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1 **Woody plant encroachment intensifies under climate change across tundra and savanna**
2 **biomes**

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4 and Nicola Stevens⁵

5

6 **Short-running title:** Woody encroachment across biomes

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17

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22 Experiment Network (ITEX), for their efforts in data collection and for making their data accessible.

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24 climatic data. We thank local and indigenous peoples of the tundra and savanna biomes for the
25 opportunity to work with data collected on their lands.

26

27 **Biosketch**

28 This work was led by Mariana García Criado as part of her PhD thesis at The University of
29 Edinburgh (Scotland, UK). Her PhD focuses on quantifying plant species' responses to climate
30 change and identifying trait and distribution shifts after global change. She is interested in the
31 macroecology and biogeography of plant biodiversity across the planet, with a particular focus in
32 the tundra biome. Mariana is supervised by Dr Isla H. Myers-Smith (www.teamshrub.com), Dr
33 Caroline E.R. Lehmann and Dr Anne D. Bjorkman. Dr Nicola Stevens contributed savanna data
34 and expertise to this project.

35 **Abstract**

36 *Aim*

37 Biomes worldwide are shifting under global change. Biomes whose extents are limited by
38 temperature or precipitation, such as the tundra and savanna, may be particularly strongly
39 affected by climate change. While woody plant encroachment is prevalent across both biomes,
40 its relationship to temperature and precipitation change remains unknown. Here, we quantify the
41 degree to which woody encroachment is related to climate change and identify its main associated
42 drivers.

43

44 *Location*

45 Tundra and savanna biomes.

46

47 *Time period*

48 1992 ± 20.27 – 2010 ± 5.62 (mean ± SD). 1876 – 2016 (range).

49

50 *Major taxa studied*

51 Woody plants (shrubs and trees).

52

53 *Methods*

54 We compiled a dataset comprising 1,089 records from 899 sites of woody plant cover over time
55 and attributed drivers of woody cover change across these two biomes. We calculated cover
56 change in each biome and assessed the degree to which cover change corresponds to concurrent
57 temperature and precipitation changes using multiple climate metrics. Finally, we conducted a
58 quantitative literature review of the relative importance of attributed drivers of cover change.

59

60 *Results*

61 Woody encroachment was widespread geographically and across climate gradients. Rates of
62 woody cover change (positive or negative) were 1.8 times lower in the tundra than in the savanna
63 (1.8% versus 3.2%), while rates of woody cover increase (i.e., encroachment) were ~1.7 times
64 lower in the tundra compared with the savanna (3.7% versus 6.3% per decade). In the tundra,
65 magnitudes of woody cover change did not correspond to climate, while in the savanna, greater
66 cover change corresponded with increases in precipitation. We found a decrease in the rate of
67 tundra cover change with warming at drier versus wetter sites, and in the savanna we found an

68 increase in the rate of cover change with precipitation increases for drier versus wetter sites.
69 However, faster rates of woody cover change were not associated with more rapid rates of climate
70 change, except for maximum precipitation in the savanna.

71

72 *Main conclusions*

73 Woody encroachment was positively related to warming in the tundra and increased rainfall in the
74 savanna. However, cover change rates were not predicted by rates of climate change, which can
75 be partially explained by climate interactions in both biomes. Additional likely influences include
76 site-level factors, time lags, plant-specific responses, and land use and other non-climate drivers.
77 Our findings highlight the complex nature of climate change impacts in biomes limited by
78 seasonality, which should be accounted for to realistically estimate future responses across open
79 biomes under global change scenarios.

80

81 *Keywords:* biomes, climate change, precipitation, savanna, shrubs, temperature, trees, tundra,
82 woody encroachment

83

84 **Introduction**

85 *Global change in open biomes at seasonality extremes*

86 Climate change is shifting biome boundaries worldwide (Beck et al., 2011; Gonzalez et al., 2010;
87 Salazar et al., 2007). Biomes experiencing seasonality in temperature and precipitation, such as
88 the tundra and the savanna, are likely to face exacerbated negative impacts of climate change
89 (Díaz et al., 2019; IPCC, 2014). The ranges and processes of these two biomes are strongly
90 limited by climate conditions. The tundra is delimited by temperature (Nemani et al., 2003) and
91 the savanna is shaped by water availability, fire and herbivory (Bond, 2005). These two biomes
92 are characterized by an open structure and dominance, to varied degrees, of non-vascular plants,
93 sedges, grasses and forbs alongside variable woody plant cover. They both have a similar
94 ecosystem composition and function but represent two climate extremes of the world's open
95 biomes.

96 The tundra and the savanna have undergone substantial compositional and structural changes
97 in recent decades (Myers-Smith & Hik, 2017; Stevens et al., 2017), and in particular, are
98 experiencing an increase in woody biomass and/or an expansion of cover into open areas, a
99 process known as woody plant encroachment (Archer et al., 2017). In the tundra, treelines and
100 shrub lines are advancing towards higher latitudes and elevations (Harsch et al., 2009; Holtmeier
101 & Broll, 2005; Myers-Smith & Hik, 2017). In the savanna, woody plants are increasing in cover
102 and density, which can lead to shifts to alternate states from grasslands to thickets or forests (Parr
103 et al., 2012). However, even though marked increases in woody cover have been documented in

104 both biomes, encroachment rates have not been directly compared, and the relationship between
105 woody encroachment and changing climate has not been disentangled.

106

107 *Climate change impacts on ecosystem services and biodiversity*

108 Both the tundra and savanna biomes are experiencing rapid climate change, and impacts are
109 already widespread (Hoegh-Guldberg et al., 2018; Post et al., 2009). The Arctic is warming at
110 more than twice the rate of the rest of the planet, with high uncertainty in precipitation projections
111 (IPCC, 2013). Temperatures across Africa are predicted to rise at 1.5 times that of the global
112 subtropics, with uncertain and heterogeneous projected rainfall patterns across the tropics
113 (Engelbrecht et al., 2015). Climate change has been linked in the tundra to advancing plant
114 phenology (Prevéy et al., 2019), and in both biomes to increased plant growth (Myneni et al.,
115 1997; Wenmin Zhang et al., 2019), species composition changes (Devine et al., 2017; Elmendorf,
116 Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012) and, most conspicuously, woody
117 encroachment (Myers-Smith et al., 2011; Stevens et al., 2017).

118 Woody encroachment can alter ecosystem function and structure, ecosystem services (Wangai
119 et al., 2016), ecohydrology (Huxman et al., 2005) and, ultimately, biome persistence (Moncrieff et
120 al., 2014; Scheiter & Higgins, 2009; Skre et al., 2002). Tundra vegetation regulates surface
121 reflectance and carbon stores (Juszak et al., 2014; Williamson et al., 2016), with greater release
122 of soil carbon predicted with warming, permafrost thaw and vegetation change (Natali et al., 2011;
123 Schuur et al., 2009). Similarly, savannas store large amounts of carbon and are essential in
124 supporting millions of people through ecosystem services, farming and tourism (Lehmann & Parr,
125 2016; Scurlock & Hall, 1998), which could be directly affected by woody encroachment (Table 1).

126 Woody encroachment has led to heterogeneous biodiversity responses. Tundra shrubs and forbs
127 are increasing at the expense of graminoids (Wahren et al., 2013), lichens and bryophytes
128 (Cornelissen et al., 2001; Vowles et al., 2017; M. D. Walker et al., 2006), with cascading effects
129 leading to decreased habitat quality for caribou (Joly et al., 2007), northward range expansions
130 for moose (Tape, Christie, et al., 2016), or loss of specialist bird species (Sokolov et al., 2012).
131 Likewise, the increasing C₃ woody plant component of savanna ecosystems (Bond & Midgley,
132 2000) alters functional group composition, with changing bird species richness (Sirami et al.,
133 2009) and decreases in specialist ant and plant species (Abreu et al., 2017). Thus, woody
134 vegetation change can lead to impacts across trophic levels in tundra and savanna food webs.

135

136 *Drivers of woody encroachment*

137 Although woody encroachment is widespread in both biomes, the hypothesized causes of
138 encroachment differ (Martin et al., 2017; Naito & Cairns, 2011; Roques et al., 2001). In the tundra,
139 warming temperatures, permafrost thaw and altered nutrient cycling are likely the main drivers of
140 shrub expansion (Myers-Smith et al., 2011; Sturm et al., 2001), with soil moisture acting as a

141 potential limiting factor (Ackerman et al., 2017). In contrast, the savanna is a disturbance-driven
142 biome whose structure and function are shaped by fire and herbivory processes. Human actions
143 altering these regimes (Archer et al., 2017; Venter et al., 2018), and changing global drivers like
144 rainfall and rising atmospheric CO₂ concentrations (Buitenwerf et al., 2012; Wenmin Zhang et al.,
145 2019) have been widely reported to determine woody encroachment. Interactions among drivers
146 of vegetation change add complexity to projections of the future abundance and distribution of
147 woody plants across these biomes.

