunity to test how ecosystems

52 respond to altered fire frequencies^{29–32}. However, the few studies comparing multi-decadal fire
53 manipulations have typically been constrained to small groups of sites within single
54 ecosystems^{31,33}. Here, we quantified the effects of fire frequency on tree cover across broad
55 biogeographic and climatic scales, incorporating additional factors that may explain variability in
56 fire effects on tree communities. We analyzed data on tree populations from 29 sites and 374
57 plots; at 27 of the sites (324 plots), surface fire frequency was experimentally manipulated for
58 16–64 years (mean of 30 years), and at two sites (50 plots), natural variation in crown fire
59 frequency presented a natural experiment. The sites cover North and South America, Africa, and
60 Australia across major biomes that experience frequent burning (Figure S1, Table S1,
61 *Supplemental Information, SI*). Each surface fire site contains replicate plots including an
62 unburned treatment and different prescribed burning frequencies (Figure S2), where fire
63 frequencies ranged from approximately one fire every decade to one fire every year (Table S1).
64 To evaluate the effects of fire alone and in combination with environmental covariates while
65 accounting for the high variability in overall tree basal area and stem density across sites, we
66 used mixed-effects models with site as a random intercept as the main test in our analysis (*SI*).
67 We focused on tree responses because trees are critical for long-term carbon storage and
68 productivity³⁴, define the ecosystem (e.g., whether a landscape is a forest or savanna)³⁵, and
69 influence several biogeochemical processes³⁶.

70 There was a clear overall effect of fire treatment on tree populations. Tree density (stems
71 per-hectare) tended to be lower in frequently burned plots relative to infrequently or unburned
72 plots (Figure 1a). A comparison between the most extreme fire frequency treatments using
73 response ratios illustrated that densities were 44±25% lower in the most frequently burned plots
74 compared with unburned plots, and that the differences between fire treatments were lower when
75 the differences in fire frequencies were lower (Figure 1b, Table S2, error defining 95%
76 confidence intervals). When fire frequency and duration of study were analyzed as continuous
77 variables across all plots and sites using mixed-effects models, sites with longer durations of
78 altered fire frequencies had larger differences between fire treatments ($F_{1,282}=47$, $p<0.001$), with
79 the slope between duration and stem density being more negative the more frequently plots were
80 burned ($F_{1,280}=8.4$, $p=0.004$, Figure 1c). For example, relative to unburned plots, stem density in
81 plots with a three-year fire-return interval was 26% lower after 30 years and 48% lower after 50
82 years (Figure 1c, Table S3). Fifty years of annual burning resulted in burned plots having 63%

83 lower stem density relative to unburned plots (Figure 1c, Table S3, see Figure S3 for non-
84 transformed results).

85 Fire type was also important, with frequent crown fires affecting tree populations to a
86 greater degree than frequent surface fires. Comparison of 50 plots in needleleaf forests that
87 experienced natural variability in the frequency of stand-replacing crown fires (i.e., wildfires)
88 illustrated that stands with shorter fire-return intervals had significantly lower tree densities,
89 especially when plots with the shortest return intervals were considered ($F_{1,26.5}=5.2$, $p=0.03$ and
90 $F_{1,21}=10.3$, $p=0.004$, Figure S4). Experimental manipulation of surface fire frequency (i.e.,
91 prescribed fires) in needleleaf forests in the USA showed that stem densities were lower in more
92 frequently burned plots, but less so than differences caused by frequent crown fires ($F_{1,47.1}=17.2$,
93 $p=0.001$, Figure S4). The large effect of short-interval crown fires on tree communities,
94 supported by studies from other regions^{37,38}, highlights the importance of higher fire intensities
95 having more severe effects.

96 Fire had similar effects on tree basal area, which we analyze in detail, because basal area
97 correlates with tree biomass, canopy cover, and tree carbon storage. Basal area was on average
98 $54\pm25\%$ lower in the most frequently burned plots relative to the unburned plots (Figure 2a,b).
99 When frequency and duration were considered in parallel across all sites, the lower basal area in
100 frequently burned plots became more apparent with increasing experimental duration and
101 frequency of burns (frequency-duration interaction, $F_{1,289}=23.3$, $p<0.001$; Figures 2c, Table S3,
102 mixed-effects models). For example, plots with 30 years of triennial burning had 27% less basal
103 area relative to unburned plots, while those with 50 years had 53% less basal area. Divergence
104 between fire treatments was even greater after 50 years of the most extreme frequencies of
105 annual burning, where burned plots had 72% less basal area than unburned plots. Consequently,
106 changing fire frequency and duration of exposure shifted tree basal area and stem abundance
107 across sites. The manifestation of fire effects began to lessen as experiments had increasingly
108 long durations, suggesting that effects will saturate as tree cover approaches a new equilibrium.

109 The effects of changing fire frequencies also depended on the fire history of the site prior
110 to the establishment of the experiment. In forest sites that burned regularly in the decades prior to
111 the onset of the experiment, fire exclusion resulted in basal area being 50% ($\pm17\%$) higher than
112 treatments that maintained historical burning frequencies ($p=0.002$, Figure S5, Table S1 for site

113 fire histories). In contrast, the reintroduction of fire into forests that had not burned for several
114 decades prior to the onset of the experiment had relatively minimal effects ($p=0.13$, Figure S5).
115 These results differ from studies on wildfires which are known to have larger effects in forests
116 that have a history of fire exclusion due to high fuel accumulation^{39,40}, which is somewhat
117 expected given the lower severity of prescribed surface fires. In savannas, where the fire
118 experiments were all initiated in landscapes that burned regularly in the decades preceding the
119 experiment, fire exclusion resulted in basal area increasing by 41% ($\pm 20\%$), but increasing fire
120 frequency resulted in basal area declining by 48% ($\pm 16\%$), relative to an intermediate interval
121 that maintained the pre-experiment frequency (statistics from log response ratios $\pm 95\%$
122 confidence intervals, $p<0.001$ for both, Figure S5, *SI*). Taken together, the largest effects of
123 altered fire frequencies were due to fire exclusion in landscapes that had burned regularly for at
124 least the past few decades.

125 Climate played an important role in modifying the effect of fire frequency on trees. Fire
126 effects were largest in areas that received more rainfall in the wet season, less rainfall in the dry
127 season, and had lower mean annual temperatures ($F_{1,292.2}=55.2$, $p<0.001$, $F_{1,284.7}=9.8$, $p=0.002$,
128 and $F_{1,283.2}=18.1$, $p<0.001$, respectively) (Figure 3a-c, Table S4, see Table S5 for stem density).
129 Sites with higher precipitation in the wet season experienced larger effects of burning. For
130 example, plots that experienced more frequent burning (2 fires every 3 years, one standard
131 deviation above mean frequency) had 67% lower tree basal area than unburned plots in sites with
132 high wet season precipitation (Figure 3a, S6, Table S4, see *SI* for details on calculations). The
133 difference between treatments was only 22% in sites with average wet season precipitation.

134 Precipitation in the dry season had opposite effects. Sites with lower precipitation in the
135 dry season experienced twice as large an effect of fire on basal area (46% vs. 22% lower tree
136 basal area in sites with low vs. average dry season precipitation Figure 3c, Table S4). The
137 contrasting response to precipitation in the wet vs. dry season is consistent with our
138 understanding that fires are most intense in areas with stronger wet seasons (leading to more
139 fuel) and more severe dry seasons (lower fuel moisture), thus contributing to potential losses
140 with more frequent burning^{41,42}. Rainfall in the dry season likely also influences fire effects by
141 determining the water available for tree growth when fire is excluded. Soil characteristics did

142 not explain sensitivity to changing fire frequencies across sites; across all sites, neither texture-
143 based classification of soils nor soil carbon content interacted with fire frequency (Table S4).

144 The effect of fire on tree basal area also differed across ecosystems ($F_{2,279}=14.5$,
145 $p<0.001$), with frequent burning having a larger effect on tree basal area in savannas relative to
146 broadleaf and needleleaf forests (accounting for climate effects and differences among
147 continents, Figure 3d, Table S4). Relative to the unburned plots, basal area in frequently burned
148 plots was 6% lower in needleleaf forests and 22% lower in broadleaf forests (Figure 3d, burn
149 frequency of two fires every three years, *SI*). In savannas, frequently burned plots had 70% lower
150 basal area relative to the unburned plots (Figure 3d, Table S4). Interestingly, stem density
151 responses to fire frequency were qualitatively different between savannas and forests (Table S5).
152 Stem densities increased with more frequent burning in forests while basal area decreased,
153 potentially due to higher light availability and recruitment of trees in the forests. We tested the
154 sensitivity of our findings that savannas were more sensitive to increased burning frequency via a
155 subdivided classification of ecosystems by partitioning broadleaf forests into oak and eucalypt
156 types and needleleaf forests into those that transitioned between oak and pine dominated (Table
157 S1). When included in the final model, the subdivided vegetation classification still had a
158 significant main effect ($F_{4,19.4}=12.4$, $p<0.0001$), and a significant interaction with fire frequency
159 ($F_{4,276.8}=7.8$, $p<0.001$, Figure S8), with basal area in savannas responding the most to changes in
160 fire frequency (Figure S8).

161 We next tested the extent to which plant traits influence tree responses to fire across
162 ecosystems²³. We analyzed only the experiments from North America (77 tree species, 16 sites,
163 181 plots) because trait data were available there to (i) categorize species by nutrient-acquisition
164 strategies, and (ii) assign wood, leaf, and root traits related to growth, survival, and nutrient-use
165 strategies. Plots with tree species having thinner bark and denser wood changed relatively more
166 with frequent burning (bark: $F_{1,154.3}=5.7$, $p=0.018$; wood density: $F_{1,154.1}=12.9$, $p<0.001$, Table
167 S6, Figure 4a,b). Within a site, mean wood density of the tree community tended to be lower in
168 frequently burned landscapes, potentially because of increasing dominance of gymnosperms,
169 which tend to have lower wood density. In contrast, we did not observe any effect of fire on the
170 mean bark investment of the tree community (Table S6), demonstrating that bark investment at

171 the community scale does not appear to change in response to fire; nevertheless, bark investment
172 may influence basal area loss patterns across broad biogeographic scales.

173 Frequent burning also shifted the nutrient use and acquisition strategies of tree
174 communities, as expected given the nitrogen (N) losses resulting from frequent burning⁴³. Plots
175 burned frequently for longer periods of time were dominated by tree species with low N
176 concentrations in green and senesced leaves and roots, and resorbed a greater proportion of N
177 before leaf senescence ($p < 0.001$ for all variables, Figure 4d, Table S7). Tissue phosphorus (P)
178 concentrations also declined with frequent burning in leaves and litter but not in roots (Figure
179 S10, Table S7).

180 Fire also affected the relative abundance of nutrient-acquisition strategies. We evaluated
181 changes in acquisition strategies using categories of trees' abilities to form symbioses, which
182 correlate with several other traits involved in acquisition⁴⁴. Trees that formed symbioses with
183 ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) fungi were the most abundant
184 nutrient-acquisition strategies across our plots; ericoid and nitrogen-fixing trees were absent
185 from most sites (Figure 4c). ECM trees, which contain fungal symbionts capable of acquiring N
186 from organic matter⁴⁵, tended to be more successful in frequently burned plots. The relative
187 abundance of ECM trees increased from 85% in unburned plots to nearly 100% in annually
188 burned plots (Figures 4c, Table S8). ECM trees were also more common in warmer climates and
189 on soils with low organic matter (Figure S11, Table S8). ECM trees typically have lower
190 concentrations of N and P in leaves, litter, and roots than AM trees⁴⁶ (Figure S12, Table S9),
191 suggesting the turnover in symbiont composition may be driving the shift in stoichiometry of the
192 tree community. The tendency for frequently burned plots to have tree communities dominated
193 by ECM trees with low N and P content in leaves, roots, and litter indicates that frequent burning
194 favors tree species with a suite of traits consistent with a conservative strategy of nutrient use and
195 acquisition.

196 Although our analysis is to our knowledge the largest compilation of results from fire
197 manipulation plots to date, it identifies several factors that highlight the need for even larger-
198 scale analyses. For one, an improved representation of fire experiments in different ecosystem
199 types across continents (e.g., tropical forests in Africa and savannas in Australia) will help
200 further unpack the variability across ecosystems. Past research has demonstrated that the

201 turnover in tree species composition can be important for explaining changes in total tree cover
202 within experiments⁴⁷. Thus, a better understanding of how fire kills trees and how these
203 processes differ across ecosystems may give a more complete picture of why fire effects vary.
204 Our analyses also demonstrated that land use history and the fire regime prior to experiment
205 establishment are critical to interpreting the magnitude of fire effects, consistent with previous
206 studies⁴⁸. Consequently, global-scale estimates of how current shifts in fire frequency alter
207 ecosystem carbon should carefully consider how uncertainties in fire history preceding the
208 satellite era may influence their estimates.

