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

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Short-running title: Woody encroachment across biomes

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Biosketch

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

Abstract

Aim

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

Location

Tundra and savanna biomes.

Time period

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

Major taxa studied

Woody plants (shrubs and trees).

Methods

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

Results

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

Main conclusions

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

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

Introduction

Global change in open biomes at seasonality extremes

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

The tundra and the savanna have undergone substantial compositional and structural changes in recent decades (Myers-Smith & Hik, 2017; Stevens et al., 2017), and in particular, are experiencing an increase in woody biomass and/or an expansion of cover into open areas, a process known as woody plant encroachment (Archer et al., 2017). In the tundra, treelines and shrub lines are advancing towards higher latitudes and elevations (Harsch et al., 2009; Holtmeier & Broll, 2005; Myers-Smith & Hik, 2017). In the savanna, woody plants are increasing in cover and density, which can lead to shifts to alternate states from grasslands to thickets or forests (Parr et al., 2012). However, even though marked increases in woody cover have been documented in both biomes, encroachment rates have not been directly compared, and the relationship between woody encroachment and changing climate has not been disentangled.

Climate change impacts on ecosystem services and biodiversity

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

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

Woody encroachment has led to heterogeneous biodiversity responses. Tundra shrubs and forbs are increasing at the expense of graminoids (Wahren et al., 2013), lichens and bryophytes (Cornelissen et al., 2001; Vowles et al., 2017; M. D. Walker et al., 2006), with cascading effects leading to decreased habitat quality for caribou (Joly et al., 2007), northward range expansions for moose (Tape, Christie, et al., 2016), or loss of specialist bird species (Sokolov et al., 2012). Likewise, the increasing C_3 woody plant component of savanna ecosystems (Bond & Midgley, 2000) alters functional group composition, with changing bird species richness (Sirami et al., 2009) and decreases in specialist ant and plant species (Abreu et al., 2017). Thus, woody vegetation change can lead to impacts across trophic levels in tundra and savanna food webs.

Drivers of woody encroachment

Although woody encroachment is widespread in both biomes, the hypothesized causes of encroachment differ (Martin et al., 2017; Naito & Cairns, 2011; Roques et al., 2001). In the tundra, warming temperatures, permafrost thaw and altered nutrient cycling are likely the main drivers of shrub expansion (Myers-Smith et al., 2011; Sturm et al., 2001), with soil moisture acting as a potential limiting factor (Ackerman et al., 2017). In contrast, the savanna is a disturbance-driven biome whose structure and function are shaped by fire and herbivory processes. Human actions altering these regimes (Archer et al., 2017; Venter et al., 2018), and changing global drivers like rainfall and rising atmospheric CO_2 concentrations (Buitenwerf et al., 2012; Wenmin Zhang et al., 2019) have been widely reported to determine woody encroachment. Interactions among drivers of vegetation change add complexity to projections of the future abundance and distribution of woody plants across these biomes.

Woody encroachment rates across biomes

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

Here, we synthesize studies of woody cover change across tundra and savanna biomes to determine the degree to which encroachment is related to regional temperature and precipitation change. This cross-biome synthesis of the current status of woody encroachment and its main drivers will improve forecasts of global change across these two open biomes and enable us to understand whether woody plant species' growth responses to climate change are generalizable or highly linked to biome context. Specifically, we tested the link between woody cover change and climate change in three ways: 1) using long-term climatologies (Figure S2a), 2) calculating magnitudes of cover change following increases in precipitation or temperature (Figure S2b) , and 3) analysing whether climate change rates predict woody encroachment rates (Figure S2c). Additionally, we compared woody encroachment rates across the tundra and the savanna biomes and conducted a literature review to assess which factors are commonly associated with cover change in both biomes. We hypothesized that woody encroachment rates are higher in the savanna, a disturbance-driven biome, due to warmer and longer growing seasons. We predicted that shrub expansion rates in the tundra have increased with warming summer temperatures, while encroachment rates in the savanna have increased with greater wet season precipitation, but were also affected by non-climate factors such as shifting fire regimes, herbivory and elevated CO_2.