148

149 *Woody encroachment rates across biomes*

150 Woody encroachment has been reported from ecosystems around the world, including the tundra
151 and the savanna. Several studies have analysed woody growth at different scales, including
152 reviews of shrub expansion (Naito & Cairns, 2011), biome-specific analyses (Martin et al., 2017;
153 Myers-Smith et al., 2011; Stevens et al., 2017), and continent-wide studies across biomes
154 (Pellizzari et al., 2017). However, woody encroachment rates and timings have not been explicitly
155 compared between open biomes limited by climate extremes, nor have the specific influences of
156 climatic factors been assessed. These two biomes can provide insights into the potential for
157 woody encroachment to alter ecosystem structure and function, biodiversity richness and wildlife
158 population abundance in open biomes.

159 Here, we synthesize studies of woody cover change across tundra and savanna biomes to
160 determine the degree to which encroachment is related to regional temperature and precipitation
161 change. This cross-biome synthesis of the current status of woody encroachment and its main
162 drivers will improve forecasts of global change across these two open biomes and enable us to
163 understand whether woody plant species' growth responses to climate change are generalizable
164 or highly linked to biome context. Specifically, we tested the link between woody cover change
165 and climate change in three ways: 1) using long-term climatologies (Figure S2a), 2) calculating
166 magnitudes of cover change following increases in precipitation or temperature (Figure S2b), and
167 3) analysing whether climate change rates predict woody encroachment rates (Figure S2c).
168 Additionally, we compared woody encroachment rates across the tundra and the savanna biomes
169 and conducted a literature review to assess which factors are commonly associated with cover
170 change in both biomes. We hypothesized that woody encroachment rates are higher in the
171 savanna, a disturbance-driven biome, due to warmer and longer growing seasons. We predicted
172 that shrub expansion rates in the tundra have increased with warming summer temperatures,
173 while encroachment rates in the savanna have increased with greater wet season precipitation,
174 but were also affected by non-climate factors such as shifting fire regimes, herbivory and elevated
175 CO₂.

176

177 **Methods**

178 *Definitions and scope*

179 Our geographical scope is tundra and savanna ecosystems globally (Figure S1). We defined the
180 tundra as the region above the latitudinal and elevational treeline (Berdanier, 2010), including
181 both alpine areas and sites at Arctic latitudes, the latter encompassing bioclimatic subzones B-E
182 of the Circumpolar Arctic Vegetation Map (D. A. Walker et al., 2005). We delimited tropical
183 savannas as the observed borders for South America, Africa and Australia outlined in Lehmann,
184 Archibald, Hoffmann, & Bond (2011) as a starting point, and complemented with expert opinion
185 (Figure S1). We included sites in transition states in order to capture woody encroachment
186 processes across a range of environmental conditions.

187

188 *Data compilation and extraction*

189 We extracted and combined the cover records compiled by the Stevens et al., (2017), Myers-
190 Smith et al., (2011) and Myers-Smith and Hik (2017) syntheses, which formed the core database.
191 We supplemented these data by searching in Web of Science and Google Scholar for the terms
192 'vegetation change', 'shrubification', 'shrub encroachment', 'shrub expansion', 'shrub decline',
193 'shrub retreat', 'cover change', 'tundra', 'arctic', 'alpine', 'woody encroachment', 'bush
194 encroachment', 'woody decline', 'savannah' and 'savanna'. Scientific papers from all available
195 years were included. We extracted additional tundra records from the International Tundra
196 Experiment (ITEX) database (see Supplementary Methods). We only retained records that
197 reported either quantitative vegetation cover in at least two time points, or total cover change over
198 time. We extracted a total of 1,089 records from 899 unique sites and 118 studies. Overall, there
199 was a larger number of records available for the savanna (776) than for the tundra (313), mainly
200 due to the extensive number of records published by Axelsson and Hanan (2018).

201 Woody cover change was documented via remote sensing (761 records), ecological monitoring
202 (287) and repeat photography (69). Some records (37) used a combination of these techniques.
203 We included information on all shrub species in both biomes, and tree species in the savanna
204 biome only because the tundra, by definition, is treeless. We recorded cover at the species level
205 when possible, and otherwise at the functional group level (i.e., deciduous shrubs, evergreen
206 shrubs, trees; Table S1).

207 For each study and each reported species/group, we extracted data on location, time period, start
208 and end observation date, initial and final cover, cover trend, methods, and attributed drivers.
209 Each site could contain different records of species/groups and their associated trends. If multiple
210 species or functional groups were reported, we used all records per site in the analyses in order
211 to provide a comprehensive overview of trends per site. In cases where the same site was
212 reported in different scientific papers including different timelines and species, we retained only
213 unique records. In the two instances when different values were reported for the same species in
214 multiple plots with the same coordinates (Ropars & Boudreau, 2012; Rundqvist et al., 2011), we
215 calculated an average value per species per site.

216 When cover values were reported in spatial units, we converted them to percent cover by dividing
217 them by the total plot/site area. We standardised all values to calculate annual woody cover
218 change rates by dividing the absolute difference in cover (end cover – start cover) by the number
219 of years between observations. We chose to calculate absolute rather than relative cover change
220 values since they are more representative of landscape-scale change and are directly
221 comparable across sites, as start and end cover values are always proportionate to land area.
222 We considered a record as 'stable' for illustration purposes when annual plant cover change
223 ranged between -0.01% and +0.01%, which is the approximate range of non-significant changes
224 in studies that reported directional change significance. Hereafter, we will refer to annual woody
225 cover change as 'cover change', and we will use 'encroachment' to refer to increasing values of
226 cover change. See Supplementary Methods for an overview of database statistics.

227 In the quantitative literature review, we included in the analysis all environmental drivers reported
228 per record. Therefore, when multiple records were reported per site, each driver has been
229 considered the same number of times in order to represent its influence towards each reported
230 trend of woody cover. It is noteworthy that drivers extracted from the literature corresponded to
231 different levels of attribution in each study. Few studies provided explicit tests of the influence of
232 some drivers on woody cover change, and in the majority of studies, the identified drivers were
233 only inferred by authors. We retained only data from control plots and not experimental treatments
234 as our study assesses unmanipulated cover change over time. Thus, the analysis in Figure 6
235 represents the current perception among the scientific community of the cover change drivers in
236 these biomes but does not necessarily represent tested causal relationships. We standardised all
237 compiled drivers into a common driver classification (Figure 6).

238

239 *Climate data extraction and analysis*

240 Firstly, we extracted temperature and precipitation climate data for the period 1979 – 2013 per
241 site from the Climatologies at High Resolution for the Earth's Surface Area (CHELSA) V1.2.1
242 dataset (Karger et al., 2017). We used Mean Annual Temperature (MAT) and Mean Annual
243 Precipitation (MAP) climatologies, which provided a single mean value over the 35 years per site,
244 to visualize the climate space of all sites (Figure 2).

245 Additionally, we extracted temperature and precipitation monthly time series, which we used to
246 then calculate the mean value per climatic variable, year and site. We calculated mean annual
247 change in 10 climate variables in order to represent the strong seasonality experienced in the
248 tundra and savanna biomes: MAT, January-February mean temperature (winter in the tundra, wet
249 season in the savanna), June-July mean temperature (summer in the tundra, dry season in the
250 savanna), minimum annual temperature (coldest month), maximum annual temperature (warmest
251 month), MAP, January-February mean precipitation (wet season in the savanna), June-July mean
252 precipitation (dry season in the savanna), minimum annual precipitation (driest month) and

253 maximum annual precipitation (wettest month). We considered precipitation in the tundra to
254 consist of rain between June and August, and snow during the rest of the year.

255 In order to examine changes in climatic conditions over time, we fitted linear models per site and
256 climate variable. These models were tailored for the duration of each study period, representing
257 the climate experienced by plants across each time series per site. Each model included climate
258 data from four years prior to the start date of each study, in order to reflect the time period over
259 which plants would have responded to previous temperature change (Bjorkman et al., 2018;
260 Elmendorf et al., 2015; Gottfried et al., 2012). For 236 records, the study start date was prior to
261 1979, in which case linear models were fitted from 1979, the starting date for our climate data, to
262 the study end date. For 580 records, the end date was later than 2013, and linear models were
263 fitted up to 2013 instead. We tested the influence of data subsetting in supplementary analyses
264 (Figure S7, Table S3, see below). The slopes from these models, representing rate of climate
265 change per variable and per year, were then used as explanatory variables in the 'rate vs rate'
266 analyses (see below).

