Frei Esther R. (Orcid ID: 0000-0003-1910-7900)

European beech dieback after premature leaf senescence during the 2018 drought in northern Switzerland

Running Title: Drought effects on European beech

Esther R. Frei[1,2,3,4,*], Martin M. Gossner[1,3,5], Yann Vitasse[1,3], Valentin Queloz[1,3], Vivanne Dubach[1], Arthur Gessler[1,3,5], Christian Ginzler[1,3], Frank Hagedorn[1,3], Katrin Meusburger[1,3], Maurice Moor[1], Eva Samblàs Vives[1], Andreas Rigling[1,3,5], Ide Uitentuis[1], Georg von Arx[1,3,6], Thomas Wohlgemuth[1,3]

[1]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zuercherstrasse 111, 8903 Birmensdorf, Switzerland

[2]WSL Institute for Snow and Avalanche Research SLF, 7260 Davos Dorf, Switzerland

[3]SwissForestLab, 8903 Birmensdorf, Switzerland

[4]Climate Change and Extremes in Alpine Regions Research Centre CERC, 7260 Davos Dorf, Switzerland

[5]ETH Zurich, Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, 8092 Zurich, Switzerland

[6]Oeschger Centre for Climate Change Research, University of Bern, 3012 Bern, Switzerland

*Correspondence: Esther R. Frei, esther.frei@wsl.ch

Keywords: bark beetles; bleeding cankers; climatic water balance; crown dieback; *Fagus sylvatica*; tree mortality

Abstract

- During the particularly severe hot summer drought in 2018, widespread premature leaf senescence was observed in several broadleaved tree species in Central Europe, particularly in European beech (*Fagus sylvatica* L.). For beech, it is yet unknown whether the drought incited a decline towards tree mortality or whether trees can recover in the longer run.

- In this study, we monitored crown dieback, tree mortality and secondary drought damage symptoms in 963 initially alive beech trees that exhibited either premature or normal leaf senescence in 2018 in three regions in northern Switzerland from 2018 to 2021. We related the observed damage to multiple climate- and stand-related parameters.

- Cumulative tree mortality continuously increased up to 7.2% and 1.3% in 2021 for trees with premature and normal leaf senescence in 2018, respectively. Mean crown dieback in surviving trees peaked at 29.2% in 2020 and 8.1% in 2019 for trees with premature and normal leaf senescence, respectively. Thereafter, trees showed first signs of recovery. Crown damage was more pronounced and recovery was slower for trees that showed premature leaf senescence in 2018, for trees growing on drier sites, and for larger trees. The presence of bleeding cankers peaked at 24.6% in 2019 and 10.7% in 2020 for trees with premature and normal leaf senescence, respectively. The presence of bark beetle holes peaked at 22.8% and 14.8% in 2021 for trees with premature and normal leaf senescence, respectively. Both secondary damage symptoms occurred more frequently in trees that had higher proportions of crown dieback and/or showed premature senescence in 2018.

- Our findings demonstrate context-specific differences in beech mortality and recovery reflecting the importance of regional and local climate and soil conditions. Adapting

management to increase forest resilience is gaining importance with the expected further beech decline on dry sites in northern Switzerland.

Introduction

Severe summer droughts and heat spells increasingly affect ecosystems globally (Choat et al. 2012, Bastos et al. 2020, Brodribb et al. 2020, Buras et al. 2020, Peters et al. 2020). Hot or prolonged droughts increase tree mortality rates (Allen et al. 2015, Choat et al. 2018, Schuldt et al. 2020, Senf et al. 2020), impact forest growth and carbon sequestration (Ciais et al. 2005, Reichstein et al. 2013, Cailleret et al. 2017) and disrupt mast seeding patterns (Bogdziewicz et al. 2020, Nussbaumer et al. 2020). Severe droughts can thus act as inciting factors that trigger a spiral of tree decline (Manion 1991) ultimately leading to large forest dieback, changes in community composition and structure, as well as shifts in species distributions (Anderegg et al. 2013, Clark et al. 2016, Brodribb et al. 2020, McDowell et al. 2020, Senf et al. 2021). These processes would in turn affect forest ecosystem services including timber production, carbon storage, climate and water regulation (Kannenberg et al. 2019) as well as impair sustainable forest management (Suarez and Kitzberger 2008, Bolte et al. 2016, Clark et al. 2016). From 2018 to 2020, Central Europe experienced an extremely hot drought period (Hanel et al. 2018, Boergens et al. 2020, Sousa et al. 2020), also severely affecting forest ecosystems (Brun et al. 2020, Schuldt et al. 2020, Senf and Seidl 2021).

As one of the most common deciduous tree species in Central European temperate forests, European beech (*Fagus sylvatica* L.) forms monospecific and mixed stands across broad temperature, moisture and edaphic gradients (Leuschner and Ellenberg 2017). In addition to its ecological value (Winter and Möller 2008, Packham et al. 2012), beech is an economically important tree species in many Central European countries, surpassed only by conifers such as Norway spruce and Scots pine (Pretzsch et al. 2020). Although beech tolerates a fairly wide range of site conditions (Leuschner et al. 2006, Leuschner and Ellenberg 2017), it has been known as a moderately drought sensitive species (Gessler et al. 2007, Meier and Leuschner 2008, Leuschner and Meier 2018, Leuschner 2020), and was

severely affected by the recent period of extreme hot droughts in Europe (Schuldt et al. 2020, Walthert et al. 2021, Arend et al. 2022). Long-term tree-ring and forest inventory-based studies revealed significant growth reductions in response to climatic drought intensity (Bircher et al. 2016, Vitasse et al. 2019, Pretzsch et al. 2020) and increased mortality rates (Archambeau et al. 2020). While past drought events mostly affected beech forests at their southern dry distribution limits (Penuelas and Boada 2003, Allen et al. 2010), recent extreme hot droughts caused extended forest dieback also in the center of the species' distribution (Leuschner 2020, Schuldt et al. 2020). Beech mortality has been related to climate variability (Hember et al. 2017, Neumann et al. 2017, Archambeau et al. 2020) and previous-year soil moisture anomaly (George et al. 2021). However, other factors can predispose beech for crown dieback and mortality such as shallow soil (Allen et al. 2010, Leuschner 2020), high sun-exposure occurring especially in gaps or at forest edges (Buras et al. 2018). Tree size can also influence mortality but findings are ambiguous: some authors reported that larger (trunk diameter) and taller (tree height) trees are more severely affected by drought due to a greater vulnerability to hydraulic stress as well as due to the higher radiation and evaporative demand experienced by their more exposed crowns (Bennett et al. 2015, Rowland et al. 2015, Grote et al. 2016, Pretzsch et al. 2018, Stovall et al. 2019, Bottero et al. 2021). By contrast, other studies observed greater vulnerability in shorter and smaller trees, which has been explained by limitations in soil water holding capacity in shallow soils and by smaller rooting systems (van Mantgem et al. 2009, Giardina et al. 2018, Ripullone et al., 2020, Nolan et al. 2021, Klesse et al. 2022). In addition, competition for light, water or nutrients can further aggravate drought stress in beech trees, which may therefore be associated with stand density (Gessler et al. 2017, Archambeau et al. 2020, Castagneri et al. 2022).

Premature leaf discoloration and leaf shedding are widely observed in beech in association with summer droughts (Bréda et al. 2006, Bigler and Vitasse 2021). On the one

hand, leaf shedding may reduce transpiration helping trees to avoid embolism by protecting branches, stem and roots from critical water loss (Pollastrini et al. 2019, Schuldt et al. 2020). On the other hand, premature leaf senescence can also result from hydraulic failure through xylem dysfunction during severe droughts (Wolfe et al. 2016, Walthert et al. 2021; Arend et al. 2022), which is one of several widely reported causes for drought-induced tree mortality in beech (Leuschner 2020). Other studies suggest that fine root failure is more strongly contributing to beech mortality by disrupting the capillary continuum from the soil to the root because of soil water deficit or fine root mortality (Johnson et al. 2018, Körner 2019, Martinez-Vilalta et al. 2019). Thermal stress can also increase stomatal conductance and thereby contribute to mortality of leaves, which could expand to twigs and eventually branches (Marchin et al. 2022). Hydraulic failure with immediate subsequent tree death occurs only rarely in beech, but embolism can lead to massive crown defoliation and dieback in subsequent years (Brodribb and Cochard 2009, Choat et al. 2012, Adams et al. 2017, Walthert et al. 2021). Although the reasons for drought damage in beech may not be fully known, crown mortality is a good proxy for vitality, reflecting a reduction of leaf mass and making trees vulnerable to lagged secondary drought impacts (Bréda et al. 2006, Schuldt et al. 2020). Impaired defence metabolism of drought-affected beech trees may increase their susceptibility to insect and pathogen attacks. As contributing factors *sensu* Manion (1991) they potentially accelerate tree death (Anderegg et al. 2015a, Brück-Dyckhoff et al. 2019, Huang et al. 2020). In addition, bark lesions due to heat and sun-burn may also open pathways for pathogens (Butin 2019). As a consequence, such drought legacy effects can negatively affect tree and forest functioning for several years after a drought event (Kannenberg et al. 2019, Kannenberg et al. 2020) and contribute to progressive vitality decline. The ability of beech trees to recover depends on the duration and intensity of the drought event but also on tree-specific factors such as size and social position (Anderegg et al.

2015b, Bennett et al. 2015). While recovery from mild droughts can occur within a short time, more severe droughts decelerate recovery processes through structural damage that provokes the need for production of new tissue (Ruehr et al. 2019). Regrowth of lost tissue may improve the competitive strength of trees indicating post-drought acclimation. Abundant post-drought re-growth can also lead to a structural overshoot of aboveground biomass potentially increasing the trees' vulnerability to recurring droughts (Jump et al. 2017, Trugman et al. 2018), i.e. predisposing them for future decline (Manion 1991).

For a better understanding of drought legacy effects and to disentangle post-drought acclimation from prolonged impairment or a decline spiral leading to tree death, there is a need to monitor drought-affected trees, forests and ecosystems over longer periods of time (Gessler et al. 2020). Here, we aim at investigating multi-year drought impacts on beech forests through a unique large-scale monitoring of 963 beech trees, which showed either premature leaf discoloration during the summer 2018 (824 affected trees) or no visible damage (139 control trees). We conducted the study in two highly drought-affected regions in northern Switzerland and one less drought-affected region located further south. We quantified the development of crown dieback and tree mortality as well as secondary drought damage, i.e. the presence of bleeding cankers and bark beetle infestations in these trees for three consecutive years. We also determined the impact of several potential climate- and stand-related (predisposing) factors on mortality and drought legacy processes. We hypothesized that: (i) Premature leaf senescence in beech indicates drought damage, eventually leading to partial or full crown mortality, to secondary damage and to continued tree mortality due to drought legacy effects or repeated droughts. (ii) Tree mortality and crown dieback as well as secondary damage are linked to water deficit, which is related to climatic water balance and soil properties. (iii) Taller trees are more vulnerable to extreme drought.

Material and Methods

Study region and tree selection

We conducted our study in three areas in northern Switzerland, where smaller or larger proportions of beech trees showed premature leaf discoloration and leaf fall during the summer 2018 (**Figure 1**). Specifically, we selected an area south-east of Basel (elevation: 271 – 817 m a.s.l., mean growing season temperature MGT between April and September: 15.9 °C, mean growing season precipitation MGP between April and September: 498 mm) and an area east of Schaffhausen (elevation: 420 – 664 m a.s.l., MGT: 15.2 °C, MGP: 534 mm), both severely affected by the drought in summer 2018, as well as a less affected area south-west of Zurich, (elevation: 360 – 667 m a.s.l., MGT: 15.0 °C, MGP: 618 mm; **Figure 2, Supplementary Table S1**).

