



# 1 What if extreme droughts occur more frequently? - Mechanisms and 2 limits of forest adaptation in pine monocultures and mixed forests in 3 Berlin-Brandenburg, Germany

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12 **Abstract.** Forests in Eastern Germany are already experiencing the detrimental effects of droughts, exemplified by the  
13 severe conditions of the 2018 drought year. With climate change, such extreme events are expected to become more frequent  
14 and severe. Previous work suggests that mixed forests exhibit greater resilience against droughts than monocultures. Our  
15 study aims to investigate the impact of increased frequency of extreme droughts, such as those seen in 2018, on biomass,  
16 structure and traits of forests in the Eastern German federal states of Berlin and Brandenburg.

17 Utilizing the flexible-trait Dynamic Global Vegetation Model LPJmL-FIT, we simulate the growth and competition of  
18 individual trees in both, pine monoculture forest and mixed forest. The trees belong to different plant functional types or in  
19 case of pine forest are parametrized as *Pinus sylvestris*. We create drought scenarios from high resolution climate input data  
20 by re-shuffling the contemporary climate with increased frequencies of the extreme drought year 2018. For each scenario, we  
21 simulated vegetation dynamics over 800 simulation years which allowed us to analyze shorter-term impacts, in the first  
22 decades of the drought scenarios, as well as the long-term adaptation of the two forest types to those new climate normals.  
23 We evaluated the resulting long-term changes in biomass, plant functional traits and forest structure to examine the new  
24 equilibrium state emerging for each scenario.

25 Our findings revealed nuanced responses to increased drought frequency. In pine monoculture forests, increased drought  
26 frequency reduced biomass and increased biomass variance, indicating higher system instability. Conversely, in mixed  
27 forests, biomass initially declined in scenarios with increased drought frequency but eventually recovered and even exceeded  
28 baseline levels after 100-150 years. We explain recovery and increase of biomass through two forest adaptation mechanisms;  
29 first, we saw a shift in the plant community towards broadleaved trees and second, plant traits shifted towards increased  
30 average wood density, decreased average tree height and increased average tree age. However, for the most extreme scenario  
31 with drought occurring each year, the adaptive capacity of the mixed forest was exceeded and the biomass halved compared  
32 to the baseline scenario. In our study, for the first time LPJmL-FIT is used with a resolution as high as 2 by 2 km<sup>2</sup>, which  
33 allows us to observe spatial heterogeneity drought impacts within the Berlin-Brandenburg area. Pine monocultures suffered,  
34 especially in the warmer urban areas and mixed forests in the central-west of Brandenburg, benefitted in the long term.



35 This study highlights the capacity of natural mixed forests in contrast to pine monocultures to adapt to increasing drought  
36 frequency up to a certain limit. The results underscore the importance of considering biodiversity in forest management  
37 strategies, especially with regard to more frequent dry periods under climate change.

## 38 1 Introduction

39 With temperatures rising at about twice the global average rate, Europe is the fastest warming continent (Copernicus 2023)  
40 and is exposed to more intense and frequent climate extremes (Pradhan et al., 2022; Treydte et al., 2024). Within Germany,  
41 Brandenburg is one of the driest regions (Dittmann et al., 2024), with a warming of 1.1°C over the last decades (LfU  
42 Brandenburg, 2022) and consequently increasing evaporation and decreasing groundwater recharge (LfU Brandenburg,  
43 2022). Increasing drought severity and frequency have been observed to damage forests in Brandenburg and to increase the  
44 severity of wildfires (Land Brandenburg, 2023; LfU Brandenburg, 2021).

45 Germany was heavily affected by two consecutive drought years in 2018-2019, where the annual precipitation amount was  
46 so low, that drought effects extended into 2020 (Büntgen et al., 2021). The extremely dry and hot growing season (March -  
47 November) in 2018 was record-breaking both in its high temperatures and low precipitation (Zscheischler and Fischer, 2020)  
48 and led to a record in burned forest area due to wildfires in Brandenburg (1664 ha burned area in Brandenburg,  
49 Landeskompetenzentrum Forst Eberswalde 2018). This compound event affected agricultural production requiring federal  
50 states to warrant aid payments of 340 million Euros to farmers with at least 30 percent of yield loss (Reinermann et al. 2019;  
51 Buras et al. 2020). During the consecutive drought years the fraction of trees with signs of damage increased from 53 % in  
52 2017 to 92% in 2022 (Land Brandenburg, 2023). In 2021, 26% of the forest area covered with pine in Brandenburg (Berlin:  
53 20%) showed significant damage in their tree crowns while the area affected in Brandenburg's beech and oak forest  
54 amounted to 40 and 42%, respectively (Bundesministerium für Ernährung und Landwirtschaft, 2021).

55 Since medieval times, natural forests have been cleared for agriculture, pastures, with natural or semi-natural forests left in  
56 only a few small regions in Europe (Barredo et al., 2021; Bengtsson et al., 2000; Lamentowicz et al., 2020). In Europe,  
57 systematic forest management roots back into the 19th century (Niedertscheider et al., 2014). Today, most European forests  
58 are highly managed, they are often planted single-species monocultures to provide people with timber from high productive  
59 forests. In Brandenburg, pine trees make up 70.1 % of the forest area, followed by oak and beech with only 6.7 % and 3.3 %,  
60 respectively (Land Brandenburg, 2023). To act against increasing forest losses from climate extremes and to support forest  
61 adaptation to a changing climate, increasing biodiversity has been suggested as one solution. According to the biological  
62 insurance hypothesis, ecosystems with high biodiversity can better maintain ecosystem functioning under external pressure.  
63 In addition, diverse forests can hold a larger portfolio of plant strategies that can help them to adapt to the new  
64 environmental conditions. Monocultural ecosystems, however, lack the required response diversity to maintain ecosystem  
65 functioning under changing environmental conditions (Mori et al., 2013; Yachi and Loreau, 1999).

66 Changing climate conditions can lead to environmental filtering and thus to a shift in the spatial domain where species can  
67 occur and be productive. Respective shifts in species' spatial distribution are among the most significant and most widely  
68 discussed ways of how forests in the northern hemisphere react/adapt to climate change (Astigarraga et al., 2024; Fei et al.,  
69 2017; Lenoir and Svenning, 2015; Parmesan and Yohe, 2003; Rabasa et al., 2013; Rubenstein et al., 2020, 2023). Due to the  
70 increase in water deficit and temperature, range shifts upward and poleward are expected by ecological theory (Bonebrake et  
71 al., 2018; Lenoir and Svenning, 2015). While there are observations of species for which these expected shifts happen (Chen  
72 et al., 2011; Lenoir and Svenning, 2015; Parmesan and Yohe, 2003), many species show multiple directions in response to  
73 climate change (Fei et al., 2017; Rabasa et al., 2013; Rubenstein et al., 2023; Zhu et al., 2014). In addition to a range shift in  
74 species, changes can also occur in stocks that persist at a specific location, particularly with regard to productivity. However,



75 the effects of climate change on European forests remain unclear (Pretzsch et al., 2023). While generally there is a trend  
76 toward more productivity temperate European forests (Charru et al., 2017; Pretzsch et al., 2014, 2023; Zhu et al., 2014),  
77 increasing drought events interrupt this trend (Martinez del Castillo et al., 2022; Piovesan et al., 2008; Schmied et al., 2023;  
78 Schuldt et al., 2020; Williams et al., 2013). Due to contrasting trends within regions (Galván et al., 2014; Pretzsch et al.,  
79 2023) and among species (Martinez del Castillo et al., 2022; Pretzsch et al., 2014, 2020, 2023), understanding of long-term  
80 shifts is still lacking.

81 Building on the knowledge that more diverse forest ecosystems could be more resilient, recent forestry programmes in  
82 Germany for example aim at increasing deciduous tree cover to adapt forests to future climate change conditions (Land  
83 Brandenburg, 2011; Wessely et al., 2024). It is supported by future projections of decadal, average changes in forest  
84 dynamics and tree species distribution (e.g., Wessely et al. 2024) and how it affects forests to provide ecosystem services in  
85 Germany (Gregor et al., 2022; Gutsch et al., 2018). Recent model applications studied the importance of functional diversity  
86 for future forest adaptation (Billing et al. 2022, 2024). However, we still have a limited understanding on the mechanisms  
87 and limits of diverse forests to adapt to an increasing frequency of climate extremes as the new climate normals.

88 In addition to biodiversity and species identity, it is also useful to consider structural and functional plant traits that  
89 determine the reactions to environmental factors and their changes but can also influence the functioning of ecosystems  
90 (Sterk et al., 2013; Suding et al., 2008). Wood density and specific leaf area might strongly impact species' responses to  
91 climate change. Some studies suggest that higher wood density correlates with drier and warmer climate (Nabais et al. 2018;  
92 S.-B. Zhang et al. 2011; Swenson and Enquist 2007; Nelson et al. 2020, Bouchard et al. 2024). Most notably, in a recent  
93 global tree inventory analysis for temperate forests Bouchard et al. (2024) found higher wood density with decreasing  
94 rainfall (below values of 1000 mm/a, which would also apply to climate conditions in Brandenburg). Fei et al. (2017)  
95 observed that in the Eastern part of the United States of America tree species that shifted to drier areas had higher median  
96 wood density. A global meta-analysis of tree mortality in response to drought found that in addition to wood density also  
97 specific leaf area (SLA) explain drought responses, where trees having a lower SLA showed lower mortality responses  
98 (Greenwood et al., 2017). Also experimental results show that individuals of different tree species from the Mediterranean  
99 area growing under drought stress had a decreased SLA in comparison to individuals of the same species growing in the  
100 control (Valladares and Sánchez-Gómez, 2006), showing that this might be a potential adaptation mechanism.

101 Because forests develop and change on decadal time scales, respective assessments of climate-extreme impacts on  
102 biodiversity-ecosystem function relationships are difficult to conduct in a field experiment. Instead, biodiversity-enhanced,  
103 process-based vegetation modeling can be applied to project and explain how climate extremes affect functional trait  
104 composition and ecosystem function in diverse forests and compare them against the performance of monoculture forests.  
105 However, climate models most likely underestimate the frequency of hot dry compound events like the 2018 drought  
106 (Zscheischler and Fischer 2020; van der Wiel et al. 2021) that were much more rare in the past. As a result, vegetation  
107 models using these data cannot accurately simulate the impact of increased drought frequency. To overcome this problem,  
108 we take a simplistic approach of designing climate scenarios with artificially increased drought frequency for the area of  
109 Berlin and Brandenburg in Germany. We use these artificial drought scenarios as input data for the flexible-individual trait  
110 Dynamic Global Vegetation Model LPJmL-FIT (Sakschewski et al. 2015, Thonicke et al. 2020) that simulates functional  
111 and structural trait changes in conjunction with ecosystem functions under varying climate and soil conditions. We then  
112 analyze how in Brandenburg and Berlin temperate mixed forests and pine monoculture forest (parameterizing *Pinus*  
113 *sylvestris* trees) perform and adapt to changing frequency of climate extremes. However, in both forest types, forest  
114 management is not considered, which means that the pine monoculture forest can be regarded as a semi-natural forest.  
115 Additionally, we assume that the entire study area is covered by forest to take advantage of the high-resolution climate data  
116 and include urban forest areas. In this context, this study aims to answer the following questions:



117 1) Does a diverse natural forest have a higher resilience against an increased frequency of extreme drought years such as  
118 2018 than a pine monoculture forest?