Methods

Definitions and scope

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

Data compilation and extraction

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

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

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

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

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

Climate data extraction and analysis

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

Additionally, we extracted temperature and precipitation monthly time series, which we used to then calculate the mean value per climatic variable, year and site. We calculated mean annual change in 10 climate variables in order to represent the strong seasonality experienced in the tundra and savanna biomes: MAT, January-February mean temperature (winter in the tundra, wet season in the savanna), June-July mean temperature (summer in the tundra, dry season in the savanna), minimum annual temperature (coldest month), maximum annual temperature (warmest month), MAP, January-February mean precipitation (wet season in the savanna), June-July mean precipitation (dry season in the savanna), minimum annual precipitation (driest month) and maximum annual precipitation (wettest month). We considered precipitation in the tundra to consist of rain between June and August, and snow during the rest of the year.

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

Statistical analyses

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

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

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

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

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

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

Software and model specifications

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

Results

Woody cover change was found across the tundra and savanna biomes

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

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

Woody encroachment occurred across climatologies

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

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

Temperature and precipitation increased across biomes over time

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

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

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

In the savanna, magnitudes of woody cover change corresponded to increases in precipitation (Table S2.28), but not to increases in temperature (Table S2.26) in our ‘magnitude vs magnitude’ analyses (Figure 4). In our ‘rates vs rates’ analyses, we found no significant relationships between rates of cover change and rates of temperature change (Figure 5a, Figure S6). However, we found a positive relationship between maximum annual precipitation and woody cover change, and a negative relationship between cover change rates and minimum annual precipitation (Figure 5b, Figure S6, Table S2.29-48). Additionally, we found a significant interaction between cover change rates, precipitation change rates and long-term precipitation climatologies in the savanna (Figure 5d, Table S2.53). The interaction indicated that rates of cover change were higher in drier versus wetter sites with increased precipitation change. We found no other significant interactions for the savanna biome (Table S2.49-56).

'Rates vs rates' relationships varied depending on record subsets

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

Reported drivers of woody encroachment differ between biomes

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

Discussion

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

Woody cover change occurred across the tundra and savanna biomes

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

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

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

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

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

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

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

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

Site heterogeneity, time lags and plant-specific responses

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

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

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

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

Non-climate environmental drivers and land use factors

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

In the savanna, the most frequently identified drivers of woody encroachment in our literature review were increased rainfall, fire suppression and rising CO_2 (Figure 6). Fire and herbivore regimes structure savanna ecosystems (Bond & Keeley, 2005), and frequent fires can prevent further woody encroachment (Roques et al., 2001). When fires are suppressed or trees can outcompete grasses to access water, precipitation increases can facilitate woody encroachment (Lehmann et al., 2009), and increases in flammable biomass can lead to more intense fires (Higgins et al., 2000). Rising CO_2 concentrations additionally enable woody plant growth (Bond & Midgley, 2000) and cover increases, shifting the competitive balance between C_3 woody plants and C_4 grasses (Buitenwerf et al., 2012). With CO_2 enrichment, plants have improved water use efficiency (Morgan et al., 2004), stimulated resprouting (Hoffmann et al., 2000), and greater tree recruitment can occur (Bond & Midgley, 2012). Global drivers have likely interacted with local land use factors leading to amplified responses (Archer et al., 2017). In addition, changing climate regimes (e.g., droughts), can strongly affect land use intensity and extent (Biazin & Sterk, 2013), creating feedbacks that could lead to further woody encroachment.

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

Ecological feedbacks and biome persistence

Woody encroachment has important implications for ecosystem functions in both biomes, which can lead to ecosystem-scale feedbacks. In the tundra, shifts in species composition can alter litter inputs to the soil and resulting decomposition, potentially leading to increased carbon turnover (McLaren et al., 2017; Myers-Smith, Thomas, & Bjorkman, 2019). Likewise, shrub cover increase can result in decreased albedo and associated alteration of snowmelt timing (Loranty & Goetz, 2012) resulting in an increase in near-surface temperatures (Rydsaa et al., 2017), ecosystem respiration (Ge et al., 2017), and permafrost thaw depth (Li et al., 2017). Tundra wildfires have increased over recent decades (Payette et al., 2008) and this trend is expected to continue (Hu et al., 2015), with climate-fire-vegetation feedbacks documented in Arctic and alpine environments (Goetz et al., 2007; Wookey et al., 2009). Fire is essential in maintaining savannas, and positive feedbacks between fire frequency and grasses limit woody plant recruitment (Beckage et al., 2009; Lehmann et al., 2014). In contrast, savanna fire suppression increases woody plant establishment, resulting in a reduced C_4 grass layer and lower light availability, thus leading to further fire intensity reduction and increased woody encroachment, with decreased albedo (Luvuno et al., 2018).