267

268 *Statistical analyses*

269 1) Linear models: We fitted multiple linear models using a Bayesian framework. Firstly, in order
270 to identify differences in cover change trends between biomes, we modelled annual cover
271 change rates as a function of biome for each categorical trend (increase, stable, decrease,
272 overall; Table S2.1-4). Secondly, to assess whether study duration influenced cover change
273 rates, we modelled cover change rates as a function of study length in both biomes (Table
274 S2.5, 6). To test whether cover change rates varied depending on whether a record was
275 reported at the species or functional group level, we modelled cover change rates as a
276 function of reported unit (species or functional group; Table S2.7-8). In order to test
277 differences in cover change in high vs low rainfall savannas, we modelled annual cover
278 change rates as a function of savanna type (high or low rainfall; Table S2.9). We additionally
279 tested whether study duration was different between biomes (Table S2.10). Finally, in order
280 to quantify the changes in climate conditions undergone at each site, we modelled changes
281 in each of the 10 climate variables over time per biome (Table S2.15-24).

282 2) 'Rate vs climatology' models (Figure S2a): In order to understand the relationship of cover
283 change with mean climatologies, we fitted Bayesian hierarchical linear models with random
284 intercepts. We modelled cover change as a function of mean climatologies of MAT, MAP,
285 and their interaction for each biome. We included location as a grid of 10x10 degrees of
286 latitude and longitude as a random effect in order to account for spatial autocorrelation (Table
287 S2.11, 12). We fitted a similar model per biome to test for an interaction between change in
288 MAT and change in MAP (Table S2.13, 14).

289 3) 'Magnitude vs magnitude' models (Figure S2b): In order to assess whether total woody cover
290 change magnitudes corresponded to total magnitudes of increasing temperature and

291 precipitation, we fitted Bayesian hierarchical linear models with random intercepts per biome
292 and gridded location as a random effect. We modelled total cover change (calculated as end
293 cover – start cover) as a function of total climate increases (calculated as end MAT or MAP
294 – start MAT or MAP). We calculated ‘Start MAT or MAP’ as the mean of the four years prior
295 to the start year, and ‘End MAT or MAP’ as the mean of the four years prior to the end of the
296 monitoring period. We used these four-year windows to provide biologically meaningful
297 climate values per site and to remove the influence of anomalies on overall relationships.
298 We retained only those sites where MAT or MAP had increased since we were interested in
299 the effect of warming and precipitation increases on woody plants and because the biological
300 responses of a woody plant to decreased temperature/precipitation are more complex – e.g.,
301 we would not necessarily expect plants to get smaller in size, while they might increase in
302 size following temperature/precipitation increases. We retained only records whose start
303 (four years prior) and end date was within the 1979 – 2013 timeframe. We fitted four models,
304 one per variable and biome with a parameter-expanded prior with an inverse Wishart
305 distribution (Table S2.25-28).

306 4) ‘Rate vs rate’ models (Figure S2c): In order to assess the relationship between cover change
307 rates and climate change rates across our sites, we fitted 20 Bayesian hierarchical linear
308 models of cover change rates as a function of change rates in the 10 climate variables, one
309 per variable and biome (Table S2.29-48). We fitted the models in three different ways: i)
310 including all woody cover change records (Table S3.41-60), ii) excluding woody cover
311 records whose start date was pre-1979 (Table S3.1-20), and iii) excluding both woody cover
312 records whose start date was pre-1979, and those whose start date was post-2013 (Table
313 S3.21-40). Analysing these different subsets of the data allowed us to understand if these
314 relationships changed when excluding those records for which we did not have climate data
315 available for part of the study duration.

316 5) ‘Rate vs rate with climatology interaction’ models: In order to understand the effect of dry
317 versus wet conditions on woody cover change in both biomes, we modelled cover change
318 rates as a function of temperature change over time, mean precipitation climatology (defined
319 by long-term climatology values), and their interaction, per biome (Table S2.49-50). Likewise,
320 in order to understand whether site temperature influences the relationship between cover
321 change and precipitation change, we modelled cover change rates as a function of
322 precipitation change over time, mean temperature climatology (defined by long-term
323 climatology values), and their interaction, per biome (Table S2.51-52). We also modelled
324 cover change rates as a function of long-term temperatures, temperature change over time
325 and their interaction; and as a function of long-term precipitation, precipitation change and
326 their interaction, in both biomes (Table S2.53-56). These models included location grid as a
327 random effect, random intercepts and a parameter-expanded priors with an inverse Wishart
328 distribution.

329

330 *Software and model specifications*

331 We used the software and programming language R version 3.4.3 (R Core Team, 2018) in
332 RStudio (RStudio Team, 2016) for all analyses. We fitted all Bayesian models using the
333 'MCMCglmm' package (Hadfield, 2010) and ran them for 100,000 to 200,000 iterations. We
334 assessed convergence through examination of the trace plots and autocorrelation values. We
335 considered a result to be statistically "significant" when the 95% credible intervals of the estimates
336 did not overlap with zero.

337

338 **Results**

339 *Woody cover change was found across the tundra and savanna biomes*

340 Woody encroachment was widespread in both biomes (Figure 1a, b, c). We found an increase in
341 woody cover for 68.1% of tundra and 67.8% of savanna records. Overall net rates of change in
342 per cent cover per year in the tundra ($0.18 \pm 0.61\%$) were marginally lower than in the savanna
343 ($0.32 \pm 0.85\%$; mean \pm SD, Table S2.4). Of the sites experiencing woody encroachment, tundra
344 mean rates of increase ($0.37 \pm 0.5\%$) were lower than savanna rates ($0.63 \pm 0.8\%$; Figure 1b, c,
345 Table S2.1). Of the sites with decreased woody cover, tundra mean rates ($-0.36 \pm 0.75\%$) were
346 marginally lower than savanna rates ($-0.4 \pm 0.45\%$; Table S2.3). Trends in increasing woody cover
347 are widespread across continents in the two biomes (Figure 1a), with the largest proportions of
348 increasing records per continent reported for South America (89.4%) and Australia (84.2%).

349 The mean duration of woody cover change studies (mean \pm SD) was slightly longer in the tundra
350 (21.4 ± 14.8 years) than in the savanna (16.9 ± 17 years, Figure S3, Table S2.10). However, we
351 did not find a relationship between cover change rates and study duration in either biome (Table
352 S2.5-6). There was no difference in rates of woody cover change when records were reported at
353 the species or functional group levels (Table S2.7-8).

354

355 *Woody encroachment occurred across climatologies*

356 Woody encroachment occurred across the range of temperature and precipitation climatologies
357 experienced in both biomes for the period 1979 – 2013 (Figure 2). There was no overlap in
358 temperatures between biomes (the savanna was always warmer), but there was substantial
359 overlap across the precipitation gradient. In the tundra, encroachment was reported widely at
360 sites between -10°C MAT and 250 mm MAP (average to warm conditions) and at 0°C MAT and
361 500 mm MAP (close to the upper limit of temperature and precipitation in the tundra). The highest
362 cover increase rate was found at 2°C MAT and 550 mm MAP (Figure S4). In the savanna, sites
363 with encroachment often had climates around 25°C and up to 600 – 700 mm MAP (Figure 2). The
364 highest rate of cover increase were found at 1,500 mm MAP and a 29°C MAT (Figure S4). In
365 addition, we found marginally higher rates of cover increase at high versus low rainfall savannas

366 (Table S2.9). Decreasing cover trends occurred throughout the climate space in both biomes.
367 There were no significant interactions in models of cover change either between temperature and
368 precipitation climatologies (Table S2.11-12) nor between MAT change and MAP change in either
369 biome (Figure S5, Table S2.13-14).

370

371 *Temperature and precipitation increased across biomes over time*

372 Changing climate conditions were observed across the tundra and savanna biomes over time.
373 Tundra sites experienced mean increases in all five temperature variables (MAT, January-
374 February, June-July, minimum and maximum temperature), while MAT, January-February, June-
375 July, and maximum temperature increased in the savanna (Figure 3, Table S2.15-24). Increases
376 in MAP and minimum precipitation were observed in the tundra biome; while the savanna sites
377 experienced increases in MAP, January-February (wet season), June-July (dry season) and
378 maximum precipitation (Figure 3, Table S2.15-24).