209 Our findings that fire effects emerge over multiple decades but then approach a new
210 (non-zero) equilibrium are in agreement with studies that have performed repeated
211 measurements of tree populations within the same experiment. Generally the treatments can
212 diverge over the first few decades¹⁵, but the rate of divergence declines through time³⁰. The
213 timescale of change is similar to the multi-decadal shifts in soil carbon and nitrogen, which likely
214 reflect a link between tree biomass inputs into soil carbon pools and potentially the turnover of
215 plant traits interacting with changes in soil nitrogen pools^{25,49,50}.

216 In conclusion, widespread changes in fire regimes are likely to have structural,
217 compositional, and functional effects on tree communities that manifest over decades.
218 Importantly, fire is an integral part of many ecosystems and can promote biodiversity, reduce
219 wildfire risk, and stimulate nutrient turnover; consequently, lower tree basal area and density in
220 more frequently burned plots is not necessarily a negative result depending on the management
221 goals for the ecosystem. Nevertheless, persistent changes in fire frequency will have, and already
222 are having, profound effects on ecosystems and need to be considered in projections of
223 communities and ecosystems in the future.

224

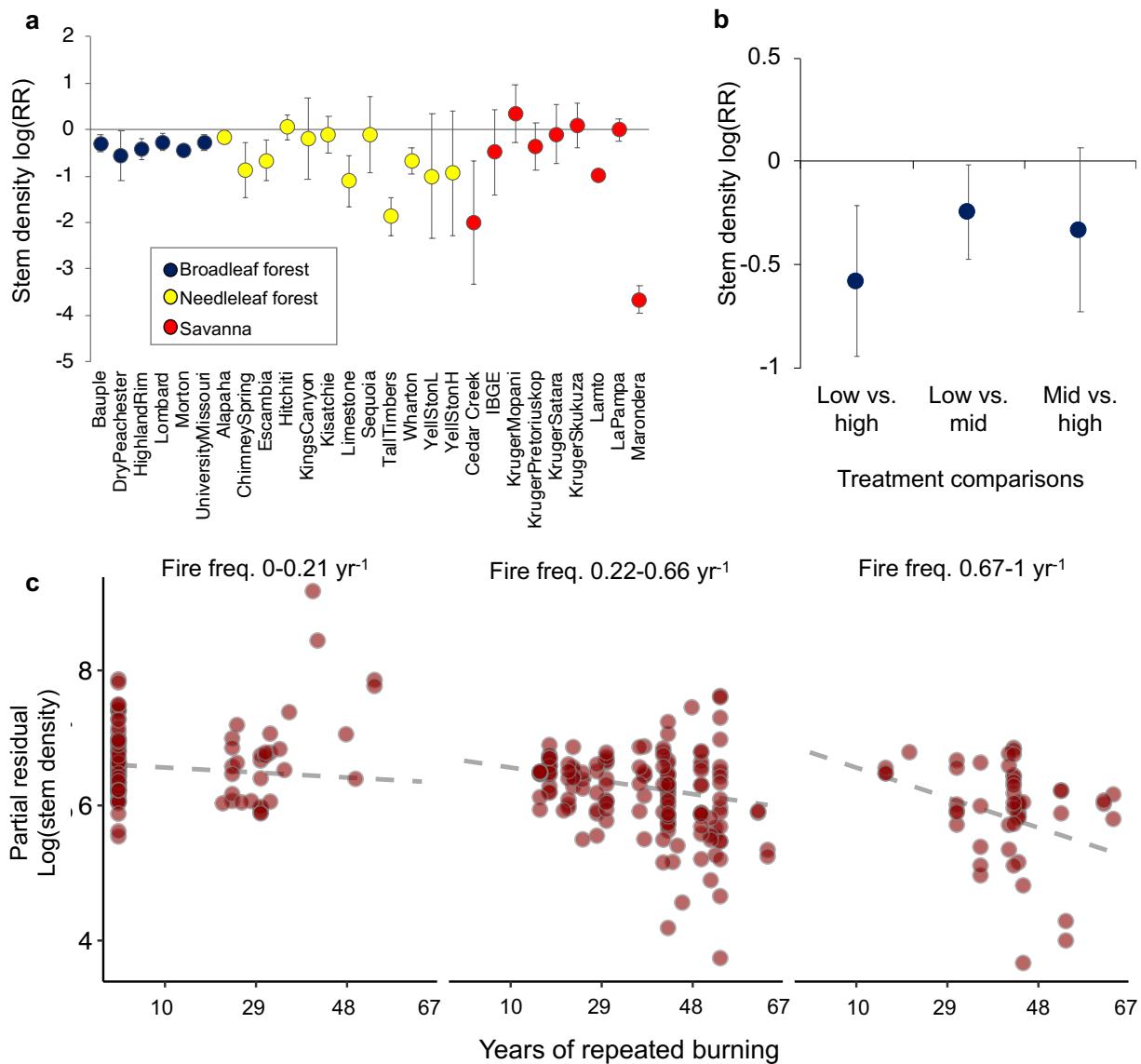
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229 **Figure 1:**

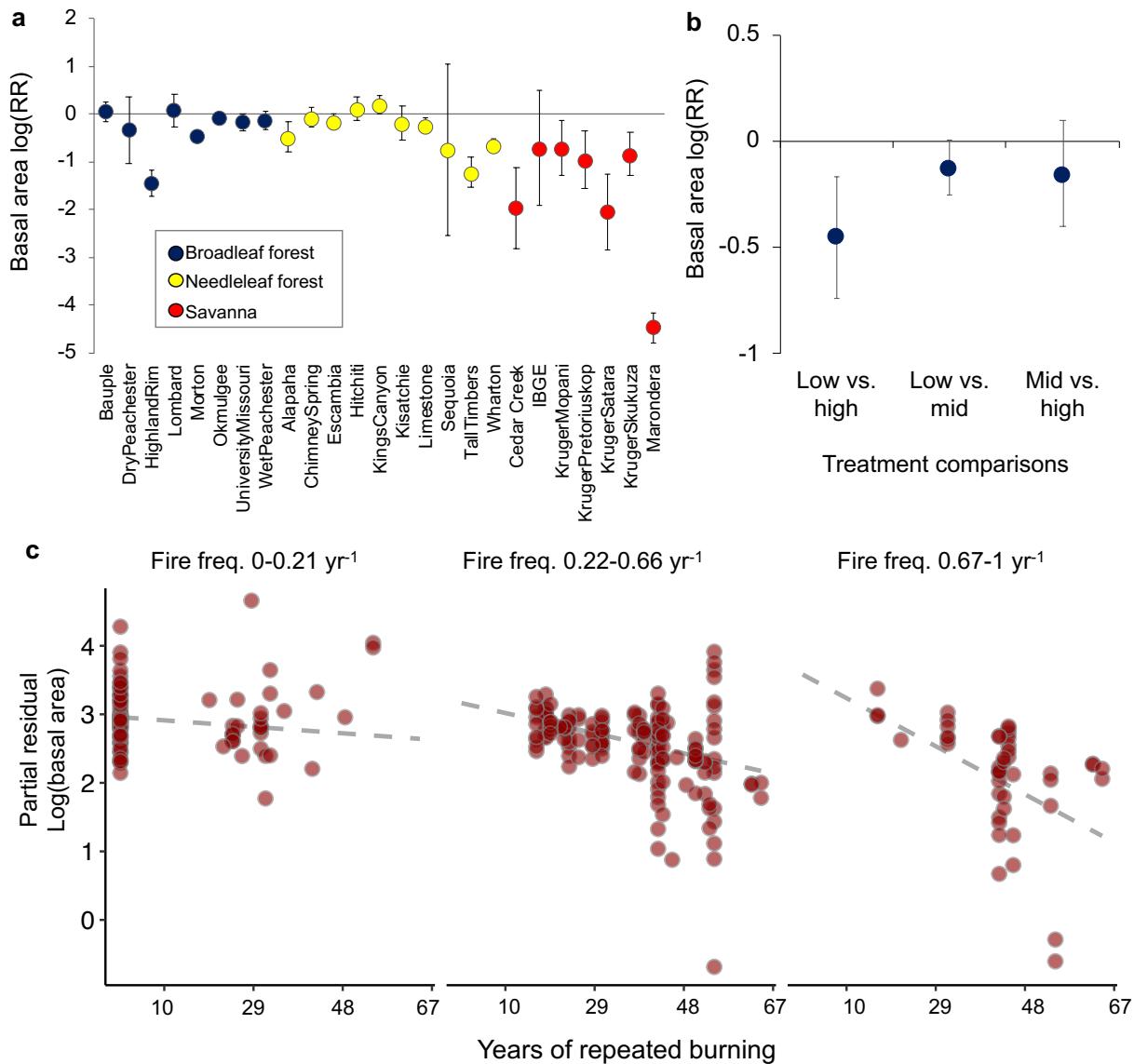


230

231 **Figure 1: Fire effects on stem density increase with degree of frequency contrast and length**
 232 **of study duration. a-b)** log response ratios of stem densities and the surrounding 95%
 233 confidence intervals. **a)** comparisons within each individual site colored by broad biome
 234 categorization in most extreme fire frequency treatments $\log_e(\text{burned}/\text{unburned})$ (Table S1). **b)**
 235 comparisons among the different levels of fire frequency in studies with ≥ 3 levels; less frequent
 236 treatment always in denominator, Table S2). **c)** partial residuals plot from a mixed effects model
 237 including fire frequency, the number of years of repeated burning, and their interaction for \log_e
 238 stem density (Table S3); site was used as a random intercept. Panels are centered on cross-
 239 section values of one fire every 10 years, 1 every 3 years, and 1 every year but encompass a
 240 range of fire frequencies within each panel.

241

242 **Figure 2:**

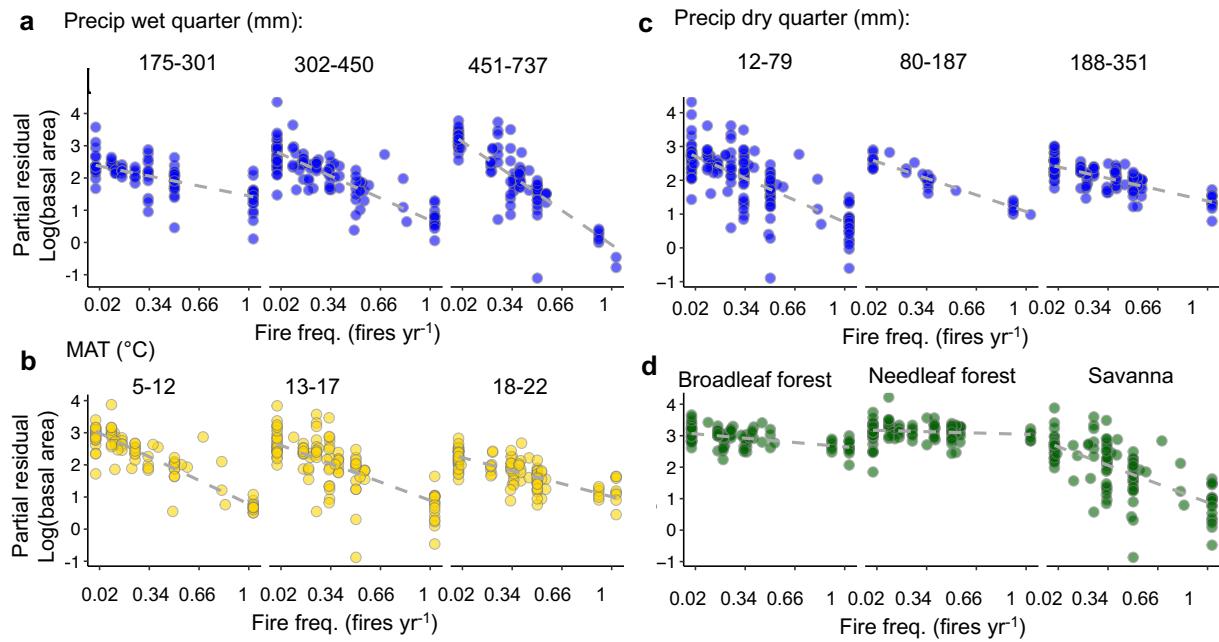


243

244 **Figure 2: Frequent burning decreases tree basal area and compounds with time of**
 245 **exposure to different fire frequencies. a-b)** log response ratios of basal area and the
 246 surrounding 95% confidence intervals. **a)** comparisons within each individual site colored by
 247 broad biome categorization in most extreme fire frequency treatments log_e(burned/unburned)
 248 (Table S1). **b)** comparisons among the different levels of fire frequency in studies with ≥ 3
 249 levels; less frequent treatment always in denominator, Table S2). **c)** partial residuals plot from a
 250 mixed effects model including fire frequency, the number of years of repeated burning, and their
 251 interaction for log_e basal area (Table S3); site was used as a random intercept. Panels are
 252 centered on cross-section values of one fire every 10 years, 1 every 3 years, and 1 every year but
 253 encompass a range of fire frequencies within each panel.

254

255 **Figure 3**



256

257 **Figure 3: Climate, ecosystem type, and plant traits modify effects of fire frequencies on tree**
258 **basal area.** Partial residual plots of the mixed-effects model illustrating the interactive effects

259 between covariates (site as a random intercept). Panels centered on cross-sectional values from

260 one standard deviations around the median (-1, 0, 1). MAT: mean annual temperature.