Between the end of August and mid-September 2018, 963 mature beech trees (394 trees in Basel, 300 trees in Schaffhausen, 268 trees in Zurich) in patches of three to five trees (207 tree groups in total) were selected and marked permanently in pure and mixed, moderately managed beech stands with natural regeneration (Wohlgemuth et al. 2020). Study trees were dominant and co-dominant trees with diameters mostly >30 cm that had no or very few dead branches. The initial set included 824 trees that exhibited premature leaf discoloration of at least 50% of the crown volume or even partial leaf shedding before mid-September (hereafter referred to as early leaf fall trees) and 139 trees whose leaves were still green by mid-September (hereafter referred to as control trees). In the area of Schaffhausen, most of the trees were showing signs of premature leaf senescence and thus, it was not possible to select control trees.

Crown condition monitoring and individual tree parameters

For three growing seasons, we assessed the crown condition of drought damaged and control trees and used multiple regression analysis to study the potential influence of several tree, stand, site, and climate parameters as potential predisposing factors on the observed damage and to determine their relative importance. Crown condition of all trees was assessed for the first time at the end of the summer drought 2018 (i.e. in August and September 2018). Further crown condition assessments were conducted in spring 2019 (April, Mai) and in the summers of 2019, 2020, and 2021 (July, August). Specifically, we visually estimated crown dieback as the volume proportion of dead branches (including lost branches) relative to the volume of the total potential crown of the healthy tree, thereby excluding naturally dying branches in the shaded part of the crown (Dobbertin et al. 2016). Crown dieback was estimated in 5%-classes, ranging from 0% (no crown dieback) to 100% (fully dead crown). A branch (> 4 cm) was considered dead if no living tissue (leaves, buds) was present. Recently lost branches (since August 2018) were also included in the proportion of dead branches by estimating their original branch volume. As a proxy of crown defoliation, crown transparency was estimated as the percentage of leaf loss (i.e. leaf buds that do not form or that have not sprouted/burst in relation to the maximum possible leaf volume) compared to a reference tree with a fully foliated crown from a photo guide with species specific reference standards (Eichhorn et al. 2016). Dead branches were excluded from the assessment of crown defoliation. Defoliation was estimated in 5%-classes, ranging from 0% (no defoliation) to 100% (fully defoliated crown). As a measure of tree recovery, we assessed the proportion of branches that produced fresh leaf biomass in the crown after the 2018 drought. Study trees that had no remaining visible living leaf tissue were considered as dead (tree mortality). As secondary damage parameters, the presence of bark beetle holes and of fresh bleeding cankers on each trunk was recorded from the root collar to a height of 2 m above ground in summer 2019, 2020 and

2021. All observations in a year were performed by the same expert-trained team and teams were calibrated against each other.

For each selected tree, we measured its diameter at breast height (DBH) with a measuring tape, assessed its social position (dominant, co-dominant) as well as the aspect and topography of its environment according to the ICP Forests definition and guidelines of the National Forest Inventory (Düggelin et al. 2020). Tree positions were recorded using a GNSS receiver (GeoXH 6000 DGNSS, Trimble Navigation Limited, Sunnyvale, CA, USA). Post-processed coordinates achieved a horizontal precision of 0.1 – 2 m. As trees are expected to be more vulnerable to drought damage with increasing height and decreasing distance to the forest edge, these parameters were determined based on tree coordinates, a vegetation height model and a forest mask from the Swiss National Forest Inventory (Waser et al. 2015). During the initial survey in early fall 2018, mast seeding of each tree was visually assessed in four classes (0 = absent, 1 = scarce, 2 = medium, 3, = high; Rohmeder 1972), because it may render trees more susceptible to drought (Hacket-Pain et al. 2017).

Climate and stand parameters

As further potentially predisposing factors we considered site climate and stand parameters. We extracted temperature, precipitation, and incoming solar radiation for the location of each tree group from MeteoSwiss data downscaled to a 25 m grid (Source: MeteoSwiss). From these parameters, the climatic water balance (CWB) for the location of each tree group was calculated as the difference between precipitation and potential evapotranspiration. The latter was approximated from temperature and solar radiation according to Turc (1961). In the statistical models, we considered the growing season CWB (April to September) averaged over the years 2013 through 2019 because these years were characterized by repeated drought phases, which may potentially have affected tree health.

Furthermore, soil properties were considered as potential predisposing factors. Average soil depth for each tree group was determined with a steel auger that was driven into the ground up to a maximum depth of 120 cm (n = 2 per group). Additionally, a sample of the mineral topsoil (0-10 cm) was collected from the center of each tree group with a steel hand probe to determine soil pH of a 1:2 soil:0.01M CaCl₂ suspension using a pH meter in the lab. Additional soil properties (gravel volume and clay content) were derived from digital soil maps based on machine learning models (Baltensweiler et al. 2021). For both parameters we calculated the weighted mean of all values up to a depth of 100 cm.

Increased competition is another factor potentially aggravating drought damage. We determined the competition index according to Hegyi (1974) for each study tree to quantify competition among individual trees. To this purpose, we measured the distances between each of our study trees (target trees i) and all of their neighboring trees j with a DBH $\geq$20 cm within a 10 m radius using a Vertex clinometer (Haglof Vertex 3). DBH of all target trees i and neighboring trees j was measured with a measuring tape in summer 2021. Based on this data we calculated the competition index CI_i for each tree according to Hegyi (1974):

$$CI_i = \sum_{j=1}^{n} \frac{DBH_j/DBH_i}{Distance_{ij}}$$

Data analysis

We used binomial generalized linear mixed effects models (GLMMs) with logit link functions to quantify the influence of explanatory variables on the proportion of dead trees per tree group (cumulative tree mortality), crown dieback percentage of individual trees, the presence of bark beetle holes on each trunk, and the presence of fresh bleeding cankers on each trunk. Logged trees were excluded from all models because data for them was incomplete. The initial models contained the explanatory variables 'Leaf fall 2018', 'Region', the climatic

water balance for the growing season (April to September) averaged over the years 2013-2019 ('CWB'), the time interval between August 2018 and the survey ('Time interval'), diameter at breast height ('DBH'), 'Tree height', 'Competition index', the distance from the nearest forest edge ('Forest edge distance'), mast seeding status 2018 ('Seed mast 2018'), 'Social position', and the proportion of 'Crown dieback' (in the models for bark beetles and bleeding cankers) for each tree as well as mean 'Soil depth', mean 'Soil pH', 'Gravel content', 'Clay content' averaged for each tree group as fixed effects (**Table 1, Supplementary Table S4**). A quadratic term for 'Time interval' was included in the models for crown dieback and bleeding cankers to account for the non-linear temporal development of these response variables. To avoid convergence problems due to overfitting, 'Tree height' and 'Gravel content' had to be excluded from the models for bark beetles and bleeding cankers. These models also included two-way interactions of 'Leaf fall 2018' with some other explanatory variables. Continuous explanatory variables were standardized to zero mean and unit variance using the function 'decostand' from the R package 'vegan' (Oksanen et al. 2019) to make effect sizes comparable. 'Tree' nested within 'Tree group' nested within 'Region' was included as random effect to account for spatial autocorrelation of trees within the same tree group and for temporal autocorrelation among multiple observations of the same tree. Models were fitted using the R package glmmTMB (Brooks et al. 2017). Variance inflation factors (VIF) were calculated based on the models containing all fixed and random effects using the R package 'performance' (Lüdecke et al. 2021) to check for multicollinearity among factors. Factors with VIF > 5 were successively removed starting with the factor with the highest VIF until VIF < 5 for all parameters. This resulted in removing 'Region' from all models. Homogeneity and homoscedasticity of simulated scaled residuals was confirmed using the R package 'DHARMa' (Hartig 2021). A stepwise model reduction procedure was applied, in which individual interactions and main factors were systematically removed, while respecting the

principle of marginality to find the most parsimonious model. In each step we removed the factor that resulted in the largest reduction of Akaike's information criterion (AIC) in comparison to the previous model. This procedure was repeated as long as a factor removal reduced AIC by more than 2 (Zuur et al. 2009). All analyses were performed with the statistical software R (R Development Core Team 2021).

Results

Tree mortality

All study trees were alive at the beginning of the project in August 2018. Thereafter, the proportion of dead trees in all regions continuously increased with mean annual mortality rates between 2018 and 2021 of 2.1% and 0.5% in early leaf fall and control trees, respectively. In summer 2021, cumulative mortality (excluding logging) reached $7.2 \pm 1.1\%$ and $1.3 \pm 0.9\%$ (mean $\pm$ 1 SE) for early leaf fall and control trees, respectively. In the same year, the cumulative percentage of standing dead trees with respect to the total number of early leaf fall trees was $10.3 \pm 2.0\%$ in Schaffhausen (31 of 249 trees), $7.2 \pm 1.6\%$ in Basel (22 of 178 trees), and $3.8 \pm 2.0\%$ in Zurich (4 of 196 trees), whereas the values for control trees were only $2.1 \pm 1.4\%$ in Basel (2 of 81 trees) and $0.0 \pm 0.0\%$ in Zurich (0 of 41 trees; no observations in Schaffhausen), respectively (**Figure 3A, Supplementary Table S2**). A substantial number of trees (207, i.e. $21.2 \pm 2.5\%$) have been logged by 2021, often to prevent damage to people and infrastructure due to uncontrolled branch and trunk breakage in damaged trees. These logged trees were excluded from the analysis because their crown condition at the time of felling was unknown and time series for these trees were incomplete. Overall, mortality and logging combined accounted for a loss of 25.6% of the 963 study trees by summer 2021. While the health status of logged trees at the time of cutting could not be recorded, only 19.7% of these trees showed $\geq 80\%$ crown dieback or were dead in the last survey before logging. At this time (the last survey before logging), mean crown dieback of logged trees was 63% higher than the highest observed mean crown dieback for all other trees ($41.3 \pm 2.4\%$ vs. $25.3 \pm 1.2\%$ for logged and remaining trees, respectively).

Mixed model analysis confirmed that tree mortality was significantly higher in early leaf fall trees ($P = 0.001$) and in locations with a greater CWB deficit ($P = 0.005$; **Table 2A**).

Beech trees with a greater DBH ($P = 0.04$) and trees that were under higher competition ($P = 0.03$) also showed higher mortality. Finally, mortality increased monotonously over time ($P < 0.001$).

Crown dieback

In the first survey in early fall 2018, crown dieback was very low with an average of $1.2 \pm 0.1\%$ dead branches in the crown for early leaf fall trees and $0.1 \pm 0.1\%$ for control trees (**Figure 3B, Supplementary Table S3A**). Crown dieback steadily increased and peaked in August 2019 for control trees at $8.1 \pm 0.4\%$ and in August 2020 for early leaf fall trees at $29.2 \pm 1.3\%$, before decreasing again in August 2021 to averages of $5.4 \pm 1.1\%$ and $25.5 \pm 1.4\%$, respectively. Crown dieback for early leaf fall trees reached peak values of $35.4 \pm 2.6\%$ in Basel, $30.2 \pm 2.2\%$ in Schaffhausen, and $22.3 \pm 2.1\%$ in Zurich in 2020. For this analysis, we excluded all logged and dead trees, as data series were not complete. In all surveys, crown dieback was about 5 times higher in early leaf fall trees than in control trees.

Crown dieback was best explained by climate, soil, and tree size variables. It was higher at sites with more negative CWB ($P < 0.001$; **Table 2B**). Dieback was elevated on soils with higher gravel content ($P = 0.01$) and with higher clay content ($P < 0.001$). Larger trees (DBH; $P = 0.02$) and taller trees (tree height; $P = 0.02$) also exhibited elevated dieback. The significant interaction of time interval $\times$ leaf fall shows that the increase in crown dieback over time was significantly higher in trees with early leaf fall compared to control trees ($P < 0.001$). Crown dieback peaked in 2020 and was followed by lower values due to partial recovery, indicated by the significant quadratic term of the time interval between August 2018 and the surveys ($P < 0.001$). All other variables in the initial model did not significantly influence crown dieback.

