1 Compound soil and atmospheric drought events and CO2 fluxes

2 of a mixed deciduous forest: Occurrence, impact, and temporal

3 contribution of main drivers

- 4 Liliana Scapucci^{1,*,•}, Ankit Shekhar^{1,•}, Sergio Aranda-Barranco², Anastasiia Bolshakova³, Lukas
- 5 Hörtnagl¹, Mana Gharun⁴, Nina Buchmann¹
- 6 Department of Environmental Systems Science, ETH Zürich, Switzerland
- 7 ² Department of Ecology, University of Granada, Granada, Spain
- 8 ³ University of Natural Resources and Life Sciences, Vienna (BOKU), Austri Austria
- ⁴ Department of Geosciences, University of Münster, Germany
- 10 *Correspondence to: Liliana Scapucci (liliana.scapucci@usys.ethz.ch)
- 11 *Both the authors contributed equally to the manuscript
- 12 Abstract. With global warming, forests are facing an increased exposure to compound soil and atmospheric drought (CSAD)
- 13 events, characterized by low soil water content (SWC) and high vapor pressure deficit (VPD). Such CSAD events trigger
- 14 responses in both ecosystem and forest floor CO2 fluxes, of which we know little about. In this study, we used multi-year daily
- and daytime above-canopy (18 years; 2005-2022) and daily forest floor (five years; 2018-2022) eddy-covariance CO₂ fluxes
- 16 of a Swiss forest site (montane mixed deciduous forest; CH-Lae). The objectives were (1) to characterize CSAD events at CH-
- 17 Lae; (2) to quantify the impact of CSAD events on ecosystem and forest floor daily CO_2 fluxes; and (3) to identify the major
- 18 drivers and their temporal contributions to changing ecosystem and forest floor CO₂ fluxes during CSAD events and CSAD
- 19 growing seasons. Our results showed that the growing seasons of 2015, 2018, and 2022; were the top three driest at CH-Lae
- 20 since 2005 (referred to as CSAD years) at CH Lae since 2005,), with similar intensity and duration of the respective CSAD
- 21 events, but with considerably different pre-drought conditions. The CSAD events reduced daily mean net ecosystem
- 22 productivity (NEP) in all three CSAD years by about 38% compared to the long-term mean, with the highest reduction during
- 23 2022 (30% decrease),41%). This reduction in daily mean NEP was largely due to decreased gross primary productivity (GPP;
- 24 >15% decrease 16% compared to the long-term mean) rather than increased ecosystem respiration (Reco) during CSAD events.
- 25 Furthermore, forest floor respiration (Rff) decreased during the CSAD events in 2018 and 2022 (no measurements in 2015),
- with a larger reduction in 2022 (>40(41/8)) than in 2018 (<25(16/8)) compared to the long-term mean (2019-2021). Using data-
- 27 driven machine learning methods, we identified the major drivers of NEP and Rff during CSAD events. While daytime mean
- 28 NEP (NEP_{DT}) during 2015 and 2018 CSAD events was limited by VPD or SWC, respectively, daytime mean NEP_{NEP_{DT}}
- 29 during the 2022 CSAD event was strongly limited by both SWC and VPD. Air temperature always had always negative effects,
- 30 while net radiation showed positive effects on daytime mean NEPNEP_{DT} during all CSAD events. Daily mean Rff during the
- 31 2018 CSAD event was driven by soil temperature and SWC, but severely limited by SWC during the 2022 CSAD event. We

Formatted: Font: 17 pt

Formatted: Font: 17 pt

Formatted: MS title

Formatted: Left

Formatted: English (United Kingdom)

- 32 found that a multi-layer analysis of CO2 fluxes in forests is necessary to better understand forest responses to CSAD events.
- 33 particularly if the first signs we saw of NEP acclimation to such CSAD events - we saw for our forest-- are found elsewhere
- 34 as well. We conclude that such CSAD events have multiple drivers with different temporal contributions, making
- prediction predictions of site-specific CSADs and forest long-term responses to such conditions more challenging. 35