379

380 *Climate was linked with woody cover change, but greater rates of climate change were not*
381 *associated with greater rates of cover change*

382 Rates and magnitudes of woody cover change were related to climate change in the tundra and
383 the savanna to varied degrees. In the tundra, magnitudes of woody cover change did not
384 correspond to increases in temperature nor precipitation in our 'magnitude vs magnitude' analysis
385 (Figure 4, Table S2.25, 27). Likewise, we did not find positive relationships between rates of
386 woody cover change and rates of climate change in our 'rates vs rates' analyses for either of the
387 10 climate variables. However, we found negative relationships between January-February mean
388 temperatures, MAT and minimum annual temperature change rates and cover change rates
389 (Figure 5a), and between minimum annual precipitation and cover change rates (Figure 5b, Figure
390 S6, Table S2.29-48). We found a significant interaction of MAT change over time with long-term
391 precipitation climatologies for the 'rates vs rates' temperature relationships (Table S2.49). This
392 interaction indicated that rates of cover change were higher in wetter versus drier sites with
393 warming temperatures (Figure 5c). We found no other significant interactions for the tundra biome
394 (Table S2.49-56).

395 In the savanna, magnitudes of woody cover change corresponded to increases in precipitation
396 (Table S2.28), but not to increases in temperature (Table S2.26) in our 'magnitude vs magnitude'
397 analyses (Figure 4). In our 'rates vs rates' analyses, we found no significant relationships between
398 rates of cover change and rates of temperature change (Figure 5a, Figure S6). However, we
399 found a positive relationship between maximum annual precipitation and woody cover change,
400 and a negative relationship between cover change rates and minimum annual precipitation
401 (Figure 5b, Figure S6, Table S2.29-48). Additionally, we found a significant interaction between
402 cover change rates, precipitation change rates and long-term precipitation climatologies in the

403 savanna (Figure 5d, Table S2.53). The interaction indicated that rates of cover change were
404 higher in drier versus wetter sites with increased precipitation change. We found no other
405 significant interactions for the savanna biome (Table S2.49-56).

406

407 *'Rates vs rates' relationships varied depending on record subsets*

408 Since the duration of woody cover data available did not correspond exactly with the climate data
409 available (1979 – 2013), we tested the 'rates vs rates' analysis in different subsets of records.
410 Excluding records pre-1979 ($n = 853$) yielded similar relationships to our main analyses including
411 all records ($n = 1,089$), except for an additional positive relationship between savanna woody
412 cover and MAP (Figure S7b, Table S3.1-20). We did not find a significant negative relationship
413 between tundra cover change and minimum annual precipitation. However, when excluding
414 records pre-1979 and post-2013 ($n = 509$), we found additional negative relationships between
415 savanna cover change rates and June-July mean temperatures and MAT, and no positive
416 relationships of cover change with precipitation variables (Figure S7c, Table S3.21-40). There
417 were no significant relationships between tundra woody cover change rates and precipitation
418 change rates (Figure S7c). Therefore, removing records pre-1979 did not substantially alter the
419 relationships found, while removing records pre-1979 and post-2013 yielded different
420 relationships, though not in a consistent manner (Figure S7).

421

422 *Reported drivers of woody encroachment differ between biomes*

423 In our literature review, warming air temperatures was the most frequently reported driver of
424 increasing woody cover in the tundra (189 records). Interestingly, warming temperatures were
425 also the most frequently reported driver of decreasing cover (63). In the savanna, increasing
426 rainfall was the most widely reported driver of increasing cover (420), while increased fire (180)
427 and increased grazing (180) were the top reported drivers of decreasing woody cover (Figure 6).

428

429 **Discussion**

430 We found woody encroachment to be prevalent in both tundra and savanna biomes, and broadly
431 linked to climate change. In the tundra, we found a significant temperature/precipitation
432 interaction, by which, following warming, drier sites had lower rates of woody cover change than
433 wetter sites. In the savanna, magnitudes of woody cover change corresponded to precipitation
434 increases. We found a significant interaction between cover change rates, precipitation change
435 rates and long-term precipitation climatologies, by which, following increasing precipitation, higher
436 rates of woody cover change were found for drier versus wetter sites. Our results suggest that
437 woody cover change climate links are more complex than previously thought across the tundra
438 and savanna biomes.

439

440 *Woody cover change occurred across the tundra and savanna biomes*

441 Woody cover increased at over two thirds of locations across both the tundra and savanna
442 biomes, but the rates of change varied with geography and over time across and within biomes
443 (Figure 1). Our data synthesis revealed a net change of 1.8% and 3.2% woody cover per decade
444 in the tundra and savanna, respectively. Of those sites experiencing cover increases, the mean
445 increase rate was 3.7% and 6.3% per decade in the tundra and savanna, respectively, but
446 reported published estimates varied widely. Tundra cover increase estimates in the literature
447 range from 1.2% per decade over the last 70 years in northern Alaska (Tape et al., 2006), to
448 modelling projections of 14% per decade across the pan-Arctic (Pearson et al., 2013). Savanna
449 mean estimates varied between continents, with a 2.5% increase per decade reported in Axelsson
450 and Hanan (2018) and Stevens et al., (2017), and a 2.6% reported in Venter, Cramer, & Hawkins
451 (2018) for Africa. In contrast, estimates for Australia are much lower at around 1% per decade,
452 while those for South America are much higher (7.4% per decade; Stevens et al., 2017). This
453 cross-biome quantification of woody encroachment agrees with previous studies of global
454 (Eldridge et al., 2011; Naito & Cairns, 2011) and regional scope from the tundra (Myers-Smith et
455 al., 2011; Tape et al., 2006) and the savanna (Mitchard et al., 2011; O'Connor & Page, 2014),
456 and is consistent with the observed heterogeneous vegetation responses within and between
457 biomes (Bjorkman et al., 2019; Myers-Smith et al., 2020; Venter et al., 2018).

458

459 *Woody cover responded to warming in the tundra and precipitation increase in the savanna*

460 Temperature change was more pronounced in the tundra versus savanna sites, and the reverse
461 was true for precipitation changes (Figure 3). These climate change trends reflect the reported
462 large-scale Arctic warming (AMAP, 2017; IPCC, 2013; McBean, 2005) and regional precipitation
463 variability in the savanna (Chou et al., 2009; Neelin et al., 2006). We found greater cover change
464 with warming at wetter versus drier tundra sites (Figure 5c), consistent with other studies
465 (Callaghan et al., 2011; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012) and
466 experiments with warming chambers (Bjorkman et al., 2019; Elmendorf, Henry, Hollister, Björk,
467 Bjorkman, et al., 2012; Hollister et al., 2015).

468 In the savanna, woody cover corresponded to precipitation increases (Figure 4b), and cover
469 change rates were marginally higher at wetter versus drier savanna sites (Table S2.9), in line with
470 studies reporting greater encroachment rates in high-rainfall savannas (Skowno et al., 2017;
471 Stevens et al., 2016). In general, woody encroachment responded to the environmental factor
472 that defined each biome's seasonality – temperature in the tundra and precipitation in the
473 savanna.

474

475 *Greater cover change rates did not occur at sites with greater climate change rates*

476 While woody cover change corresponded to temperature and precipitation changes, contrary to
477 our initial hypothesis and certain studies (Axelsson & Hanan, 2018; Pearson et al., 2013; Wenmin
478 Zhang et al., 2019), we found that higher cover change rates did not correspond with greater rates
479 of increase in temperature or precipitation over time (Figure 5a,b).

480 In the tundra, plant responses to temperature change are heterogeneous across studies and
481 regions (Bjorkman et al., 2019; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al.,
482 2012; Myers-Smith et al., 2015; Prevéy et al., 2017). Heterogeneity in climate-cover change
483 relationships among sites could be partially explained by the observed interactions where lower
484 rates of woody cover change were found for drier relative to wetter sites with tundra warming.
485 (Figure 5c).

486 In the savanna, increased cover change rates were not associated with increased precipitation
487 rates. Sankaran et al. (2005) found that maximum woody cover increased linearly with MAP up
488 to c. 650 mm in African savannas. Above this threshold, higher precipitation results in canopy
489 closure and disturbances regulate tree-grass coexistence. Such rainfall boundaries vary between
490 continents (Lehmann et al., 2011). Rates of savanna cover change were more positively related
491 to increasing MAP in drier versus wetter savanna sites (Figure 5d, Table S2.53). Our finding
492 suggests that woody cover change saturates at wet sites, while woody cover can increase at dry
493 sites with precipitation increases. Almost half (40.7%) of the records included in this synthesis are
494 found above 650 mm MAP, which could partially account for the lack of an overall positive
495 relationship between MAP change rates and woody cover change rates in the savanna.
496 Additionally, fire and herbivory could be restricting the potential for increasing cover with
497 increasing MAP up to the 650 mm breakpoint.