119 2) What are the underlying mechanisms that enable forests in Brandenburg to adapt to the increased frequency of extreme  
120 droughts? In particular, how do these mechanisms manifest in the shifts in tree community composition, and changes in the  
121 traits spectrum within individual plant functional types?

122 3) Is there spatial variability in the response of the two forest types towards droughts across Berlin and Brandenburg?

123 We first describe how biomass of the pine monoculture vs. temperate mixed forest is changing under the different drought  
124 extreme scenarios, before we analyze how structural and functional traits explain the underlying mechanisms and how these  
125 mechanisms differ between PFTs.

## 126 2 Methods

127 We created artificial climate data sets with increased drought frequencies using high-resolution climate data compiled for the  
128 study area Berlin-Brandenburg as the baseline (Bart et al., under review). Our new drought scenarios contain weather data  
129 from 1980-2022, to which we have added the drought year 2018 with varying frequency. We investigated the impact that  
130 these scenarios might have on pine monocultures which currently dominate managed forests in the study area and on mixed  
131 forest as its natural analogue. We applied the flexible individual traits Dynamic Global Vegetation Model LPJmL-FIT to two  
132 plant community configurations, i) a pine monoculture forest and ii) a mixed forest and calculated resulting forest  
133 development for a baseline scenario (the original climate data set) and to our new drought scenarios (see below). We  
134 simulate the study area to be fully covered by vegetation, neglecting land used for settlements and agriculture. Forest  
135 management, such as thinning or logging, was not simulated in any of the configurations. We then analyzed changes in  
136 vegetation dynamics and in plant characteristics at the centennial time scale to analyze the short- and long-term ability of  
137 forests to adapt to an increased frequency of extreme droughts.

### 138 2.1 Model description: The flexible-trait DGVM LPJmL-FIT

139 The dynamic flexible-trait vegetation model LPJmL-FIT ('Lund-Potsdam-Jena managed Land – Flexible Individual Traits')  
140 is a process-based Dynamic Global Vegetation Model (DGVM). It simulates the establishment, growth, competition and  
141 mortality of individual trees using a forest gap approach. Tree individuals can differ in their functional traits according to the  
142 leaf and stem economics spectrum (Sakschewski et al., 2015; Thonicke et al., 2020). The spatial resolution of model  
143 simulations depend on the resolution of the input data. For each grid cell, the model requires soil texture as well as daily  
144 climate input data (temperature, precipitation, and radiation) and atmospheric CO<sub>2</sub> concentration to calculate soil hydrology  
145 and vegetation dynamics. Grid cells are further subdivided into independent forest patches of 10 m by 10 m on which tree  
146 individuals compete for water and light. The present study uses the model version as described in Thonicke et al. (2020) and  
147 Billing et al. (2024) and has been extensively validated. In addition, we adopted the variable rooting scheme described in  
148 Sakschewski et al. (2020) to allow for diverse tree rooting strategies and excluded grass PFTs from our simulations.

149 Tree individuals are typically categorized into broad Plant Functional Types (PFTs) representing main ecological  
150 characteristics of natural vegetation at the biome level as in the standard model LPJmL (Schaphoff et al. 2018). However, the  
151 model can also be parameterized for specific species. In LPJmL-FIT newly established tree individuals are randomly  
152 assigned to PFTs, if there is more than one PFT simulated at the same time. Key functional traits, such as specific leaf area  
153 (SLA) and wood density (WD), are then randomly sampled out of the PFT- or species-specific ranges and remain constant



154 over a tree’s life. Other functional traits (e.g. leaf nitrogen content) are connected to SLA and WD via trade-offs according to  
 155 the plant economics spectrum. Trees compete for light and water in independent 10 m by 10 m forest patches. Their crown  
 156 area and leaf area index control their capacity to absorb photosynthetic active radiation. Water uptake depends on root depth  
 157 and soil moisture availability. The amount of absorbed photosynthetic active radiation, soil water uptake and other  
 158 environmental factors such as temperature and atmospheric CO<sub>2</sub> concentration determine the gross primary production  
 159 (GPP) via the process of photosynthesis. Autotrophic respiration is divided into maintenance and growth respiration, both of  
 160 which are temperature-dependent and linked to the tree’s biomass and GPP. Carbon that is lost through autotrophic  
 161 respiration is subtracted from GPP, resulting in net primary productivity (NPP), which represents the carbon available for  
 162 new growth. The allocation of NPP to various parts of each individual tree—roots, stems and leaves—is modeled based on  
 163 the specific strategies of each PFT to optimize resource use in different environmental conditions (Schaphoff et al., 2018).  
 164 Over time, performance and competition determine tree survival and growth. Via these processes, climate, soil properties  
 165 and competition conditions filter locally best adapted (environmental filtering) and best performing (competitive filtering)  
 166 tree individuals. That is, LPJmL-FIT can simulate functionally diverse forests but also monocultures that would grow under  
 167 the sole influence of climate and soil conditions. An illustrative video of forest community assembly is available in Billing et  
 168 al. (2024), Video 1, and can be found under the following link: [https://www.pik-](https://www.pik-potsdam.de/~billing/video/2023/spinup_LPJmLFIT.mp4)  
 169 [potsdam.de/~billing/video/2023/spinup\\_LPJmLFIT.mp4](https://www.pik-potsdam.de/~billing/video/2023/spinup_LPJmLFIT.mp4). In this animation, each tree is colored according to its SLA or WD  
 170 value assigned at establishment.

## 171 2.2 Data and simulation experiments

172 In our simulations the area of Brandenburg and Berlin was represented by a grid of 7073 cells with ~2 x 2 km resolution. For  
 173 each grid cell, 80 patches of 10 m x 10 m patch size were simulated, representing the forest of the total grid cell. We run the  
 174 model with climate data derived from the Central Europe Refined analysis version 2 (CER v2) (Bart et al., under review).  
 175 This dataset was generated by dynamical downscaling of ERA5 reanalysis forcing data provided by the European Centre for  
 176 Medium-Range Weather Forecasts (ECMWF) for the area of Berlin and Brandenburg, utilizing the Weather Research and  
 177 Forecasting (WRF) model version 4.3.3. The climate data covers the period from 1980 to 2022 with daily temporal  
 178 resolution and 2 x 2 km spatial resolution. We first created a climate set for a 1000-year model spin up, randomly drawing  
 179 from the climate input years 1980-2022. To assess the effects of droughts, we afterwards manipulated the original climate  
 180 dataset by artificially adding the drought year 2018 to the data in increasing frequencies. For a slightly wetter scenario  
 181 (Scenario A), we only used data from 1980-2001 (i.e. frequency of drought year 2018 = 0), and for the baseline scenario  
 182 (Scenario B, frequency = 0.02), we used the original full dataset from 1980-2022 without any manipulation. Five additional  
 183 scenarios contained the years 2001-2022 plus the drought year 2018 at varying frequencies (Scenario C: 0.05 to Scenario G:  
 184 0.68). For the last scenario we only took data from the year 2018 (Scenario H: 1.0). Increasing the frequency of the 2018  
 185 drought year also changed the mean climate. To quantify the drought effect, we calculated the mean annual Maximum  
 186 Climatic Water Deficit (MCWD) following (Sakschewski et al., 2021). The absolute values and their deviation from the  
 187 baseline climate as well as the frequency the year 2018 for each scenario are shown in Table 1. To create the full weather  
 188 data sets to run the model for different drought scenarios (Scenarios A-H), we randomly draw 800 years from the respective  
 189 manipulated climate dataset (Figure 1).

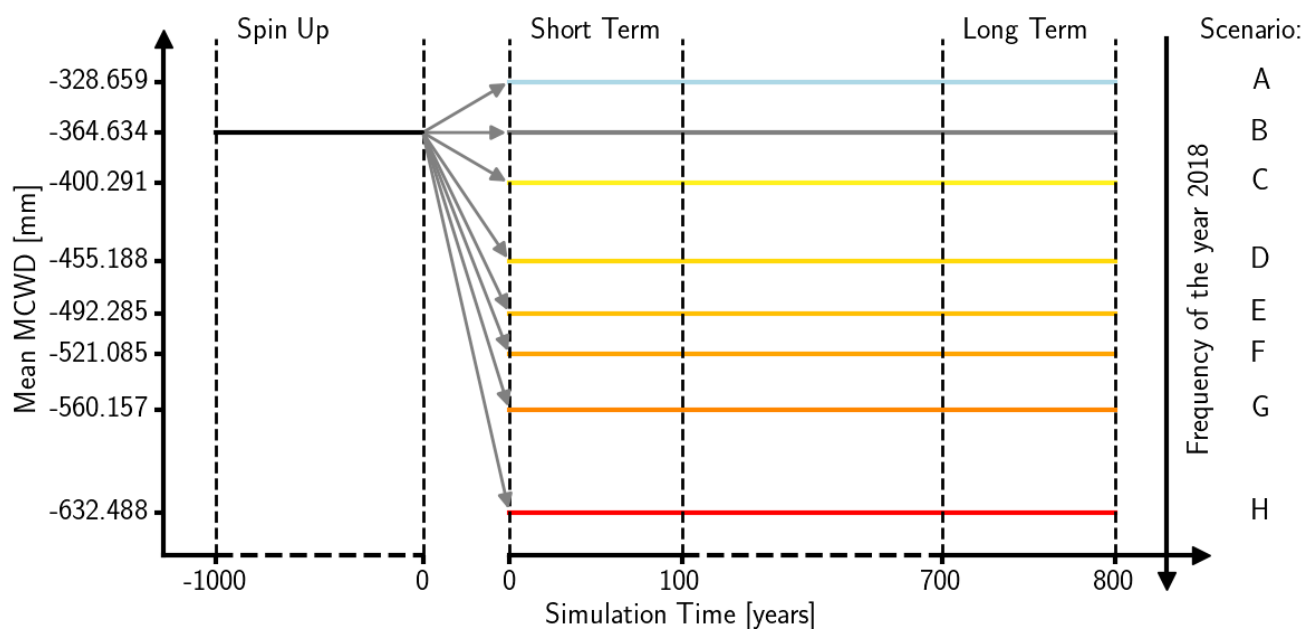
190 **Table 1:** Characteristics of drought scenarios. Frequency of the year 2018 in manipulated data and resulting mean  
 191 maximum climatic water deficit (MCWD) and mean temperature (T) and deviation from baseline (Scenario B) for each of  
 192 the scenarios.