1 Introduction 36

- 37 Forests play an essential role in mitigating climate change thanks to their ability to partially offset anthropogenic CO2 emissions
- 38 (Harris et al., 2021). However, the increasing frequency of droughts and heatwayes is compromising the carbon uptake capacity
- of forests worldwide (Anderegg et al., 2022). According to IPCC (2022), the temperature increase over Europe (1850-1990) 39
- 40 has been about twice the global mean since the pre-industrial period, accompanied with an increase in frequency of drought
- events (Spinoni et al., 2018). Recent studies have revealed that European forests are showing increasing rates of tree mortality, 41
- induced by low soil water content (SWC) (George et al., 2022). In addition, recent studies have highlighted the role of high 42
- 43 vapor pressure deficit (VPD), an indicator of atmospheric drought and a distinct characteristic of heatwaves, in further
- exacerbating tree mortality (Birami et al., 2018; Gazol and Camarero, 2022; Grossiord et al., 2017, 2020). Due to enhanced
- 44
- land-atmosphere feedback duein response to climate change, the frequency of co-occurrence of occurring low soil moisture 45
- and high VPD conditions has also increased (Dirmeyer et al., 2021; Miralles et al., 2019; Orth 2021; Zhou et al., 2019), 46
- resulting in so-called compound soil and atmospheric drought (CSAD) conditions. The 21st century European droughts in 47
- 48 2003, 2015, 2018, and the most recent one in 2022, were indeed characterized by CSAD conditions (Dirmeyer et al., 2021;
- Ionita et al., 2021, 2017; Lu et al., 2023; Tripathy and Mishra, 2023). In 2022, Europe experienced its hottest and driest year 49
- on record, with the summer being the warmest ever recorded, which ultimately led to numerous CSAD events across the 50
- 51 continent (Copernicus Climate Change Service, 2023).
- 52 Such CSAD events have multiple impacts on forest ecosystems. They can lead to reduced net ecosystem productivity (NEP)
- by decreasing gross primary productivity (GPP) and/or increasing ecosystem respiration (Reco) (Xu et al., 2020). Additionally, 53
- 54 soil respiration (SR) can be reduced due to water scarcity in the soil, which limits both heterotrophic and autotrophic respiration
- 55 (Ruehr and Buchmann, 2009; Ruehr et al., 2010; van Straaten et al., 2011; Sun et al., 2019; Schindlbacher et al., 2012).
- 56 Still However, high soil temperature (TS) can increase SR rates when soil moisture is not limiting metabolic reactions in the
- 57 soil (Schindlbacher et al., 2012), affecting the sensitivity of respiration to soil temperature (Sun et al., 2019). Thus, to better
- understand the ecological consequences of climate change on forest ecosystems, the capacity of forests to acclimate to stress 58
- 59 conditions like CSAD events, e.g., by changing the NEP sensitivity to abiotic drivers like air temperature (Tair), VPD, and
- 60 SWC during a growing season or among growing seasons, needs to be known (Grossman, 2023).
- 61 The summer of 2022 in Europe, characterized by strong CSAD conditions (Tripathy and Mishra, 2023; van der Woude et al.,
- 2023), showed an extensive reduction in forest greenness (about 30% of temperate and Mediterranean European forest area; 62
- Hermann et al., 2023), and a reduction in GPP (van der Woude et al., 2023), comparable to summer 2018 CSAD events. In

65 L.) forests (Haberstroh et al., 2022; Obladen et al., 2021; Rukh et al., 2023; Schuldt et al., 2020). Clearly, most drought impact studies use data measured above the canopy, be iti.e., net carbon dioxide (CO₂) exchange or remote sensing of vegetation, 66 particular. Particularly the latter is largely neglecting the below--canopy component of the forest (also known as forest floor), 67 68 which although it might show contrasting responses to drought conditions compared to the top canopy sensed from above (Chi 69 et al., 2021). The forest floor, composed of soil, tree roots, woody debris, and understory vegetation, provides an essential 70 interface for soil-atmosphere CO₂ exchange, with photosynthesis of understory vegetation and forest floor respiration (Rff), 71 both representing major CO₂ exchange pathways processes (Chi et al., 2017; Paul-Limoges et al., 2017), Therefore, separating the ecosystem-level drought response from the forest floor drought response provides a more comprehensive insight into 72 73 drought impacts than one level alone (Chi et al., 2017; Martinez-Garcia et al., 2022). Furthermore, the intensity and duration 74 of CSAD events, and their impacts on forests can largely vary at regional scale (Pei et al., 2013; Kim et al., 2020). Thus, more 75 attention is needed on temperate forest ecosystems across Central Europe, such as in Switzerland, where forests are accustomed 76 to humid and cool climates, with ample amount of summer rainfalls (Schuldt and Ruehr, 2022). 77 In Switzerland, 2022 was the warmest year on record since the beginning of instrumental measurements in 1864, with average 78 air temperatures 1.6 °C above the long-term mean (1991-2020), and annual precipitation amounting to only 60% of the long-79 term average (MeteoSvizzera, 2023). Such hot and dry conditions as in 2022 were bound to result in CSAD events which 80 could ultimately compromise the carbon dioxideCO2 uptake capacity of forests. Thus, the objectives of this study were as follows: (1) to characterize compound soil and atmospheric drought (CSAD) events at a Swiss montane mixed deciduous 81