Secondary damage

The proportion of trees with bleeding cankers was <2% in the first inventory in 2018 (**Figure 4A, Supplementary Table S3B**). In the aftermath of the 2018 drought, proportions peaked in summer 2019 for trees in Zurich at 26.5% and 4.9% for early leaf fall and control trees, respectively, and in summer 2020 for trees in Basel (23.2% vs. 16.0%, respectively) and Schaffhausen (26.3% for early leaf fall trees). Thereafter, the proportion of trees with bleeding cankers decreased to less than 6% in summer 2021. Proportions were more than three times higher in early leaf fall than in control trees. The cumulative proportion of trees with bark beetle holes continuously increased in the three years after the 2018 drought (**Figure 4B, Supplementary Table S3C**). In 2021, bark beetle holes were present on 21.5% of all trees. There was a non-significant tendency that early leaf fall trees were more affected than control trees (22.8% v. 14.8%; $P = 0.84$). The highest percentage of affected trees was found among early leaf fall trees in Schaffhausen (31.5%).

Mixed models showed that bleeding cankers were more frequently found on early leaf fall trees ($P = 0.002$; **Table 2C**) and on trees with higher crown dieback values ($P < 0.001$). They were most frequently observed 1–2 years after 2018, indicated by the significant quadratic term for time interval ($P < 0.001$). Presence of bleeding cankers was also more frequent on trees with a greater DBH ($P < 0.001$) and at locations with more negative CWB ($P < 0.001$) and higher soil pH ($P = 0.05$), as well as on trees located closer to the forest edge ($P = 0.03$). The other factors in the initial model did not significantly influence bleeding canker occurrence. The number of trees with presence of bark beetle holes increased with the percentage of crown dieback ($P < 0.001$; **Table 2D**) and with the time elapsed after August 2018 ($P < 0.001$). None of the other factors in the initial model significantly influenced the presence of bark beetle holes.

Discussion

The large-scale monitoring of nearly a thousand beech trees for three consecutive years following the extreme 2018 drought showed continuously increasing tree mortality, which was potentially exacerbated by the repeated hot and dry weather conditions in 2019 and 2020. Significantly higher mortality and crown dieback were observed in trees that showed premature leaf senescence during summer 2018 as well as for trees growing on drier sites, i.e. where average CWB was more negative. Similarly, the frequency of bleeding cankers and bark beetles as typical symptoms of secondary damage increased for at least two years after the extreme drought in 2018. Partial decreases in crown dieback and bleeding cankers in the third year suggest that European beech can slowly recover, provided there are no additional disturbances or recurring droughts. Our results also reveal that larger and taller trees (defined by DBH and/or tree height) were more affected by drought. Finally, elevated crown dieback was found on soils with higher gravel and clay contents, whereas bleeding cankers and bark beetle holes occurred more frequently in trees that had higher proportions of crown dieback indicating a predisposition for drought damage.

Drought-induced mortality

Our repeated beech monitoring after the 2018 drought showed substantial tree mortality one year after the drought and a continued increase in the two subsequent years **(Figure 3)**. The resulting mean annual mortality rate of 2.1% in early leaf fall trees was 1.6 times higher than the long-term background annual mortality rate of beech (DBH >5 cm; Etzold et al. 2019). The observed increasing beech mortality for at least three years confirms earlier observations indicating that severe droughts and heat-waves can not only cause direct heat-induced damage (Marchin et al. 2022) and immediate tree mortality (Williams et al. 2013, Schuldt et al. 2020), but can also incite tree decline leading to mortality over several years or even decades after a

drought (Peterken and Mountford 1996, Cavin et al. 2013). Such lagged mortality after drought may be the result of preferential carbon allocation to rebuild damaged tissue, which could lead to carbon starvation in the long-term (Trugman et al. 2018, Massonnet et al. 2021) or of insect and pathogen attacks that contribute to the decline by negatively affecting tree functioning for several years (Anderegg et al. 2015a, Huang et al. 2020, Kannenberg et al. 2020). The years 2014 to 2018 were the five driest years recorded in Central Europe in the 253-year period 1766–2018 with respect to soil moisture (Moravec et al. 2021). They were followed by recurring droughts in 2019 and 2020 **(Figure 2)**. This extraordinary series of dry years may have aggravated stress on already weakened trees and accelerated vitality decline (Schuldt et al. 2020). In summary, impacts of this prolonged drought, evident in long-term growth declines in large-scale tree ring chronologies (Cailleret et al. 2017, Kannenberg et al. 2019, Vitasse et al. 2019), may have contributed to the observed mortality. By combining data from several forest health monitoring networks, George et al. (2021) found significantly increased beech mortality in Europe over the last 25 years. Primary weaknesses of such assessments based on national forest monitoring networks are the multi-year inventory intervals and the timing of assessments that may dilute the climate signal on mortality and thus underestimate mortality rates (Hülsmann et al. 2016, Hember et al. 2017). In order to more efficiently detect effects of severe drought on tree decline, high spatial and temporal resolution in forest monitoring should be re-considered (Hartmann et al. 2018, Rohner et al. 2021). Such fine-scale assessments were initiated during the forest decline debate of the 1980ies, but efforts were reduced again after the year 2000 (Ferretti 2021). Furthermore, combining ground-based monitoring with remote sensing methods is important to bridge spatial scales as suggested by the IUFRO-initiated International Tree Mortality Network (Hartmann et al. 2018).

Although we identified logging as a cause of additional mortality that we were able to disentangle from drought-induced mortality **(Supplementary Table S2)**, the large number of trees lost through logging renders our interpretation of crown dieback and secondary damage conservative, given that the percentage of felled early leaf fall trees was double the one of control trees and logged early leaf fall trees showed almost four times larger crown dieback ($23.0 \pm 0.6\%$ vs $6.0 \pm 0.4\%$). Nevertheless, the relatively low average dieback values of the trees before logging suggest that crown dieback increased drastically between the last survey and the logging, or that not only severely damaged or dead trees but also quite healthy trees were cut, probably for operational and technical reasons.

Premature leaf senescence as a preliminary sign of drought-induced damage

Drought-induced leaf discoloration and early leaf fall were widely observed phenomena in summer 2018 (Schuldt et al. 2020, Bigler and Vitasse 2021) and remote sensing data confirmed that large parts of the natural range of European beech were affected (Baltensweiler et al. 2020, Brun et al. 2020, Sturm et al. 2022). Our ground-measured data show that trees with early leaf fall in 2018 had increased proportions of crown dieback and tree mortality as well as an increased susceptibility to secondary damage for at least two consecutive years as compared to trees that exhibited normal senescence timing in 2018 **(Figures 3, 4)**. These results suggest that early leaf fall is an indicator of a predisposition of beech trees for decline incited by the drought event (Manion 1991, Walthert et al. 2021). They are in line with our predictions and with recent findings of Walthert et al. (2021) demonstrating clear relationships between soil water potential, leaf water potential and crown dieback in years following an extreme drought. Although early leaf fall may initially have been a physiological response to reduce water loss and xylem tension with the aim to avoid embolism (Wolfe et al. 2016), our results suggest that the 2018 drought was so severe that it

was – in particular in dry regions – an inciting event causing widespread hydraulic failure (Brodribb et al. 2020, Wohlgemuth et al. 2020, Arend et al. 2021, Walthert et al. 2021, Arend et al. 2022) with subsequent crown-dieback, which ultimately leads to higher tree mortality (Chakraborty et al. 2017, Leuschner 2020, Schuldt et al. 2020). In these regions, the observed early leaf senescence during summer 2018 was in fact an indicator of stress and a predisposition for eventual crown dieback and tree mortality.

The presence of bleeding cankers and bark beetle holes increased for at least two years after the drought, with early leaf fall trees being more frequently affected than control trees **(Figure 4)**, which also suggests that these trees were predisposed for decline. Both secondary damage symptoms were also positively correlated with the percentage of crown dieback, suggesting that drought legacy had increased susceptibility of these beech trees to secondary damage (Schuldt et al. 2020). This phenomenon is particularly known for bark beetle attacks in Norway spruce (Biedermann et al. 2019) but was also observed in other species (e.g., Bigler et al. 2006). For beech, it has been shown that drought-affected trees are more vulnerable to infestations by beech splendor beetle (*Agrilus viridis*) and microfungi (Bolte et al. 2009, Jung 2009, Gösswein et al. 2017, Corcobado et al. 2020), acting as factors contributing to decline. *Agrilus* infestations were also observed in our study, but the beetle occurred mainly in the canopy and its population size could thus not be quantified. As contributing factors, such insect infestations can exacerbate the vitality decline of trees, driving the 'decline spiral' towards mortality (Manion 1991). Accordingly, Jung (2009) related beech decline in Central Europe after the 2003 drought to the interaction between climatic extremes (inciting factors) and *Phytophthora* sp. infections (contributing factor). Yet, we detected only a few *Phytophthora* sp. infections in our study trees (data not shown) suggesting that the occurrence of bleeding cankers was rather due to physiological stress or other non-targeted biotic agents.

Contrary to our expectation that premature leaf senescence eventually leads to partial or full crown mortality and to secondary damage, proportions of crown dieback and the presence of bleeding cankers and bark beetle holes remained constant or slightly decreased between 2020 and 2021 **(Figures 3, 4)**, indicating partial recovery. The reduced proportion of crown dieback in the rather wet summer 2021 was likely due to regrowth of new crown biomass, such as twigs and leaves (Jump et al. 2017, Gessler et al. 2020), as indicated by decreasing crown transparency and an increasing proportion of trees that produced epicormic branches in the crown (**Supplementary Figure S1; Supplementary Table S3**). While full recovery from mild droughts is possible within a short time, more severe events cause structural damage that can only be compensated by the regrowth of new tissue, which is a relatively slow process (Ruehr et al. 2019). On the one hand, rapid recovery of radial growth within a few years after drought has repeatedly been described in beech (e.g., Bolte et al. 2010, Scharnweber et al. 2011, Pretzsch et al. 2020). On the other hand, longer-term growth decline (Peterken and Mountford 1996, Cavin et al. 2013) and aggravated negative growth impacts by the consecutive summer drought 2019 have also been reported (Schnabel et al. 2021). The three-year observation period of our study was too short to quantify to which extent drought damaged beech trees are able to recover because full recovery of tree vigor can take much longer and delayed mortality may also occur several years to decades post-drought (Trugman et al. 2018), particularly under recurring droughts (Mitchell et al. 2016).

Regional and local scale drivers of drought damage

Our monitoring showed that drought damage often affected patches of several beech trees next to unaffected individuals. Such small-scale variation in damage patterns have been described repeatedly but the causes are still unclear (Bréda et al. 2006, Trugman et al. 2021). These studies suggested local variability in site conditions, such as soil properties,

microtopography and stand structure, as predisposing factors for the variation in damage on small spatial scales. On a regional scale, our results showed higher tree mortality, higher degrees of crown dieback, and more bleeding cankers in the drier regions as indicated by the negative relation between these responses and the CWB **(Table 2)**. These findings are in line with our hypothesis that the proportions of mortality and secondary damage increase with increasing CWB deficit. Beech trees in drier regions operate closer to their physiological limits, and thus the extreme conditions of the 2018 drought and/or the sequence of multiple drought years in a row pushed them beyond these limits. The fact that regional climate is an important factor predisposing for drought damage was confirmed by evaluations of forest inventory data across the entire species range of beech in Europe demonstrating that climatic drought intensity was the most important driver for beech mortality (Neumann et al. 2017, Archambeau et al. 2020). Mortality of beech and several other tree species was also related to soil moisture in an analysis of ICP Forests data over 25 years (George et al. 2021) and mortality was related to water stress in several tree species across North America (Hember et al. 2017). In contrast, no long-term trend of increased beech mortality under drier conditions has been detected in data from the Swiss forest health monitoring network across broad ecological amplitudes (Etzold et al. 2019).