Scenario	Frequency of Year 2018 [year <sup>-1</sup> ]	MCWD [mm]	Δ MCWD [mm]	T [Celsius]	ΔT [Celsius]
A: 1980-2001	0	-328.7	36.0	8.9	-0.42



<b>B: 1980-2022 (Baseline)</b>	0.02	-364.6	0	9.31	0
<b>C: 2001-2022</b>	0.05	-400.3	-35.7	9.71	0.4
<b>D: 2001-2022+7x2018</b>	0.28	-455.2	-90.6	9.94	0.63
<b>E: 2001-2022+14x2018</b>	0.42	-492.3	-127.7	10.08	0.77
<b>F: 2001-2022+22x2018</b>	0.52	-521.1	-156.5	10.19	0.88
<b>G: 2001-2022+44x2018</b>	0.68	-560.2	-195.5	10.35	1.04
<b>H: 2018 only</b>	1	-632.5	-267.9	10.67	1.36

193



194

195 **Figure 1:** Scheme of the simulation protocol. After 1000 years of spin up with shuffled Central Europe Refined analysis  
 196 version 2 (CER v2) data from 1980 - 2022, 800 years of Scenarios A-H with decreasing mean Maximum Water Deficit  
 197 (MCWD) and increasing frequency of the year 2018 follow. The frequency of the year 2018 was increased by adding an  
 198 increasing number of the year 2018 to the pool from which each year was drawn (see Table 1 for details).

199 Soil depth data was sourced from Pelletier et al. (2016) and subsequently re-gridded from an original resolution of about 1  
 200 km to match the climate-data grid resolution. Soil type information was obtained from the Harmonized World Soil Database  
 201 (HWSD) (FAO and IIASA, 2023) and aggregated to match the grid cell resolution using the LandInG package (Ostberg et  
 202 al., 2023).



203 We ran the model for two forest configurations, a monoculture including only trees of *Pinus sylvestris* (pine monoculture,  
204 hereafter) and a diverse temperate mixed forest (mixed forest, hereafter). The temperate mixed forest included four major  
205 PFTs; temperate broad-leaved summergreen (T-BL), temperate needle-leaved evergreen (T-NL), boreal needle-leaved  
206 evergreen (B-NL), and boreal broad-leaved summergreen (B-BL). In the mixed forest configuration, any PFT can be  
207 established in any forest patch at any time, following the approach used in Thonicke et al. (2020), with the establishment rate  
208 of new trees depending on light availability on the forest floor. As described above, their key functional traits are randomly  
209 sampled out of the PFT-specific ranges. These are obtained from the TRY database (Kattge et al., 2011) as described by  
210 Sakschewski et al. (2015). For the pine monoculture, only pine trees can be established, which were parameterized using the  
211 boreal needle-leaved PFT and restricting the ranges for SLA and WD to the 25th and 75th percentile of their respective  
212 distributions in the TRY database (Kattge et al., 2011) for *Pinus sylvestris*. SLA and WD ranges of all PFTs and *Pinus*  
213 *sylvestris* are provided in Appendix A, Table A1. Other important differences between the tree types are their temperature  
214 limits for establishment which reflects chilling requirements and frost tolerance as well as their optimum temperature range  
215 for photosynthesis (see Appendix A, Table A2).

216 The model spin up started with the establishment of saplings on bare ground (illustrated in Billing et al. 2024, Video 1) and  
217 was run for 1000 years of simulation for each forest configuration with the spin up climate dataset. Afterwards, we ran the  
218 model for 800 years with the different drought scenarios for each forest configuration (Figure 1).

### 219 **2.3 Evaluation of simulation outcomes**

220 We evaluated the overall resilience of both pine monoculture and mixed forests against an increased frequency of extreme  
221 droughts by calculating the mean for the above- and belowground biomass ( $\text{kgC/m}^2$ ) across the entire study area for each  
222 year. We compared the short-term (years 1 - 100) and the equilibrium (long-term, years 701-800) biomass of each scenario  
223 with the baseline scenario (Scenario B). Then we analyzed different adaptation mechanisms to increased drought frequencies  
224 by calculating the mean above - and belowground biomass [ $\text{kgC/m}^2$ ], the mean number of trees per  $\text{m}^2$  (tree density), the  
225 mean tree height [m], the mean tree wood density [ $\text{kg/m}^3$ ] and the mean tree age [years] over the e study region for the last  
226 hundred years of the simulation for each scenario and forest configuration. We further investigated how these mechanisms  
227 manifested in the mixed forest including changes in the tree community composition and changes in traits for all tree  
228 individuals belonging to a particular PFT. For this, we calculate the mean tree height [m], tree wood density [ $\text{kg/m}^3$ ], tree age  
229 [years], SLA [ $\text{m}^2/\text{g}$ ], mortality [probability/year] and mean growth speed [years] for each PFT during the last 100 simulation  
230 years of each experiment. The growth speed of an individual tree was defined as the time to reach a height of 15 meters.  
231 Trees that did not reach this size were not evaluated. For the calculation of the means for tree density, height, wood density,  
232 SLA, mortality and age, trees were weighted with their biomass and trees smaller than 5 m height were excluded to prevent  
233 an evaluation bias towards the multiple small trees.

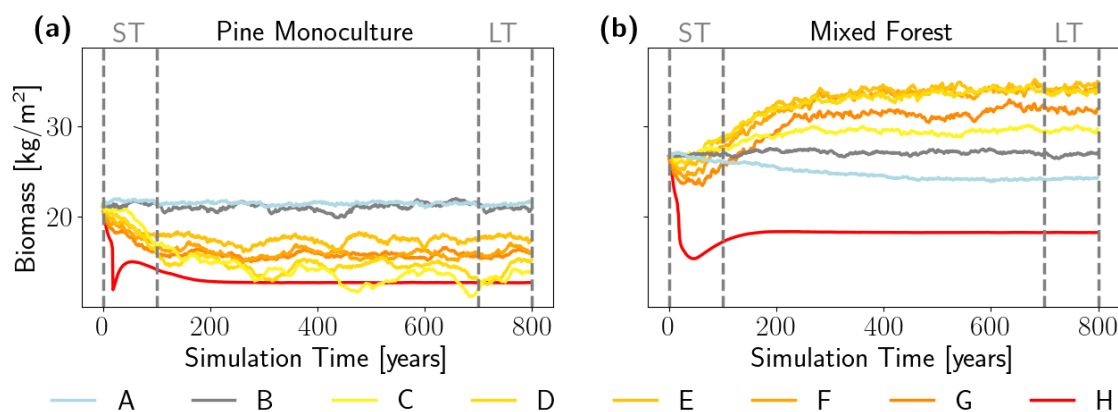
234 To assess spatial heterogeneity in forest responses, we computed the long-term (i.e. mean over the last 100 simulation years)  
235 impact of our drought scenarios on the spatial biomass variation of the pine monoculture and the mixed forest configuration  
236 across Berlin and Brandenburg.

### 237 **3 Results**

238 The overall resilience in the pine monoculture and mixed forests against a higher frequency of droughts was assessed by  
239 calculating mean biomass over the entire simulation domain, assuming the Berlin-Brandenburg area is covered by vegetation  
240 only, for each simulated year and scenario (Fig. 2). While the wet scenario (Scenario A, without the 2018 drought year) and  
241 the baseline scenario B show stable biomass in the pine monoculture forest over the entire simulation period, all drought



242 scenarios lead to biomass loss and biomass remains lower than under the Scenarios A and B (Fig. 2a). In the mixed forest,  
 243 biomass increased again after an initial phase of biomass decline of 50-150 years (Fig. 2b). Exceptions are the wet Scenario  
 244 A and the most extreme climate Scenario H, where biomass declines and remains at a lower level (Fig. 2b). After an initial  
 245 phase of decrease in biomass in both forest configurations, the biomass stabilized under all drought scenarios, fluctuating  
 246 around a new stable state.