forest site, (2) to quantify the impact of CSAD events on ecosystem and forest floor CO₂ fluxes, and (3) to identify the major

drivers of ecosystem and forest floor CO2 fluxes and their temporal contributions during CSAD events and CSAD growing

2018, this resulted in drought-induced tree mortality in Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica

Formatted: Subscript

85 2 Material and methods

86 2.1 Forest site

seasons.

82 83

84

64

87 The study was conducted in a managed mixed deciduous mountain forest (CH-Lae at 682 m a.s.l.) located at the Lägeren, in 88 the far east of the Jura Mountain range in Switzerland. The CH-Lae forest has a complex canopy structure with a rather high species diversity, the dominant species are European beech (Fagus sylvatica; L., 40% cover), ash (Fraxinus excelsior; L., 19% 89 90 cover), Sycamore maple (Acer pseudoplatanus, L., 13% cover), European silver fir (Abies alba, Mill., 8% cover), large-leaved 91 linden (Tilia platyphyllos, Scop., 8%) and Norway spruce (Picea abies, (L.) H. Karst., 4% cover) (Paul-Limoges et al., 2020). 92 showing no significant trend of leaf area index (LAI) over the years. The soils at CH-Lae are characterized by two main types, 93 rendzic leptosols and haplic cambiosols, with bedrocks of limestone marl, sandstone, and transition zones between the two 94 (Ruehr et al., 2010). The mean annual air temperature at CH-Lae was 8.8 ± 1.3 °C (mean \pm sdSD), and mean annual precipitation was 831 ± 121 mm (mean 2005-2022). The understory vegetation at CH-Lae is dominated by wild garlic (Allium

96 ursinum, L., height ~ 30 cm) which grows for a short period in spring and early summer (March-June) (Ruehr and Buchmann,

Measurements In this study, we used measurements of ecosystem CO₂ fluxes from above the forest canopy using the eddy

97 2009). The net carbon uptake period of CH-Lae is from May to September (Figure A1, appendix A).