261 Comparisons of rainfall scenarios relative to the mean in the text used wet-season precipitation

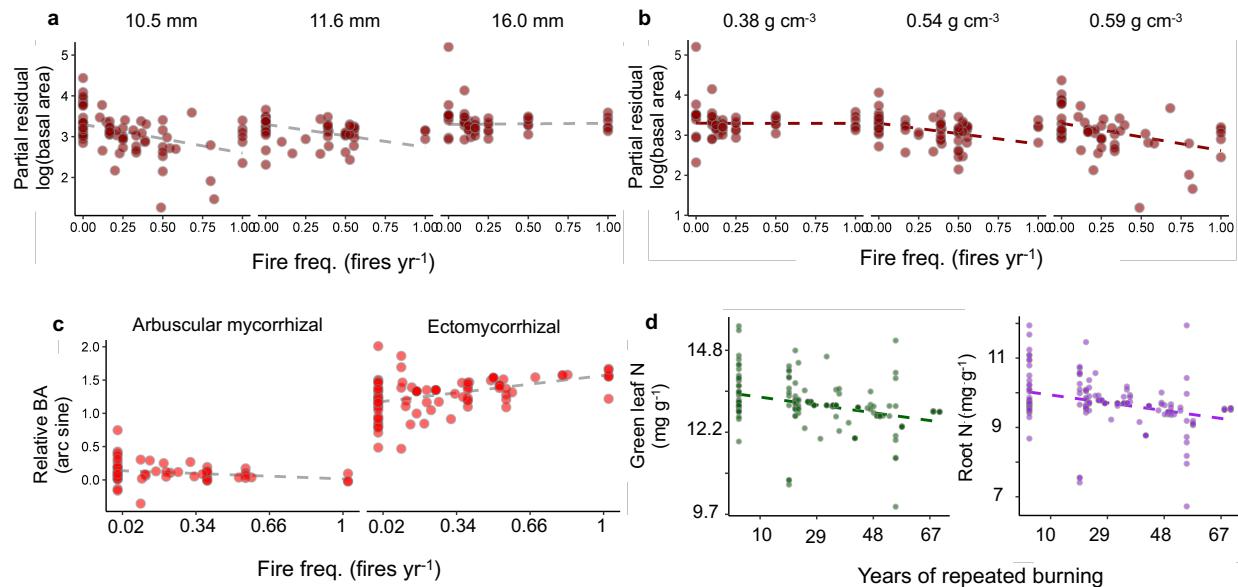
262 of +1 standard deviation above the mean (525 vs. 375 mm yr⁻¹) and dry season precipitation of -1

263 standard deviation below the mean (25 vs. 133 mm yr⁻¹). The duration of experiment held at its

264 mean of 28 years. All model fits are $p < 0.05$; statistics are in Table S4.

265

266 **Figure 4**



267

268 **Figure 4: Frequent burning filters for conservative nutrient-use and acquisition strategies**
269 **across North America.** Partial regression plots from mixed-effects models with community
270 weighted means of (a) bark investment scaled to a 10 cm stem size and (b) wood density (WD)
271 as modifying variables. Bark and wood density were included in the same model and were
272 negatively correlated $\sigma = -0.86$. Statistics are in Table S6. Basal area is \log_e transformed. c-d)
273 community weighted means of nutrient acquisition (c) and nutrient use (d) strategies. c) relative
274 basal area (arc sine transformed) of arbuscular vs. ectomycorrhizal trees as a function of fire
275 frequency. d) green leaf and live root N as a function of study duration. Statistics are in Tables
276 S7-S9. Data on litter N and resorption are in the Tables and phosphorus content data are in
277 Figure S8.

278

279

Supplemental Information

280

281 Experimental design and site descriptions

282 The majority of sites sampled comprise ecosystems that experience surface fires (from
283 fire manipulation experiments, n=27). Our main analyses are based on the surface fire
284 experiments, but we compare these data with a network of plots across n=2 sites with natural
285 variability in the frequency of stand-replacing crown fires to evaluate the effect of fire regime.
286 We describe the sites briefly in Table S1, and present detailed descriptions of site history in
287 Dataset 1.

288 The surface fire experiments mostly are experimental prescribed burn plots. The
289 managers generally try to burn in a broad seasonal window (e.g., a spring fire in North America
290 may occur anytime from March-May) to optimize burn timing for the local fire conditions most
291 suitable to their planned fire intensities. The sites contained different land use histories before the
292 establishment of the experiment, which was not always documented in detail, but we describe
293 key factors in Tables S1 and Dataset 1. We describe how we evaluated the potential role of land
294 use history in *Testing role of fire and land use history* below.

295 Because these experimental sites utilized different survey methods, the classification of a
296 plant as a tree differed. In some cases, such as savannas with relatively small woody plants, all
297 woody plants over a basal diameter of 5 cm were measured (which includes shrubs). In other
298 cases, stems only above 10 cm diameter at breast height were measured. Consequently, the
299 definition of 'tree' is based on the local knowledge of what is the relevant size threshold for a
300 particular ecosystem, and in some cases it includes all woody plants.

301 The stand-replacing crown fires are from one extensive ecosystem type that accounts for
302 a large amount of forest fire area in North American temperate regions. Specifically, we used
303 data from 50 plots in lodgepole pine forest in the Western United States²³ (n=50) spanning
304 different elevations and plots along a continuum of fire return intervals²³. Because this ecosystem
305 experiences stand-replacing fires, time-since-fire is critical for determining tree abundance
306 because it determines the stage of regrowth. We dealt with this by sampling plots that differed in

307 their fire return interval over the past several hundred years but shared the same time since last
308 fire because of a large fire that burned forests with different times since the previous fire. Given
309 the previous study found elevation to be important, we included elevation categories in the
310 model (<2400 m and >2400 m, respectively).

311

312 **Choice of plots within 27 sites with surface fires**

313 Within each site, we only used one sampling time period for our analysis. Eight sites
314 contained time series data: Cedar Creek, Lombard, Sequoia, Kings Canyon, and the four Kruger
315 sites. For Lombard, we used the surveys from 2002, for Cedar Creek we used 2010, for Kruger
316 we used 1996-98 and for Sequoia and Kings Canyon it varied according to the replicate plots
317 because their most recent surveys occurred in different years. For Cedar Creek, more recent
318 surveys exist, but the outbreak of oak wilt has resulted in large amounts of tree mortality not due
319 to fire (Reich *personal communication*). For Highland Rim, we used two different sets of data:
320 the first dataset contains plot-level data (thereby allowing us to determine a variance around the
321 mean) but no tree species identities; the second dataset contains no plot-level data but has
322 treatment-level averages within each tree species, which allowed us to analyze composition
323 changes. We utilized the plot-level data for analyses of basal area and stem density. For Morton
324 and Okmulgee, there are not always true replicates in each fire treatment. Morton contains two
325 true replicates for the unburned, but no true replicates for the burned plots. Okmulgee contains
326 no true replicates.

327 In sites where fires were prescribed in different seasons, we used a single burn season in
328 the analysis in an attempt to match seasons of burns within a particular ecosystem type within a
329 particular region. In North America, we standardized fire season to burning conducted in the
330 winter to early spring because not all sites contained fire treatments with summer burns. For
331 Hitchiti, we used the December-March burns, dropping the June burns. For Kisatchie we used
332 March, dropping July and May. For Kruger, we used August, dropping all the other seasons. For
333 Lombard, we used March-May, dropping the June-Aug.

334 Lamto and La Pampa only contained data on the number of tree stems. Consequently,
335 these were incorporated into the stem abundance analysis only.

336

337 **Soil chemistry data**

338 We collected and analyzed soil data using several methods. First, we determined the
339 dominant soil type using either author descriptions or reported soil texture analysis. Second, we
340 used the highest resolution soil data as possible (e.g., soil samples from each replicate plot within
341 a fire treatment), but some sites only contained site-level soil properties. Consequently, we
342 analyze overall effects of fire on all sites without any covariates, followed by a model that uses
343 model selection to account for collinearities among variables when testing for factors that modify
344 fire effects. To extend data on soils across plots, we sampled soils (top 0-5 cm of the mineral
345 horizon) in 24 plots across four sites: Kings Canyon, Sequoia, Limestone Flats, and Chimney
346 Springs. Each site contained three replicate plots of an unburned treatment and a high fire
347 frequency treatment. We collected n=5 pseudo-replicates within the true replicate plot, analyzed
348 the soils for carbon, nitrogen, and texture, and averaged within each plot.

349

350 **Climate data**

351 To obtain long-term climate averages at each site, we used WorldClim⁵¹. Managers timed
352 burning to coincide with consistent weather conditions over the course of the experiment,
353 therefore we did not obtain high resolution inter-annual variability in climate. We focused on
354 several climate variables based on ecologically relevant *a priori* hypotheses: (i) precipitation
355 partitioned into the driest and wettest quarters of the year because precipitation influences fuel
356 accumulation (primarily in the wettest quarter) and fire conditions (primarily in the driest
357 quarter) and (ii) mean annual temperature because of its large effect on a variety of
358 biogeochemical processes. Precipitation in wet and dry quarters are not as correlated with one
359 another but are highly correlated with mean annual precipitation and temperature (Table S10).

360

361 **Calculation of fire effects in different environmental conditions**

362 Several methods exist to calculate variable importance, with no clear optimal method⁵².
363 We chose to use the regression coefficients in the model to understand the sensitivity of basal

364 area and stem density to changes in relative values of each variable. Importantly, the models
365 were fit to re-scaled data by subtracting each value by the mean and dividing by the standard
366 deviation of the variable. Consequently, the product between the mean value of a variable and its
367 coefficient is always zero. Thus, we can compare the relative impact of variables by comparing
368 the magnitude of the fitted coefficients because they reflect the potential change in basal area for
369 a one standard deviation change in a variable value.

370 To perform meaningful comparisons, we use the standard deviations of variables to
371 illustrate the sensitivity of basal area to a change in the value. For example, using the model to
372 estimate the effect of increasing fire by 1 standard deviation from the mean (mean = 0.34, mean
373 + 1σ = 0.67) tells us the sensitivity of basal area to fire, with all other variables held at their
374 means. Interactions can be tested by moving two variables away from their means: for example,
375 changing the fire value in conjunction with precipitation in the wet quarter. Because the model is
376 fit to re-scaled data, the intercept of the model is not representative of the unburned fire
377 treatment, which is calculated by re-scaling the fire frequency data $(0-\mu)/\sigma$, which gives a value
378 of -1.081, making the unburned calculation of $25.6 \text{ m}^2 \text{ ha}^{-1}$ when all other variables are held at
379 their means.

380 Here are the different levels of comparisons we used in the results and the corresponding
381 figures.

382 *Wet season precipitation* (Figure 3a): wet season precipitation varied one standard deviation
383 above the mean vs. at the mean (525 vs. 375 mm yr⁻¹, respectively). Fire frequency varied from
384 unburned to one standard deviation above the mean (2 fires every 3 years).

385 *Dry season precipitation* (Figure 3c): dry-season precipitation was one standard deviation below
386 the mean vs. at the mean (25 vs. 133 mm yr⁻¹, respectively). Fire frequency varied from
387 unburned to one standard deviation above the mean (2 fires every 3 years).

388 *Vegetation type* (Figure 3d): fire frequency effects were made using two levels of comparisons.
389 Unburned plots vs. burning at the mean frequency (1 fire every 3 years) and unburned plots vs.
390 burning at one standard deviation above the mean frequency (2 fires every 3 years).

391

392 **Testing overall fire effects**

393 We first tested the overall effects of the fire treatments across sites with log response
394 ratios using techniques employed meta-analyses^{53,54}. First, we calculated the log response ratio
395 between the different fire frequency categories (low, medium, and high) for basal area and stem
396 density averaged within each category, with the lowest fire frequency in the comparison always
397 in the denominator. Next, we determined the variance based on the number of true replicates
398 within each treatment in a site and the standard deviations within the fire frequency category.
399 These values across sites were then used to determine the effects of fire treatments on tree basal
400 area and stem density.

401 We first evaluated the overall effect of fire frequency and length of time frequency was
402 altered on tree basal area and stem density without considering any potential modifying role of
403 covariates to test the general effect of fire across all sites. To accomplish this we analyzed (i) a
404 mixed-effects model containing fire frequency, fire period, and their interaction, and (ii) log
405 response ratios of stem density and basal area relativized within each site. We excluded the 50
406 crown fire plots for this initial analysis. We fit the mixed-effects models with site as a random
407 intercept. The statistical design is nested because each site has several replicate plots receiving
408 different fire treatments. As a result of this design, the responses to fire at the plot level are likely
409 more related within sites than between sites, necessitating a random intercept. Although our
410 design is not balanced (sites differ in their number of replicate plots), models are generally robust
411 to unbalanced designs unless sample sizes are low and/or a random slope is being estimated⁵²,
412 neither of which are applicable here. Models were constructed based on our *a priori* hypotheses
413 of how fire would influence tree population sizes and the potential to interact with covariates. In
414 all cases of mixed-effects models, we tested for model significance using Satterwaith's
415 approximation for degrees of freedom and a Type III ANOVA⁵⁵. In the event of an insignificant
416 main effect but significant interaction, we tested whether the main effect could be dropped from
417 the model using a change in Aikake Information Criterion (AIC) with a threshold of two.