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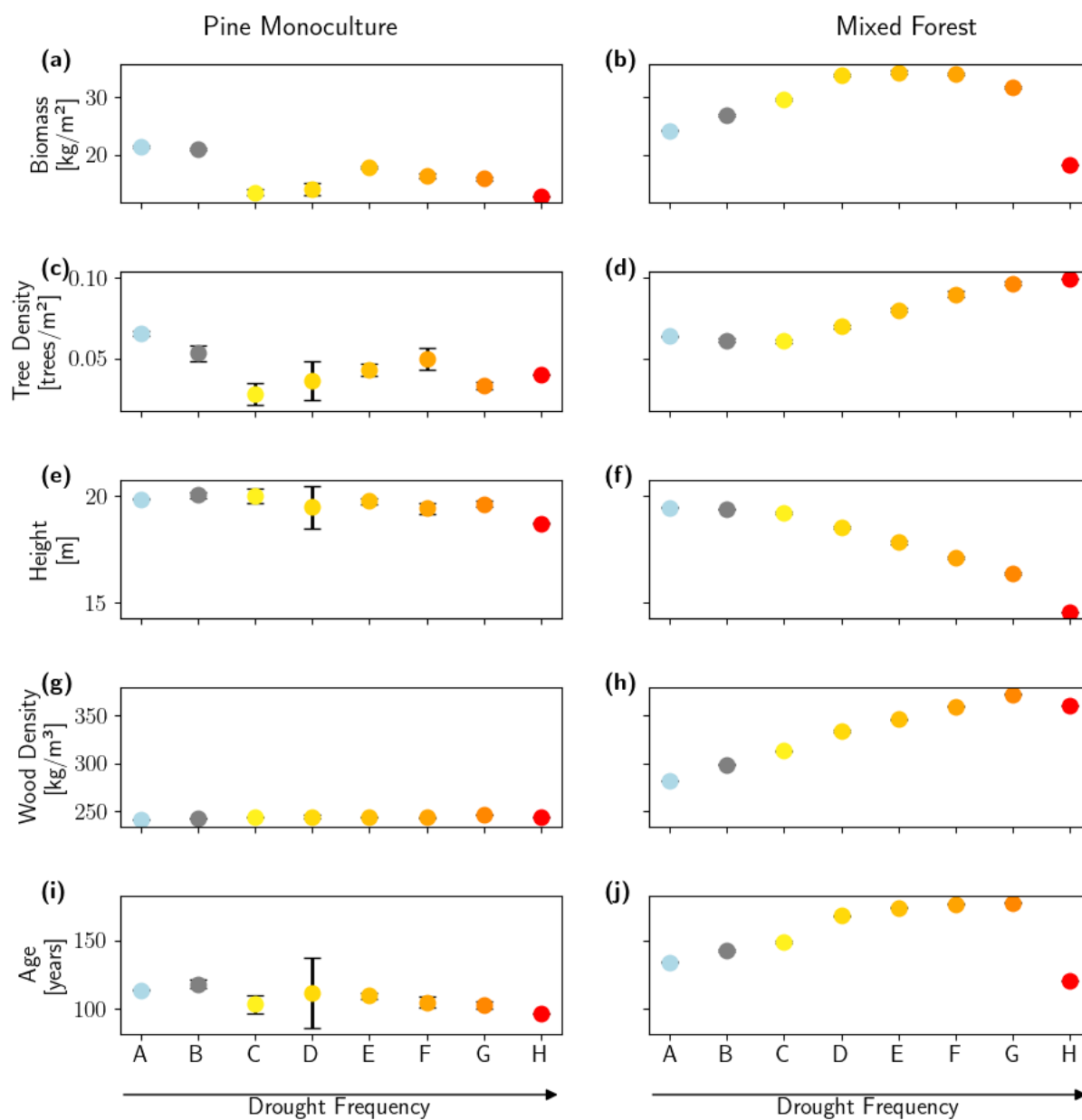
248 **Figure 2:** Living biomass in pine monoculture forest (*Pinus sylvestris*, panel (a)) and mixed forest (b) simulated by the  
 249 LPJmL-FIT DGVM and averaged over Berlin-Brandenburg study area. Living biomass includes above- and belowground  
 250 biomass [ $\text{kgC}/\text{m}^2$ ] and was averaged over all patches and grid cells for each year for each drought scenario (Scenarios A-H,  
 251 see Table 1 for details about the scenarios). Dashed vertical lines mark the limits of the short-term (ST), i.e. the first 100  
 252 simulation years, and the long-term (LT), i.e. the last 100 simulation years. The wetter-than-the-baseline Scenario A and the  
 253 baseline Scenario B are shown in blue and grey lines, respectively. The color values of the other points range from yellow to  
 254 red illustrating the increasing frequency of extreme drought years.

255

256 In the pine monoculture, the amplitude of these fluctuations varied significantly across the different scenarios, and on  
 257 average, these fluctuations were much larger than those observed in mixed forests. The standard deviation of the biomass  
 258 time series over the last 100 simulated years was, on average, twice as high in the monoculture ( $0.37 \text{ kg}/\text{m}^2$ ) compared to the  
 259 mixed forest ( $0.18 \text{ kg}/\text{m}^2$ ), reflecting a stronger response to individual drought years (Fig. 2a).

260 Both the decrease in biomass for pine monoculture forests and the increase in long-term biomass for mixed forests were non-  
 261 linear and non-monotonic, i.e., the variations in biomass levels did not linearly or monotonically correspond to the  
 262 differences in drought frequencies or MCWDs among the scenarios (compare to Table 1). The lower drought frequency in  
 263 Scenarios C and D resulted in a stronger decrease in biomass compared to the higher drought frequency in Scenarios E, F, G  
 264 in the pine monoculture (see Fig. 2a). In the mixed forests, the Scenarios D, E, F have a stronger increase despite a lower  
 265 drought frequency than for G and H (see Fig. 2b). Under Scenarios D, E and F, the drought-frequency ranged between 0.28  
 266 and 0.53 that resulted in MCWD values of  $-455$ ,  $-492$  and  $-521$  mm, respectively (Table 1). Surprisingly, despite the large  
 267 differences in drought frequency and MCWD, the resulting biomass levels were very close under all three scenarios (Fig.  
 268 2b).



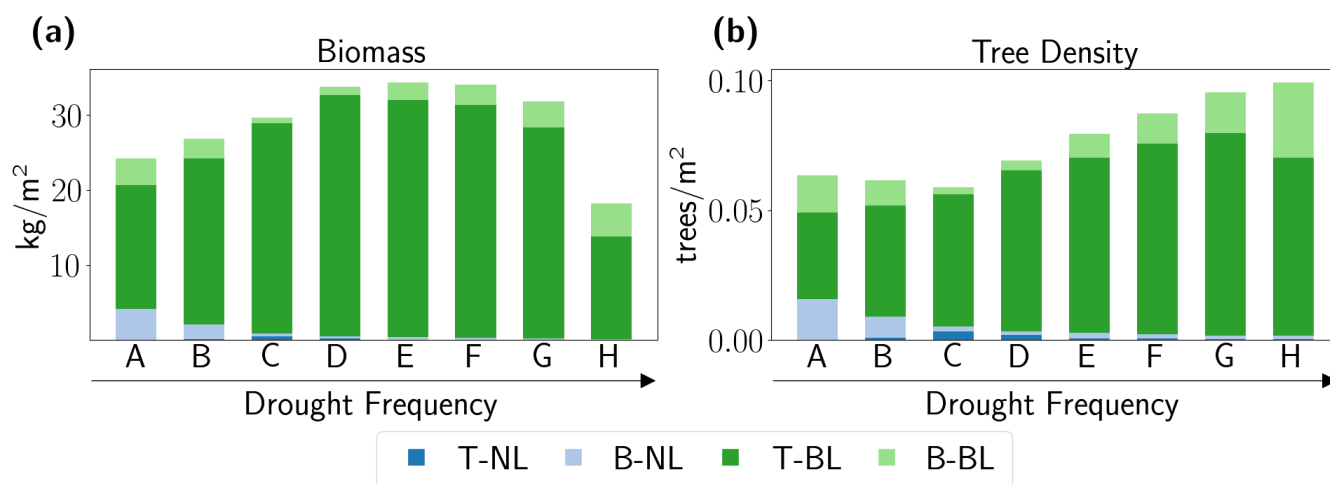


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270 **Figure 3:** Long-term impact of drought frequency on selected forest characteristics under Scenarios A-H as simulated by  
 271 LPJmL-FIT for the pine monoculture forest (left panels a, c, e, g and i) and the mixed forest (right panels b, d, f, h and j)  
 272 averaged over the Berlin-Brandenburg study area. Biomass (panel (a) and (b)), Tree Density ((c) and (d)), Height ((e) and  
 273 (f)), Wood Density ((g) and (h)) and Age ((i) and (j)) are displayed as means over the last simulated 100 years (simulation  
 274 years 701-800).



275 The long-term responses of monocultures and mixed forests to increased drought frequency differed both, at the community  
 276 level and at the level of individual trees (Figure 3). At the community level, monoculture vs. mixed forests showed opposing  
 277 responses towards increased drought frequency. In the pine monoculture forest, long-term biomass (Fig. 3a) and number of  
 278 trees (Fig. 3c) were lower in Scenarios A and B compared to all the drier scenarios (Scenarios C-H). The mixed forest  
 279 showed a different pattern. Here, biomass (Fig. 3b) and tree density (Fig. 3d) were higher at the end of the simulation period  
 280 the higher the drought frequency became. However, under the extreme Scenario H biomass was lower than Scenario A and  
 281 B, while the number of trees was highest (Fig. 3b and d). While height and wood density showed little variation or no trend  
 282 across the scenarios for the pine trees growing in monoculture forest (Fig. 3 e and g), increasing drought frequency in the  
 283 mixed forest led to decreasing tree height (Fig. 3f) and increased wood density (except under Scenario H, see Fig. 3h). Mean  
 284 forest age was lower under Scenarios C-H in the pine monoculture forest compared to Scenarios A and B and showed little  
 285 variation (Fig. 3i). On the contrary, trees in the mixed forest grew older the higher the drought frequency became, again with  
 286 the exception of Scenario H where average tree age was approx. 50 years lower (Fig. 3j). In general, there was much less  
 287 adaptation in individual tree properties and total stand properties in the monocultures compared to the mixed forests. In  
 288 mixed forests, trees got smaller, had a higher wood density and grew older with increasing drought frequency while the  
 289 monocultures did not show clear trends in the properties of individual trees. It seems that tree demography effects in  
 290 conjunction with trait adaptation at the individual level dominate forest adaptation that resulted in the hump-shaped biomass  
 291 pattern (Fig. 3b).