98 2.2 Ecosystem-level measurements

99

100 covariance (EC) technique (Aubinet et al., 2012) started in April 2004. Here we used data (Aubinet et al., 2012), spanning from 101 2005 to 2022 (full years) of net ecosystem productivity (NEP), gross primary productivity (GPP), and ecosystem respiration 102 (Reco).. The EC system (eddy tower coordinates: 47°28'42.0" N and 8°21'51.8" E) was mounted at a height of 47 m (mean 103 canopy height of 30 m). We performed) above the ground. The EC technique utilizes high frequency (20 Hz) measurements 104 of wind speed and _wind direction-using , measured with a three-dimensional sonic anemometer, and usedgas (here CO2) 105 concentration, measured with an infrared gas analyser (IRGA) to measure as CO2 molar density (with an open-path IRGA from 106 2004-2015) or as dry mole fraction (with a closed-path IRGA from 2016-2022; for details of instrumentation used in the EC 107 system, see Table A1, appendix A). The time-lag between turbulent fluctuations of vertical wind speed and CO₂ molar density 108 or dry mole fraction was calculated by covariance maximization (Fan et al., 1990), and (Fan et al., 1990); half-hourly fluxes of 109 CO₂ (FC, µmol CO₂ m²s² s⁻¹) were then calculated from the 20 Hz measurements using the EddyPro software v7 (v7.0.9, LI-110 COR Inc., Lincoln, NE, USA), following established community guidelines (Aubinet et al., 2012; Sabbatini et al., 2018). 111 Fluxes (Aubinet et al., 2012; Sabbatini et al., 2018). The FC from the open-path IRGA LI-7500 were corrected for air density 112 fluctuations (Webb et al., 1980). Spectral (Webb et al., 1980), all FC underwent spectral corrections for high-pass (Moncrieff 113 et al., 2004)(Moncrieff et al., 2004) and low-pass filtering (Fratini et al., 2012; (Fratini et al., 2012; Horst, 1997)) losses-were 114 applied to the raw fluxes. The impact of self-heating of the open-path IRGA on EC was corrected following thebased on a 115 method described by Kittler et al. (2017). Thereafter, F_C were filtered for turbulent conditions based on the steady state test 116 statistic and integrated turbulence criterion test (Foken et al., 2004). Additional quality control flags (OCF) for each half-hourly 117 CO₂ flux were calculated based on Sabbatini et al. (2018); fluxes with QCF=2 (unreliable flux value) were removed. Kittler et 118 al. (2017). The net ecosystem CO₂ exchange (NEE) was then calculated as the sum of FC and the CO₂ storage term. Thereafter, 119 four quality checks were applied to the calculated NEE, namely (1) despiking using a Hampel filter to reject NEE values higher 120 or lower than five times the standard deviation estimated from the median absolute deviation in a 9-day running window, (2) 121 absolute threshold filtering to remove values outside a physically plausible range concentrations based on 1-point 122 measurements (Greco and Baldocchi, 1996). The quality of -50 to 50 μmol m²s⁻¹, (3) removal of potential non-biotic fluxes 123 during cold season using a trimming mean approach (see Etzold et al., 2011), (4) constant u* (friction velocity) filtering of 0.3 ms⁻¹-for CH-Lae (Etzold et al., 2010). Then, the missinghalf-hourly NEE flux values was ensured by applying a comprehensive 124 125 quality screening process that combined several well-tested methods into a single quality flag (0-1-2 system; Mauder and 126 filtered NEE time series was Foken, 2006; Sabbatini et al., 2018). Fluxes of low quality (flag = 2) were removed from further 127 analyses. Fluxes that passed the quality-screening process were then gap-filled using the marginal distribution sampling (MDS) approach as implemented in the ReddyProc v1.3.2 R-package (Reichstein et al., 2005; Wutzler et al., 2018). Finally, the gap-128

Formatted: Not Superscript/ Subscript

Formatted: Not Superscript/ Subscript

Formatted: Not Superscript/ Subscript

Formatted: Not Superscript/ Subscript

- 129 filled NEE was (Reichstein et al., 2005) and partitioned into gross primary productivity (GPP) and ecosystem respiration
- 130 (Reco) using the day-time partitioning method (Lasslop et al., 2010). (Lasslop et al., 2010). More details about quality-
- 131 screening, gap-filling and partitioning can be found in Shekhar et al. (2024). In this study, we used net ecosystem productivity
- 132 (NEP = -NEE) for further data analyses. Positive NEP fluxes represent CO₂ uptake by the forest, whereas negative NEP
- 133 represent represents CO₂ release. Along with fluxes, we also measured half-hourly air temperature (Tair), relative humidity
- 134 (RH), incoming short-wave radiation (Rg), and precipitation (Precip) at the top of the EC tower from 2005-2022 (see Table
- 135 A1 for instrumentation details). We estimated half-hourly VPD from half-hourly measurements of air temperature and relative
- 136 humidity. For more information about the processing chain refer to Shekhar et al., 2024.