498

499 *Site heterogeneity, time lags and plant-specific responses*

500 Variation in cover change rates could be related to landscape factors such as topography, soils
501 and microhabitats (Auger & Payette, 2010; Körner & Paulsen, 2004; Scherrer et al., 2011). Soil
502 moisture influences the establishment of tundra plants (Boulanger-Lapointe et al., 2014), with
503 shrubs showing increased climate sensitivity of growth in wet versus dry habitats (Figure 5c;
504 Ackerman et al., 2017; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012;
505 Myers-Smith et al., 2015). Dynamics might also differ between arid and mesic savannas, where
506 fine-scale water availability can facilitate woody recruitment and establishment (Table S2.9;
507 Luvuno et al., 2018). Our study may not capture these site-level explanatory factors driving cross-
508 site heterogeneity and climate-plant relationships.

509 A delayed response of plants to changing conditions (Wu et al., 2015) might also account for the
510 lack of correspondence between cover change rates and climate change rates. Recruitment
511 changes are dependent on successful reproduction, germination and survival, and tundra plants
512 may require several favourable growing seasons (Chapin & Starfield, 1997), and up to decades
513 of temperature increases (Buntgen et al., 2015; Myers-Smith & Hik, 2017) or herbivory exclusion

514 (Olofsson & Post, 2018) to respond with increased cover. Similarly, lags of 3-5 years have been
515 observed in the savanna following herbivore exclusion (Koerner et al., 2014), and substantial lags
516 following precipitation are characteristic of regions with a sudden onset of precipitation change
517 (Schultz & Halpert, 1993). Longer-term data collection with higher temporal resolution may be
518 required to capture lag effects of climate change on woody cover change.

519 Plant responses to climate change can also be species-dependant and thus lead to heterogeneity
520 in cover change rates (Bjorkman et al., 2018, 2019; Myers-Smith et al., 2020). Species with fast
521 and opportunistic growth strategies, like *Betula* and *Salix* in the tundra (Ackerman et al., 2017;
522 Bjorkman et al., 2018; Williamson et al., 2016) or *Acacia* in the savanna (Archibald & Bond, 2003)
523 will increase faster since they can take advantage of changes in their environment (Bond &
524 Midgley, 2000; Osborne et al., 2018; Sonesson & Callaghan, 1991). Nitrogen-fixing species (e.g.
525 *Alnus* in the tundra, *Acacia* in the savanna) can alter nitrogen cycling, reshaping nutrient
526 availability across the landscape (Hu et al., 2001), and in the case of the savanna leading to
527 further woody encroachment and legume proliferation (Ritchie et al., 1998). Therefore, species
528 traits can influence their responses to changing environmental conditions across these two
529 biomes (Bjorkman et al., 2018; Osborne et al., 2018).

530

531 *Non-climate environmental drivers and land use factors*

532 Other environmental processes that are indirectly influenced by climate change could be just as
533 or more important than the direct effects of temperature and precipitation shifts in driving woody
534 encroachment. In the tundra, warming summer air temperatures were the most frequently
535 reported direct driver of plant growth in our literature review (Figure 6; Wilson & Nilsson, 2009;
536 Hallinger et al., 2010; Myers-Smith et al., 2015). Warming, together with longer growing seasons,
537 could lead to permafrost thaw and a deepening of the active layer (Natali et al., 2012), which
538 could increase nutrient release, stimulate plant growth (Aerts et al., 2006; Shaver et al., 2001)
539 and result in expanded shrub cover (Myers-Smith et al., 2019). Thus, climate can influence other
540 mechanistic processes which can in turn enhance woody encroachment.

541 In the savanna, the most frequently identified drivers of woody encroachment in our literature
542 review were increased rainfall, fire suppression and rising CO₂ (Figure 6). Fire and herbivore
543 regimes structure savanna ecosystems (Bond & Keeley, 2005), and frequent fires can prevent
544 further woody encroachment (Roques et al., 2001). When fires are suppressed or trees can
545 outcompete grasses to access water, precipitation increases can facilitate woody encroachment
546 (Lehmann et al., 2009), and increases in flammable biomass can lead to more intense fires
547 (Higgins et al., 2000). Rising CO₂ concentrations additionally enable woody plant growth (Bond &
548 Midgley, 2000) and cover increases, shifting the competitive balance between C₃ woody plants
549 and C₄ grasses (Buitenwerf et al., 2012). With CO₂ enrichment, plants have improved water use
550 efficiency (Morgan et al., 2004), stimulated resprouting (Hoffmann et al., 2000), and greater tree
551 recruitment can occur (Bond & Midgley, 2012). Global drivers have likely interacted with local land

552 use factors leading to amplified responses (Archer et al., 2017). In addition, changing climate
553 regimes (e.g., droughts), can strongly affect land use intensity and extent (Biazin & Sterk, 2013),
554 creating feedbacks that could lead to further woody encroachment.

555 Plant responses to climate do not act in isolation from other trophic levels (Bale et al., 2002;
556 Olofsson & Post, 2018; Ravolainen et al., 2014; Tape, Gustine, et al., 2016; Vowles et al., 2017).
557 Herbivory has a contrasting role in shaping woody encroachment in these biomes. While in the
558 tundra grazing often inhibits shrub growth (Ravolainen et al., 2014; Vowles et al., 2017), in the
559 savanna it is a key regulator of woody cover. Browsers decrease woody cover and grazers
560 increase woody cover via removal of grass, ameliorating tree–grass competition (Sankaran et al.,
561 2008). Only 51 (4.7%) of our records identified excluded herbivory and 238 (21.85%) identified
562 increased grazing as a cover change driver across both biomes (Figure 6). Thus, while capturing
563 the influence of trophic interactions on vegetation change remains challenging (Olofsson et al.,
564 2013), the importance of herbivory may be under-reported in the ecological literature.

565

566 *Ecological feedbacks and biome persistence*

567 Woody encroachment has important implications for ecosystem functions in both biomes, which
568 can lead to ecosystem-scale feedbacks. In the tundra, shifts in species composition can alter litter
569 inputs to the soil and resulting decomposition, potentially leading to increased carbon turnover
570 (McLaren et al., 2017; Myers-Smith, Thomas, & Bjorkman, 2019). Likewise, shrub cover increase
571 can result in decreased albedo and associated alteration of snowmelt timing (Loranty & Goetz,
572 2012) resulting in an increase in near-surface temperatures (Rydsaa et al., 2017), ecosystem
573 respiration (Ge et al., 2017), and permafrost thaw depth (Li et al., 2017). Tundra wildfires have
574 increased over recent decades (Payette et al., 2008) and this trend is expected to continue (Hu
575 et al., 2015), with climate-fire-vegetation feedbacks documented in Arctic and alpine
576 environments (Goetz et al., 2007; Wookey et al., 2009). Fire is essential in maintaining savannas,
577 and positive feedbacks between fire frequency and grasses limit woody plant recruitment
578 (Beckage et al., 2009; Lehmann et al., 2014). In contrast, savanna fire suppression increases
579 woody plant establishment, resulting in a reduced C₄ grass layer and lower light availability, thus
580 leading to further fire intensity reduction and increased woody encroachment, with decreased
581 albedo (Luvuno et al., 2018).

582 When amplified, woody encroachment could translate into wide-scale transformations of both
583 biomes. Shrub lines and boreal forest treelines are moving northwards or upwards in tundra
584 regions (Harsch et al., 2009; Myers-Smith & Hik, 2017). Shrubs are the characteristic dominant
585 vegetation component in four of the five Arctic bioclimatic subzones (D. A. Walker et al., 2005),
586 with this coverage increasing with warming temperatures (Wenxin Zhang et al., 2013) and driving
587 certain areas to a state of phase transition towards shrubland (Naito & Cairns, 2015). Therefore,
588 latitudinal or elevational shrub line movement could lead the tundra biome to decrease in size as
589 the climate warms. In contrast, the savanna/forest ecotone is an inherently dynamic boundary

590 due to its fire dependency (Bond et al., 2005). Thus, the direct consequences of climate change
591 on biome extent are less likely to be detected in savannas. However, land use change or shifting
592 fire regimes will interact with climate change (including elevated CO₂), such that the savanna
593 could either expand into grasslands, be invaded by forest (Hoffmann et al., 2009; Osborne et al.,
594 2018; Stevens et al., 2017), or result in grassless shrublands or forests that can no longer be
595 defined as savannas (Bond & Midgley, 2012; Parr et al., 2012, 2014).