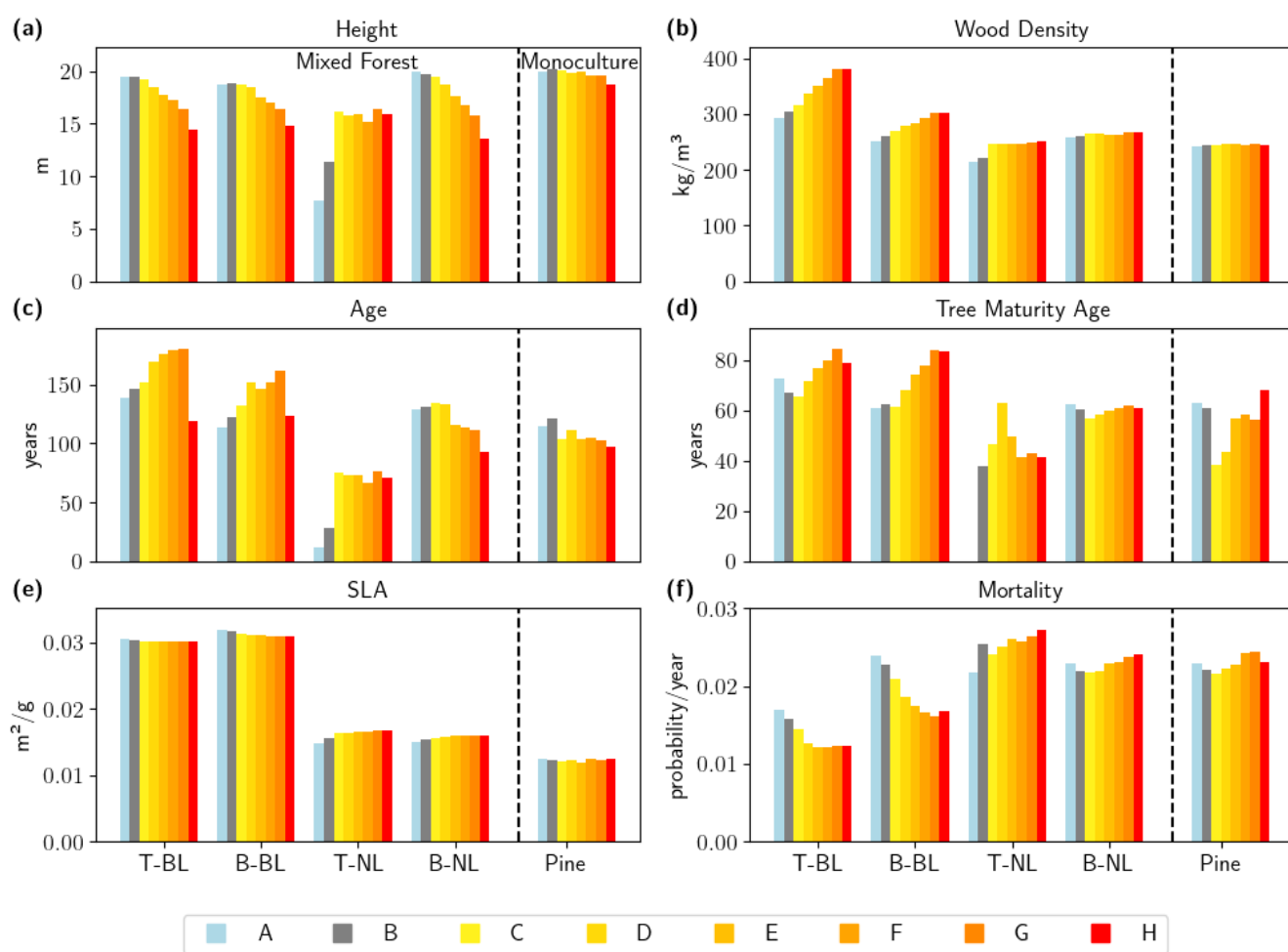
292

293 **Figure 4:** Composition of the plant community in the mixed forests averaged over the Berlin-Brandenburg simulation  
 294 domain and the last 100 simulation years (701-800). Biomass [kg/m<sup>2</sup>] (a) and Tree Density [trees/m<sup>2</sup>] (b) of tree individuals  
 295 belonging to temperate needle-leaved evergreen PFT (T-NL, dark blue), boreal needle-leaved evergreen PFT (B-NL, light  
 296 blue), temperate broadleaved summergreen PFT (T-BL, dark green) and boreal broad-leaved summergreen PFT (B-BL,  
 297 light green) for each drought frequency scenario.

298 In addition to changes in biomass and tree density in the mixed forests (as seen in Fig. 3), also their functional composition  
 299 shifted in response to increasing drought frequency (Fig. 4). The higher the drought frequency, the lower the proportion of  
 300 needle-leaved trees belonging to the T-NL and B-NL PFTs was. Even though needle-leaved trees could still adapt under  
 301 Scenarios D and E, their contribution to the overall biomass was marginal in the equilibrium state. Generally, broadleaved  
 302 trees dominated the forest community with their biomass being 12 times as high as needle-leaved trees and their tree density  
 303 became six times as high as in the baseline Scenario B. While the biomass and tree number of needle-leaved trees further



304 declined with increasing drought frequency, the number of broadleaved trees increased, as well as their total biomass until  
 305 drought frequency was too high (Scenarios F-H). That is, the patterns observed in Figure 3 can be mainly attributed to the  
 306 increasing dominance of broadleaved trees. In particular, the temperate broadleaved tree is the dominant PFT in all  
 307 scenarios, with its highest fraction in intermediate drought scenarios (Scenarios C-E) and its lowest fraction in the wettest  
 308 scenario. In contrast, the fraction of the boreal broadleaved PFT is highest in wettest and driest scenarios, and the boreal  
 309 needle-leaved PFT plays only a minor role in the composition, with its highest fraction in Scenario C. Interestingly, the tree  
 310 density of boreal broadleaved trees (B-BL) is small under scenarios A and B, is the lowest under Scenario C, and is  
 311 increasingly higher under scenarios D-H (Fig. 4b), but does not contribute to biomass at the same proportion (Fig. 4a). Given  
 312 those patterns found, it seems that the tree individuals in each PFTs adapt differently to the new climate normals.



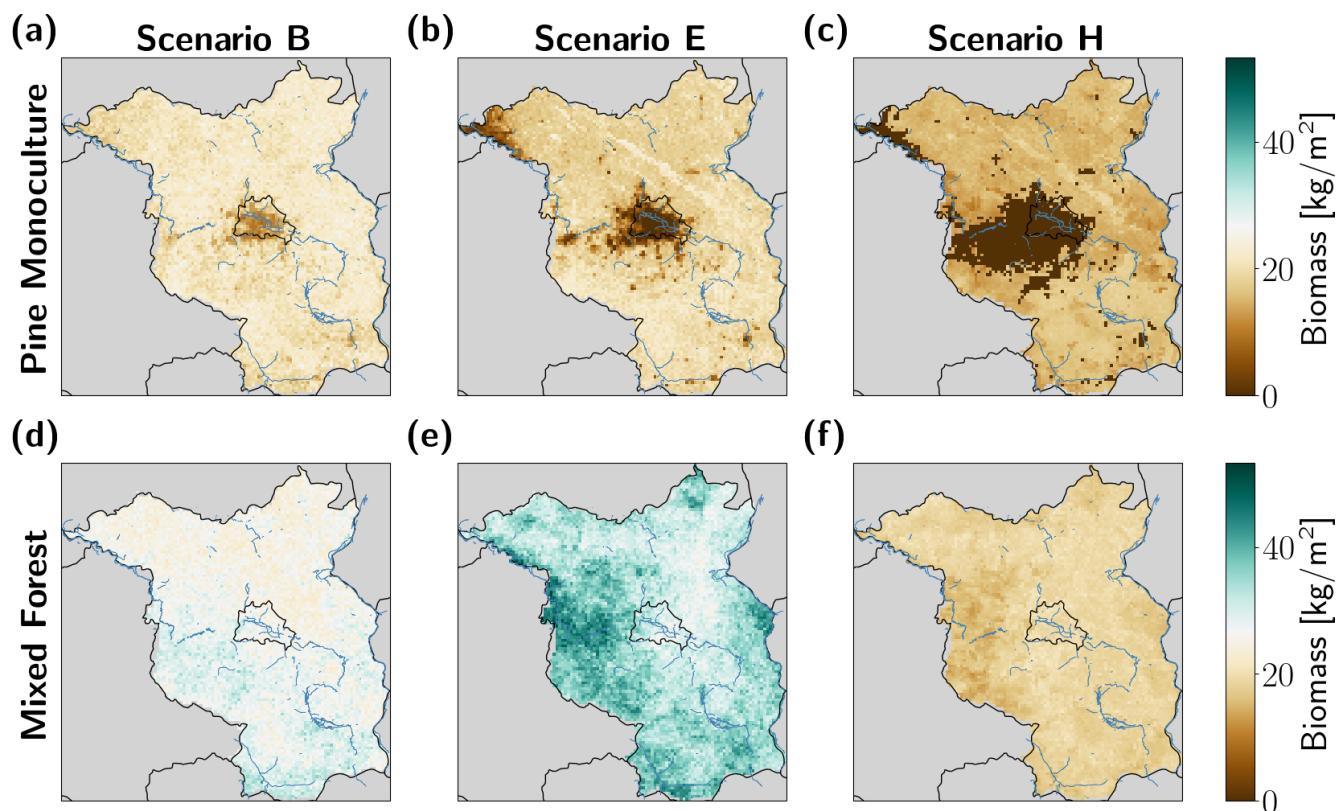
313

314 **Figure 5:** Long-term impact of drought frequency on selected tree characteristics. Biomass-weighted mean values are shown  
 315 for (a) height [m], (b) wood density [kg/m³], (c) age [years] and (d) tree maturity age [years] (also referred to as growth  
 316 speed, defined as tree height at which a tree reached a height of 15m), specific leaf area [m²/g] (SLA) and mortality  
 317 [probability/year] at the end of the simulation period (simulation years 701-800) in pine monoculture forest (Pine) and for  
 318 each PFT in mixed forests under drought frequency Scenarios A-H. Temperate broad-leaved trees (T-BL), boreal broad-  
 319 leaved trees (B-BL), temperate needle-leaved trees (T-NL) and boreal needle-leaved trees (B-NL). Please note that values



320 for T-NL are based on very low numbers of individuals (see Fig. 4b) and that the sample size for the calculation of tree  
321 maturity age is less compared to the data in the other panels, as not all trees reach a height of 15m.

322 Figure 4 showed that changes in biomass and tree numbers could mainly be explained by shifts in the functional composition  
323 of mixed forests, i.e. how much biomass and how many trees belonging to a particular PFT contributed to the forest  
324 community. In addition, we observed drought-induced changes in the characteristics of individual trees across PFTs  
325 concerning their height, wood density and age (Fig. 3e-j). In Figure 5, we can show that these changes were rather attributed  
326 to trait adaptation *within* each PFT leading to shifts in mean characteristics of each PFT than to shifts in PFT dominance. The  
327 trends in drought-induced shifts were mostly similar between PFTs for height and wood density but differed for the age of  
328 individual trees. Except for temperate needle-leaved trees (which are very low in number, and therefore need to be treated  
329 with care), the mean height of all PFTs decreased from around 20 m to around 15 m in mixed forests (Fig. 5a). Pine trees  
330 growing in a monoculture only slightly decreased in height, i.e. intra-species plant competition seems to strongly impact  
331 drought adaptation. For wood density (Fig. 5b) we observed differences between broadleaved species, which strongly  
332 increased in density (by 29.6% for T-BL and 19.8% for B-BL), and needle-leaved species, which initially started with a  
333 lower wood density and showed only marginal increases from Scenarios C to H. Pine trees in monocultures showed even  
334 less response than the boreal needle-leaved type. For mean tree age, broadleaved trees generally grew older, while at least  
335 the boreal needle-leaved PFT showed a younger age structure with increasing drought. Again, the results of the temperate  
336 needle-leaved PFT need to be treated with care because of low numbers. In monocultures, the mean age of pine trees was  
337 slightly lower than of their pendant in the mixed forest. Growth speed was generally faster for needle-leaved trees (40-65  
338 years to reach a size of 15 m) than for broadleaved trees (60-85 years). While boreal and temperate broadleaved trees have a  
339 similar growth speed despite their differing wood density, boreal needle-leaved trees seem to grow slower than temperate  
340 ones. In most cases, a higher drought frequency slows down the growth speed, i.e. trees need longer to reach a height of 15  
341 m. However, pine trees in monocultures seem to reach this height faster under mild drought scenarios (Scenarios C and D)  
342 and similar to the baseline scenario for more frequent droughts (Scenarios E-H). For broadleaved trees mortality decreased  
343 with increasing drought frequency and in all drier-than-baseline scenarios (Scenarios C-H) it was lower than for the needle-  
344 leaved trees (Fig. 5f). In contrast, for needle-leaved trees the mortality for the driest scenarios (Scenarios D-H) was higher  
345 than for the baseline scenario. Also for SLA, broadleaved and needle-leaved trees showed opposing trends, although changes  
346 were relatively small for all tree types (Fig. 5e). For the needle-leaved trees SLA increased with drought frequency, while for  
347 the broadleaved trees SLA decreased slightly and for pine there was no significant trend (Fig. 5e). For broad-leaved trees  
348 SLA was higher than for needle-leaved trees, for which in turn SLA was higher than for pine trees and even exceeded the  
349 upper limit of the *Pinus sylvestris* parametrization range.