When amplified, woody encroachment could translate into wide-scale transformations of both biomes. Shrub lines and boreal forest treelines are moving northwards or upwards in tundra regions (Harsch et al., 2009; Myers-Smith & Hik, 2017). Shrubs are the characteristic dominant vegetation component in four of the five Arctic bioclimatic subzones (D. A. Walker et al., 2005), with this coverage increasing with warming temperatures (Wenxin Zhang et al., 2013) and driving certain areas to a state of phase transition towards shrubland (Naito & Cairns, 2015). Therefore, latitudinal or elevational shrub line movement could lead the tundra biome to decrease in size as the climate warms. In contrast, the savanna/forest ecotone is an inherently dynamic boundary due to its fire dependency (Bond et al., 2005). Thus, the direct consequences of climate change on biome extent are less likely to be detected in savannas. However, land use change or shifting fire regimes will interact with climate change (including elevated CO_2), such that the savanna could either expand into grasslands, be invaded by forest (Hoffmann et al., 2009; Osborne et al., 2018; Stevens et al., 2017), or result in grassless shrublands or forests that can no longer be defined as savannas (Bond & Midgley, 2012; Parr et al., 2012, 2014).

Study limitations

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

Conclusions

Woody encroachment occurred across the tundra and savanna biomes and, while this process was related to climate change, the relationships were complex. We found that woody cover change was higher in wetter versus drier sites following warming in the tundra biome, and that woody cover change magnitudes corresponded to MAP increases in the savanna. However, we found no overall positive relationships between climate change rates and woody cover change rates. The lack of climate-woody cover relationships was due in part to interactions among site climatology and climate change variables in both biomes. Additional factors are likely also important, including site heterogeneity, time lags, plant-specific responses, and non-climate processes such as increased active layer in the tundra and disturbance processes, such as shifting fire and herbivory regimes, driving woody encroachment in the savanna. Our findings, together with those previously reported, highlight the role of current and projected climate change on woody encroachment. However, simple extrapolations of increased woody encroachment rates with temperature warming or increased precipitation will likely poorly represent plant cover change across biomes that are strongly influenced by seasonality. Thus, woody encroachment projections should account for complex climate-biome interactions to better estimate future changes under global change scenarios.

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Data accessibility

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

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)

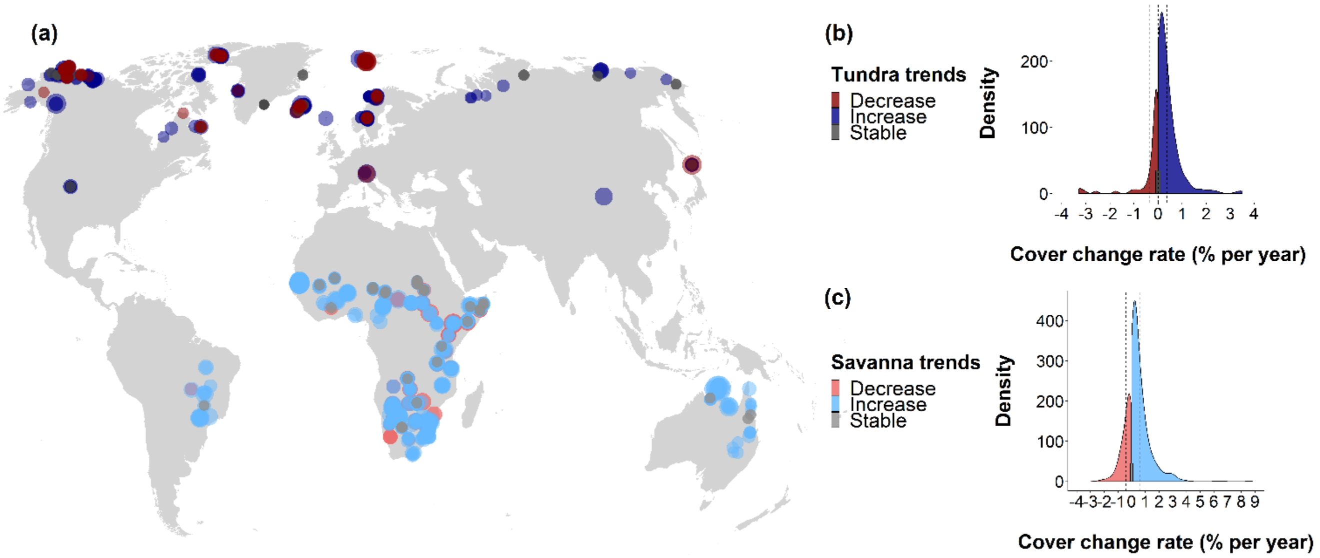

Figure 1. a) Woody cover increased in all continents across the tundra and savanna biomes. Points represent the woody cover change records compiled for analysis, coloured according to their biome and direction of cover trend. The size of the points is scaled to the annual rate of plant cover change at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