596

597 *Study limitations*

598 Woody cover change data reported in our study could be influenced by a number of limitations:
599 1) Publication bias could influence results, since stable or negative trends in plant cover are rarely
600 reported. We also observed spatial bias, with woody cover change reported widely from well-
601 studied areas such as Toolik Lake (Alaska) or Abisko (Sweden), and very few records from
602 Siberia or the Brazilian Cerrado. 2) Estimations of woody cover can differ depending on the
603 methods used, but we reported only absolute percentages to partially account for inconsistent
604 methods. 3) Cover trends were reported both at the functional group and at the species levels,
605 which could mask species-specific trends. We found no significant differences in woody cover
606 change rates when presented at the species or functional group levels (Table S2.7-8). 4) Woody
607 cover trend periods for multiple records extended beyond the available duration from 1979 – 2013
608 of the climate data. We did not find evidence of a consistent positive relationship between cover
609 change rates and rates of climate change when subsetting these records, which we attribute to a
610 change in sample size (Figure S7, Table S3). 5) Gridded climate data do not capture microclimate
611 and site-level conditions, which could play an important role in explaining heterogeneity in cover
612 change at the landscape scale. However, site-level meteorological data were not consistently
613 available for our sites and the use of the CHELSA dataset provides a standardised and robust
614 way to test for the effects of climate change across biomes. 6) Reported driver data from the
615 literature may not capture all components of mechanisms influencing woody cover change. These
616 reported drivers are likely to be biased, and driver attribution differs between studies. Certain
617 studies attribute woody encroachment to one particular cause, while the process could be the
618 result of synergies between different drivers.

619

620 **Conclusions**

621 Woody encroachment occurred across the tundra and savanna biomes and, while this process
622 was related to climate change, the relationships were complex. We found that woody cover
623 change was higher in wetter versus drier sites following warming in the tundra biome, and that
624 woody cover change magnitudes corresponded to MAP increases in the savanna. However, we
625 found no overall positive relationships between climate change rates and woody cover change
626 rates. The lack of climate-woody cover relationships was due in part to interactions among site
627 climatology and climate change variables in both biomes. Additional factors are likely also

628 important, including site heterogeneity, time lags, plant-specific responses, and non-climate
629 processes such as increased active layer in the tundra and disturbance processes, such as
630 shifting fire and herbivory regimes, driving woody encroachment in the savanna. Our findings,
631 together with those previously reported, highlight the role of current and projected climate change
632 on woody encroachment. However, simple extrapolations of increased woody encroachment
633 rates with temperature warming or increased precipitation will likely poorly represent plant cover
634 change across biomes that are strongly influenced by seasonality. Thus, woody encroachment
635 projections should account for complex climate-biome interactions to better estimate future
636 changes under global change scenarios.

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1147

1148

1149 **Data accessibility**

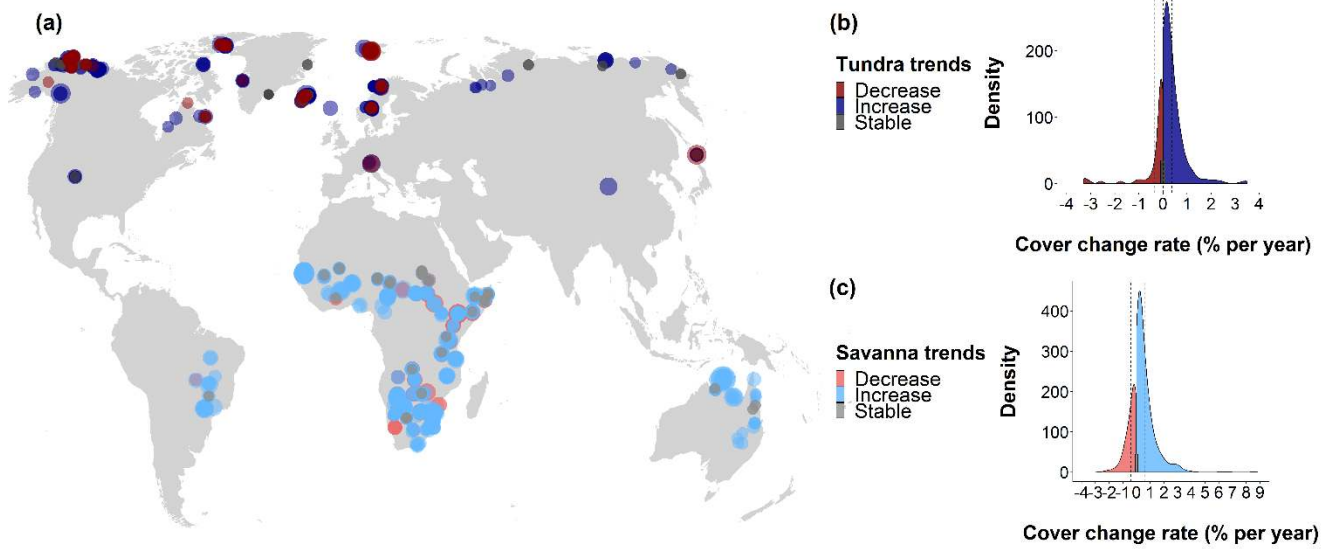
1150 Code and data are freely available here: <https://doi.org/10.5281/zenodo.3601454>. CHELSA
1151 climatic data can be downloaded from <http://chelsa-climate.org/>.

1152 **Table 1.** Summary of the main characteristics of both the tundra and savanna study biomes.

Biome characteristics	Tundra	Reference	Savanna	Reference
Earth's land surface	15-20%	(Wilsey, 2018)	~20%	(Scholes & Hall, 1996)
Terrestrial Net Primary Production	2.16%	(Saugier et al., 2001)	30%	(Grace et al., 2006)
Earth's population	0.05%	(National Snow & Ice Data Center, 2019)	20%	(Scholes & Archer, 1997)
Human land uses	Herding and hunting	(Nuttall, 2007)	Ranging and farming	(Scholes & Archer, 1997)
Distinctive features	Permafrost layer	(Schuur et al., 2009)	Coexistence of C ₄ grasses and trees	(Scholes & Hall, 1996)
Biome limiting factors	Temperature	(IPCC, 2013)	Disturbance (fire, herbivory, etc.) and precipitation	(Bond, 2008)
Grass cover	18% (mean, range 0.7 – 90%)	Unpublished analysis.	50-100%	Unpublished analysis.
World's carbon storage	50% (northern circumpolar region)	(Tarnocai et al., 2009)	15%	(Grace et al., 2006)