137 2.3 Forest floor measurements

- 138 We measured forest floor fluxes of CO₂ based on the EC technique (Aubinet et al., 2012) below the canopy from 2018 to 2022
- 139 to estimate net ecosystem exchange of the forest floor (NEE_{ff}), which includes CO₂ fluxes from the soil and the understory
- 140 vegetation. We partitioned NEEff into gross primary productivity of the forest floor (GPPff) and respiration of the forest floor
- 141 (Rff; Lasslop et al., 2010). The below-canopy station at CH-Lae site was located in a distance of c. 100 m from the main tower
- 142 (47°28'42.9" N and 8°21'27.6" E) and hashad a height of 1.5 m. Wind speed and direction were measured with a sonic
- anemometer and CO₂ concentrations with an open-path IRGA (LI-7500; Table A1) at a frequency of 20 Hz. We calculated
- NEE_{ff}, and the partitioned fluxes, using the same process and corrections as for above—canopy measurements, (except for the
- 145 self-heating correction). We used a seasonal u* filtering to account for changes in the understory canopy, with 0.024 ms⁻¹ for
- $146 \quad \text{spring (day 60-151), 0.027 ms}^{-1} \text{ for summer (day 152-243), 0.039 ms}^{-1} \text{ for autumn (day 244-334), and 0.025 ms}^{-1} \text{ for winter (day 152-243), 0.039 ms}^{-1} \text{ for autumn (day 244-334), and 0.025 ms}^{-1} \text{ for winter (day 152-243), 0.039 ms}^{-1} \text{ for autumn (day 244-334), and 0.025 ms}^{-1} \text{ for winter (day 152-243), 0.039 ms}^{-1} \text{ for autumn (day 244-334), and 0.025 ms}^{-1} \text{ for winter (day 152-243), 0.039 ms}^{-1} \text{ for autumn (day 244-334), and 0.025 ms}^{-1} \text{ for winter (day 152-243), 0.039 ms}^{-1} \text{ for autumn (day 244-334), and 0.025 ms}^{-1} \text{ for winter (day 152-243), 0.039 ms}^{-1} \text{ for autumn (day 244-334), and 0.025 ms}^{-1} \text{ for autum$
- (day 335-60). Additionally, we continuously measured air temperature ($(\text{Tair}_{\text{ff}})$), relative humidity ((RH_{ff})), incoming short-wave
- 148 radiation (Rgff), soil temperature (TS) and soil water content (SWC) at multiple depths 5, 10, 20, 30, 50 cm depth at the forest
- 149 floor meteorological station next to the below-canopy EC system (Table A1, appendix A). In 2020, we installed an additional
- soil moisture profile. To account for spatial heterogeneity, we centre normalised normalized the SWC data and and are arranged a z-score
- 151 transformation, we then used z-scores of SWC for further analyses.

152 2.4 Soil respiration measurements

- 153 Ten PVC collars (diameter 20 cm, height 13 cm, depth = 2 cm) were installed at CH-Lae in spring 2022, at the same locations
- 154 within the footprint of the tower as described in Ruehr et al. (2010). Soil respiration (SR) measurement campaigns were
- 155 performed at least once a month from March until November 2022, with a LI-8100-103 analyser and a closed chamber (Table
- 156 Al, appendix A). Collars were measured once a day in a random order during each campaign. Every measurement lasted 90
- 157 seconds from the moment the LI-8100 chamber closed on top of the collar. Next to each collar, we measured SWC_s (SWC
- from survey measurements) at 5 cm with a soil moisture sensor, and TS_S (TS from survey measurements) at 5 cm with a
- temperature sensor (Table A1, appendix A). When the Swiss meteorological service (MeteoSwiss) forecasted a two-week
- 160 heatwave starting on 14th of July 2022, we intensified the measurements of SR to one campaign every second day with two

161 rounds of measurements per day for two weeks (at 09:00 and at 16:00). The order of measurements was inverted every

fieldwork day. Since the portable soil moisture sensor broke on 22 nd of July 2022 and was only available on 11th of August 162

163 2022, we calculated the SWC based on continuous measurements at the forest floor meteorological station for these days

 $(SWCs = 1.34 * SWC - 10.7; R^2 = 0.82).$ 164

165 2.5 Data analyses

169

170

171

173

180

In this study, we focused all our analysis analyses on the growing season, between May and September, when the long-term 166

mean of ecosystem NEP (2005-2022) was positive, implying that GPP of the vegetation overcompensated all respiratory losses 167

168 (Figure A1, appendix A; Körner et al., 2023). We conducted all data analyses using the R programming language (R version

4.3.3, R core team, 2021). We compared cumulative precipitation (indicating total water supply to the forest) and cumulative

VPD (indicating total atmospheric water demand) during the growing seasons of 18 years at our forest site and chose the three

years with the driest growing seasons, i.e., with low cumulative precipitation and high VPD₅, called compound soil and