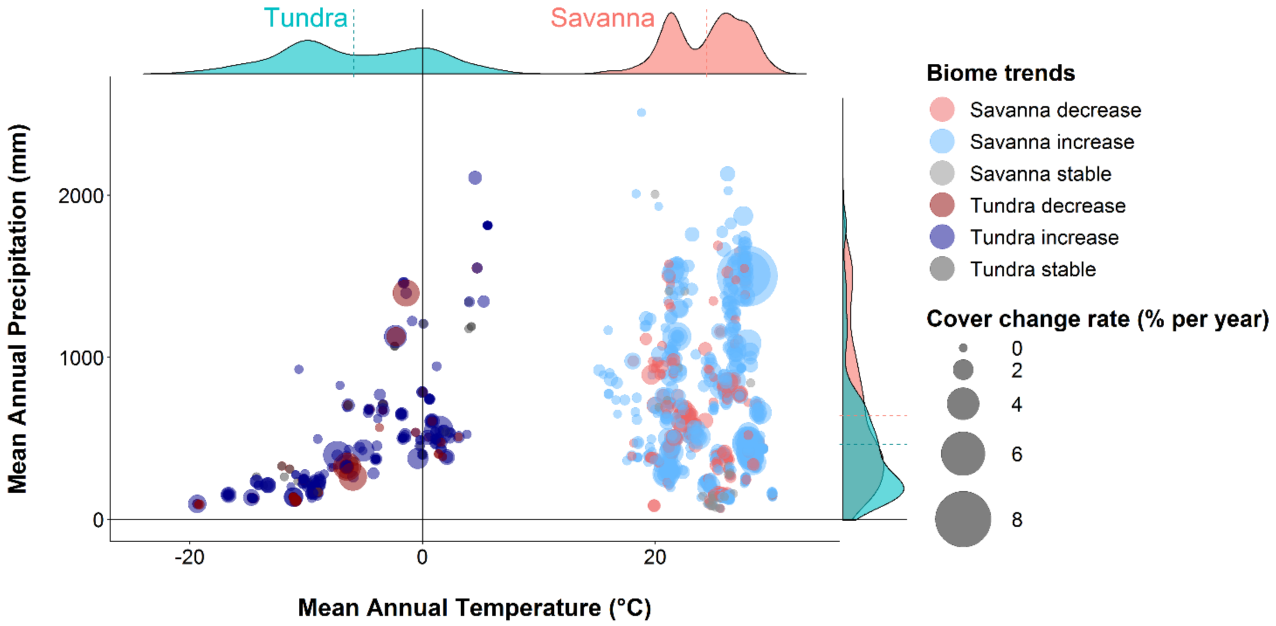

Figure 2. Woody cover change was found across the gradient of temperature and precipitation in the two biomes. Each point represents a cover change record. The size of the points is relative to the woody cover change rate (% per year) in each location. The colour of the points represents the direction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