418

419 **Comparison between surface vs. crown fire regimes**

420 To analyze the effect of crown vs. surface fire types, we analyzed stem density data from
421 50 plots (paired within 25 locations) in the Western USA in a separate model. All plots had the
422 same time since fire of 12 years. For this analysis, we used a mixed-effects model to test the
423 relationship between fire return interval and stem density for all locations across the entire return
424 interval span with location as a random intercept. As a further test of fire return interval effects,
425 we selected the short fire return interval (<100 years) in each paired plot and analyzed the
426 relationship with a linear model.

427

428 **Testing the role of fire and land use history**

429 We partitioned studies into three categories based on their disturbance history. Using
430 knowledge of fire history for several decades prior to the fire experiments, we determined if the
431 fire treatments within a site reflected (i) an increase in fire frequency above a historical mean, (ii)
432 fire exclusion after decades of repeated burning prior to the experiment, and (iii) reintroduced
433 fire after decades of pre-experiment fire exclusion (Table S1); the historical mean was defined
434 based on fire activity data for several decades prior to initialization of the experiment (Dataset 1).

435 The fire experiments in the savannas were all initiated in sites that had regularly burned
436 for several decades before the establishment of the experiment. The intermediate fire frequency
437 treatments were reflective of the historical mean, but the most frequently burned plots in those
438 sites were burned at a frequency higher than the historical mean. Consequently, we could use the
439 intermediate frequency plots to evaluate the relative changes due to fire exclusion (unburned vs.
440 intermediate) or tree cover declines because of more frequent burning (frequent vs.
441 intermediate). In one savanna site, Marondera, all trees were removed before the onset of the
442 experiment, and consequently we are not able to assume that the difference between the
443 intermediate and high frequency treatment is due to declines in trees since the onset of the
444 experiment, rather, it is likely due to a restriction on recovery. Consequently, we omit Marondera
445 from these calculations.

446 The fire experiments in the forests varied in their historical fire frequency and the
447 occurrence of other disturbances. Several sites were in some stage of recovery from previous
448 land use (e.g., selective logging, agriculture, etc.), but we focused on the variability in fire

449 history to categorize the sites into fire response categories. We partitioned forests into those that
450 had remained unburned for several decades before the onset of the fire treatments (i.e.,
451 reintroduction burns) vs. sites that burned regularly before the experiment. We assume that in the
452 case of the reintroduction burns, changes in tree cover arises from losses due to more frequent
453 burning.

454 In the sites that burned regularly prior to the establishment of the experiment, the
455 differences between the unburned plots and those burned at the historical mean was assumed to
456 arise from gains under fire exclusion, and not necessarily increased losses due to frequent
457 burning (although that can clearly occur).

458 We analyze the effect sizes of fire in the comparisons of the unburned vs. intermediate
459 vs. frequent treatments using the same meta-analysis method described above.

460

461 **Model selection to determine parsimonious variable combinations**

462 For the plots with surface fires, we performed model selection by incorporating
463 covariates of climate, soil, and plant composition into mixed-effects models to test for pairwise
464 interactions and possible collinearities (see discussion below of collinearities). Finally, we
465 constructed a full model containing fire, climate, soil, and composition variables based on our
466 hypotheses that these factors will interact with fire frequency as well as information gained from
467 the pairwise tests. There were several insignificant effects in the final model, which we tested for
468 removal using model selection with a threshold AIC of two. All variables were re-scaled by
469 subtracting the mean and dividing by their standard deviation.

470 Our selection process in the tables illustrates the sensitivity of the final model to the
471 inclusion of additional interactive effects that are not in the final model as well as main effects of
472 the climate, geography, and soil variables. We do not present the exhaustive comparisons
473 because they are not guided by our *a priori* hypotheses of factors modifying fire effects. Soil
474 type was not reported for one location with stem density measurements in South America, so we
475 just use soil carbon content in the model selection analysis.

476

477 **Evaluating assumptions of aggregating ecosystem types**

478 The vegetation composition at each site differs substantially, ranging from diverse
479 tropical savannas with dozens of tree species (e.g., Kruger sites) to monodominant coniferous
480 forests (e.g., Limestone Flats and Chimney Springs). Classifying the sites into broad categories
481 was done methodologically, by balancing the need to maintain parsimony (and thus statistical
482 power) with accurately capturing how plant composition may modify fire effects. Consequently,
483 we performed two levels of classification: (i) a coarse categorization based on biomes, as
484 savannas vs. forests, and within forests treating broadleaf and needleleaf forests separately,
485 which we refer to as a vegetation type; and (ii) accounting for variability within forest types by
486 partitioning broadleaf forests into Myrtaceae (eucalypt) vs. Fagaceae (oak) dominated, and
487 needleleaf forests into forests that are near completely dominated by needleleaf trees vs. a mixed
488 forest containing both needleleaf and broadleaf trees, which we refer to as a sub-vegetation type.

489

490 **Collinearity among climate variables:**

491 Climate variables can be highly collinear, which can inflate the risk of error in statistical
492 inference. To evaluate collinearity, we first determined the Pearson correlation coefficients
493 between the main climate variables. We excluded variable combinations with a correlation
494 >0.70 . Most climate variables relating to water availability were not correlated with mean annual
495 temperature. For water availability, we used precipitation in the driest quarter and the wettest
496 quarter because their correlation coefficient was relatively low and they are ecologically more
497 relevant than annual means because they determine the potential productivity in the wet season
498 when most growth occurs but also potential water stress and fire conditions in the dry season
499 (Table S10). In contrast, mean annual precipitation and aridity were tightly correlated with one
500 another, as well as with the precipitation values in the separate quarters.

501

502 **Species classifications and functional traits**

503 Bark thickness data were collected from a dataset in the Fire and Fuels Extension of the
504 Forest Vegetation Simulator. <https://www.fs.fed.us/fmsc/ftp/fvs/docs/gtr/FFEaddendum.pdf>.

505 Although broad syntheses of bark investment exist for many tree species in North America, not
506 all species contained data from empirical measurements, and thus we used the data from the Fire
507 and Fuels Extension. Bark thickness was assumed to scale linearly with stem diameter, which is
508 generally valid for smaller stems, but it is known bark saturates with increasing stem diameter⁵⁶.
509 The ability of bark investment to predict fire effects will likely improve with better consideration
510 of the non-linear relationship between bark and stem diameter. We evaluate the relative bark
511 investment, and not absolute bark thickness, which is based on bark investment as well as stem
512 size.

513 Wood density was compiled from the literature using a global wood density database⁵⁷,
514 supplemented with additional data^{58,59}. We assigned a genus-level average for 19 species lacking
515 data.

516 Plant tissue stoichiometry and mycorrhizal type were determined using both trait data as
517 well as phylogenetic trait estimates calibrated to trait data used in a previous global analysis of
518 plant mycorrhizal traits⁴⁶. Full data selection criteria are presented in⁴⁶, but we describe them
519 briefly below.

520 The plant phylogeny contained >49,000 plant species⁶⁰. Plant species were added to this
521 phylogeny as needed using the *congeneric.merge* method⁶¹. This method uses congeners to add
522 species missing genetic data to the phylogeny, conservatively replacing genera with polytomies
523 where more than one member of the genus is present in the analysis.

524 We next generated a species-level phylogenetically estimated trait value for each species
525 and trait by fitting models to all data for a particular trait as a function of phylogenetic distance,
526 leaving out each species one at a time using the *phyEstimate* function within the *picante* package
527 for R statistical software⁶². This way, each species trait estimate is based on its own phylogenetic
528 position and a phylogenetic model of evolution (Brownian motion) parameterized without that
529 specific species trait observation. For species without trait data, we estimated trait values based on
530 a model fit to all available trait data.

531

532 **Testing the interactions between species composition and fire**

533 To test for fire effects on the relative abundance of symbiotic strategies, we calculated the
534 relative basal area of the different strategies (ectomycorrhizal, arbuscular mycorrhizal and the
535 less abundant ericoid mycorrhizal, non-mycorrhizal, and nitrogen-fixing tree species). Given the
536 low occurrences of ericoid, non-mycorrhizal, and nitrogen-fixing species, we analyzed the
537 relative abundance of arbuscular mycorrhizal and ectomycorrhizal species only. We then fit
538 mixed-effects models with relative basal area as the dependent variable and fire, climate, broad
539 vegetation type (broadleaf, needleleaf, savanna), and soil conditions as the independent
540 variables, each modified by a symbiont term. Relative basal area was arcsine transformed. This
541 analysis was conducted in the North American plots.

542 To test how functional traits correlated with the effects of fire frequency and duration of
543 experiment, we calculated community trait means in plot j by averaging the traits of each species
544 i by their relative basal area (BA) in a plot. Bark thickness (Bark) for example:

545

$$\mu_j = \sum_{i=1}^S BA_i Bark_i$$

546 We calculated community weighted means (CWM) for wood density, bark thickness, live and
547 senesced leaf nitrogen (N) and phosphorus (P) and live root N and P. We also calculated
548 retranslocation of N and P from a live leaf before senescence using the data from live and
549 senesced leaf N and P (i.e., not directly measured). Calculations using N as an example:

550

$$Retranslocation = \frac{N_{green} - N_{senesced}}{N_{green}}$$

551 Bark thickness was calculated as a scaling coefficient relative to stem diameter (β)

552

$$Absolute\ bark\ thickness = \beta * stem\ diameter + \alpha$$

553 To test the potential for traits to predict the response of trees to fire, we fit linear mixed-effects
554 models with the CWM modifying fire effects but allowing for main effects of fire. For example,

555

$$(plot\ basal\ area) \sim FirePeriod + FireFreq + FireFreq: WD_{CWM} + FirePeriod: WD_{CWM}$$

556

$$+ FireFreq: BT_{CWD} + FirePeriod: BT_{CWM} + (1|Site)$$

557

558 To test how fire influenced the trait composition of the community we fit mixed-effects
559 models to test the effect of both fire as well as environmental factors in explaining the
560 community weighted mean trait values.

561 We do not include an independent effect of either wood density or bark thickness because
562 we are primarily concerned with how they may modify fire effects.

563 We also tested for whether the symbiotic strategies differed in their traits. To do so, we
564 assigned symbiotic strategies and the dominant ecosystem in which they occurred to different
565 species. We then analyzed linear models incorporating symbiotic strategy and ecosystem type as
566 additive effects.

567

568

569 Table S1: List of sites with key meta-data. Cont=continent (AU=Australia, NA=North America,
570 SA=South America, AF=Africa). Vegetation type present in broad categories (NL=needleleaf,
571 BL=broadleaf) and the families of the dominant tree species. Sites with a pine-dominated ecosystem that
572 can change from pine to oak depending on fire regime are noted. Number of plots is the total within the
573 entire site. Duration is the number of years over which fire frequencies have differed across plots.
574 Frequency is in # fires yr⁻¹. Prior conditions describe the ecosystem type at the beginning of the
575 ecosystem, whether the site experienced regular burning prior to the experiment and if not, how long it
576 had remained unburned (reintroduction burns).

577

578 *In attached document.*

579

580 Table S2: Meta-analysis statistics. The sample size indicates true replicates. The top section analyzes
581 basal area, the bottom analyzes stem abundance.

Variable measured	Fire comparison	Response ratio	Standard error	Z value	p value	Lower CI	Upper CI
Basal area	Low vs. high						
	n=22	-0.78	0.22	-3.53	0.0004	-1.22	-0.35
	Low vs. mid						
	n=16	-0.40	0.12	-3.41	0.0006	-0.63	-0.17
	Mid vs. high						
	n=16	-0.43	0.23	-1.86	0.0632	-0.88	0.02
Stem abundance	Low vs. high						
	n=23	-0.58	0.19	-3.13	0.002	-0.94	-0.22
	Low vs. mid						
	n=17	-0.25	0.12	-2.12	0.034	-0.48	-0.02
	Mid vs. high						
	n=18	-0.33	0.20	-1.65	0.0985	-0.73	0.06

582

583

584

585 Table S3: Results from mixed-effects model fit to log basal area and stem density (ANOVA for
586 significance of terms, and then fitted model coefficients) testing the effect of fire frequency (FireFreq),
587 the length of time plots were exposed to different frequencies (Duration) and their interaction
588 (FireFreq:Duration). The means and standard deviations used to re-scale the data were: Basal area: fire
589 frequency, mean=0.34, standard deviation=0.32; duration of experiment, mean=28, standard
590 deviation=19. Stem density: fire frequency, mean=0.35, standard deviation=0.33; duration of experiment,
591 mean=29, standard deviation=19. Units for frequency are fires per-year and duration are years. The main
592 effect of fire frequency was dropped from the top model based on the AIC being lower.