Contrary to our expectations and in contrast to reports of increased drought-induced beech mortality on shallow soils (Mueller et al. 2005, Allen et al. 2010, Schuldt et al. 2020), soil depth did not significantly predispose beech for drought damage in our study. One reason might be that sites with very shallow soils were not well represented. Also, the modeled soil parameters (Baltensweiler et al. 2021) may not have reproduced small scale variation in soil properties with sufficient accuracy. We found higher crown dieback on soils with higher gravel and clay contents, which may reduce soil water retention capacity as high gravel content increases soil drainage whereas high clay content reduces the amount of extractable

water (Hillel 1980). This result is in line with reports by Bréda et al. (2006) and Crouchet et al. (2019), suggesting small scale variation in soil parameters as driving factors for the diffuse or patchy distribution of drought damaged trees in forest stands. Likewise, Obladen et al. (2021) identified soil properties as key drivers of drought-induced beech mortality in central Germany. Similar to our results, they reported significant growth reduction in beech and Norway spruce at the study site with the highest soil clay content. Recurring droughts may have resulted in soil water depletion, while clay shrinkage might have truncated roots (Sanders et al. 2012).

As hypothesized, we found higher mortality, greater proportions of crown dieback and higher occurrence of bleeding cankers in larger trees **(Table 2)**. Elevated mortality in taller trees was reported from natural beech forests in Sweden and Ukraine, whereas no or an opposite size effect was described in Germany and Switzerland (Fuentes et al. 2010, Hülsmann et al. 2016). Likewise, Hember et al. (2017) found decreasing sensitivity to soil water deficit with increasing tree height in an analysis of North American forest inventory data. A possible explanation for these diverging findings may be that the influence of tree size on drought susceptibility depends on the severity of a drought, as larger trees were found to be more resilient to mild droughts but more vulnerable to severe events than smaller trees (Bottero et al. 2021). Additional factors, such as forest openings due to management, may potentially have amplified crown damage by increasing sun-burn of leaves. However, they are unlikely to have affected crown condition at our study sites because the degree of crown damage did not correlate with the proportion of missing trees (stumps) in the neighborhood (data not shown). Tree mortality in our study increased with increasing competition by neighboring trees. Similarly, Klesse et al. (2022) found that drought-induced crown damage was more severe in shorter and slower-growing beech trees that experience stronger

competition. These differences among individual trees further emphasize the importance of local-scale processes in determining drought effects on trees.

Conclusions

Our large-scale beech monitoring for three consecutive years following the extreme 2018 hot drought found increasing crown and tree mortality, as well as secondary damage symptoms after early leaf senescence providing evidence for adverse drought legacy effects. These findings suggest that premature leaf senescence was an indicator of predisposition of beech trees for decline on dry sites. The severe drought in summer 2018 incited a decline, which may end in tree mortality, particularly if contributing insect and pathogen attacks exacerbate the tree condition. Recurring droughts in the two subsequent years have likely aggravated the stress for beech trees. While climatic drought intensity determined drought damage at regional scale, soil properties, tree and stand characteristics modulated local damage patterns resulting in patches of trees suffering severe damage located in proximity to patches of more drought-resistant trees. Crown tissue regrowth in later years of the monitoring indicates the beginning of partial canopy recovery, which may ultimately result in either long-term tree resilience or increased drought susceptibility. Under future climate change with increasing frequency and intensity of droughts and heat spells, further beech decline may be expected on dry sites in northern Switzerland. This underlines the importance of adapting forest management to the changing climate for example by promoting mixed stands with better heat- and drought-adapted species in order to increase forest resilience.

Acknowledgements

References

Adams, H.D., Zeppel, M.J.B., Anderegg, W.R.L., Hartmann, H., Landhausser, S.M., Tissue, D.T., et al. 2017. A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. Nature Ecology & Evolution **1**:1285-1291. doi: 10.1038/s41559-017-0248-x.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management **259**:660-684. doi: 10.1016/j.foreco.2009.09.001.

Allen, C.D., Breshears, D.D., and McDowell, N.G. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere **6**. doi: 10.1890/es15-00203.1.

Anderegg, W.R.L., Kane, J.M., and Anderegg, L.D.L. 2013. Consequences of widespread tree Mortality triggered by drought and temperature stress. Nature Climate Change **3**:30-36. doi: 10.1038/nclimate1635.

Anderegg, W.R.L., Hicke, J.A., Fisher, R.A., Allen, C.D., Aukema, J., Bentz, B., et al. 2015a. Tree mortality from drought, insects, and their interactions in a changing climate. New Phytologist **208**:674-683. doi: 10.1111/nph.13477.

Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., et al. 2015b. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science **349**:528-532. doi: 10.1126/science.aab1833.

Archambeau, J., Ruiz-Benito, P., Ratcliffe, S., Frejaville, T., Changenet, A., Castaneda, J.M.M., et al. 2020. Similar patterns of background mortality across Europe are mostly driven by drought in European beech and a combination of drought and competition in Scots pine. Agricultural and Forest Meteorology **280**. doi: 10.1016/j.agrformet.2019.107772.

Arend, M., Link, R.M., Patthey, R., Hoch, G., Schuldt, B., and Kahmen, A. 2021. Rapid hydraulic collapse as cause of drought-induced mortality in conifers. Proceedings of the National Academy of Sciences of the United States of America **118**. doi: 10.1073/pnas.2025251118.

Arend, M., Link, R.M., Zahnd, C., Hoch, G., Schuldt, B., and Kahmen, A. 2022. Lack of hydraulic recovery as a cause of post-drought foliage reduction and canopy decline in European beech. New Phytologist **234**:1195-1205. doi: 10.1111/nph.18065.

Baltensweiler, A., Brun, P., Pranga, J., Psomas, A., Zimmermann, N.E., and Ginzler, C. 2020. Räumliche Analyse von Trockenheitssymptomen im Schweizer Wald mit Sentinel-2-Satellitendaten. Schweizerische Zeitschrift für Forstwesen **171**:298-301. doi: 10.3188/szf.2020.0298.

Baltensweiler, A., Walthert, L., Hanewinkel, M., Zimmermann, S., and Nussbaum, M. 2021. Machine learning based soil maps for a wide range of soil properties for the forested area of Switzerland. Geoderma Regional **27**. doi: 10.1016/j.geodrs.2021.e00437.

Bastos, A., Ciais, P., Friedlingstein, P., Sitch, S., Pongratz, J., Fan, L., et al. 2020. Direct and seasonal legacy effects of the 2018 heat wave and drought on European ecosystem productivity. Science Advances **6**. doi: 10.1126/sciadv.aba2724.

Bennett, A.C., McDowell, N.G., Allen, C.D., and Anderson-Teixeira, K.J. 2015. Larger trees suffer most during drought in forests worldwide. Nature Plants **1**. doi: 10.1038/nplants.2015.139.

Biedermann, P.H.W., Muller, J., Gregoire, J.C., Gruppe, A., Hagge, J., Hammerbacher, A., et al. 2019. Bark Beetle Population Dynamics in the Anthropocene: Challenges and

Solutions. Trends in Ecology & Evolution **34**:914-924. doi: 10.1016/j.tree.2019.06.002.

Bigler, C., Braker, O.U., Bugmann, H., Dobbertin, M., and Rigling, A. 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems **9**:330-343. doi: 10.1007/s10021-005-0126-2.

Bigler, C., and Vitasse, Y. 2021. Premature leaf discoloration of European deciduous trees is caused by drought and heat in late spring and cold spells in early fall. Agricultural and Forest Meteorology **307**. doi: 10.1016/j.agrformet.2021.108492.

Bircher, N., Cailleret, M., Zingg, A., and Bugmann, H. 2016. Potenzielle Grundflächenveränderungen auf Bestandesebene im Klimawandel. *In* Wald und Klimawandel. Grundlagen für Adaptationsstrategien. *Edited by* A. R. Pluess, S. Augustin, and P. Brang. Haupt, Bern. pp. 157-171.

Boergens, E., Guntner, A., Dobslaw, H., and Dahle, C. 2020. Quantifying the Central European Droughts in 2018 and 2019 With GRACE Follow-On. Geophysical Research Letters **47**. doi: 10.1029/2020gl087285.

Bogdziewicz, M., Kelly, D., Thomas, P.A., Lageard, J.G.A., and Hacket-Pain, A. 2020. Climate warming disrupts mast seeding and its fitness benefits in European beech. Nature Plants **6**:88-94. doi: 10.1038/s41477-020-0592-8.

Bolte, A., Ammer, C., Lof, M., Madsen, P., Nabuurs, G.J., Schall, P., et al. 2009. Adaptive forest management in central Europe: Climate change impacts, strategies and integrative concept. Scandinavian Journal of Forest Research **24**:473-482. doi: 10.1080/02827580903418224.

Bolte, A., Hilbrig, L., Grundmann, B., Kampf, F., Brunet, J., and Roloff, A. 2010. Climate change impacts on stand structure and competitive interactions in a southern Swedish spruce-beech forest. European Journal of Forest Research **129**:261-276. doi: 10.1007/s10342-009-0323-1.

Bolte, A., Czajkowski, T., Cocozza, C., Tognetti, R., de Miguel, M., Psidova, E., et al. 2016. Desiccation and Mortality Dynamics in Seedlings of Different European Beech (*Fagus sylvatica* L.) Populations under Extreme Drought Conditions. Frontiers in Plant Science **7**. doi: 10.3389/fpls.2016.00751.

Bottero, A., Forrester, D.I., Cailleret, M., Kohnle, U., Gessler, A., Michel, D., et al. 2021. Growth resistance and resilience of mixed silver fir and Norway spruce forests in central Europe: Contrasting responses to mild and severe droughts. Global Change Biology **27**:4403-4419. doi: 10.1111/gcb.15737.

Bréda, N., Huc, R., Granier, A., and Dreyer, E. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Annals of Forest Science **63**:625-644. doi: 10.1051/forest:2006042.

Brodribb, T.J., and Cochard, H. 2009. Hydraulic Failure Defines the Recovery and Point of Death in Water-Stressed Conifers. Plant Physiology **149**:575-584. doi: 10.1104/pp.108.129783.

Brodribb, T.J., Powers, J., Cochard, H., and Choat, B. 2020. Hanging by a thread? Forests and drought. Science **368**:261-266. doi: 10.1126/science.aat7631.

Brooks, M.E., Bates, D.M., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., et al. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal **9**: 378-400.

Brück-Dyckhoff, C., Petercord, R., and Schopf, R. 2019. Vitality loss of European beech (*Fagus sylvatica* L.) and infestation by the European beech splendour beetle (*Agrilus viridis* L., Buprestidae, Coleoptera). Forest Ecology and Management **432**:150-156. doi: 10.1016/j.foreco.2018.09.001.

Brun, P., Psomas, A., Ginzler, C., Thuiller, W., Zappa, M., and Zimmermann, N.E. 2020. Large-scale early-wilting response of Central European forests to the 2018 extreme drought. Global Change Biology **26**:7021-7035. doi: 10.1111/gcb.15360.

Buras, A., Schunk, C., Zeitrag, C., Herrmann, C., Kaiser, L., Lemme, H., et al. 2018. Are Scots pine forest edges particularly prone to drought-induced mortality? Environmental Research Letters **13**:025001. doi: 10.1088/1748-9326/aaa0b4.

Buras, A., Rammig, A., and Zang, C.S. 2020. Quantifying impacts of the 2018 drought on European ecosystems in comparison to 2003. Biogeosciences **17**:1655-1672. doi: 10.5194/bg-17-1655-2020.

Butin, H. 2019. Krankheiten der Wald- und Parkbäume. Eugen Ulmer Verlag, Stuttgart.

Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., et al. 2017. A synthesis of radial growth patterns preceding tree mortality. Global Change Biology **23**:1675-1690. doi: 10.1111/gcb.13535.

Castagneri, D., Vacchiano, G., Hacket-Pain, A., DeRose, R.J., Klein, T., and Bottero, A. 2022. Meta-analysis Reveals Different Competition Effects on Tree Growth Resistance and Resilience to Drought. Ecosystems **25**:30-43. doi: 10.1007/s10021-021-00638-4.

Caudullo, G., Welk, E., San-Miguel-Ayanz, J., 2017. Chorological maps for the main European woody species. Data in Brief **12**:662-666. doi: 10.1016/j.dib.2017.05.007.