172 atmospheric drought (CSAD) years hereafter. Then, we identified the CSAD events during thethese CSAD years as periods

when both soil and atmosphere were significantly drier than usual for more than 10 consecutive days, implying a compound

174 drought condition. To identify drier than usual periods, we compared 5-day moving daily means (assigned to the centre of 5

175

days) of SWC and VPD with their long-term (2005-2022) means. So, a period of 10 or more consecutive days with SWC being

176 significantly lower (p<0.05) and VPD being significantly higher (p<0.05) than the long-term mean, werewas identified as

177

We quantified the impact of CSAD events based on anomalies of NEP, GPP, Reco, and Rff by comparing them with their 178

179 respective long-term means (NEP, GPP, Reco: mean of 2005-2022; Rff: mean of 2019-2021). Since CSAD events occurred

in two of the five years of flux data available at the forest floor station (Rff), we excluded 2018 and 2022 from the calculation

181 of the Rff long-term mean. To understand the major drivers of NEP and Rff, we performed two different driver analyses in

182 this study, first focusing on the CSAD years; (I), and second focusing on the CSAD events in the CSAD years; (II).

183 (I) For the first driver analysis, we used the conditional variable importance (CVI) feature based on random forest regression

184 model (Breiman, 2001). For modelling daily mean NEP₇ (NEP), the predictors were Rg, VPD, and Tair measured above the

canopy, and SWC measured at the forest floor station, whereas for modelling daily mean Rff, (Rff), the predictors were Rg 185

186 (Rg_{ff}) and Tair (Tair_{ff}) as well as soil temperature (TS) and SWC, measured at the forest floor station. The model was run for

187 each year separately. The CVI considers is specifically designed to consider the multi-collinearity between the among predictors

188 (i.e., Tair, VPD, Rg), while estimating the importance of each predictor variables variable (Strobl, et al., 2008), and thus

considered a very reliable method to estimate overall feature importance. For estimating CVI, we used the cforest and varimp 189

190 function from the R-package party (Hothorn et al., 2006).

191 (II) For the second driver analysis, we used daytime mean NEP (NEP_{DT}, excluding nighttime data to highlight the effects of

environmental drivers when photosynthesis is dominating) to avoid potential biases if GPP were used, since some predictors, 192

(i.e., Tair and Rg.) were used for the partitioning of to partition NEE into GPP and Reco. We used a TreeExplainer-based 193