Basal area	df	F value		p value	del AIC
FireFreq					-FireFreq=9.4
Duration	1	290.5	94.3	<0.0001	
FireFreq:Duration	1	288.6	23.3	<0.0001	
Stem density	df	F value		p value	-FireFreq=3.8
FireFreq					
Duration	1	281.6	47.3	<0.0001	
FireFreq:Duration	1	279.9	8.4	0.004	
Model coefficients					
		Intercept	FireFreq	Duration	FireFreq:Duration
Log basal area		2.7408		-0.4268	-0.2204
		Intercept	FireFreq	Duration	FireFreq:Duration
Log stem density		6.3765		-0.3427	-0.1515

593

594

595

596

597

598 Table S4: Results from mixed-effects model fit to log basal area a) ANOVA for significance of terms, b)
599 fitted model coefficients, and c) change in the model AIC with altered additions and removals. All
600 analyses performed on mean centered and standard deviation scaled data for continuous variables with
601 site as a random intercept. ANOVA uses Satterthwaite's method to estimate degrees of freedom. Colon
602 denotes interactions. Variable abbreviations are: FireFreq= fire frequency (fires yr⁻¹), Veg=vegetation
603 type (needleleaf forest, broadleaf forest, savanna), MAT=mean annual temperature (°C),
604 PWQ=precipitation in wet quarter (mm), PDQ=precipitation in dry quarter (mm), Duration=length of
605 time plots have experienced the repeated burning regime (years). For the fitted model coefficients, the
606 intercept gives the value for broadleaf forest (so to calculate the basal area in a savanna, you would
607 exponentiate the sum of the coefficient of “VegSavanna” and the intercept). See Figures 3, S7 for the
608 effects. Independent effects of PWQ, PDQ, and Continent were not included in the model because the
609 models did not pass the criterion that an improved model needed to have a >2 AIC difference. C)
610 Sensitivity of model to changes in terms illustrates what happens when the model only includes
611 interactions and the effect of adding or removing independent effects, as well as the interactions between
612 fire and soil.

a) Type III ANOVA	df	F value	P value	Mean	SD
FireFreq	1	287.5	29.0	<0.001	0.34
Veg	2	17.8	1.9	0.172	
MAT	1	18.6	2.7	0.115	
Continent	3	19.2	4.2	0.020	14
FireFreq:Veg	2	279.7	14.0	<0.001	
FireFreq:PWQ	1	285.1	50.3	<0.001	375
FireFreq:PDQ	1	285.6	7.5	0.007	133
FireFreq:MAT	1	280.8	16.8	<0.001	4
FirePeriod:Continent	4	283.4	7.2	<0.001	28
					19

b) Fitted model coefficients

Variable	Estimate	SE	df	t value	P value
(Intercept)	1.8	0.6	17.2	2.9	0.011
FireFreq	-0.1	0.1	284.7	-1.5	0.135
VegetationNeedleleaf	0.2	0.3	18.5	0.8	0.451
VegetationSavgrass	-0.9	0.6	17.1	-1.5	0.142
MAT	-0.2	0.1	18.6	-1.7	0.115
ContinentAustralia	1.6	0.7	17.2	2.4	0.025
ContinentNorthAmer	1.1	0.6	17.1	1.9	0.078
ContinentSouthAmer	1.7	0.6	23.2	2.8	0.010
FireFreq:VegetationNeedleleaf	0.1	0.1	278.8	1.0	0.310
FireFreq:VegetationSavgrass	-0.5	0.1	281.1	-3.5	<0.001

FireFreq:PWQ	-0.4	0.1	285.1	-7.1	<0.001
FireFreq:PDQ	0.2	0.1	285.6	2.7	0.007
FireFreq:MAT	0.2	0.0	280.8	4.1	0.000
FirePeriod:ContinentAfrica	-0.2	0.1	285.1	-2.1	0.039
FirePeriod:ContinentAustralia	0.3	0.1	283.2	1.9	0.059
FirePeriod:ContinentNorthAmer	-0.2	0.1	291.3	-4.3	<0.001
FirePeriod:ContinentSouthAmer	-0.2	0.2	274.7	-0.8	0.418

**Intercept using broadleaf for vegetation

c) Sensitivity of model terms

Model	df	AIC	ΔAIC
~FireFreq+Veg+MAT+Veg:FireFreq+PWQ:FireFreq+PDQ:FireFreq			Top
+MAT:FireFreq+Continent:Duration+Continent	19	556.3	model
Only interactions	13	582.0	25.76
+PWQ	17	561.0	4.70
+PDQ	17	566.4	10.18
-MAT	16	567.3	11.03
-VegType	15	589.1	32.83
-Continent	16	562.8	6.5394
+SoilType	26	559.3	3.0709
+%C	20	561.4	5.1847
+SoilType:FireFreq	23	581.3	25.06
+%C:FireFreq	17	569.1	25.76

613

614

615 Table S5: Results from mixed-effects model fit to log stem density a) ANOVA for significance of terms,
 616 b) fitted model coefficients, and c) sensitivity of model terms. All analyses performed on mean centered
 617 and standard deviation scaled data for continuous variables with site as a random intercept. ANOVA uses
 618 Satterthwaite's method to estimate degrees of freedom. Colons denote interactions. Variable abbreviations
 619 are: FireFreq= fire frequency (fires yr⁻¹), Veg=vegetation type (needleleaf forest, broadleaf forest,
 620 savanna), MAT=mean annual temperature (°C), PWQ=precipitation in wet quarter (mm),
 621 Duration=length of time plots have experienced the repeated burning regime (years). For the fitted model
 622 coefficients, the intercept gives the value for broadleaf forest (so to calculate the basal area in a savanna,
 623 exponentiate the sum of the coefficient of “VegSavanna” and the intercept). See Figures S7, S9 for
 624 effects. Model terms are presented relative to the top model (given in the first row), the only interactions
 625 refers to all main effects removed.

a) Type III ANOVA	df	F value	P value	Mean	SD
FireFreq	1	271.8	<0.001	0.35	0.33
FireFreq:Duration	1	272.8	0.026	29	19
FireFreq:Vegetation	2	270.4	<0.001		
FireFreq:PWQ	1	272.2	<0.001	389	165
FireFreq:MAT	1	270.2	<0.001	15	6
Duration:Continent	3	275.7	<0.001		

b) Fitted model coefficients

Variable	Estimate	SE	df	t value	P value
(Intercept)	6.30	0.28	23.9	22.3	< 2e-16
FireFreq	0.31	0.08	271.8	3.8	<0.001
FireFreq:Duration	-0.10	0.05	272.8	-2.2	0.026
FireFreq:VegNeedleleaf	-0.19	0.10	270.3	-2.0	0.051
FireFreq:VegSavanna	-0.85	0.11	270.8	-8.0	<0.001
FireFreq:PWQ	-0.21	0.04	272.2	-6.0	<0.001
FireFreq:MAT	0.36	0.05	270.2	7.2	<0.001
Duration:ContinentAustralia	-0.73	0.18	271.0	-4.1	<0.001
Duration:ContinentNorthAmer	-0.42	0.07	275.5	-6.0	<0.001
Duration:ContinentSouthAmer	-0.07	0.21	281.6	-0.4	0.719

Intercept using broadleaf for vegetation

c) Sensitivity of model terms

Model	Df	AIC	ΔAIC
~FireFreq+ FireFreq:Veg+ FireFreq:PWQ+FireFreq:MAT+ Duration:Continent+Veg+Continent	17	630.6	0
Only interactions	12	639.6	9.0
+PDQ	18	632.8	2.2

+PWQ	18	631.3	0.6
+MAT	18	632.5	1.9
+%C	18	635.3	4.6
-Veg	15	630.6	0.0
-Continent	14	637.0	6.3
+PDQ:FireFreq	18	636.0	5.4
+%C:FireFreq	18	633.0	2.4

626

627

628

629

630 Table S6: Results from mixed-effects models testing how: a) wood traits modified fire effects on tree
631 basal area and b) fire altered the trait values within plots. Whether the site was a savanna, broadleaf
632 forest, or needleleaf forest was included in the model because of the large difference in wood traits
633 between needleleaf forests and the other ecosystems.

<u>a) Basal area ~ wood traits</u>	df	F value	P value
FireFreq	1	154.4	<0.001
FireFreq:Bark	1	154.3	0.018
FireFreq:WD	1	154.1	<0.001
<u>b) Wood traits ~ fire</u>			
<i>Bark</i>			
Duration	1	157.3	0.4
FireFreq	1	156.3	0.2
Vegetation	2	12.9	0.006
<i>Wood density</i>			
Duration	1	156.4	0.022
Vegetation	2	13.0	0.003

634

635

636 Table S7: Results from mixed-effects models testing the effect of fire on nitrogen (N) and phosphorus (P)
637 concentrations in green and senesced leaves, the proportion of N and P retranslocated before senescence,
638 and root N and P concentrations. Vegetation type was included as a term given the strong differences in
639 traits between needleleaf vs. broadleaf trees.

Green N	df	F value	P value	Green P	df	F value	P value	
Duration	1	158.9	13.8	<0.001	Duration	1	157.3	11.8
Vegetation	2	12.7	33.6	<0.001	Vegetation	2	12.6	12.4
Senesced N								
Duration	1	158.9	19.7	<0.001	Duration	1	158.3	21.3
Vegetation	2	12.4	19.1	<0.001	Vegetation	2	12.5	27.2
Retrans N								
Duration	1	157.8	14.2	<0.001	Duration	1	159.8	24.1
Vegetation	2	12.3	3.0	0.088	Vegetation	2	12.5	43.3
Root N								
Duration	1	160.0	14.3	<0.001	Duration	1	157.2	3.1
Vegetation	2	12.6	30.7	<0.001	Vegetation	2	12.4	1.1
Root P								
Duration	1							
Vegetation	2							

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643

644 Table S8: Results from top mixed-effects model on the relative abundance of trees summed within a
645 symbiotic strategy within a plot with site as a random intercept conducted in North America where
646 taxonomic resolution was the highest (relative basal area was arcsine transformed). The statistics were
647 only run on ectomycorrhizal and arbuscular mycorrhizal groups because they were sufficiently abundant
648 across plots, but all other strategies (ericoid, non-mycorrhizal, nitrogen fixer) were included in relative
649 basal area calculation.

Variable	df	df	F value	P value
Symb	1	138.3	49.1	<0.001
Symb:Soil C	2	34.4	23.4	<0.001
Symb:FireFreq	2	140.1	7.8	<0.001
Symb:MAT	2	18.6	12.5	<0.001
Symb:Family	4	14.0	4.4	0.017
Symb:Duration:FireFreq	2	135.0	4.0	0.021

650

651

652 Table S9: Type III ANOVAs on linear models testing the differences in tissue stoichiometry between the
653 symbiotic strategy grouped in the different ecosystem vegetation types (broadleaf forest, needleleaf forest,
654 or savanna). Inferred statistics are using phylogenetic relationships to infer trait values for species with
655 missing data (see supporting information and⁴⁶) while observed are based on direct trait measurements.
656 The inferred vs. observed do not refer to the classification of mycorrhizal type.

Inferred				Observed			
N green				N green			
n=61	DF	F value	p value	n=48	Df	F value	p value
Symb	1	12.4	0.001	Symb	1	4.2	0.046
Veg	2	5.4	0.007	Veg	2	4.0	0.025
N senesced				N senesced			
n=61	Df	F value	p value	n=25	Df	F value	p value
Symb	1	90.8	0.000	Symb	1	1.1	0.310
Veg	2	4.5	0.016	Veg	2	1.5	0.237
N roots				N roots			
n=61	Df	F value	p value	n=31	Df	F value	p value
Symb	1	15.8	0.000	Symb	1	0.6	0.427
Veg	2	1.8	0.181	Veg	2	0.7	0.489
P green				P green			
n=61	DF	F value	p value	n=38	Df	F value	p value
Symb	1	8.5	0.005	Symb	1	3.9	0.054
Veg	2	1.8	0.176	Veg	2	5.7	0.007
P senesced				P senesced			
n=61	DF	F value	p value	n=21	Df	F value	p value
Symb	1	27.8	0.000	Symb	1	6.6	0.018
Veg	2	6.1	0.004	Veg	2	1.6	0.216
P roots				P roots			
n=61	DF	F value	p value	n=9	Df	F value	p value
Symb	1	11.0	0.002	Symb	1	9.3	0.014
Veg	2	0.6	0.572	Veg	2	1.2	0.346

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661

662 Table S10: Pearson correlation coefficients between climate variables., PWQ=precipitation in wet quarter
663 (mm), PDQ=precipitation in dry quarter (mm), MAT=mean annual temperature (°C), MAP=mean annual
664 precipitation (mm yr⁻¹). Data derived from WorldClim.