Cavin, L., Mountford, E.P., Peterken, G.F., and Jump, A.S. 2013. Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. Functional Ecology **27**:1424-1435. doi: 10.1111/1365-2435.12126.

Chakraborty, T., Saha, S., Matzarakis, A., and Reif, A. 2017. Influence of multiple biotic and abiotic factors on the crown die-back of European beech trees at their drought limit. Flora **229**:58-70. doi: 10.1016/j.flora.2017.02.012.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., et al. 2012. Global convergence in the vulnerability of forests to drought. Nature **491**:752-755. doi: 10.1038/nature11688.

Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., Lopez, R., and Medlyn, B.E. 2018. Triggers of tree mortality under drought. Nature **558**:531-539. doi: 10.1038/s41586-018-0240-x.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., et al. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature **437**:529-533. doi: 10.1038/nature03972.

Clark, J.S., Iverson, L., Woodall, C.W., Allen, C.D., Bell, D.M., Bragg, D.C., et al. 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. Global Change Biology **22**:2329-2352. doi: 10.1111/gcb.13160.

Corcobado, T., Cech, T.L., Brandstetter, M., Daxer, A., Huttler, C., Kudlacek, T., et al. 2020. Decline of European Beech in Austria: Involvement of *Phytophthora* spp. and Contributing Biotic and Abiotic Factors. Forests **11**. doi: 10.3390/f11080895.

Crouchet, S.E., Jensen, J., Schwartz, B.F., and Schwinning, S. 2019. Tree Mortality After a Hot Drought: Distinguishing Density-Dependent and -Independent Drivers and Why It Matters. Frontiers in Forests and Global Change **2**. doi: 10.3389/ffgc.2019.00021.

Dobbertin, M., Hug, C., Schwyzer, A., Borer, S., Schmalz, H., 2016. Aufnahmeanleitung - Kronenansprachen auf den Sanasilva- und den LWF-Flächen, V10-16. Swiss Federal Research Institute WSL, Birmensdorf, Switzerland.

Düggelin, C., Abegg, M., Bischof, S., Brändli, U.-B., Cioldi, F., Fischer, C., et al. 2020. Schweizerisches Landesforstinventar. Anleitung für die Feldaufnahmen der fünften Erhebung 2018–2026. Swiss Federal Research Institute WSL, Birmensdorf, Switzerland.

Eichhorn, J., Roskams, P., Potočić, N., Timmermann, V., Ferretti, M., Mues, V., et al. 2016. Visual Assessment of Crown Condition and Damaging Agents. Manual Part IV. *In* Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests. *Edited by* U. I. F. P. C. Centre. Thünen Institute of Forest Ecosystems, Eberswalde, Germany. pp. 54.

Etzold, S., Zieminska, K., Rohner, B., Bottero, A., Bose, A.K., Ruehr, N.K., et al. 2019. One Century of Forest Monitoring Data in Switzerland Reveals Species- and Site-Specific Trends of Climate-Induced Tree Mortality. Frontiers in Plant Science **10**. doi: 10.3389/fpls.2019.00307.

Ferretti, M. 2021. Origin, features, vision and objectives of the Swiss AIM initiative. In M. Ferretti, C. Fischer, & A. Gessler (Eds.), WSL Berichte: Vol. 106. Towards an advanced inventorying and monitoring system for the Swiss forest (pp. 7-15). Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland.

Fuentes, M., Niklasson, M., Drobyshev, I., and Karlsson, M. 2010. Tree mortality in a semi-natural beech forest in SW Sweden. Ecological Bulletins **53**:117–130.

Giardina, F., Konings, A.G., Kennedy, D., Alemohammad, S.H., Oliveira, R.S., and Gentine, P. 2018. Tall Amazonian forests are less sensitive to precipitation variability. Nature Geoscience **11**:405-409. doi:10.1038/s41561-018-0133-5.

George, J.-P., Sanders, T.G., Neumann, M., Cammalleri, C., Vogt, J.V., and Lang, M. 2021. Long-term forest monitoring unravels constant mortality rise in European forests. bioRxiv **2021.11.01.466723**. doi: 10.1101/2021.11.01.466723.

Gessler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., and Rennenberg, H. 2007. Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. Trees - Structure and Function **21**:1-11. doi: 10.1007/s00468-006-0107-x.

Gessler, A., Schaub, M., and McDowell, N.G. 2017. The role of nutrients in drought-induced tree mortality and recovery. New Phytologist **214**:513-520. doi: 10.1111/nph.14340.

Gessler, A., Bottero, A., Marshall, J., and Arend, M. 2020. The way back: recovery of trees from drought and its implication for acclimation. New Phytologist **228**:1704-1709. doi: 10.1111/nph.16703.

Gösswein, S., Lemme, H., and Petercord, R. 2017. Prachtkäfer profitieren vom Trockensommer 2015. LWF Wissen **1**:14–17. doi:

Grote, R., Gessler, A., Hommel, R., Poschenrieder, W., and Priesack, E. 2016. Importance of tree height and social position for drought-related stress on tree growth and mortality. Trees-Structure and Function **30**:1467-1482. doi: 10.1007/s00468-016-1446-x.

Hacket-Pain, A.J., Lageard, J.G.A., and Thomas, P.A. 2017. Drought and reproductive effort interact to control growth of a temperate broadleaved tree species (*Fagus sylvatica*). Tree Physiology **37**:744-754. doi: 10.1093/treephys/tpx025.

Hanel, M., Rakovec, O., Markonis, Y., Maca, P., Samaniego, L., Kysely, J., et al. 2018. Revisiting the recent European droughts from a long-term perspective. Scientific Reports **8**. doi: 10.1038/s41598-018-27464-4.

Hartig, F. 2021. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.4.

Hartmann, H., Schuldt, B., Sanders, T.G.M., Macinnis-Ng, C., Boehmer, H.J., Allen, C.D., et al. 2018. Monitoring global tree mortality patterns and trends. Report from the VW symposium 'Crossing scales and disciplines to identify global trends of tree mortality as indicators of forest health'. New Phytologist **217**:984-987. doi: 10.1111/nph.14988.

Hegyi, F. 1974. A simulation model for managing jack-pine stands. In Fries, J. (Ed.), Growth models for tree and stand simulation, Royal College of Forestry, Department of Forest Yield Research, Stockholm, Sweden. p.74–90.

Hember, R.A., Kurz, W.A., and Coops, N.C. 2017. Relationships between individual-tree mortality and water-balance variables indicate positive trends in water stress-induced tree mortality across North America. Global Change Biology **23**:1691-1710. doi: 10.1111/gcb.13428.

Hillel, D. 1980. Applications of Soil Physics. Academic Press, New York.

Huang, J.B., Kautz, M., Trowbridge, A.M., Hammerbacher, A., Raffa, K.F., Adams, H.D., et al. 2020. Tree defence and bark beetles in a drying world: carbon partitioning, functioning and modelling. New Phytologist **225**:26-36. doi: 10.1111/nph.16173.

Hülsmann, L., Bugmann, H.K.M., Commarmot, B., Meyer, P., Zimmermann, S., and Brang, P. 2016. Does one model fit all? Patterns of beech mortality in natural forests of three European regions. Ecological Applications **26**:2463-2477. doi: 10.1002/eap.1388.

Johnson, D.M., Domec, J.C., Berry, Z.C., Schwantes, A.M., McCulloh, K.A., Woodruff, D.R., et al. 2018. Co-occurring woody species have diverse hydraulic strategies and mortality rates during an extreme drought. Plant Cell and Environment **41**:576-588. doi: 10.1111/pce.13121.

Jump, A.S., Ruiz-Benito, P., Greenwood, S., Allen, C.D., Kitzberger, T., Fensham, R., et al. 2017. Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. Global Change Biology **23**:3742-3757. doi: 10.1111/gcb.13636.

Jung, T. 2009. Beech decline in Central Europe driven by the interaction between Phytophthora infections and climatic extremes. Forest Pathology **39**:73-94. doi: 10.1111/j.1439-0329.2008.00566.x.

Kannenberg, S.A., Maxwell, J.T., Pederson, N., D'Orangeville, L., Ficklin, D.L., and Phillips, R.P. 2019. Drought legacies are dependent on water table depth, wood anatomy and drought timing across the eastern US. Ecology Letters **22**:119-127. doi: 10.1111/ele.13173.

Kannenberg, S.A., Schwalm, C.R., and Anderegg, W.R.L. 2020. Ghosts of the past: how drought legacy effects shape forest functioning and carbon cycling. Ecology Letters **23**:891-901. doi: 10.1111/ele.13485.

Klesse, S., Wohlgemuth T., Meusburger K., Vitasse, Y., von Arx, G., Lévesque, M., et al. 2022. Long-term soil water limitation and previous tree vigor drive local variability of drought-induced crown dieback in *Fagus sylvatica*. Science of the Total Environment **851**:157926. doi: 10.1016/j.scitotenv.2022.157926.

Körner, C. 2019. No need for pipes when the well is dry-a comment on hydraulic failure in trees. Tree Physiology **39**:695-700. doi: 10.1093/treephys/tpz030.

Leuschner, C., Meier, I.C., and Hertel, D. 2006. On the niche breadth of *Fagus sylvatica*: soil nutrient status in 50 Central European beech stands on a broad range of bedrock types. Annals of Forest Science **63**:355-368. doi: 10.1051/forest:2006016.

Leuschner, C., and Ellenberg, H. 2017. Ecology of Central European Forests - Vegetation Ecology of Central Europe, Volume I 6th edition. Springer Nature, Stuttgart, Germany.

Leuschner, C., and Meier, I.C. 2018. The ecology of Central European tree species: Trait spectra, functional trade-offs, and ecological classification of adult trees. Perspectives in Plant Ecology Evolution and Systematics **33**:89-103. doi: 10.1016/j.ppees.2018.05.003.

Leuschner, C. 2020. Drought response of European beech (*Fagus sylvatica* L.)—A review. Perspectives in Plant Ecology, Evolution and Systematics **47**. doi: 10.1016/j.ppees.2020.125576.

Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., and Makowsk, D. 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. Journal of Open Source Software **6**:3139. doi: 10.21105/joss.03139.

Manion, P.D. 1991. Tree disease concepts. 2nd ed. Englewood Cliffs, N.J., Prentice-Hall, New Jersey.

Marchin, R.M., Backes, D., Ossola, A., Leishman, M.R., Tjoelker, M.G., and Ellsworth, D.S. 2022. Extreme heat increases stomatal conductance and drought-induced mortality risk in vulnerable plant species. Global Change Biology **28**:1133-1146. doi: 10.1111/gcb.15976.

Martinez-Vilalta, J., Anderegg, W.R.L., Sapes, G., and Sala, A. 2019. Greater focus on water pools may improve our ability to understand and anticipate drought-induced mortality in plants. New Phytologist **223**:22-32. doi: 10.1111/nph.15644.

Massonnet, C., Chuste, P.A., Levillain, J., Gérémia, F., E Silva, D., Maillard, P., et al. 2021. Leafy season length is reduced by a prolonged soil water deficit but not by repeated defoliation in beech trees (*Fagus sylvatica* L.): comparison of response among regional populations grown in a common garden. Agricultural and Forest Meteorology **297**. doi: 10.1016/j.agrformet.2020.108228.

McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., et al. 2020. Pervasive shifts in forest dynamics in a changing world. Science **368**: (eaaz9463). doi: 10.1126/science.aaz9463.

Meier, I.C., and Leuschner, C. 2008. Belowground drought response of European beech: Fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. Global Change Biology **14**:2081-2095. doi: 10.1111/j.1365-2486.2008.01634.x.

Mitchell, P.J., O'Grady, A.P., Pinkard, E.A., Brodribb, T.J., Arndt, S.K., Blackman, C.J., et al. 2016. An ecoclimatic framework for evaluating the resilience of vegetation to water deficit. Global Change Biology **22**:1677-1689. doi: 10.1111/gcb.13177.