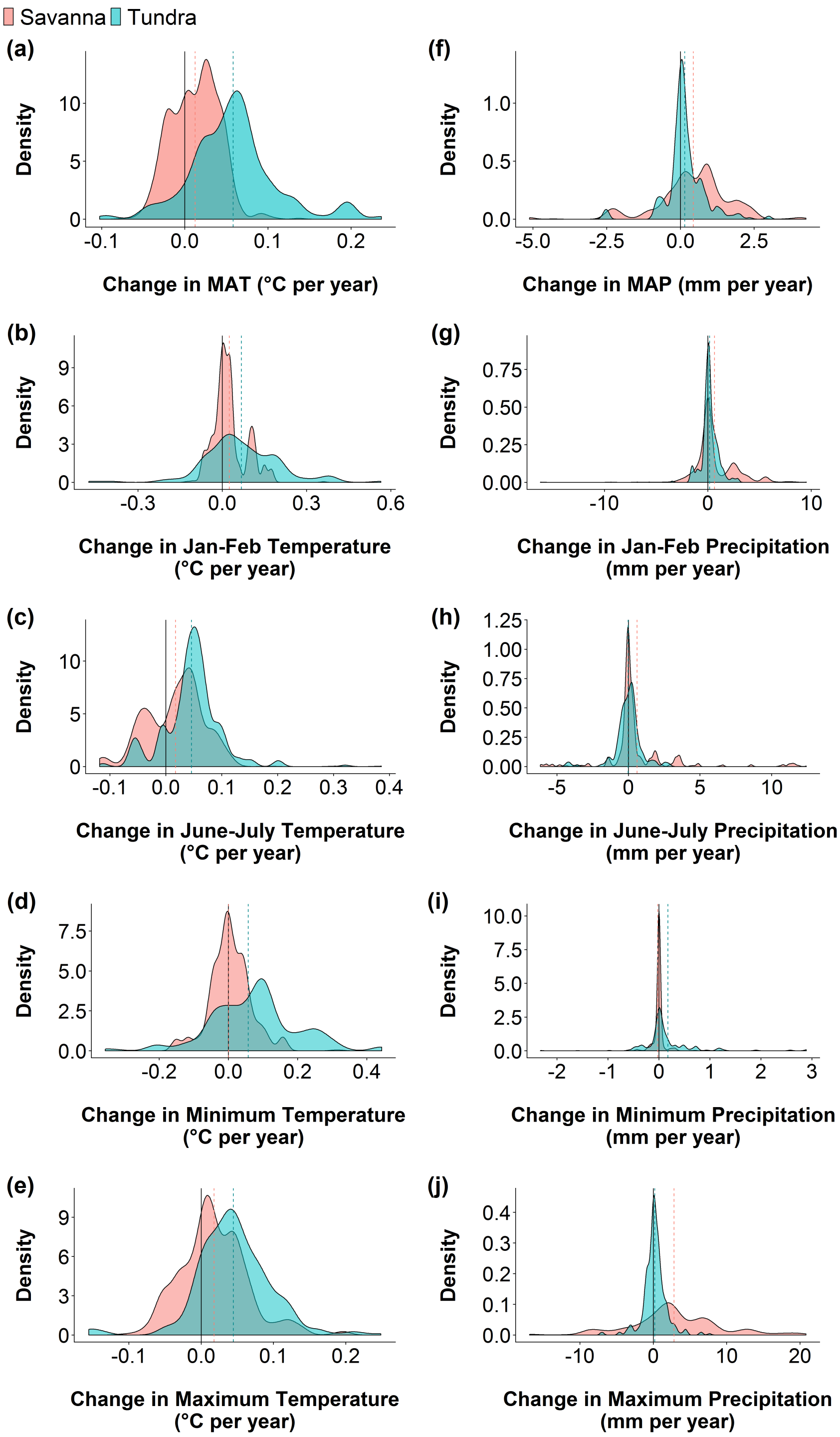

Figure 3. Both tundra and savanna sites warmed over time (**a-e**), with the exception of minimum temperature in the savanna (**d**). MAP and minimum precipitation have increased in the tundra (**f, i**), while in the savanna precipitation increased in all variables (**f-h, j**) except for minimum precipitation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