665

	PDQ	PWQ	MAT	MAP	Aridity
PDQ		0.28	-0.05	0.82	0.88
PWQ	0.28		0.44	0.77	0.54
MAT	-0.05	0.44		0.19	-0.04
MAP	0.82	0.77	0.19		0.91
Aridity	0.88	0.54	-0.04	0.91	

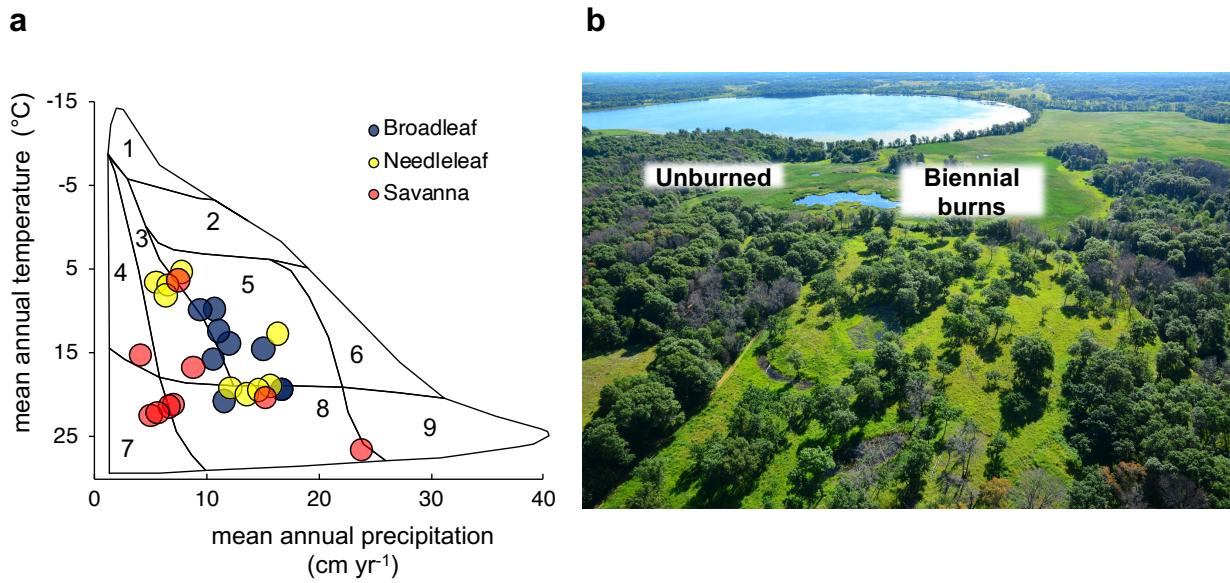
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Supplemental figures

669 **Figure S1:**



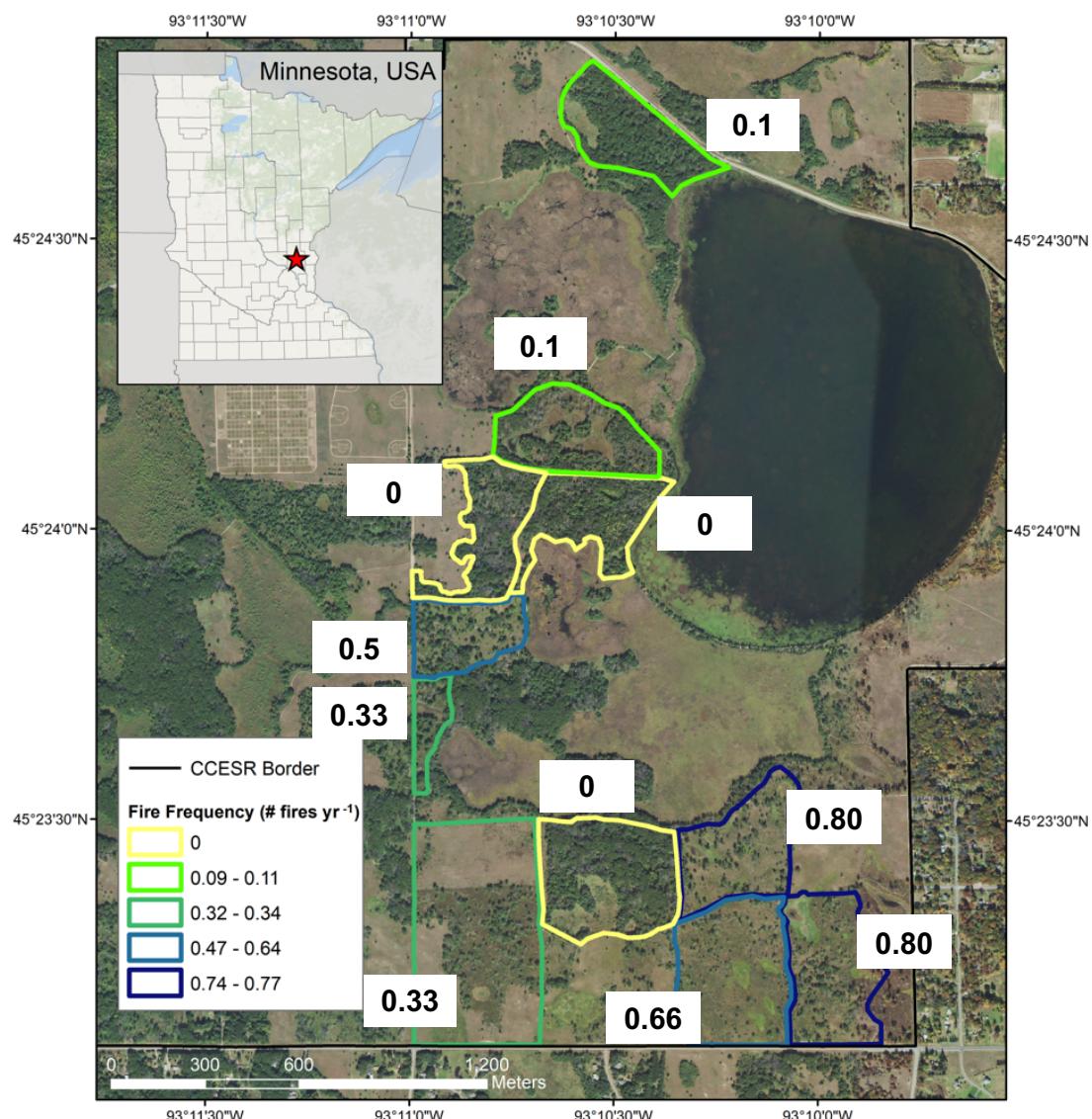
670

671 **Figure S1:** a) distribution of sites in climate space overlying Whittaker's biome distribution ⁸¹. (1=tundra,
672 2=boreal forest, 3=woodland/shrubland, 4=temperate grassland/desert, 5=temperate forest, 6=temperate
673 rainforest, 7=subtropical desert, 8=tropical forest and savanna, 9=tropical rainforest). Dots colored
674 according to broad vegetation type category. Plots span a mean annual temperature range from 5.2-27.3° C
675 and a mean annual precipitation range from 408-2378 mm yr^{-1} . b) aerial picture of two different fire
676 treatment plots from Cedar Creek, a temperate oak savanna, where different fire frequencies have created
677 a stark biome boundary between forests in unburned plots and savannas in biennial burn plots (Pellegrini
678 et al. 2019).

679

680

681 **Figure S2:**

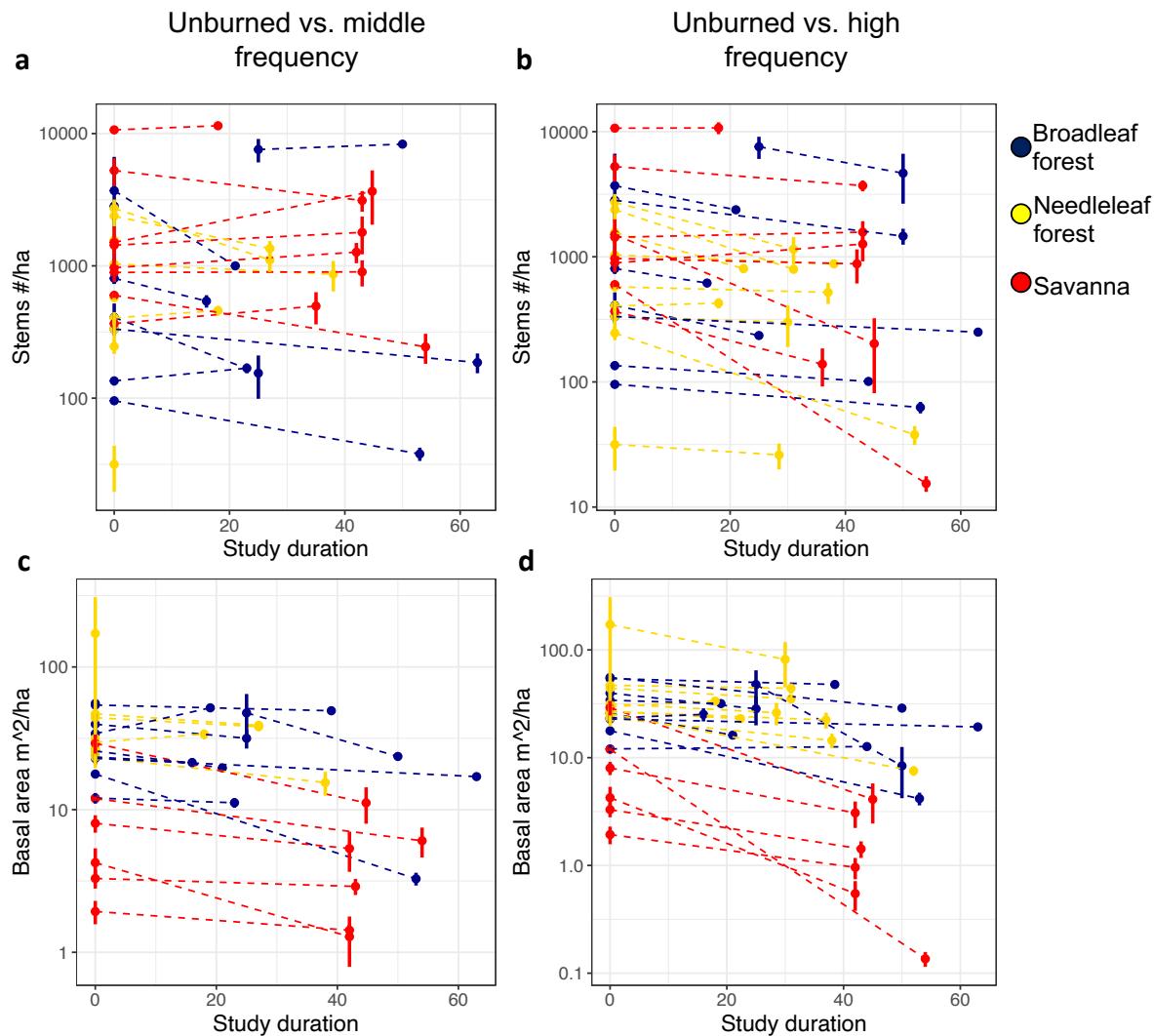


682

683 **Figure S2:** Example of the experimental layout of a fire manipulation experiment taken from Cedar
684 Creek (a temperate savanna in Minnesota, USA), where fires have been manipulated since 1964. Aerial
685 imagery (taken in 2017) from the National Agriculture Imagery Program from the Farm Service Agency.
686 Plots are outlined with a color corresponding to their fire frequencies expressed in terms of number of
687 fires per year (e.g. 0.33 is one fire every 3 years).

688

689 **Figure S3:**



690

691 **Figure S3:** Untransformed data on stem density (a-b) and basal area (c-d) as a function of the duration
692 that plots have been exposed to burning in the experiment (0=unburned plots). Each dot represents a site
693 and the dashed lines connect treatments within sites. Columns represent two sets of fire frequency
694 contrasts comparing unburned vs. the intermediate frequency in a and c, and unburned vs. the high
695 frequency in b and d (levels defined based on treatments within sites). Dots and bars based on mean and
696 standard error calculated across the replicate plots within a fire treatment in a site. Note y-axis is on a
697 log10 scale.