Moravec, V., Markonis, Y., Rakovec, O., Svoboda, M., Trnka, M., Kumar, R., et al. 2021. Europe under multi-year droughts: How severe was the 2014–2018 drought period? Environmental Research Letters **16**. doi: 10.1088/1748-9326/abe828.

Mueller, R.C., Scudder, C.M., Porter, M.E., Trotter, R.T., Gehring, C.A., and Whitham, T.G. 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. Journal of Ecology **93**:1085-1093. doi: 10.1111/j.1365-2745.2005.01042.x.

Neumann, M., Mues, V., Moreno, A., Hasenauer, H., and Seidl, R. 2017. Climate variability drives recent tree mortality in Europe. Global Change Biology **23**:4788-4797. doi: 10.1111/gcb.13724.

Nolan, R.H., Gauthey, A, Losso, A., Medlyn, B.E., Smith, R., Chhajed, S.S., et al. 2021. Hydraulic failure and tree size linked with canopy die-back in eucalypt forest during extreme drought. New Phytologist **230**: 1354–1365. doi: 10.1111/nph.17298.

Nussbaumer, A., Meusburger, K., Schmitt, M., Waldner, P., Gehrig, R., Haeni, M., et al. 2020. Extreme summer heat and drought lead to early fruit abortion in European beech. Scientific Reports **10**. doi: 10.1038/s41598-020-62073-0.

Obladen, N., Dechering, P., Skiadaresis, G., Tegel, W., Keßler, J., Höllerl, S., et al. 2021. Tree mortality of European beech and Norway spruce induced by 2018-2019 hot droughts in central Germany. Agricultural and Forest Meteorology **307**. doi: 10.1016/j.agrformet.2021.108482.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. 2019. vegan: community ecology package. R package version 2.5-6.

Packham, J.R., Thomas, P.A., Atkinson, M.D., and Degen, T. 2012. Biological Flora of the British Isles: *Fagus sylvatica*. Journal of Ecology **100**:1557-1608. doi: 10.1111/j.1365-2745.2012.02017.x.

Penuelas, J., and Boada, M. 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). Global Change Biology **9**:131-140. doi: 10.1046/j.1365-2486.2003.00566.x.

Peterken, G.F., and Mountford, E.P. 1996. Effects of drought on beech in Lady Park Wood, an unmanaged mixed deciduous woodland. Forestry **69**:125-136. doi: 10.1093/forestry/69.2.125.

Peters, W., Bastos, A., Ciais, P., and Vermeulen, A. 2020. A historical, geographical and ecological perspective on the 2018 European summer drought. Philosophical Transactions of the Royal Society B-Biological Sciences **375**. doi: 10.1098/rstb.2019.0505.

Pollastrini, M., Puletti, N., Selvi, F., Iacopetti, G., and Bussotti, F. 2019. Widespread Crown Defoliation After a Drought and Heat Wave in the Forests of Tuscany (Central Italy) and Their Recovery-A Case Study From Summer 2017. Frontiers in Forests and Global Change **2**. doi: 10.3389/ffgc.2019.00074.

Pretzsch, H., Schutze, G., and Biber, P. 2018. Drought can favour the growth of small in relation to tall trees in mature stands of Norway spruce and European beech. Forest Ecosystems **5**. doi: 10.1186/s40663-018-0139-x.

Pretzsch, H., Grams, T., Haberle, K.H., Pritsch, K., Bauerle, T., and Rotzer, T. 2020. Growth and mortality of Norway spruce and European beech in monospecific and mixed-species stands under natural episodic and experimentally extended drought. Results of the KROOF throughfall exclusion experiment. Trees-Structure and Function **34**:957-970. doi: 10.1007/s00468-020-01973-0.

R Development Core Team. 2021. R: A language and environment for statistical computing, Vienna, Austria.

Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M.D., Seneviratne, S.I., et al. 2013. Climate extremes and the carbon cycle. Nature **500**:287-295. doi: 10.1038/nature12350.

Ripullone, F., Camarero, J.J., Colangelo, M., and Voltas, J. 2020. Variation in the access to deep soil water pools explains tree-to-tree differences in drought-triggered dieback of Mediterranean oaks. Tree Physiology, 40:591-604. doi: 10.1093/treephys/tpaa026.

Rohmeder, E. 1972. Das Saatgut in der Forstwirtschaft. Paul Parey, Hamburg, Berlin.

Rohner, B., Kumar, S., Liechti, K., Gessler, A., and Ferretti, M. 2021. Tree vitality indicators revealed a rapid response of beech forests to the 2018 drought. Ecological Indicators **120**. doi: 10.1016/j.ecolind.2020.106903.

Rowland, L., da Costa, A., Galbraith, D., Oliveira, R.S., Binks, O.J., Oliveira, A.A.R., et al. 2015. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. Nature **528**:119-122. doi: 10.1038/nature15539.

Ruehr, N.K., Grote, R., Mayr, S., and Arneth, A. 2019. Beyond the extreme: recovery of carbon and water relations in woody plants following heat and drought stress. Tree Physiology **39**:1285-1299. doi: 10.1093/treephys/tpz032.

Sanders, T.G.M., Pitman, R., and Broadmeadow, M. 2012. Soil type modifies climate-growth response of beech in Southern Britain. In Proceedings of the DENDROSYMPOSIUM 2011: May 11th - 14th, 2011 in Orléans, France, (Scientific Technical Report; 12/03), 10th TRACE conference (Tree Rings in Archaeology, Climatology and Ecology) (Orléans, France 2011). Edited by H. Gärtner, P. Rozenberg, P. Montès, O. Bertel, I. Heinrich, and G. Helle. Deutsches GeoForschungsZentrum GFZ Potsdam. pp. 106-110.

Scharnweber, T., Manthey, M., Criegee, C., Bauwe, A., Schroder, C., and Wilmking, M. 2011. Drought matters - Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. Forest Ecology and Management **262**:947-961. doi: 10.1016/j.foreco.2011.05.026.

Schnabel, F., Purrucker, S., Schmitt, L., Engelmann, R.A., Kahl, A., Richter, R., et al. 2021. Cumulative growth and stress responses to the 2018-2019 drought in a European floodplain forest. Global Change Biology. doi: 10.1111/gcb.16028.

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., et al. 2020. A first assessment of the impact of the extreme 2018 summer drought on Central European forests. Basic and Applied Ecology **45**:86-103. doi: 10.1016/j.baae.2020.04.003.

Senf, C., Buras, A., Zang, C.S., Rammig, A., and Seidl, R. 2020. Excess forest mortality is consistently linked to drought across Europe. Nature Communications **11**. doi: 10.1038/s41467-020-19924-1.

Senf, C., and Seidl, R. 2021. Persistent impacts of the 2018 drought on forest disturbance regimes in Europe. Biogeosciences **18**:5223-5230. doi: 10.5194/bg-18-5223-2021.

Senf, C., Sebald, J., and Seidl, R. 2021. Increasing canopy mortality affects the future demographic structure of Europe's forests. One Earth **4**:749-755. doi: 10.1016/j.oneear.2021.04.008.

Sousa, P.M., Barriopedro, D., Garcia-Herrera, R., Ordonez, C., Soares, P.M.M., and Trigo, R.M. 2020. Distinct influences of large-scale circulation and regional feedbacks in two exceptional 2019 European heatwaves. Communications Earth & Environment **1**. doi: 10.1038/s43247-020-00048-9.

Stovall, A.E.L., Shugart, H., and Yang, X. 2019. Tree height explains mortality risk during an intense drought. Nature Communications **10**. doi: 10.1038/s41467-019-12380-6.

Sturm, J., Santos, M.J., Schmid, B., and Damm, A. 2022. Satellite data reveal differential responses of Swiss forests to unprecedented 2018 drought. Global Change Biology. doi: 10.1111/gcb.16136.

Suarez, M.L., and Kitzberger, T. 2008. Recruitment patterns following a severe drought: long-term compositional shifts in Patagonian forests. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **38**:3002-3010. doi: 10.1139/x08-149.

Trugman, A.T., Detto, M., Bartlett, M.K., Medvigy, D., Anderegg, W.R.L., Schwalm, C., et al. 2018. Tree carbon allocation explains forest drought-kill and recovery patterns. Ecology Letters **21**:1552-1560. doi: 10.1111/ele.13136.

Trugman, A.T., Anderegg, L.D.L., Anderegg, W.R.L., Das, A.J., and Stephenson, N.L. 2021. Why is Tree Drought Mortality so Hard to Predict? Trends in Ecology & Evolution **36**:520-532. doi: 10.1016/j.tree.2021.02.001.

Turc, L. 1961. Evaluation des besoins en eau d'irrigation, évapotranspiration potentielle, formule simplifié et mise à jour. Annales Agronomiques **12**:13-49.

van Mantgem, P. J., Stephenson, N.L., Byrne J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., and Veblen, T.T. 2009. Widespread Increase of Tree Mortality Rates in the Western United States Science **323**: 521-524. doi: 10.1126/science.1165000.

Vitasse, Y., Bottero, A., Cailleret, M., Bigler, C., Fonti, P., Gessler, A., et al. 2019. Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. Global Change Biology **25**:3781-3792. doi: 10.1111/gcb.14803.

Walthert, L., Ganthaler, A., Mayr, S., Saurer, M., Waldner, P., Walser, M., et al. 2021. From the comfort zone to crown dieback: Sequence of physiological stress thresholds in

mature European beech trees across progressive drought. Science of the Total Environment **753**. doi: 10.1016/j.scitotenv.2020.141792.

Waser, L.T., Fischer, C., Wang, Z.Y., and Ginzler, C. 2015. Wall-to-Wall Forest Mapping Based on Digital Surface Models from Image-Based Point Clouds and a NFI Forest Definition. Forests **6**:4510-4528. doi: 10.3390/f6124386.

Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., et al. 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change **3**:292-297. doi: 10.1038/nclimate1693.

Winter, S., and Möller, G.C. 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecology and Management **255**:1251-1261. doi: 10.1016/j.foreco.2007.10.029.

Wohlgemuth, T., Kistler, M., Aymon, C., Hagedorn, F., Gessler, A., Gossner, M.M., et al. 2020. Early leaf fall of European beech during the hot and dry summer of 2018: Resistance or sign of weakness? Schweizerische Zeitschrift für Forstwesen **171**:257-269. doi: 10.3188/szf.2020.0257.

Wolfe, B.T., Sperry, J.S., and Kursar, T.A. 2016. Does leaf shedding protect stems from cavitation during seasonal droughts? A test of the hydraulic fuse hypothesis. New Phytologist **212**:1007-1018. doi: 10.1111/nph.14087.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, United States.

Figure and table captions

Figure 1. Location of groups of beech trees monitored for drought damage from 2018 – 2021 in the three study regions near Basel, Schaffhausen and Zurich located in northern Switzerland. Map data derived from ©swisstopo, Esri® Data & Maps, and Caudullo et al. 2017.

Figure 2. Mean growing season (April to September) air temperature (a), growing season precipitation sum (b), and climatic water balance (CWB), i.e. precipitation minus potential evapotranspiration (c) for the period 1981 – 2021 for the three regions Basel (BL, red line), Schaffhausen (SH, green line), and Zurich (ZH, blue line) in northern Switzerland. Horizontal dashed lines indicate the corresponding value for the climate norm period 1981 – 2010 and grey shading the observation period of this study (2018 – 2021). Climate data derived from © MeteoSwiss (see Table S1 for details).

Figure 3. Development of cumulative tree mortality (A) and crown dieback (B) (mean ± SE) in early leaf fall (dashed lines) and control trees (solid lines) in the three regions Basel (BL), Schaffhausen (SH) and Zurich (ZH) in northern Switzerland from 2018 to 2021. Logged trees were excluded and in Panel B trees were excluded if time series were incomplete (N = 745; for numbers see also Supplementary Table S3).

Figure 4. Presence of fresh bleeding cankers (A) and bark beetle holes (B) in early leaf fall (dashed lines) and control trees (solid lines) in the three regions Basel (BL), Schaffhausen (SH) and Zurich (ZH) in northern Switzerland from 2018 to 2021. Trees with incomplete time series due to logging were excluded (N = 745; for numbers see also Supplementary Table S3).