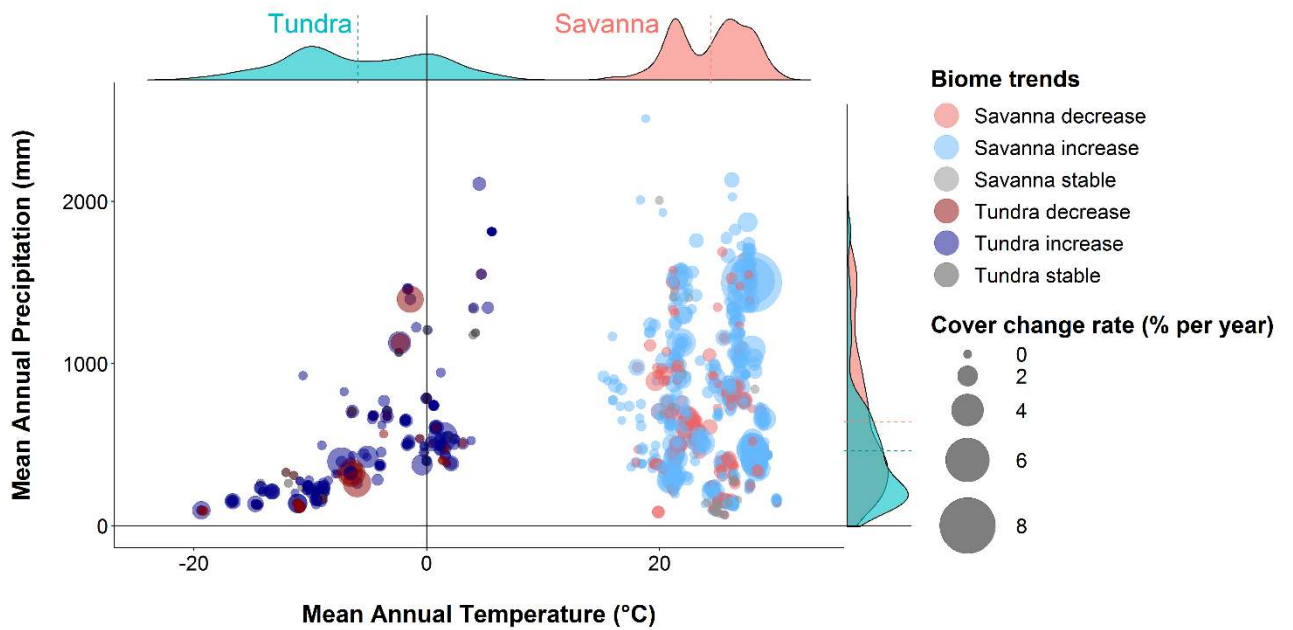
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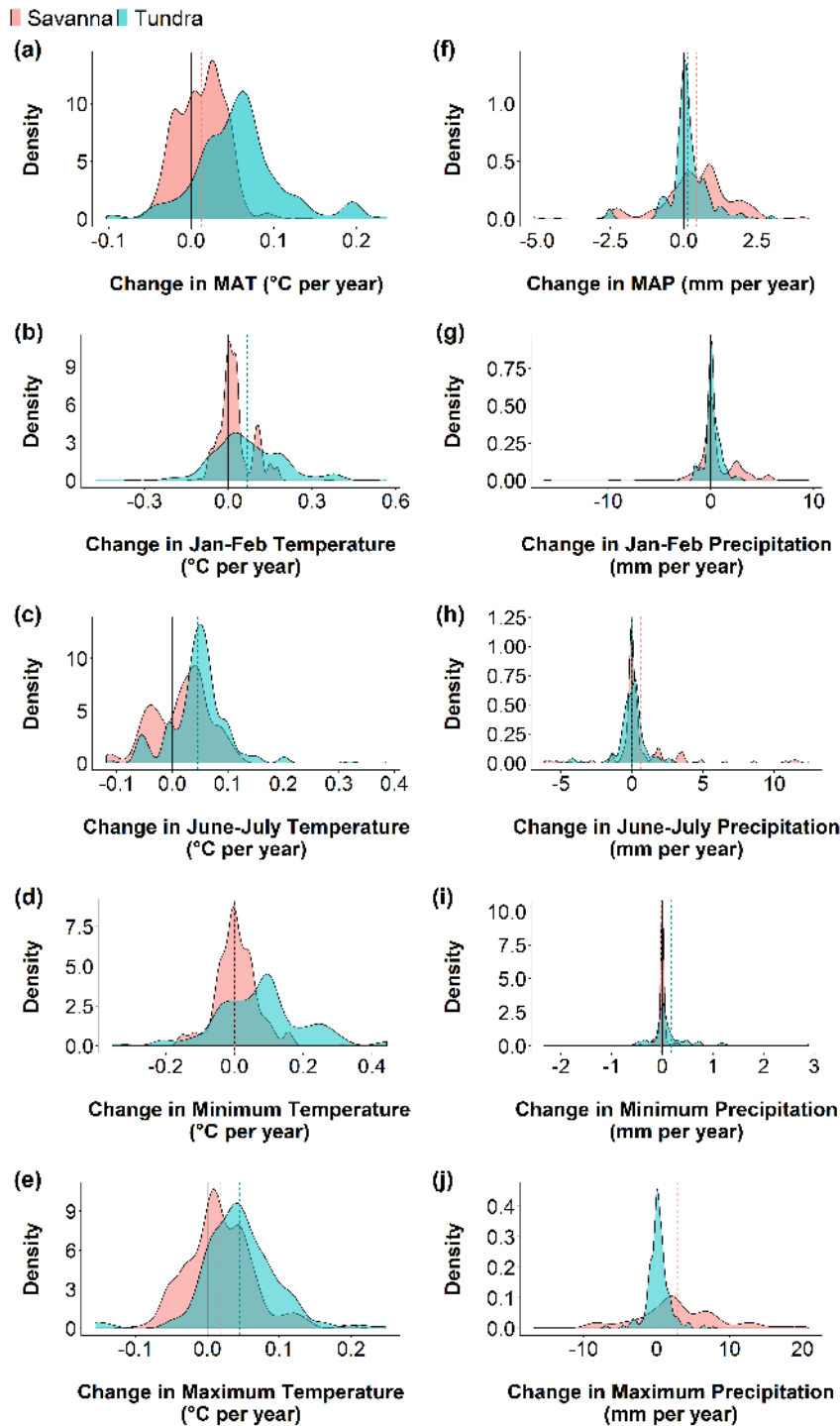
1155

1156 **Figure 1. a)** Woody cover increased in all continents across the tundra and savanna biomes.
1157 Points represent the woody cover change records compiled for analysis, coloured according to
1158 their biome and direction of cover trend. The size of the points is scaled to the annual rate of plant
1159 cover change at each location. Map projection is Winkel-Tripel. **b)** In the tundra, 68.05% records
1160 reported an increase in woody cover. **c)** In the savanna, 67.78% records reported an increase in
1161 woody cover. Of those records that reported increased woody cover, we found higher rates in the
1162 savanna ($0.63 \pm 0.82\%$) than in the tundra ($0.37 \pm 0.5\%$, mean \pm SD per year). Stable trends are
1163 presented as a bar in the density plots for visualization purposes. We defined stable trends as an
1164 annual plant cover change between -0.01% and $+0.01\%$. Dashed lines represent mean values
1165 per qualitative trend.



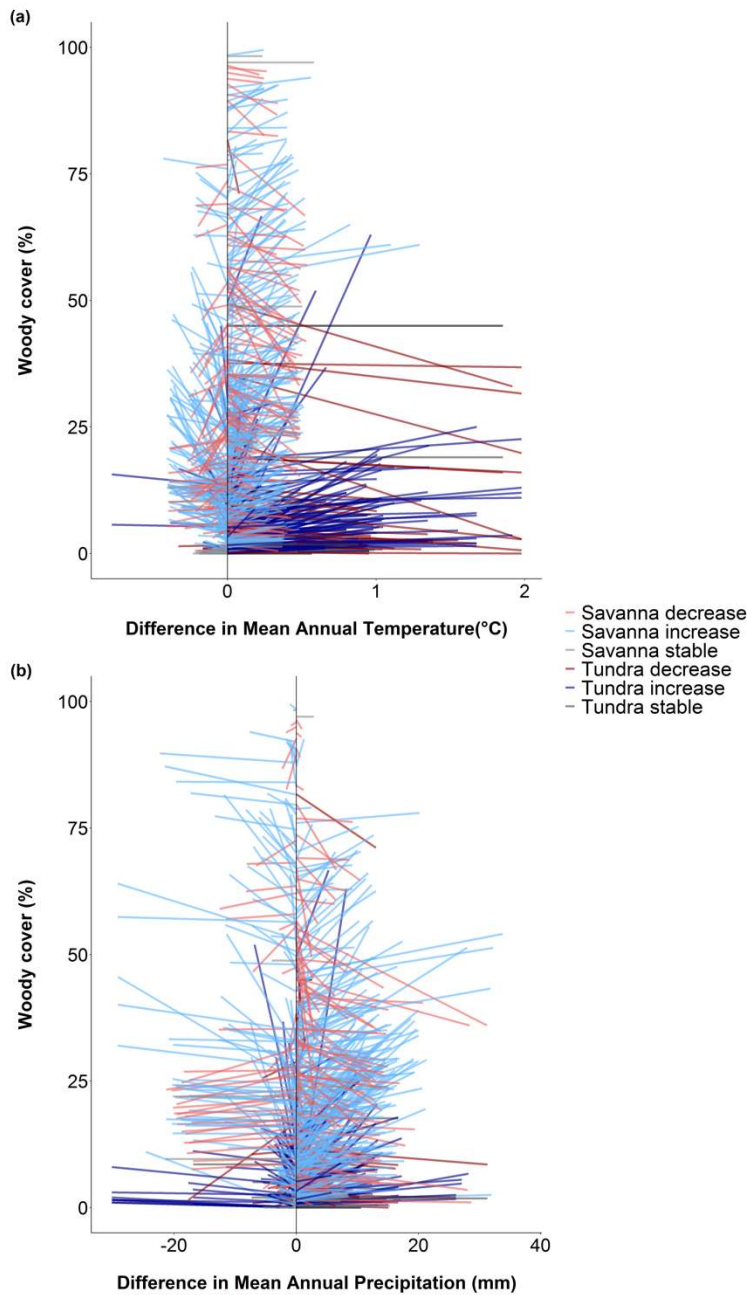
1166

1167 **Figure 2.** Woody cover change was found across the gradient of temperature and precipitation
 1168 in the two biomes. Each point represents a cover change record. The size of the points is relative
 1169 to the woody cover change rate (% per year) in each location. The colour of the points represents
 1170 the direction of the trend in each biome. Climate data here are climatologies (mean values of MAT
 1171 and MAP) for the period 1979 – 2013. The marginal density plots represent MAT (top density plot)
 1172 and MAP (right density plot) conditions across sites in both biomes. Dashed lines represent the
 1173 means per climate variable and biome.