194 SHapley Additive exPlanations (SHAP) framework (Lundberg and Lee, 2017; Lundberg et al., 2020), with a tree-based 195 ensemble learning extreme gradient boosting (XGB) model (Chen and Guestrin, 2016). The XGB model was used to model 196 daytime mean NEPNEP_{DT} and daily mean Rff, applying the GridSearchCV methodology to optimize the parameters of the XGB model for NEP and Rff (see Wang et al., 2022 for more details). The TreeExplainer-based SHAP framework integrates 197 198 explanatory models (here the XGM model) with game theory (Shapley, 1953), which allowed us to estimate the marginal 199 contribution (known as SHAP value) of each predictor variable (i.e., Tair, VPD, SWC, TS) to predicted the response variables. 200 (NEP_{DT}, Rff). We used the function xgboost (eXtreme Boosting Training) from the R-package xgboost to train the model, and the functions shap, values and shap, prep from the R-package SHAPforxgboost (Chen and Guestrin, 2016) to obtain the SHAP 201 202 values of each predictor variable for daytime mean NEPNEPDT (for 2005-2022) and daily mean Rff (for 2018-2022). The 203 models were run for each year separately, and we obtained the marginal contributions of each feature for each day of each growing season, which allowed to observe their temporal course. Then we calculated the mean SHAP value during the CSAD 204 205 events for each predictor of daytime mean NEPNEP_{DT} and daily mean Rff for the CSAD years. For comparison to determine 206 the dominant direction of the effect of each feature. To determine differences to the long-term means, we also calculated the 207 mean SHAP values of the predictors during the respective reference periods (long-term means: 2005-2022 for daytime mean 208 NEPNEPDT; 2019-2021 for daily Rff). The respective reference period includes included all days, in which a CSAD event 209 occurred independent of the year, i.e., ranging from 7th July to 23rd August for daytime mean NEPNEPDT during 2005-2022 210 (including CSAD years due to the large number of years available with measurements), and from 14th July to 23rd August for 211 daily mean-Rff during 2019-2021 (excluding CSAD years due to the small number of years available with measurements; 212 Figure A2, appendix A)...). For comparison with the first model (based on CVI), we also calculated the mean and standard 213 error of the absolute SHAP values for NEP in 2015, 2018, 2022, and the long-term mean 2005-2022 (Figure A3). However, 214 since we were interested in the short-term changes in driver importance, including the direction of their effect, we did not 215 follow up using absolute SHAP values in this study. 216 Moreover, weWe then used the SHAP values of drivers (VPD, Tair and SWC for NEPNEPDT; TS and SWC for Rff) to derive 217 driver thresholds, i.e., estimate acclimation of NEP_{DT} and Rff to abiotic drivers by estimating the absolute driver values 218 (thresholds) related to the largest effects, as indicated by highest the maximum marginal contributions to the response variables 219 NEPNEP_{DT} and Rff for each CSAD year (Gou et al., 2023; Wang et al., 2022). For this, we fitted a local polynomial regression (LOESS curve) between the SHAP values of the driver variable and the driver variable itself, and i.e., a loess curve, and 220 221 calculated the residual standard error from the loess function of the stats R-package. We then identified the absolute driver 222 value corresponding to the highest SHAP value. We specifically derived (feature_NEPmax, feature_Rffmax) for each CSAD 223 year, i.e., VPD_NEP_{max}, Tair_NEP_{max}, SWC_NEP_{max}, i.e., the VPD, Tair and SWC, values associated with the highest marginal 224 contributions to daytime mean NEP, and NEPDT, as well as TS_Rffmax and SWC_Rffmax, i.e., TS and SWC_values associated 225 with the highest marginal contributions to dailyRff. These absolute driver values provided information about the NEP_{DT} and 226 Rff sensitivities to abiotic drivers during the growing season of each CSAD year. For example, a shift in the SWC_NEP_{max} towards drier conditions in one growing season compared to others thus translated to an acclimation of NEP_{DT} to drier 227

- 228 conditions in that growing season. To test if the feature NEPmax values varied with the corresponding mean feature values
- 229 during the respective growing season, we fitted a linear regression between the mean RffVPD, SWC and Tair and their
- 230 corresponding values of NEPmax for each CSAD-year- from 2005 to 2022.
- 231 Finally, we used linear models to explain daily mean SR responses to TS and SWC during the CSAD events and the rest of
- the years, based on the measurements from the survey campaigns in 2022. The amount of SR data was not sufficient to use 232
- 233 machine learning approaches.

234 3 Results

235 3.1 Detected CSAD events

- 236 The growing seasons (May to September) of 2015, 2018, and 2022 were the three driest in the last 18 years (2005-2022) which
- 237 the mountain forest site experienced (Figure 1). The growing seasons in these three years were characterized by very high
- 238 atmospheric drought (indicated by cumulative VPD) and low water supply (indicated by cumulative precipitation, a proxy for
- 239 soil drought), called compound soil and atmospheric drought (CSAD) years hereafter.) In particular, the summer months (June-
- 240 August) of these three years were significantly warmer and drier (Figures 1, 2). Mean summer temperatures of 2018 (19.8 °C)
- 241 and 2022 (20.3 °C) were more than 2.5 °C higher than the long-term mean summer temperature at the forest site (17.2 °C);
- 242 summer precipitation sums in 2018 and 2022 were more than 20% and 10% lower than the long-term mean cumulative summer
- precipitation (300 mm), respectively. Furthermore, during the month July of both years 2015 and 2022, less than one-third of 243
- 244 long-term mean cumulative summer precipitation was recorded. Coupled with a more than 50% increase in average VPD, this
- 245 resulted in intense soil and atmospheric drought conditions.
- 246 Moreover, we detected two distinct CSAD events in 2015, i.e., periods of 10 or more consecutive days with significantly lower
- 247 SWC and significantly higher VPD than the long-term mean: one from 7th July 2015 to 21st July 2015, and a second one from
- 2nd August 2015 to 13th August 2015 (Figure 2a, d, g), comprising a total of 2527 days with a mean maximum temperature of 248
- 249 26.9 °C, mean maximum VPD of 2.24 kPa, and mean minimum normalized SWC of -1.83 (Table 1). For comparison, in 2018,
- 250 the CSAD event lasted for 3132 days, from 23rd July 2018 to 23rd August 2018 (Figure 2b, e, h), with a mean maximum
- 251 temperature of 27.7 °C, mean maximum VPD of 2.19 kPa, and mean minimum normalized SWC of -1.94 (Table 1). In 2022,
- 252 the CSAD event lasted 2+22 days, from 14th July 2022 to 4th August 2022. Thus, although it was shorter than in those in 2015
- 253 and 2018 (Figure 2c, f, i), it was more intense than those in 2015 and 2018, with mean maximum temperature of 28.3 °C, mean
- 254 minimum VPD of 2.43 kPa, and mean minimum normalized SWC of -2.51 (Table 1). We measured the highest air temperature
- 255 (33.56 °C) and the third highest VPD (3.83 kPa) ever recorded at the forest site in the past 18 years (2005-2022) on the last
- 256 day of the 2022 CSAD event, i.e., on 4th August 2022 between 16:30 and 17:00 (Figure A3, appendix AA4). Furthermore, the
- 257
- 2022 CSAD event was characterized by multiple tropical nights (i.e., nighttime temperature > 20 °C; Figure A3, appendix
- 258 AA4) and progressive soil drying (Figure 2).