350

351 **Figure 6:** Simulated long-term (mean over last 100 simulation years) biomass under selected drought frequency scenarios  
 352 (baseline (Scenario B), example for medium-frequency scenario (Scenario E) and highest drought frequency (Scenario H))  
 353 for pine monocultures (top row) and mixed forests (bottom row) for the Berlin-Brandenburg study area. The state borders of  
 354 Berlin and Brandenburg are shown in black, major riverbanks in blue. Biomass in pine monoculture decreased under all  
 355 scenarios (panels (a) to (c)), especially in central and western parts, whereas spatial patterns of biomass increased  
 356 differently in mixed forests under each scenario (panels (d) to (f)). See Appendix B, Fig B1 for Scenarios A, C, D, F and G.

357 The spatial pattern of simulated long-term biomass in the Berlin-Brandenburg study area confirmed the differences between  
 358 the performance of pine monocultures and mixed forests under increasing drought frequencies (Fig. 6). A new aspect was,  
 359 however, that we saw large spatial heterogeneity for the performance of both, the pine monoculture and the mixed forest,  
 360 under baseline climate (Scenario B, Fig. 6a,d). Pine monocultures seemed especially heat sensitive, as Berlin and urban areas  
 361 of Brandenburg, which have a higher temperature (see Appendix B, Fig B2), showed much less biomass than in rural areas  
 362 (Fig. 6a-c). In contrast, mixed forests seemed to respond to both: temperature increase and water deficits (see Appendix, Fig  
 363 B3). Under the baseline scenario, the more or less temporarily stable biomass levels (Fig. 2b) result from biomass values of  
 364 around 30 kg/m<sup>2</sup> in southern Brandenburg and slightly lower biomass values of around 20 kg/m<sup>2</sup> in northern parts (Fig. 6d).  
 365 The higher biomass under medium-frequency Scenario E compared to the baseline (Fig. 2b) which is driven by changes in  
 366 structural and functional traits (Figs. 3 and 4) is mainly found in central western and southern parts, and also in isolated areas  
 367 in eastern parts of Brandenburg, where biomass reaches values of around 40 kg/m<sup>2</sup> (Fig. 6e). When the 2018-drought  
 368 becomes the new climate normal (Scenario H), lower biomass values (<20 kg/m<sup>2</sup>) show little spatial variation across the  
 369 study area with slightly lower values in western Brandenburg.



370 Under increased drought frequency (here shown Scenarios E and H), areas of very low biomass in pine monocultures  
371 became larger. In the extreme scenario H, they basically collapsed in the western-central Berlin-Brandenburg area and near  
372 the river Elbe in north-west Brandenburg (Fig. 6c). As shown before, an increase in drought frequency led to an overall  
373 increase in biomass of mixed forests, if drought was not occurring every year (scenario H, Fig. 6e). As a result, biomass in  
374 the western-central part of Brandenburg, but not in Berlin was higher in Scenario E, but drastically lower in Scenario H (Fig.  
375 6f).

376 Summarizing all above results, we observed that mixed forests could better adapt to increasing drought frequency than pine  
377 monoculture forests. Mixed forest can adapt via shifts in PFT composition, functional and structural trait shift at the  
378 community level which resulted from changes in the characteristics of the tree individuals: The fraction of broadleaved trees  
379 increased, and these became sturdier (smaller with higher wood density) and grew older. However there were spatial  
380 differences throughout the study areas, with pinus monocultures especially suffering along urban areas and mixed forests  
381 responding stronger in the western-central part.

## 382 4 Discussion

### 383 4.1 Differences between Pine monocultures and mixed forests under current conditions

384 Generally, our results for pine monocultures show lower total biomass (around 21 kg/m<sup>2</sup>) under present conditions (baseline  
385 scenario) than mixed forests (around 27 kg/m<sup>2</sup>). This is in line with a study across forests in northern Germany (Förster et al.  
386 2021) that compared landscape-scale aboveground biomass of different forest types and found much lower values for old-  
387 grown pine forests (19 kg/m<sup>2</sup>) than for forests with natural development (32 kg/m<sup>2</sup>). Moreover, multiple forest studies show a  
388 positive productivity-biodiversity relationship and higher carbon stocks in more diverse forests (Watson et al. 2018; Ali et al.  
389 2017; Y. Zhang and Chen 2015), which can, however, strongly depend on species identity (Chisholm and Dutta Gupta, 2023)  
390 and climatic conditions. In a US-scale analysis on forests, Fei et al. (2018) found a positive biodiversity-productivity  
391 relationship in arid to semi-arid areas, which turned negative under a more humid climate.

392 Also the difference in mean tree age between monocultures (118 years) and mixed forests (143 years) is similar to observed  
393 values from Förster et al. (2021) who found a mean stand age of 112 years for old-grown pine forests and 146 years for natural  
394 developed forests. However, our findings on stem density, which show a slightly higher number of trees per area in mixed  
395 forests, deviate from their results, as they find a much higher number of trees in young- and old-grown pine forests than in  
396 mixed forests with natural development. This can rather be an effect of management than of tree species composition. However,  
397 other studies confirm our results, with higher tree numbers per area in mixed forests than in pine monocultures, e.g. due to a  
398 higher use efficiency of light, water, or nutrients by species mixing (Pretzsch and Biber, 2016; Pretzsch and Schütze, 2016).  
399 Also our results on slightly higher tree heights and faster growth speed in monocultures are confirmed by other studies  
400 (Pretzsch and Forrester, 2017) which is one of the reasons why pine forests have been promoted in forestry of the past decades  
401 (Spathelf and Ammer, 2015).

### 402 4.2 Effects of droughts on biomass and structure of pine monocultures versus mixed forests

403 Under drier and warmer conditions the difference in total biomass between pine monocultures and mixed forests increases  
404 strongly, as the biomass of the monocultures declines further, while the biomass of mixed forests increases in the long-term.  
405 Also the stronger fluctuations in the biomass time series show that the pine forest responded stronger to individual drought  
406 years, which indicates increased system instability. This is in accordance with observations, which found that pine  
407 monocultures were affected by the European drought year 2018, which led to high mortalities of *Pinus sylvestris* and a



408 vegetation shift to other species (Haberstroh et al., 2022). In addition to the drier conditions, one major reason for the  
409 biomass decline in the pine monoculture were the warmer temperatures negatively affecting the establishment of pine trees  
410 (compare Figure 6 a-c with Table A2), which germinate better with cold stratification (Houšková et al., 2021), and have a  
411 lower thermostability of photosystem II during photosynthesis compared to other important temperate tree species  
412 (Húdoková et al., 2022). However, the model might estimate the chilling temperature needed for cold stratification as too  
413 low for the B-NL PFT and pine trees in Brandenburg, as germination requirements vary with provenance (Hannerz et al.,  
414 2003; Rampart, 2018; Tillman-Sutela and Kauppi, 1995) and might be different for temperate lowlands like Brandenburg  
415 compared to colder regions.

416 Also broadleaved trees, e.g. European beech *Fagus sylvatica* or even pedunculate oak *Quercus robur*, strongly suffered from  
417 the 2018-drought, but these were less strong and the mixing of appropriate species might have been able to mitigate drought  
418 impacts (Schuldt et al., 2020). In our simulations, we also see that the biomass of mixed forests drops in the first decades, as  
419 they need time to adjust to altered climate conditions. However, after this phase of adjustment, biomass in mixed forests  
420 increases in the long-term (except for the extreme Scenario H). As comparative data on such long-term forest dynamics is  
421 difficult to obtain, it is helpful to assess the validity of our results with the help of a spatial aridity gradient. A comprehensive  
422 study on data from a tree ring database along an aridity gradient in Europe (Pardos et al., 2021) tested the growth response to  
423 site specific drought events between 1975 and 2015 for monospecific and mixed stands. They generally found a higher  
424 resilience and resistance to drought events in mixed forests compared to monocultures but especially an increased resilience  
425 to drought in drier sites with slight increases in productivity in post-drought years for mixed forests but not for monocultures.  
426 Also a long-term study using inventory data of boreal forests of western Canada from 1958 to 2011 confirmed that with  
427 increasing temperature and decreasing water availability, biomass declined in species poor forests while increasing in  
428 species-rich forests (Hisano et al., 2019). These two studies might be an indicator that well adapted species compositions  
429 might indeed become more productive and increase their biomass over centuries in mixed forests. However, the increased  
430 biomass simulated by LPJmL-FIT might be overestimated because the model did not include nutrient limitation, e.g.  
431 nitrogen, which might limit tree growth to a greater extent under drier conditions.

432 A higher drought frequency does not only impact the biomass of forests, but also their structure. We found large differences  
433 between the pine monoculture and a mixed forest, where different properties of the mixed forest responded much stronger to  
434 increased drought frequency. In the pine forest, tree density decreased in response to more droughts and higher temperatures,  
435 which was also found by Haberstroh et al. (2022). Surprisingly, the pine monoculture does not exhibit the expected shift  
436 towards higher wood density under drought conditions. One explanation lies in the inherent structure of the pinus stands,  
437 which contain a dense population of fast-growing trees with lower wood density under present conditions. These trees,  
438 characterized by rather fast vertical growth, may outcompete new tree saplings with higher wood densities due to light  
439 competition. Therefore, the presence of trees with lower wood densities could hinder the success of slower growing tree  
440 saplings to grow, although trees with higher wood densities might be better adapted to drought conditions. This competition  
441 effect could lead to lower drought resistance of pines growing in a monoculture compared to pines in more diverse forests, as  
442 also found in an empirical study (Granda et al., 2018). Such a phenomenon suggests that light competition in the understorey  
443 plays a significant role in developing certain drought adapted plant strategies. Similar shifts in wood densities as a response  
444 to increased competition has been previously observed in earlier studies (Billing et al., 2024). As the mean height and age  
445 only decreased slightly, the decrease in pine forest biomass seems to be especially caused by lower tree densities and not by  
446 changes in tree morphology.