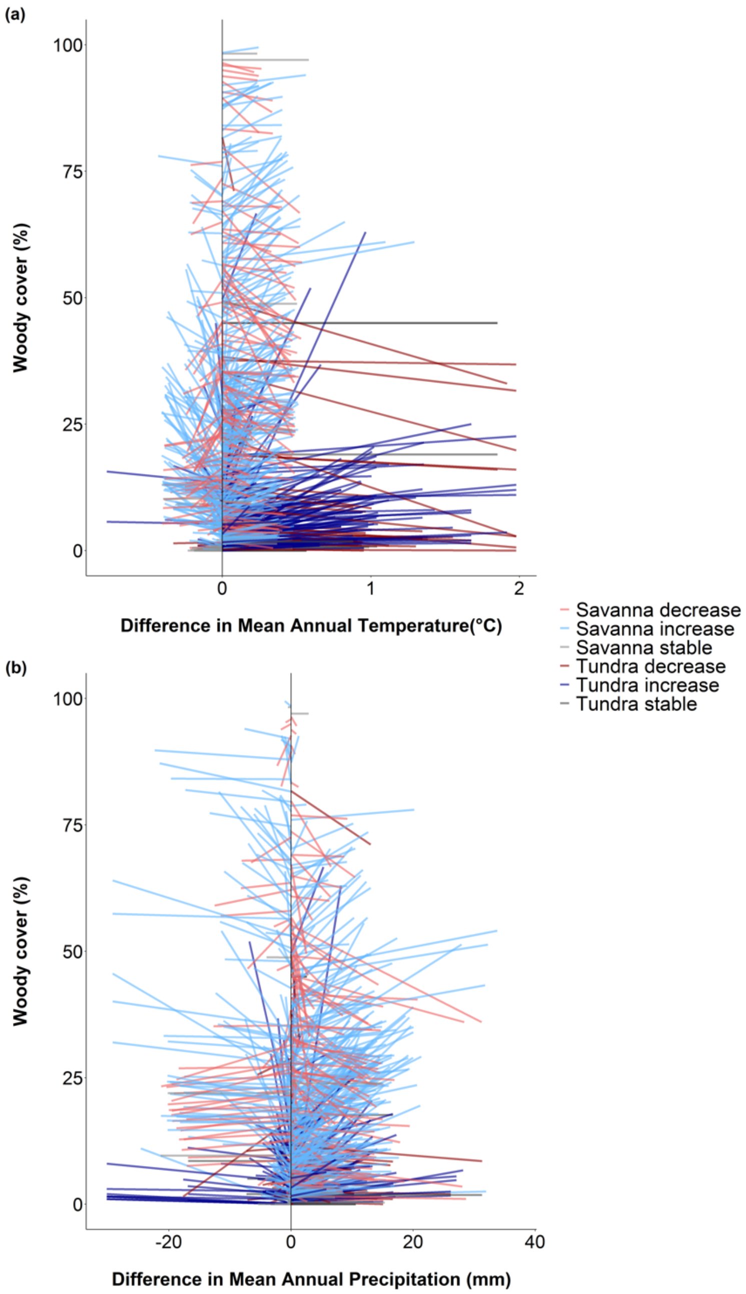

Figure 4. There was a positive relationship between total woody cover change magnitude and magnitude of MAP increases over time in the savanna but not in the tundra (Table S2.27-28). Cover change magnitude was not related to the magnitude of MAT increase in either biome (Table S2.25-26). Each line represents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