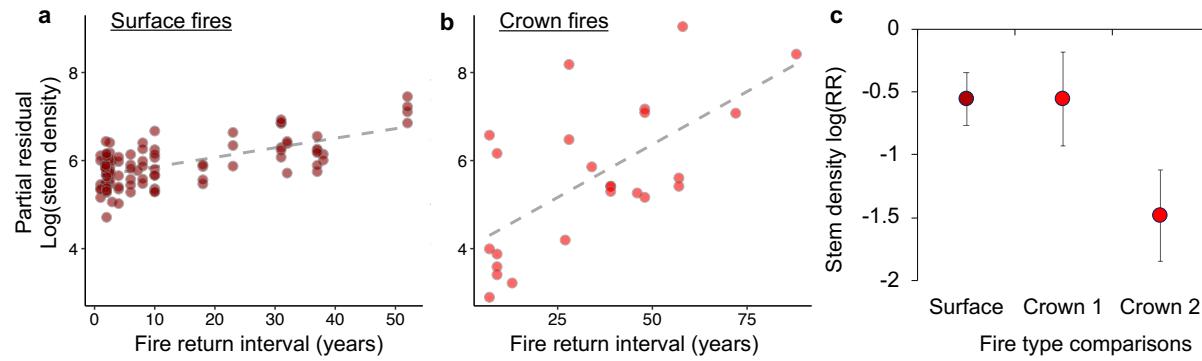
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701 **Figure S4:**

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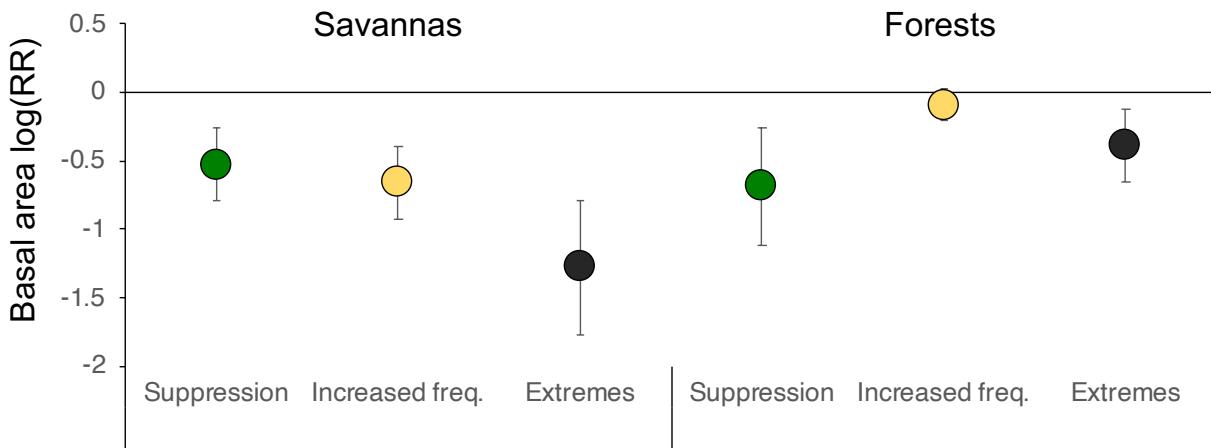
703

704 **Figure S4:** Comparison between fire types (surface in **a**, $F_{1,94,3}=50.6$, $p<0.001$, and crown in **b**,
705 $F_{1,21}=10.3$, $p=0.004$) in needleleaf forests with fire expressed in terms of return period (crown fire
706 plots are all 12 years postfire, data subset to include short-interval burn plots). **c**) illustrates the
707 mean response ratios +/- standard error for the fire types with crown fires split into high ($>2,400$
708 m) and low ($<2,400$) elevation sites (Crown 1 and Crown 2, respectively). Analyses were robust to
709 considering surface fires in only Western US needleleaf forests: $F_{1,47,1}=17.2$, $p=0.001$. Response ratios
710 were split into long and short fire return interval plots (Crown 1 and 2, respectively), with the justification
711 for definition of interval in ²³.

712

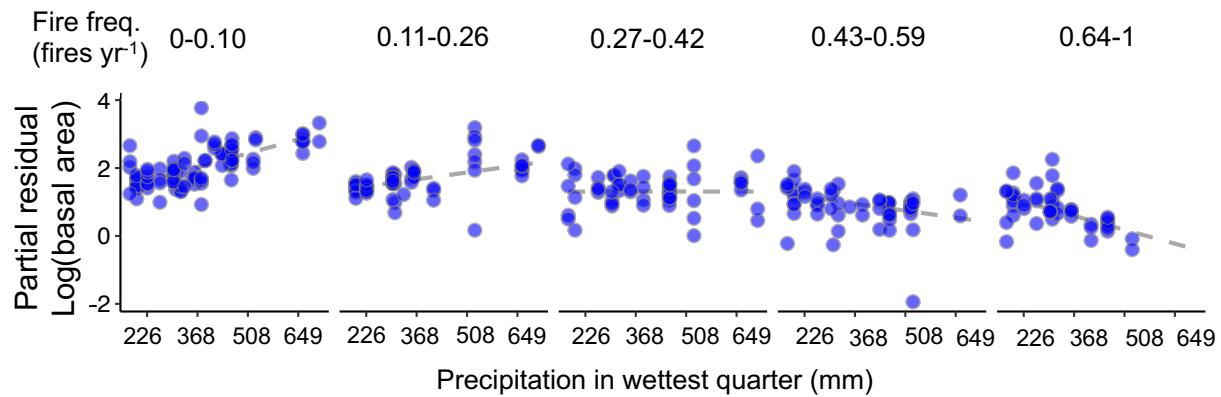
713

714 **Figure S5:**



716 **Figure S5:** Log response ratios of basal area under different fire history scenarios. In savannas,
717 suppression compares the unburned vs. intermediate burn in a historically burned environment. The
718 increased frequency compares higher than historical frequency with historical frequency. The extremes
719 compare the highest frequency vs. suppression. The main difference in forests is the increased frequency,
720 which is the reintroduction of fire into a historically fire suppressed forest.

721 **Figure S6:**



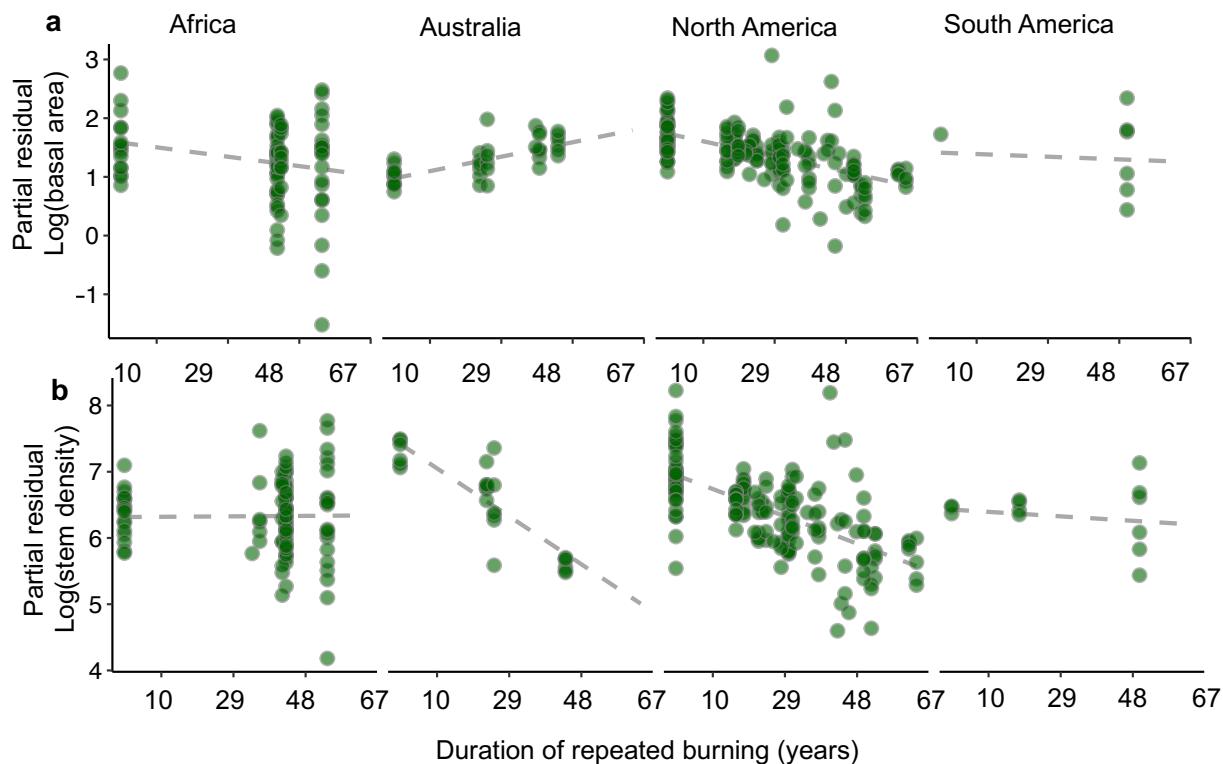
722

723 **Figure S6:** partial residual plot displaying the relationship between \log_e basal area and precipitation in the
724 wettest quarter cross-sectioned based on fire frequency. This plot is based on the same mixed-effects
725 model presented in Figure 3 and Table S4, just re-arranged to emphasize how precipitation-basal area
726 relationship changes with more frequent burning.

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728

729 **Figure S7:**

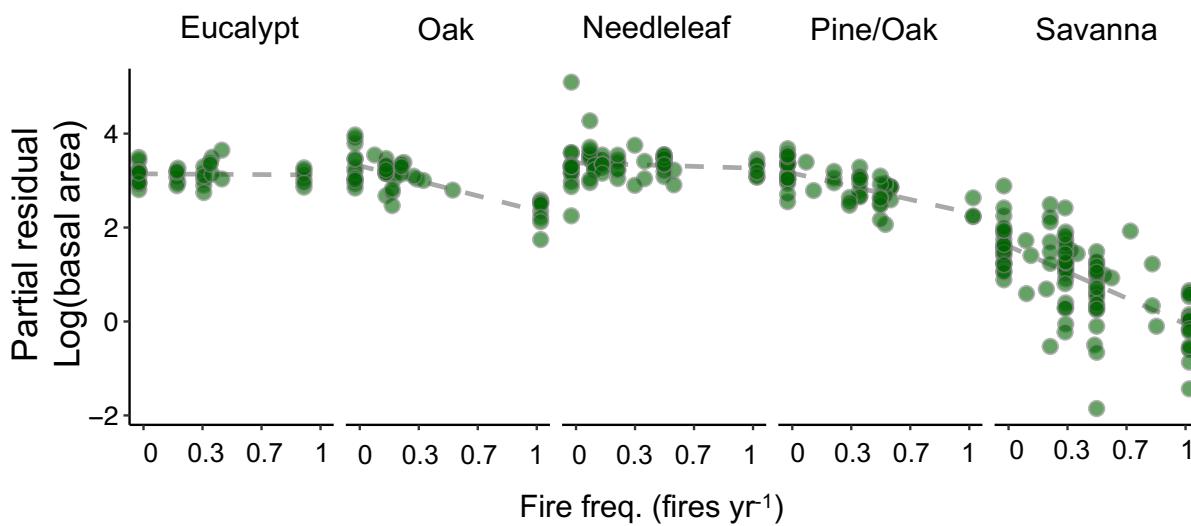


730

731 Figure S7: partial residual plot between the length of time plots were exposed to frequent burning and the
732 log basal area (a) and stem density (b) in the different continents (from the main mixed-effects model
733 with site as a random intercept in Tables S4-S5).

734

735 **Figure S8**



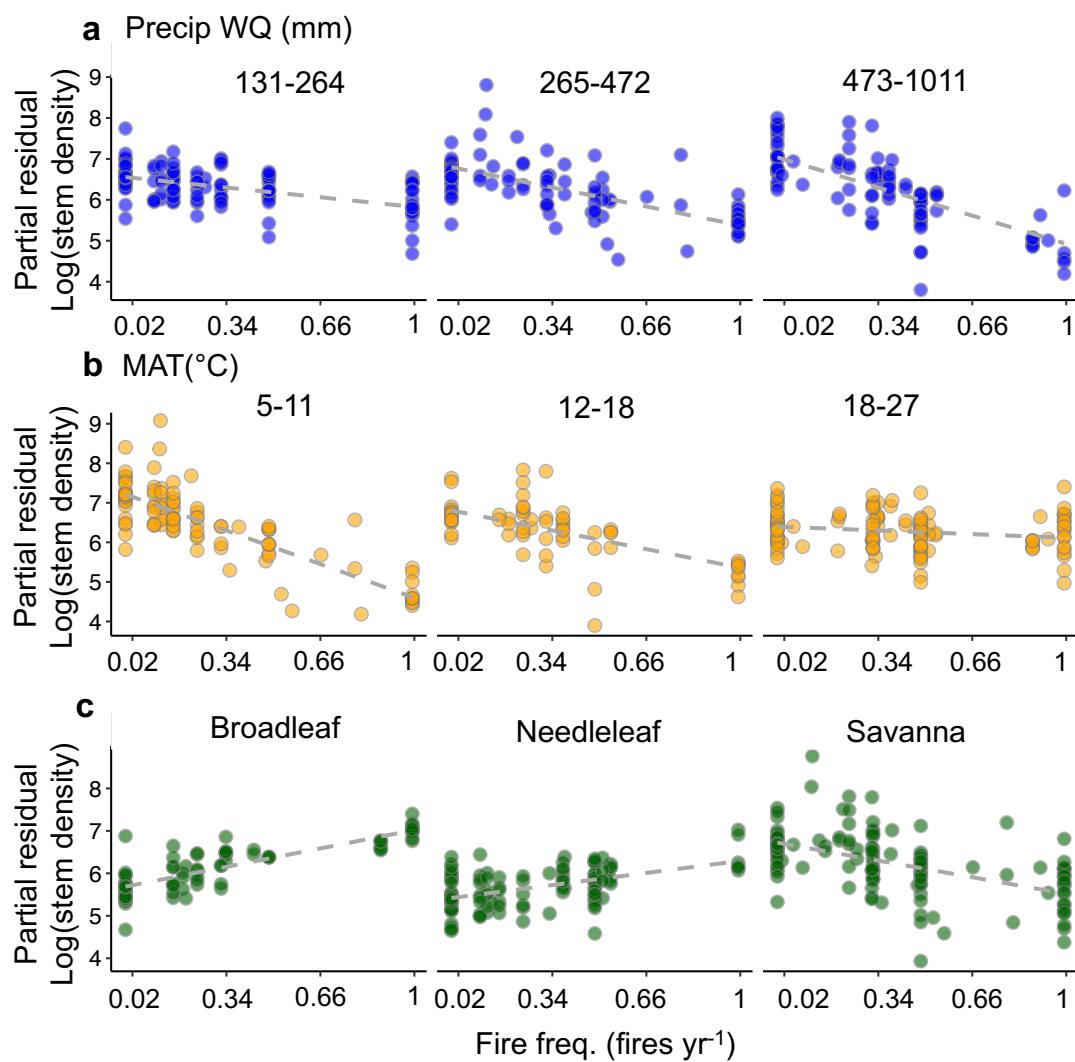
736

737 **Figure S8:** partial residual plot between the length of time plots were exposed to frequent burning and the
738 log basal area in the different sub-vegetation types (from the main mixed-effects model, presented in
739 Table S4 but substituting the broad vegetation effect with the more detailed classification. We found no
740 evidence that accounting for the finer-scale variability in ecosystem classification increased the accuracy
741 of the model or changed our conclusions