447 In contrast, tree density increased in mixed forests, even for the most extreme drought Scenario H. Individual trees, however,  
448 had higher wood density leading to slower growth, reduced mortality, smaller SLA and smaller height, while getting older.  
449 Higher wood density with decreasing annual rainfall (below values of 1000 mm/a, which is the case in our study area) was  
450 also found in a global tree inventory analysis for temperate forests (Bouchard et al., 2024). But also species-specific



451 investigations showed increasing wood densities for the same species from different provenances across the world with  
452 higher aridity (Nabais et al., 2018). Also Fei et al. (2017) observed that in the Eastern part of the US, tree species whose  
453 range shifted to drier areas had higher median wood density. When trees invest more carbon into their wood density, this can  
454 lead to a decrease in growth rate and size (Aiba and Nakashizuka, 2009; Kallarackal and Ramírez, 2024). Moreover, it makes  
455 sense that trees optimize their height towards smaller sizes, as found in our study, as large trees suffer stronger from droughts  
456 (Bennett et al. 2015, ). Also Ryan and Yoder (1997) found that for the same species, its maximal height can differ strongly  
457 between locations, with smaller tree sizes found in more arid environments. Slower growing forests also have a lower  
458 turnover-rate (Black et al., 2008; Johnson and Abrams, 2009), which is reflected in our finding of an older mean tree age  
459 under higher drought frequency (except for the most extreme Scenario H).

### 460 **4.3 Underlying mechanisms leading to a higher resilience of the mixed forest**

461 As discussed in the previous section, mixed forests seemed to have a higher resilience towards droughts: their biomass  
462 stabilized at high values after an initial adaptation phase, and trees had a higher wood density, grew slower but got older and  
463 reached a lower height. Here, we discuss (i) if the higher resilience is rather a result of a shift in the composition of the  
464 community or in the traits of individual PFTs towards more optimized values, as well as (ii) the general role of species diversity  
465 on forest resilience.

466 Our results showed a shift in PFT composition in the mixed forest: while needle-leaved trees declined strongly in their  
467 biomass and tree density, playing only a marginal role under increased drought, the biomass and tree density of broadleaved  
468 trees increased. These higher tree densities with increasing aridity have also been observed in a study in northern Germany  
469 on *Fagus sylvatica* monocultural stands (Weigel et al., 2023). Such a community shift from pine trees to broadleaved trees in  
470 response to the drought in 2018 has also been observed in satellite data and tree mortality data in Germany (Haberstroh et al.,  
471 2022). Particularly, temperate broad-leaved trees overall benefited from an increased frequency of the drought-year 2018, as  
472 they are less limited by higher temperatures (Table A2). Looking back at our question if rather the shift in the plant  
473 community composition or a shift in individual tree traits increases the forest resilience of mixed forests, we can say at this  
474 point that a shift towards more temperate broadleaved trees (and the associated shift in community weighted mean traits) can  
475 at least partly explain the higher resilience of mixed forests.

476 Much more important seems however, the trait shift in individual PFTs as a response to a higher drought frequency. The  
477 flexible-trait scheme of our model allows the emergence of different plant strategies to optimize plant performance under  
478 stressful conditions within a PFT. That is, from our model results, we can learn about PFT-specific plant trait combinations  
479 that are best adapted under different drought conditions. In contrast to needle-leaved species, it seems to be optimal for  
480 broadleaved species to strongly invest into wood density under higher drought frequency. This resembles the well known  
481 coping mechanisms towards high wood densities and slightly smaller SLAs under drought or dry summer conditions  
482 observed at broader scales (Greenwood et al., 2017; Serra-Maluquer et al., 2022) and explains the decrease in mortality  
483 (Greenwood et al. 2017) for broadleaved trees and the overall increase in wood density at the community level. Also in the  
484 study on *Fagus sylvatica* monoculture stands in Germany, lower growth was observed in response to a decadal decrease in  
485 the climatic water balance (Weigel et al., 2023). In general, there seems to be a shift for both broadleaved PFTs towards a  
486 more conservative strategy, where they invest into wood density, grow slower (Chave et al., 2009; Poorter et al., 2010) and  
487 less tall (Aiba and Nakashizuka, 2009; Kallarackal and Ramírez, 2024), but become older (Laurance et al. 2004; Black,  
488 Colbert, and Pederson 2008; Bigler and Veblen 2009). In contrast, boreal needle-leaved trees are less productive, have a  
489 lower wood density thus a higher mortality and consequently the forests are composed of younger and smaller individual  
490 trees with little trait adaptations, which we also see for pine monocultures.





491 In general, mixed-species forests have been discussed as an adaptation strategy to reduce the risk for forest ecosystems under  
492 global change (Forrester et al., 2016). One reason is the potential niche complementary of different species, reducing  
493 competition for resources (Morin et al., 2011) and improving the resource supply, and uptake (Richards et al., 2010).  
494 Moreover, interspecific facilitation can partly release trees from stress, leading to higher resistance and resilience of mixed  
495 forests especially to climate extremes such as droughts (Pretzsch et al., 2013). However, these findings can strongly depend  
496 on species identity and the environmental context (Decarsin et al., 2024; Forrester et al., 2016). Therefore, the forest species  
497 mixture has to be appropriately chosen for a specific stand to increase the likelihood that beneficiary effects mitigate drought  
498 impacts (Ammer, 2017). As we do not account for these facilitative effects in our simulations, we might even underestimate  
499 the positive effects of mixed forests on drought resilience in our assessments.

500 In conclusion, it can be summarized that numerous mechanisms lead to the higher resilience via adaptation of mixed forests  
501 to an increased drought frequency, which we have only partially considered in this study. The higher adaptive capacity of  
502 broadleaved trees to drought via shifts in their traits, but also shifts in species composition are both playing a major role.  
503 However, the observation that biomass decreased again when drought frequency was too high shows that also in a mixed  
504 forest the adaptation capacity has limits beyond which productivity decreases.

#### 505 **4.4 Implications**

506 We found that an increased drought frequency along with increased mean temperatures adversely affect the productivity of  
507 forests in Berlin-Brandenburg in the first decades. This leads to a massive biomass decline in both forest types, pine  
508 monocultures as well as mixed forests with multiple implications for ecosystem functions and services (for examples see  
509 here: Brockerhoff et al. 2017). However, we also saw that mixed forests can adapt in the long term (as long as extreme  
510 droughts do not occur too often) by a change in species composition towards more broad-leaved trees, but also by shifts in  
511 species traits. Such a shift towards a higher fraction of broad-leaved trees was also suggested in a European-wide study  
512 combining forest inventory data with climate data driven by different Representative Concentration Pathways (RCP)  
513 scenarios which found a retraction in *Pinus sylvestris* and *Picea abies* (Norway spruce) from lowlands in Central Europe to  
514 higher altitudes or more northern areas, but extended areas for *Quercus robur* (pedunculate oak) and ambivalent results for  
515 *Fagus sylvatica* (Buras and Menzel, 2019).

516 The current and potential future impacts of climate change have concerned practitioners and scientists for more than two  
517 decades (Hanewinkel et al. 2022). However, a case study with forest practitioners in four regions of Germany by Milad et al.  
518 (2013) showed that strategies for adapting forest management were at that point still in early stages. Recently, the Scientific  
519 Advisory Board for Forest Policy of the German Federal Ministry of Food and Agriculture proposed mixed forests to better  
520 cope with climate change, but also the active introduction of better-adapted tree species that are taxonomically, spatially and  
521 ecophysiologicaly closely related to current species to also support native biodiversity (Bauhus et al., 2021). Moreover,  
522 using seeds from seed provenances adapted to future climates for reseeded rather than local seed provenances might further  
523 mitigate the initial biomass declines that we found in our simulations, as a recent study on assisted tree migration in Europe  
524 showed (Chakraborty et al., 2024). In order to apply these suggested methods for increasing the resilience towards possible  
525 new climate normals, knowing which traits combinations and species communities perform best under these conditions is  
526 crucial. With our study we contribute to this quest by showing which forest structure and tree characteristics result under  
527 increased drought frequencies in unmanaged forests in Berlin and Brandenburg.

528 Due to the small grid size of only 2 x 2 km we were able to observe large heterogeneity in the forest biomass across Berlin-  
529 Brandenburg. This heterogeneity increased under increased drought frequencies. However, this could also be a consequence  
530 of the specific spatial heterogeneity in the climate of the year 2018, which has an increasing influence on the results the  
531 higher the frequency becomes. The observed heterogeneity underscores that for the management of forests site-specific



532 solutions, accounting, e.g. for temperature differences between more urban and more rural areas, for the rainfall gradient in  
 533 Berlin-Brandenburg and for different soil textures are required. Furthermore they highlight that in addition to local studies  
 534 there is a strong need for high-resolved climate projections that accurately reflect possible increases in extreme drought  
 535 frequencies and models that accurately simulate the impacts of these climate projections on vegetation.

## 536 5 Conclusions

537 Our results suggest that increased drought frequencies could lead to a drastic reduction in biomass in both pine monoculture  
 538 forests and mixed forests in Brandenburg and Berlin. Mixed forests, however, might eventually recover and even exceed  
 539 initial biomass levels in the long-term, as long as drought frequencies are not too high. The higher resilience of mixed forests  
 540 in our simulations was due to higher adaptive capacity. The adaptation, however, profoundly changed forest characteristics:  
 541 Mixed forests were predominantly composed of smaller, broad-leaved trees with higher wood density and slower growth,  
 542 which can be summarized as a shift towards more conservative strategies. These changes would have significant  
 543 implications for forestry, even when sustainably managed, related industries, and other ecosystem functions and services.  
 544 Our results thus highlight the importance of incorporating biodiversity into forest management and preparing for shifts in the  
 545 ecosystem services provided by forests in Brandenburg and Berlin in the future.

## 546 Appendices

### 547 Appendix A: Selected characteristics of plant Functional Types and *Pinus sylvestris* parametrization

548 **Table A1:** Specific leaf area [m<sup>2</sup>/g] (SLA) and wood density [kg/m<sup>3</sup>] (WD) ranges for the simulated plant functional types and *Pinus*  
 549 *sylvestris*.