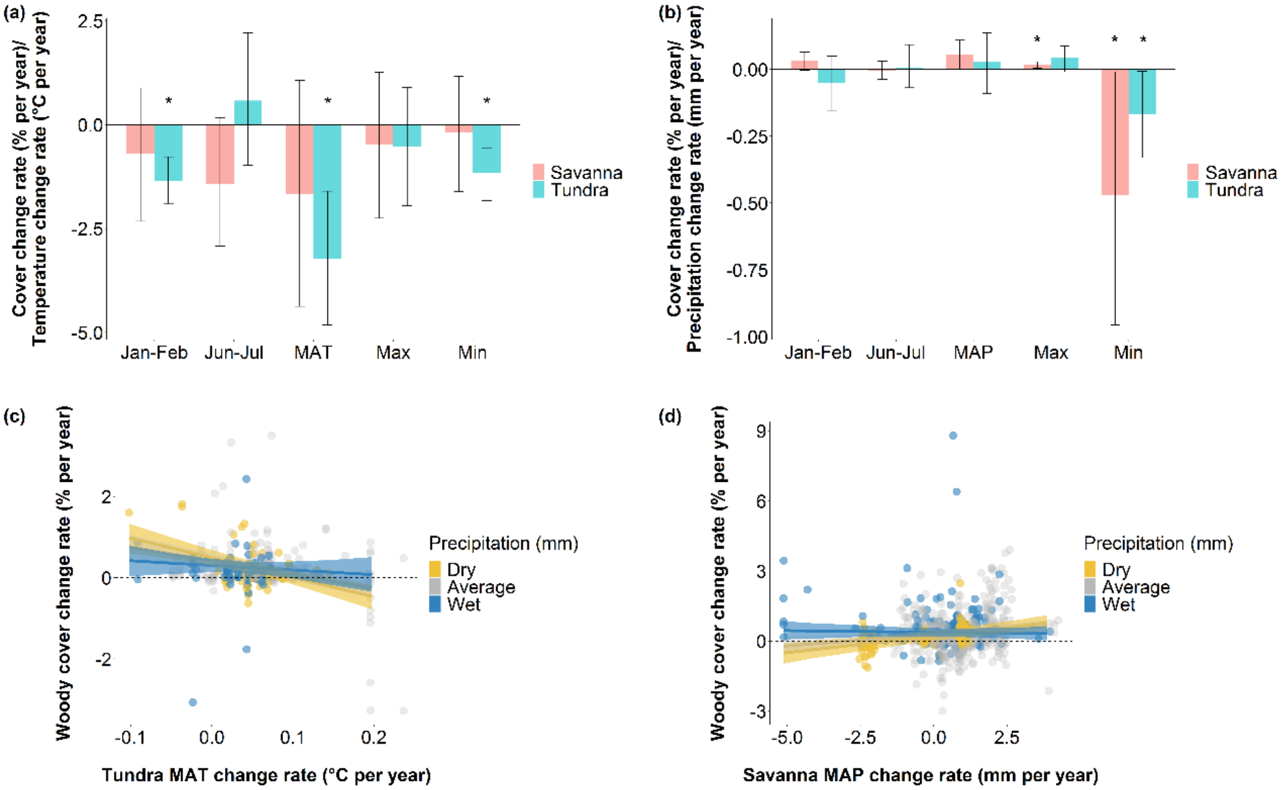

Figure 5. There were no positive linear relationships between woody cover change rates and rates of changing climate conditions in either the tundra or savanna biomes, except for maximum MAP in the savanna (Table S2.29-48). **a**) and **b**) slopes are Bayesian models of cover change rates per year as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

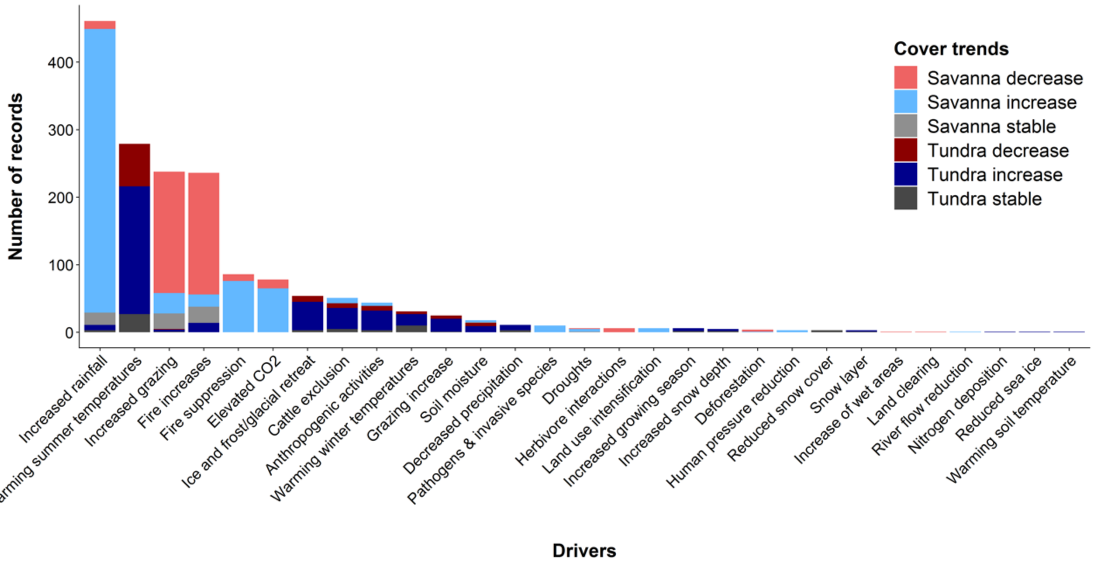

Figure 6. The most commonly reported drivers of increasing woody cover are warming summer temperatures in the tundra and increased rainfall in the savanna. The stacked bars show the total values per driver and are coloured by the biome and direction of the cover trend. The bars display all reported records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

Summary of numbered items in the supplementary material

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

Figure S2. Conceptual diagrams of main climatic analyses.

Figure S3. Timelines of woody cover change studies.

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

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

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

Figure S7. ‘Rate vs rate’ analyses in different record subsets.

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

Table S2. Results of all fitted Bayesian models.

Table S3. Results of all fitted Bayesian ‘rate vs rate’ models in different record subsets.