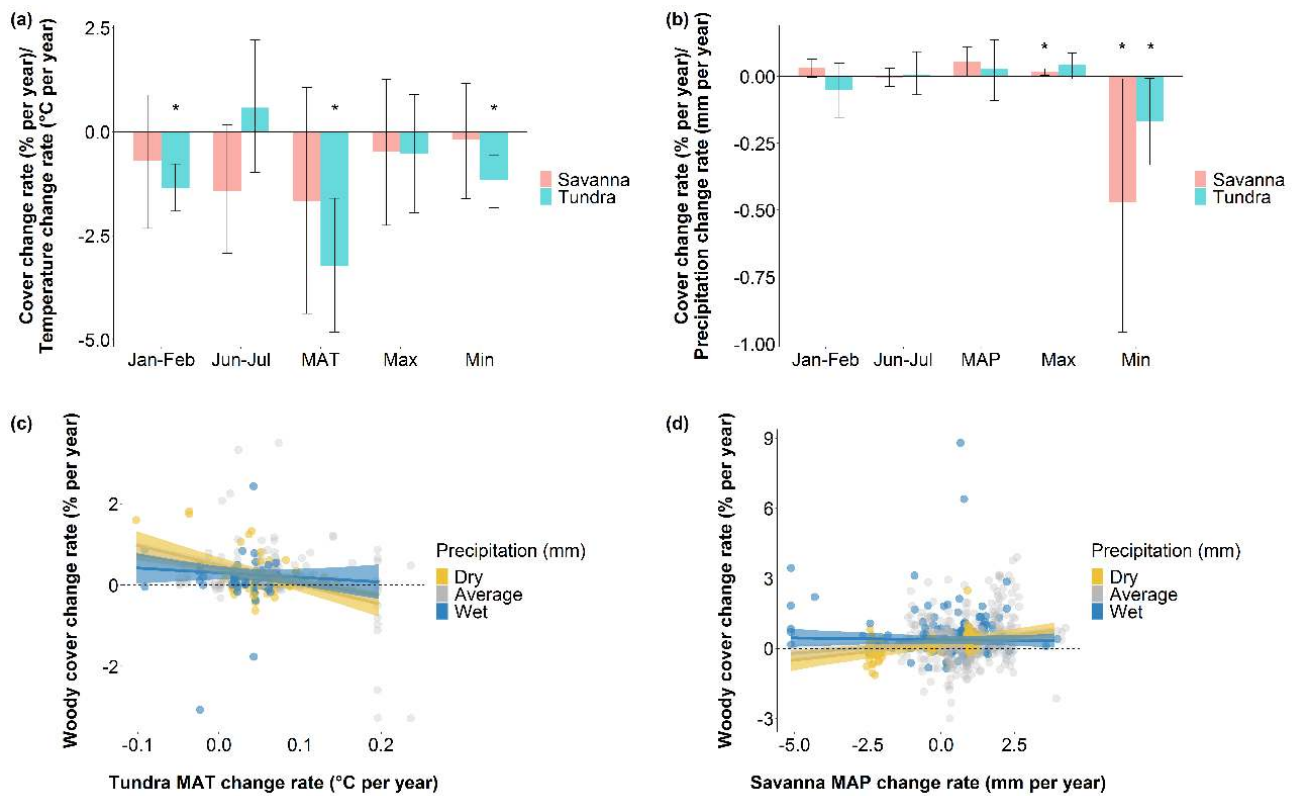
1174

1175 **Figure 3.** Both tundra and savanna sites warmed over time (a-e), with the exception of
 1176 minimum temperature in the savanna (d). MAP and minimum precipitation have
 1177 increased in the tundra (f, i), while in the savanna precipitation increased in all variables
 1178 (f-h, j) except for minimum precipitation (i). Each density plot represents annual change
 1179 in each climate variable across sites, with climate data fitted to each site-specific study
 1180 duration. Dashed lines represent the mean of the posterior distribution in each biome
 1181 (i.e., the mean slope of climate change).



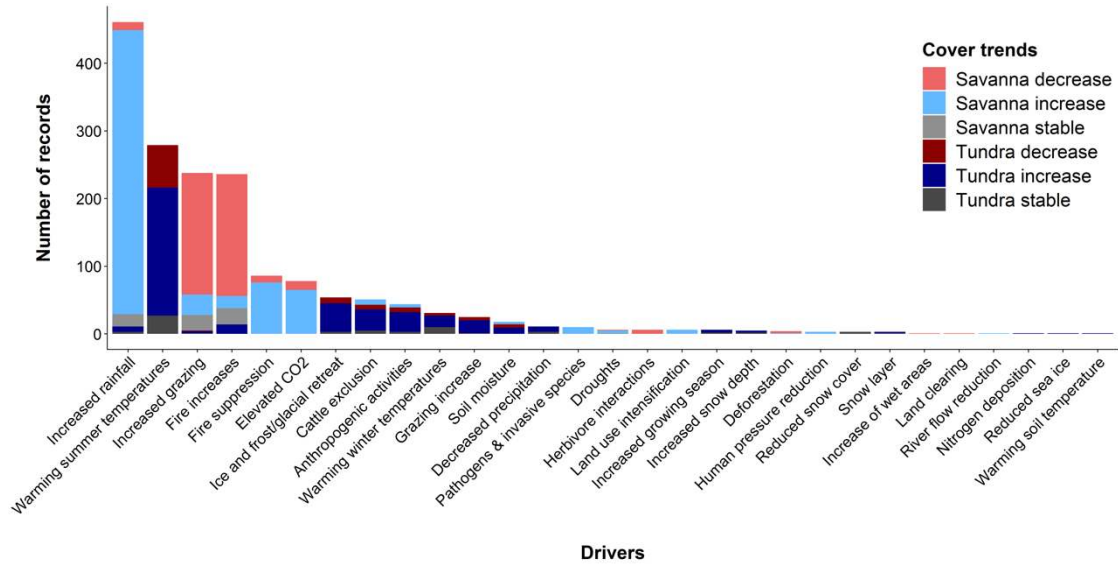
1182

1183 **Figure 4.** There was a positive relationship between total woody cover change magnitude and
 1184 magnitude of MAP increases over time in the savanna but not in the tundra (Table S2.27-28).
 1185 Cover change magnitude was not related to the magnitude of MAT increase in either biome (Table
 1186 S2.25-26). Each line represents a particular record (species or functional group per site
 1187 combination), with a start cover value emanating from the 0 line on the x-axis, and an end cover
 1188 value at the opposite end of the line, representing the cover values at the start and end of the
 1189 monitoring period. Climate values at the start of the monitoring period are centred on 0, and the
 1190 line represents the magnitude of change in cover and in **a)** Mean Annual Temperature and **b)**
 1191 Mean Annual Precipitation over each particular monitoring time period. The colour of the line
 1192 represents the trend direction for each biome.



1193

1194 **Figure 5.** There were no positive linear relationships between woody cover change rates and
 1195 rates of changing climate conditions in either the tundra or savanna biomes, except for maximum
 1196 MAP in the savanna (Table S2.29-48). **a)** and **b)** slopes are Bayesian models of cover change
 1197 rates per year as a function of annual change rate for all climate variables for **a)** temperature and
 1198 **b)** precipitation. Location grid was included as a random effect in all models. Vertical error lines
 1199 represent the 95% credible intervals of the slope estimates. The relationships between cover
 1200 change rates and climate change rates that had credible intervals that did not overlap zero are
 1201 represented by the asterisk. **c)** Rates of tundra woody cover change were lower in drier versus
 1202 wetter sites with increasing MAT. **d)** Rates of savanna woody cover change were higher in drier
 1203 versus wetter sites with increasing MAP. Points are annual woody cover change values coloured
 1204 depending on their quantile category in the precipitation gradient, as climatologies for the 1979 –
 1205 2013 period. Points are coloured according to three categories: below the 20% quantile (dry),
 1206 between 20% and 80% quantiles (average), and above the 80% quantile (wet). Regression lines
 1207 represent predicted values from the fitted models for the 20% (dry) and 80% (wet) quantiles of
 1208 climatologies (with grid cell as a random factor), and ribbons represent the 95% credible intervals.



1209

1210 **Figure 6.** The most commonly reported drivers of increasing woody cover are warming summer
 1211 temperatures in the tundra and increased rainfall in the savanna. The stacked bars show the total
 1212 values per driver and are coloured by the biome and direction of the cover trend. The bars display
 1213 all reported records per driver ($n = 1,670$).

1214 **Summary of numbered items in the supplementary material**

1215 **Figure S1.** Distribution maps of the tundra and savanna biomes.

1216 **Figure S2.** Conceptual diagrams of main climatic analyses.

1217 **Figure S3.** Timelines of woody cover change studies.

1218 **Figure S4.** Woody cover change across MAT and MAP climatologies.

1219 **Figure S5.** Woody cover change under MAT and MAP changes over time.

1220 **Figure S6.** Woody cover change rates versus climate change rates in all 10 variables.

1221 **Figure S7.** 'Rate vs rate' analyses in different record subsets.

1222 **Table S1.** Summary of all published references used in this synthesis.

1223 **Table S2.** Results of all fitted Bayesian models.

1224 **Table S3.** Results of all fitted Bayesian 'rate vs rate' models in different record subsets.