742

743

744 **Figure S9:**

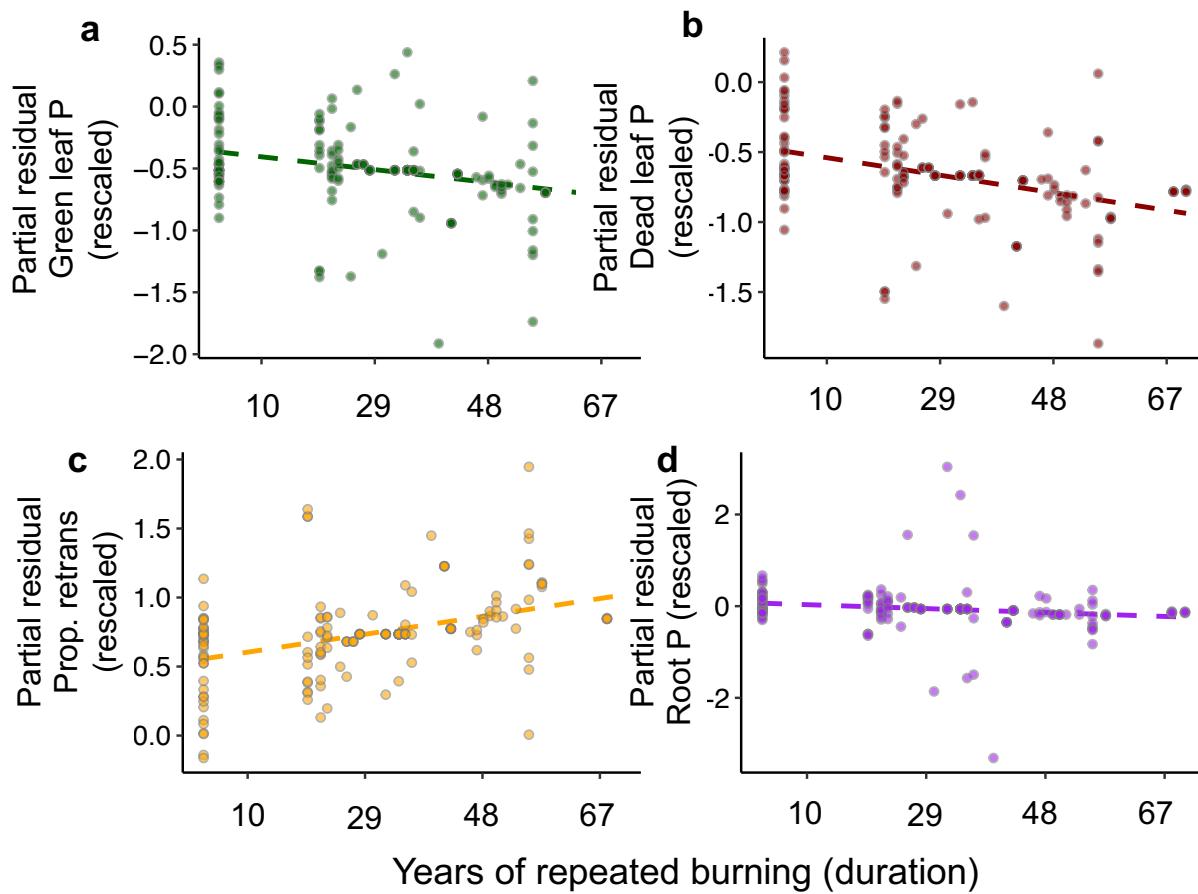


746 **Figure S9:** Partial residual plots of the mixed-effects model for stem densities illustrating how fire
747 frequency effects changed according to wet-season precipitation, mean annual temperature, and
748 ecosystem type. Panels structured by standard deviations around the median to visualize the spread (-1,
749 0,1), PWQ: precipitation in the wet quarter, MAT: mean annual temperature. All model fits are $p < 0.05$
750 and specific results can be found in Table S5. The predictor variables are mean-centered and standard
751 deviations are scaled to facilitate comparisons of variable influence. In needleleaf and broadleaf forests,
752 stem densities actually increased with more frequent burning initially, but declined with increasing
753 experiment duration, potentially because of increased light availability initially stimulating recruitment of
754 small trees (Figure S7, Table S5). Stem density in African sites changed little through time (Figure S7).
755 The trends in density may reflect the ability of many of the tree species to re-sprout in between fire
756 events⁸².

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759 **Figure S10:**



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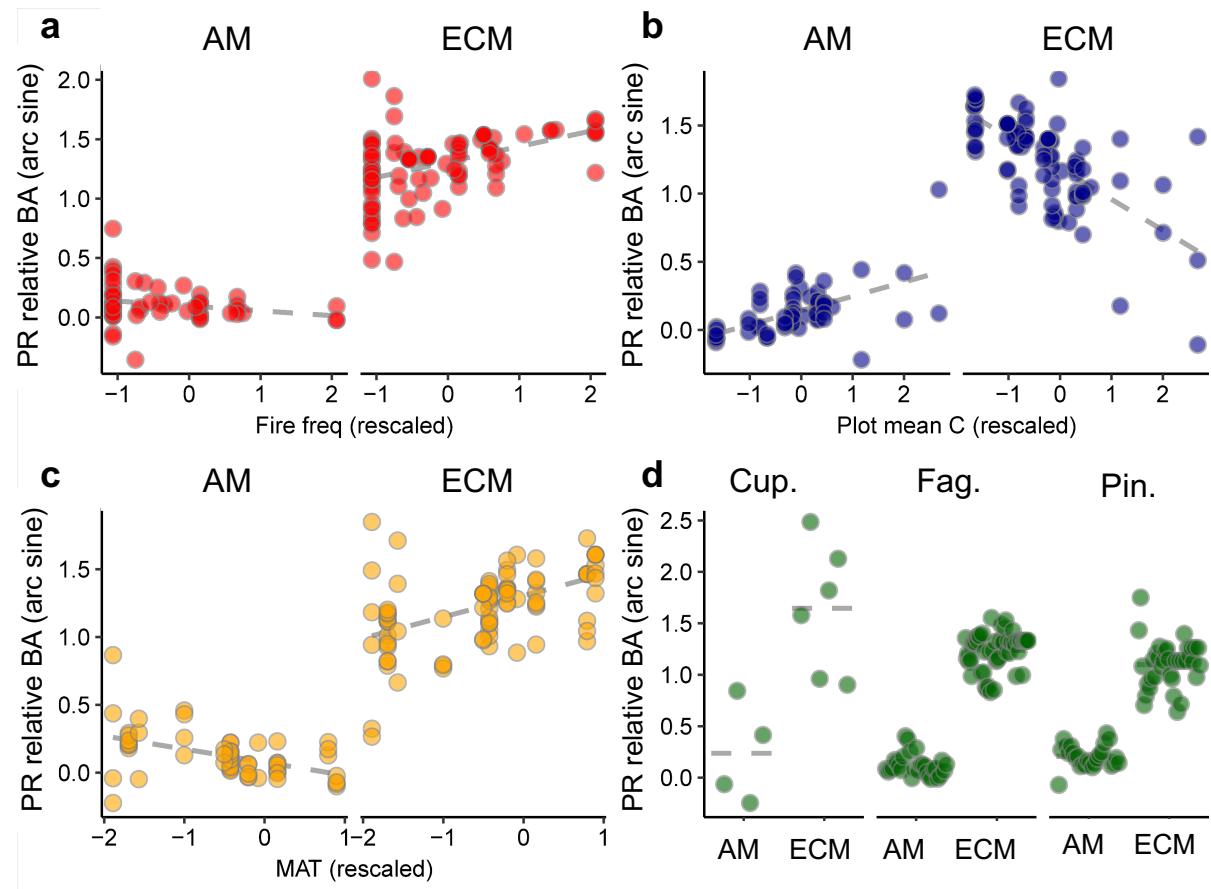
761 **Figure S10:** Partial residual plots of the phosphorus (P) stoichiometry of community weighted means as a
762 function of years of repeated burning. Taken from mixed-effects models presented in Table S7. The
763 models include a vegetation type effect. Tissue P is rescaled by subtracting the mean and dividing by the
764 standard deviation.

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767 **Figure S11:**

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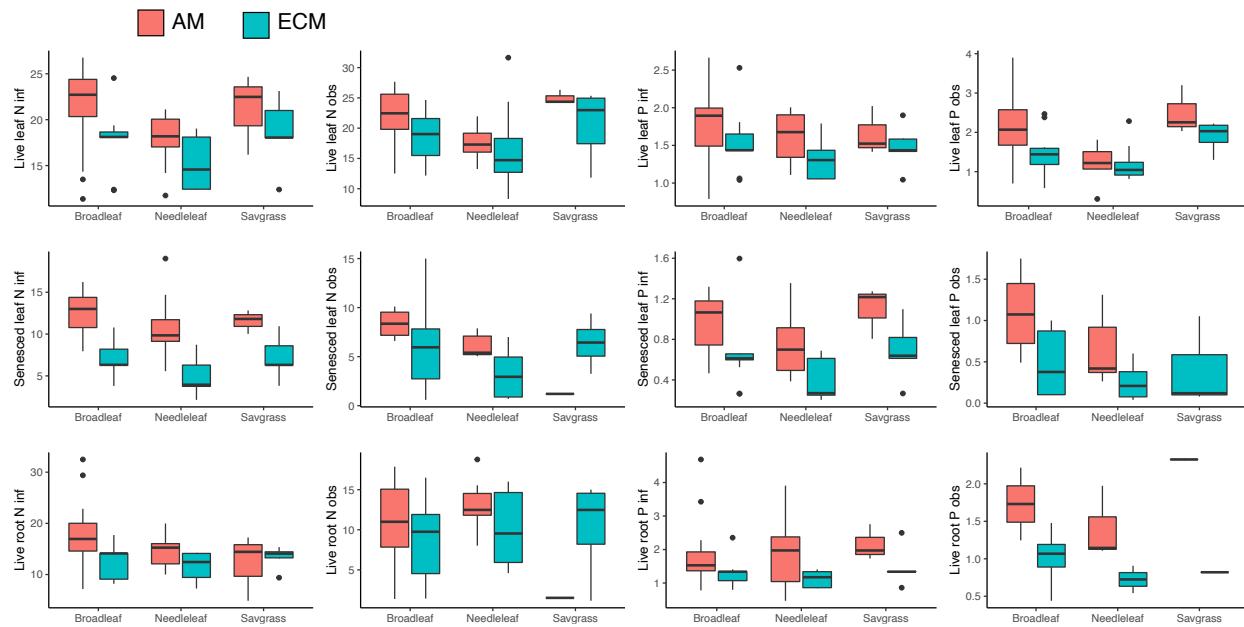
770 **Figure S11:** Partial residual (PR) plots of the mixed-effects model between relative basal area different
771 symbiotic groups within a plot (AM=arbuscular mycorrhizal and ECM=ectomycorrhizal on the left- and
772 right-hand side of each panel, respectively). Relative basal area was arcsine transformed. In all panels, the
773 continuous predictor variables were re-scaled by mean centering and dividing by the standard deviation
774 for comparability testing the relationship with fire frequency (a), soil total carbon content (b). mean
775 annual temperature (c). d) illustrates composition across different plant communities grouped based on
776 the family of the dominant tree species (Cup= *Cupressaceae*, Fag= *Fagaceae*, Pin= *Pinaceae*). Statistics
777 are given in Table S8.

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781 **Figure S12:**



782

783 **Figure S12:** Box and whiskers plot displaying the tissue stoichiometry for tree species averaged within
784 symbiont strategy (AM= arbuscular mycorrhizal; ECM=ectomycorrhizal) and then grouped according to
785 which overall ecosystem type the species generally occurred in (broadleaf forest, needleleaf forest, or a
786 savanna-grassland). For both N and P, we conducted our comparisons using data that were either based on
787 direct observations ("obs" in the y-axis), or inferred via a phylogenetic relatedness statistical filling ("inf"
788 in the y-axis). Statistics are in Table S9.

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