Table 1. Response and explanatory variables that were used in regression models.

Table 2. Results of binomial generalized linear mixed effect models after stepwise model reduction for tree mortality (A), the proportion of crown dieback (B), the presence of bleeding cankers (C), and the presence of bark beetle holes (D). All models used a logit link function and included 'Tree' nested within 'Tree group' and 'Region' as random effect. Models were based on data from N = 176 tree groups for tree mortality, from N = 745 individual trees for crown dieback, bleeding cankers and bark beetles. Continuous explanatory variables were standardized to zero mean and unit variance. Significant explanatory variables are **in bold text** and non-significant factors that were dropped during model reduction are indicated with 'ns'. Factors that were not included in the initial models are indicated with '-'.

Tables

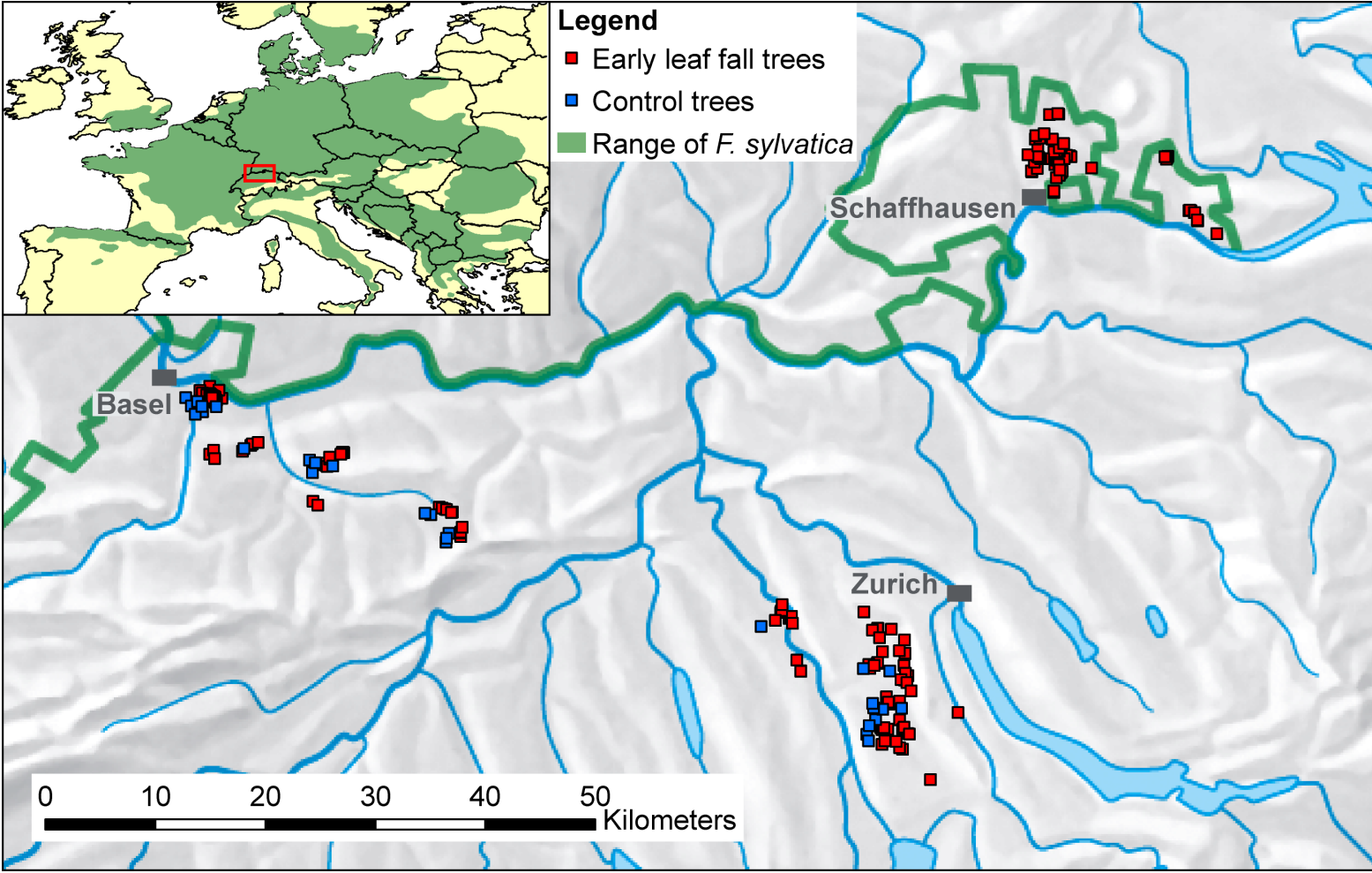**Table 1.** Response and explanatory variables that were used in regression models.

Variable	Description	Type	Survey
Response variables			
Bark beetles	Presence of bark beetle holes on the trunk	binary	t_1, t_2, t_4, t_5
Bleeding cankers	Presence of fresh bleeding cankers on the trunk	binary	t_1, t_2, t_4, t_5
Crown dieback	Proportion of crown dieback	proportion	t_0, t_1, t_2, t_4, t_5
Tree mortality	Proportion of dead trees per tree group	proportion	$t_0 - t_5$
Explanatory variables			
Clay content[1]	Weight fraction of clay in the fine earth	proportion	modeled
Competition index[1]	Hegyi's competition index, showing competition by neighboring trees (r = 10 m)	continuous	t_5
Crown dieback[2]	Proportion of crown dieback	proportion	t_2, t_4, t_5
CWB[1,2]	Mean climatic water balance of the growing season for 2013 – 2019	continuous	modeled
DBH[1]	Tree trunk diameter at breast height	continuous	t_0
Forest edge distance[1]	Distance from the nearest forest edge	continuous	modeled
Gravel content[1]	Volume fraction of gravel in the soil	proportion	modeled
Leaf fall 2018	Timing of leaf fall in 2018 (0 = normal, 1 = early)	binary	t_0
Region	Study region (Basel, Schaffhausen, Zurich)	categorical	–
Seed mast	Mast seeding status 2018 (0 = absent, 1 = scarce, 2 = medium, 3 = high)	ordinal	t_0
Social position	Social position of the tree (1 = dominant, 2 = co-dominant, 3 = sub-dominant)	ordinal	t_0
Soil depth[1]	Mean soil depth at stand level	continuous	t_4
Soil pH	Mean soil pH at stand level	continuous	t_4
Time interval[1,2]	Time interval between August 2018 and survey date	continuous	–
Tree height[1]	Tree height derived from the LFI vegetation height model	continuous	modeled

Superscript numbers after explanatory variables indicate two-way interactions with 'Leaf fall 2018' in the model with crown dieback (1), in the model with bleeding cankers (2) and in both models (1,2). Competition index, calculated according to (Hegyi 1974). CWB, climatic water balance of the growing season (April to September) averaged over the years 2013 through 2019, i.e. precipitation minus potential evapotranspiration. Type, variable type. Survey, dates of survey (t_0 = August 2018, t_1 = April 2019, t_2 = August 2019 t_3 = May 2020, t_4 = August 2020, t_5 = August 2021). Tree mortality was recorded during all six surveys. Modeled, variables derived from interpolated climate data, digital soil maps and vegetation height models.
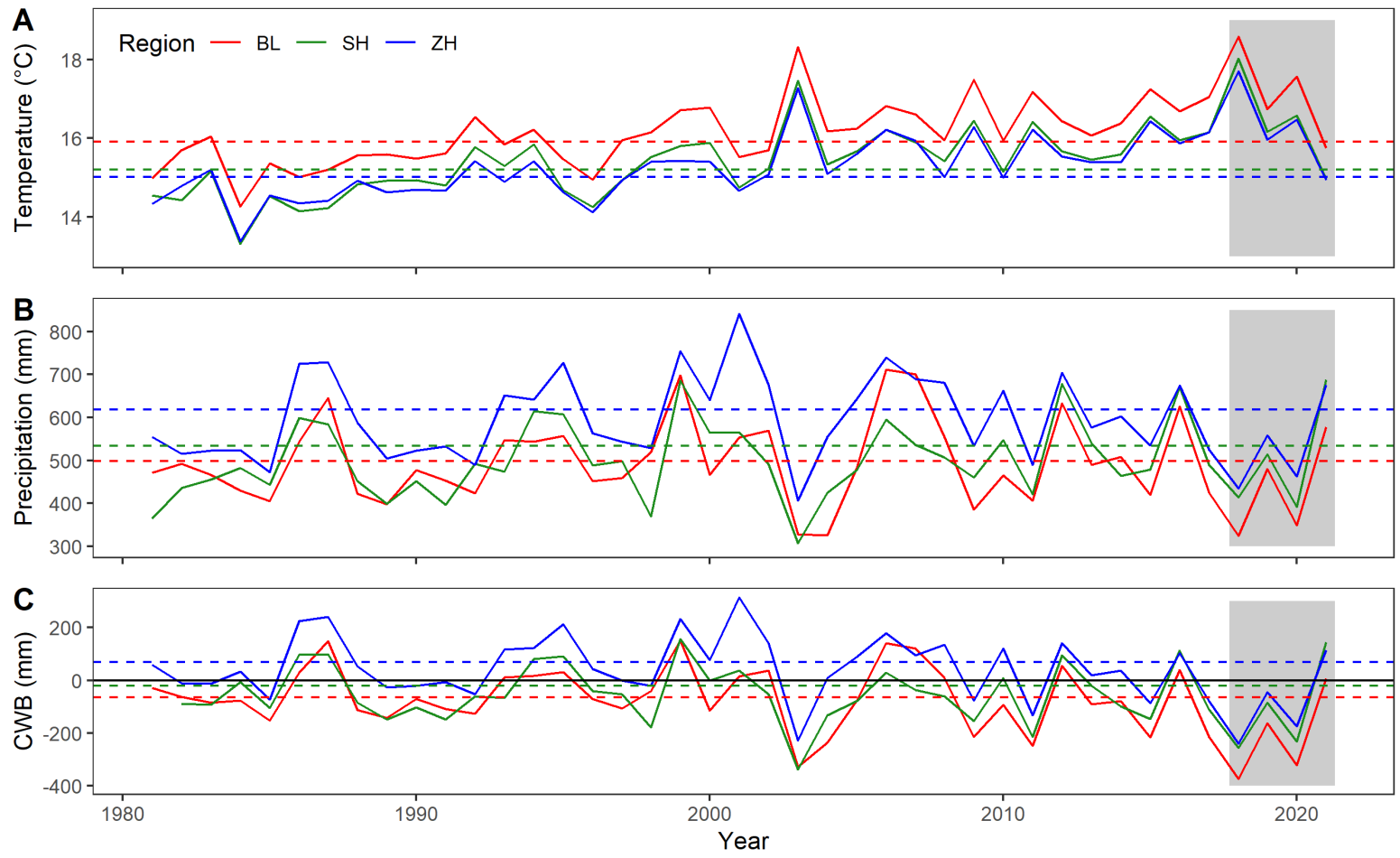
Table 2. Results of binomial generalized linear mixed effect models after stepwise model reduction for tree mortality (A), the proportion of crown dieback (B), the presence of bleeding cankers (C), and the presence of bark beetle holes (D). All models used a logit link function and included 'Tree' nested within 'Tree group' and 'Region' as random effect. Models were based on data from N = 176 tree groups for tree mortality, from N = 745 individual trees for crown dieback, bleeding cankers and bark beetles. Continuous explanatory variables were standardized to zero mean and unit variance. Significant explanatory variables are **in bold text** and non-significant factors that were dropped during model reduction are indicated with 'ns'. Factors that were not included in the initial models are indicated with '-'.