Plant Functional Type (PFT)/Species	Specific Leaf Area [m <sup>2</sup> /g]	Wood Density [kg/m <sup>3</sup> ]
Temperate Broadleaved Summergreen (T-BL)	0.0242 - 0.0547	147.9 - 637.0
Boreal Broadleaved Summergreen (B-BL)	0.0242 - 0.0547	147.9 - 637.0
Temperate Needle-leaved Evergreen (T-NL)	0.005 - 0.0187	117.0 - 418.5
Boreal Needle-leaved Evergreen (B-NL)	0.005 - 0.0187	117.0 - 418.5
<i>Pinus sylvestris</i>	0.0094 - 0.0135	223.0 - 268.5

550

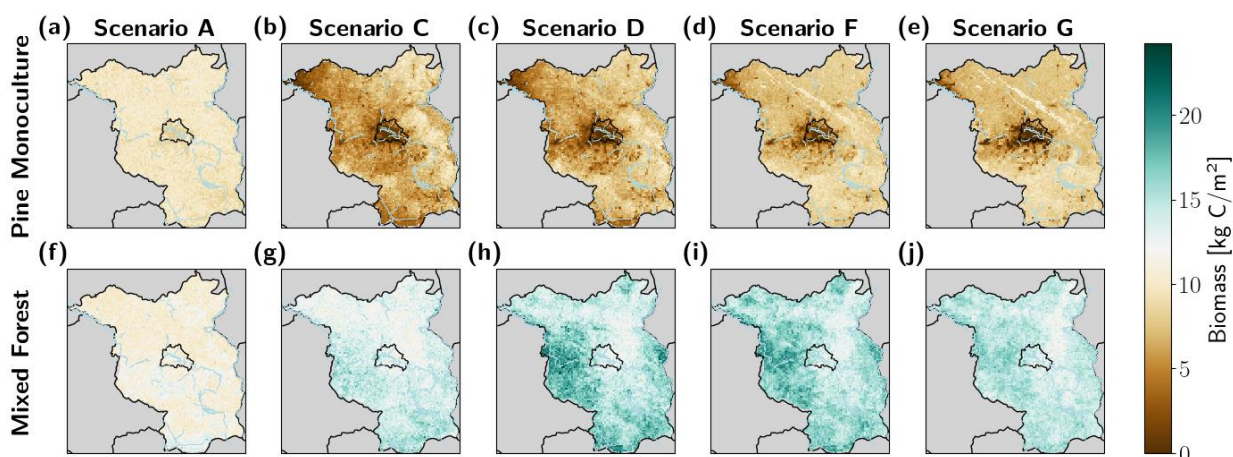


551 **Table A2:** Temperature limits for tree establishment and survival as well as optimum temperature range for photosynthesis. For  
 552 establishment to happen, the mean of the annual minimum temperature over the last 20 years must be larger or equal to the Frost  
 553 Tolerance Temperature [°C] and smaller or equal to the Chilling Requirement Temperature [°C]. Trees die if the mean of the annual  
 554 minimum temperature over the last 20 years is smaller than the Frost Tolerance Temperature [°C]. The Temperature Optimum for  
 555 Photosynthesis is the temperature range in which photosynthesis is not inhibited by too low or too high temperatures.

Plant Functional Type (PFT)/Species	Chilling Requirement Temperature [°C]	Frost Tolerance Temperature [°C]	Temperature Optimum for Photosynthesis [°C]
Temperate Broadleaved Summergreen (T-BL)	15.5	-17.0	20.0 - 25.0
Boreal Broadleaved Summergreen (B-BL)	10	-35.0	15.0 - 25.0
Temperate Needle-leaved Evergreen (T-NL)	38.0	-4.0	20.0 - 30.0
Boreal Needle-leaved Evergreen (B-NL)	-2.0	-32.5	15.0 - 25.0
<i>Pinus sylvestris</i>	-2.0	-32.5	15.0 - 25.0

556

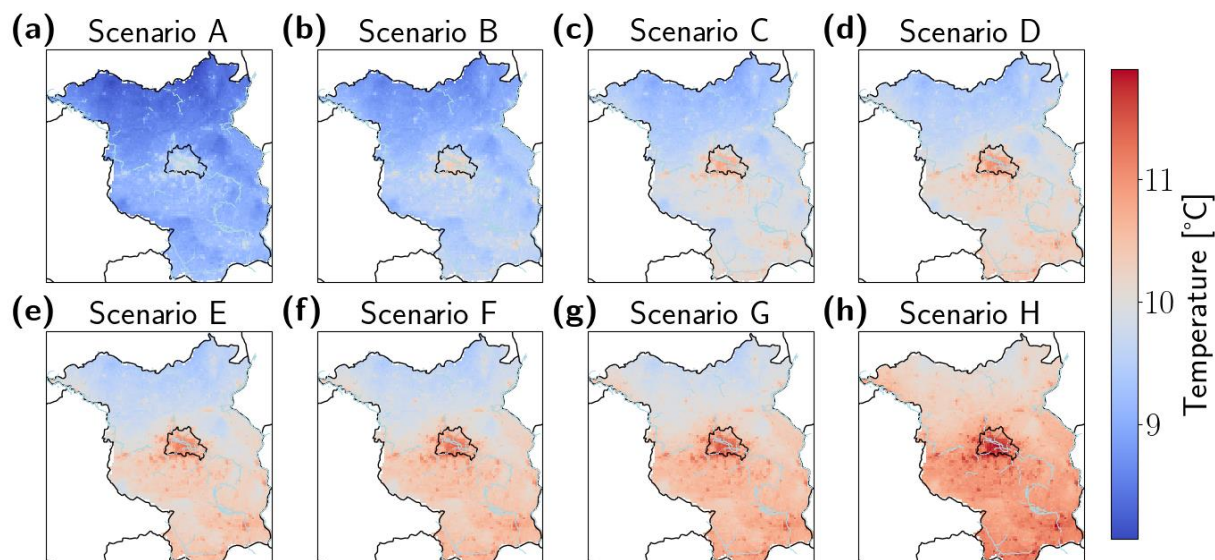
557 **Appendix B: Biomass, Temperature and Maximum Climatic Water Deficit maps for Berlin-Brandenburg**



558

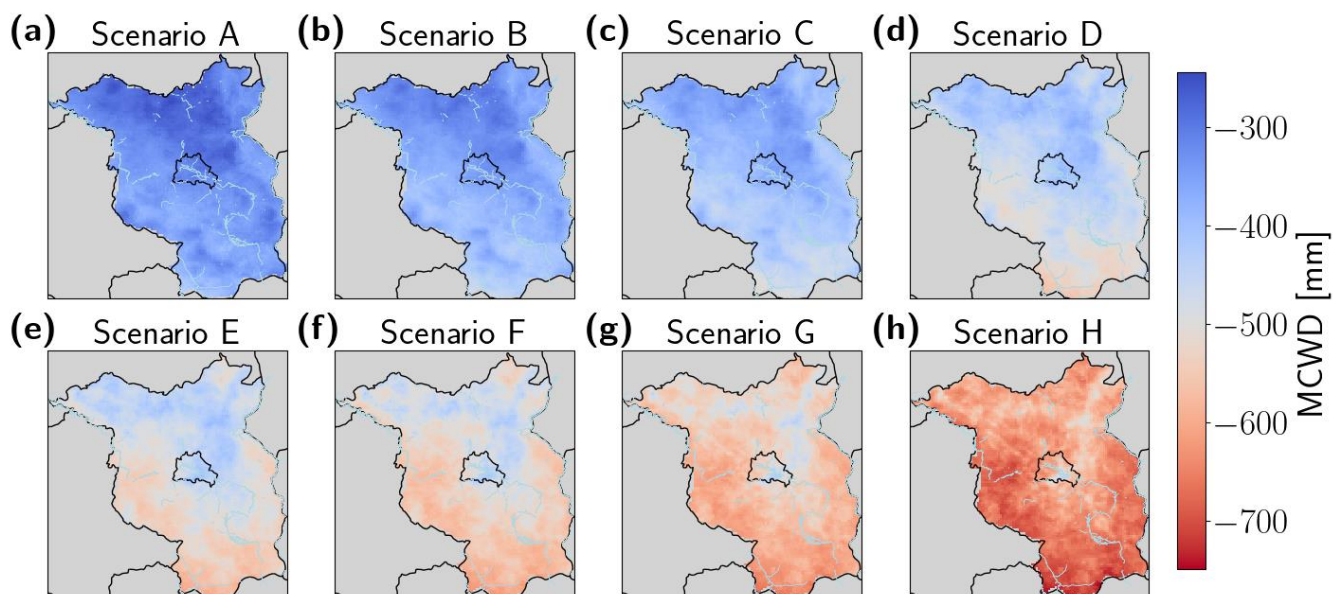


559 **Figure B1:** Simulated long-term (mean over last 100 simulation years) biomass under selected drought frequency scenarios A, C, D, F  
560 and G for pine monocultures (top row) and mixed forests (bottom row) for the Berlin-Brandenburg study area. The state borders of Berlin  
561 and Brandenburg are shown in black, major river banks in blue.



562

563 **Figure B2:** Mean daily Temperatures [°C] over all simulation years for the Berlin-Brandenburg area for scenarios with increasing  
564 frequency of the year 2018 from A-H (a-h). The state borders of Berlin and Brandenburg are shown in black, major river banks in blue.



565



566 **Figure B3:** Mean Maximum annual Climatic Water Deficit (MCWD) [mm] over all simulation years for the Berlin-Brandenburg area for  
567 scenarios with increasing frequency of the year 2018 from A-H (a-h). The state borders of Berlin and Brandenburg are shown in black,  
568 major river banks in blue.

569 **Code availability:** Programming code can be provided by Potsdam Institute for Climate Impact Research (PIK e. V.) upon  
570 reasonable request and pending scientific review.

571 **Data availability:** All data needed to evaluate the conclusions in the manuscript are present in the manuscript The data can  
572 be provided by Potsdam Institute for Climate Impact Research (PIK e. V.) upon reasonable request and pending scientific  
573 review.

574 **Author contribution:** Jamir Priesner, Britta Tietjen, Kirsten Thonicke, Boris Sakschewski and Maik Billing made the study  
575 design. Kirsten Thonicke, Boris Sakschewski, Sarah Bereswill, Werner von Bloh and Maik Billing developed the LPJml-FIT  
576 model version used in this study. Jamir Priesner carried out the simulations. Jamir Priesner, Britta Tietjen, Kirsten Thonicke,  
577 Boris Sakschewski, Maik Billing and Sebastian Fiedler analyzed and interpreted the simulation outputs. Jamir Priesner,  
578 Britta Tietjen and Kirsten Thonicke prepared the manuscript with contributions from all co-authors.

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