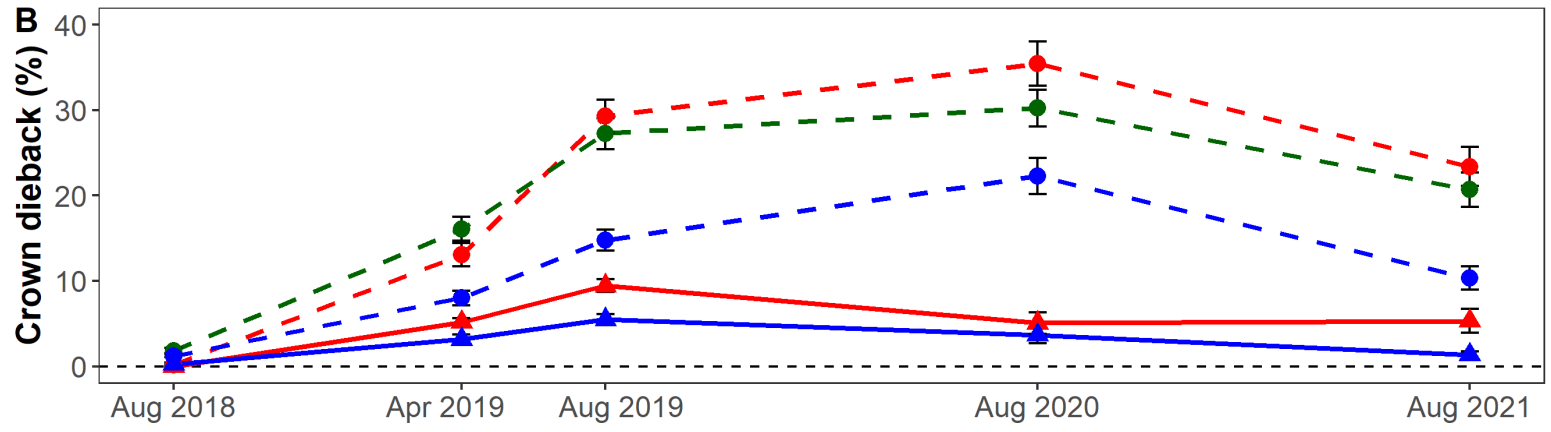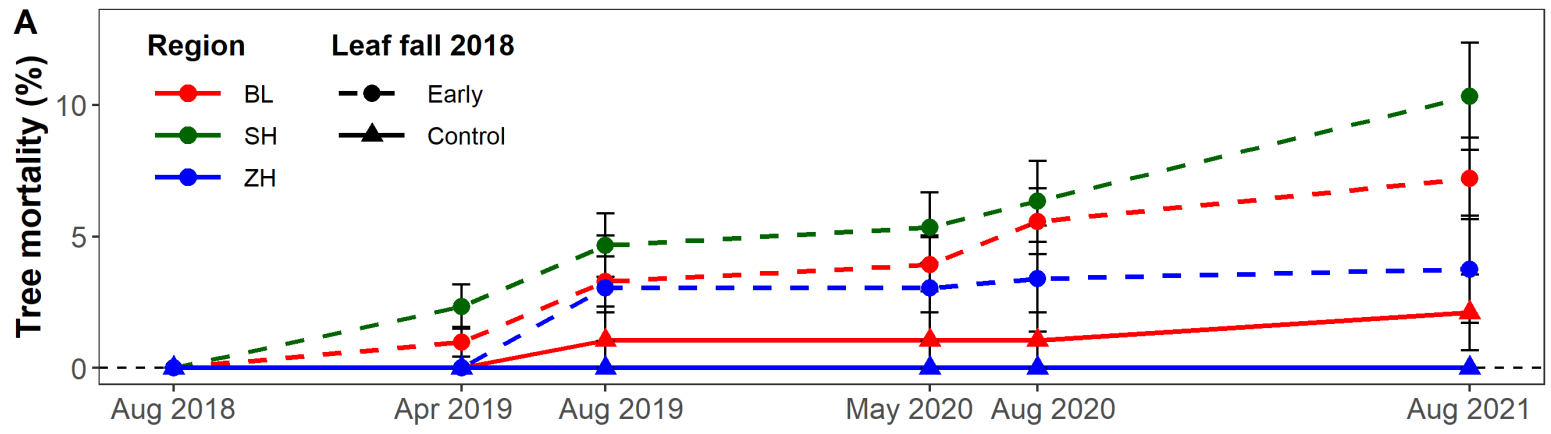| Explanatory variable	(A) Tree mortality			(B) Crown dieback			(C) Bleeding cankers			(D) Bark beetles		
	Est.	*SE*	*P*	*Est.*	*SE*	*P*	*Est.*	*SE*	*P*	*Est.*	*SE*	*P*
Leaf fall 2018	5.17	1.63	**0.001**	1.03	0.27	**<0.001**	1.04	0.34	**0.002**	0.17	0.85	0.839
Competition index	1.62	0.73	**0.026**	0.09	0.08	0.303	ns	ns	ns	-0.09	0.37	0.804
Seed mast 2018	-1.08	0.68	0.109	ns	ns	ns	ns	ns	ns	ns	ns	ns
Social position	0.39	0.78	0.622	ns	ns	ns	ns	ns	ns	ns	ns	ns
DBH	0.10	0.05	**0.035**	0.45	0.19	**0.015**	0.86	0.12	**<0.001**	0.34	0.37	0.350
Tree height	0.10	0.11	0.348	0.18	0.08	**0.019**	-	-	-	-	-	-
Clay content	0.09	0.07	0.189	0.41	0.08	**<0.001**	ns	ns	ns	ns	ns	ns
Time interval	0.08	0.01	**<0.001**	0.33	0.01	**<0.001**	1.08	0.30	**<0.001**	2.93	0.26	**<0.001**
Time interval^2	-	-	-	-0.01	0.00	**<0.001**	-1.72	0.14	**<0.001**	-	-	-
Gravel content	0.07	0.04	0.109	0.22	0.09	**0.010**	-	-	-	-	-	-
Soil pH	-0.06	0.33	0.851	ns	ns	ns	0.23	0.11	**0.044**	0.18	0.29	0.538
CWB	-0.02	0.01	**0.005**	-0.33	0.09	**<0.001**	-0.61	0.14	**<0.001**	0.48	0.79	0.545
Forest edge distance	-0.01	0.00	0.135	-0.11	0.08	0.170	-0.26	0.12	**0.032**	0.14	0.29	0.631
Soil depth	-0.01	0.01	0.565	0.03	0.08	0.685	0.04	0.11	0.725	0.05	0.27	0.844
Crown dieback	-	-	-	-	-	-	0.39	0.08	**<0.001**	1.50	0.21	**<0.001**
Leaf fall 2018 × DBH	-	-	-	-0.28	0.19	0.148	-	-	-	-	-	-
Leaf fall 2018 × Tree height	-	-	-	0.23	0.19	0.238	-	-	-	-	-	-
Leaf fall 2018 × Time	ns	ns	ns	0.04	0.01	**<0.001**	-0.54	0.31	0.072	ns	ns	ns
Leaf fall 2018 × CWB	-	-	-	ns	ns	ns	ns	ns	ns	-0.57	0.85	0.505

Est., estimate. SE, standard error. P, P-value. Time interval^2, quadratic term for factor time interval. For description of explanatory variables see Table 1. Interaction terms that were dropped during model reduction were not included in this table.

Legend
- Early leaf fall trees
- Control trees
- Range of *F. sylvatica*

Schaffhausen

Basel

Zurich

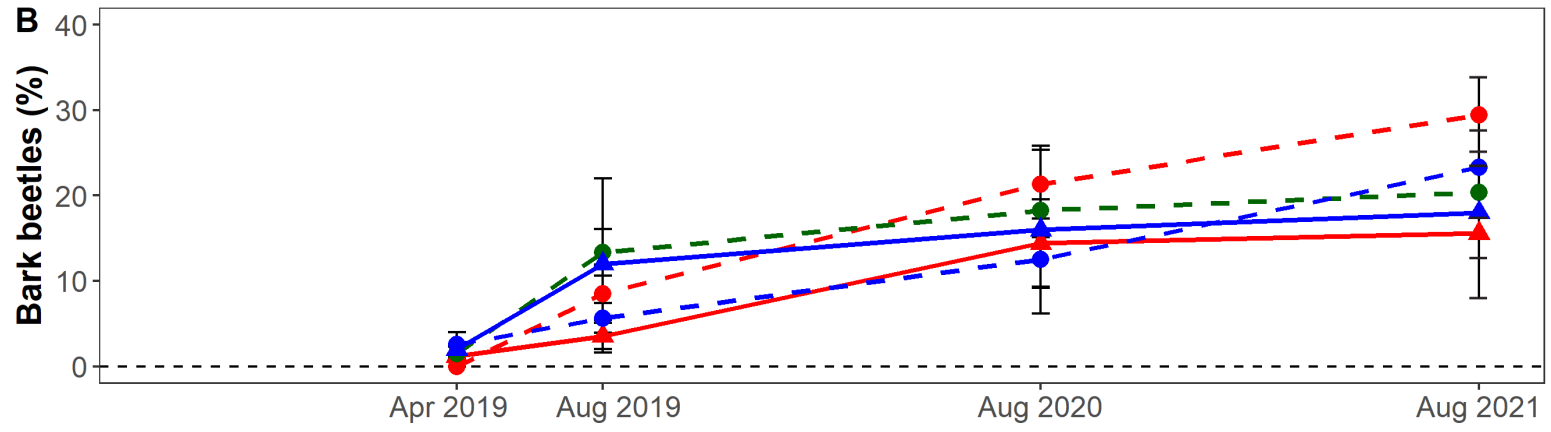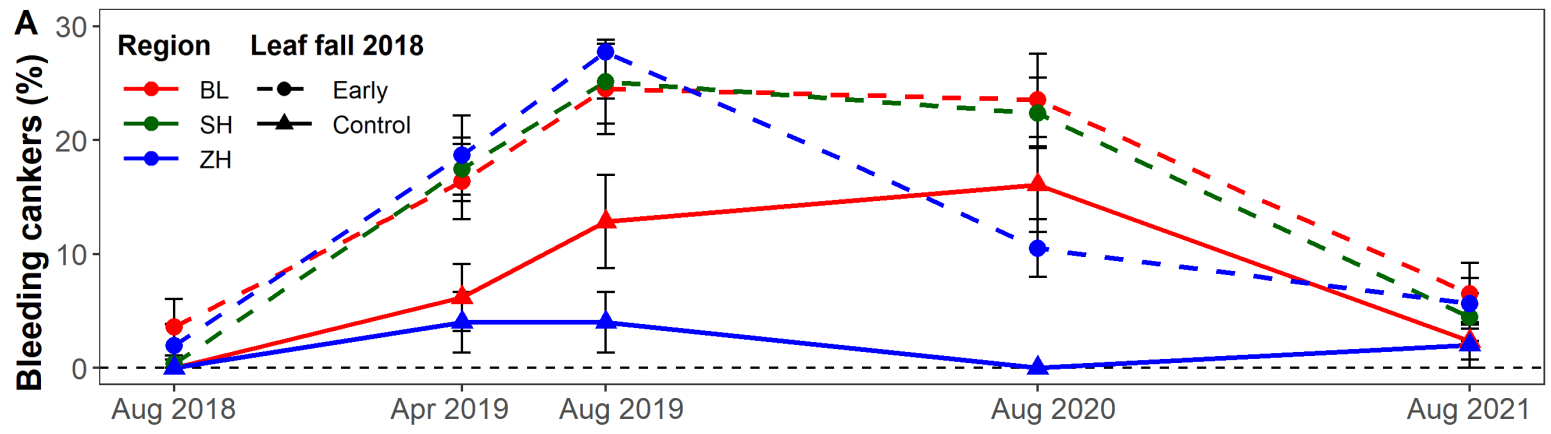0   10   20   30   40   50
Kilometers

PLB_13467_Frei_etal_Figure1_revised.tif

PLB_13467_Frei_etal_Figure2_revised.png

PLB_13467_Frei_etal_Figure3_revised.png

PLB_13467_Frei_etal_Figure4_for_Production.png