Thus, the CSAD events were not only slightly different in terms of intensities, but also in terms of time of CSAD occurrence (Table 1), and initial drought development. In both years 2015 and 2018, wetter (than long-term mean; 2015) or normal (2018) soil conditions continued from late spring (mid-May) until end of June, with a quick soil drought intensification in July due to high air temperatures (> 30°C), high VPD (>3.8 kPa) (Figure 2), and low precipitation (more than 40% lower than the long-term July average). The year 2022, however, was already characterized by exceptionally low soil water content and high VPD (> 2.5 kPa) in May (Figure 2i), which intensified with low precipitation and high temperatures into early summer. Nighttime VPD exceeded 2 kPa on a few days in June, before the CSAD event occurred mid-July to beginning of August (see Figure A3, appendix AA4). Even the heavy rainfall on 5th August 2022 (28 mm) only resulted in a minor increase of SWC. Nevertheless, after 4th August, air temperature and VPD conditions became near-normal, thereby marking the end of the 2022 CSAD event (Figure 2).

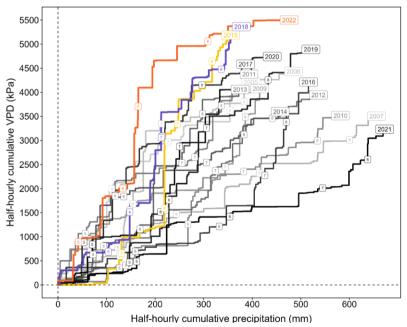


Figure 1. Cumulative VPD and cumulative precipitation from May to September (growing season of the Lägeren forest) of each year (2005-2022). The numbers (5-9) on the cumulative lines depict the end of each month.

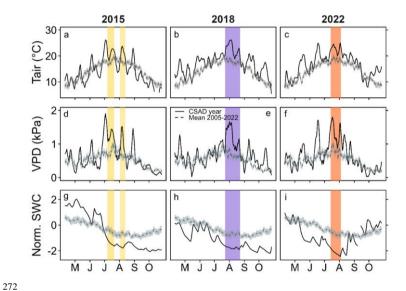


Figure 2. Comparison of 5 day moving averages of daily mean (a-c) Tair, (d-f) VPD, and (g-i) SWC in the years when a CSAD event happened against the long-term means (2005-2022). The band around the dashed line indicates the standard error of the long-term mean 2005-2022. The coloured areas mark the CSAD events, i.e., periods with co-occurring lowest SWC and highest VPD.

Table 1. Characterization of CSAD events in 2015, 2018 and 2022. Duration, maximum (Max.) and standard deviation (\pm SD) of daily mean Tair, maximum (Max.) and standard deviation (\pm SD) of daily mean VPD, and minimum (Min.) and standard deviation (\pm SD) of daily mean normalized SWC recorded during the CSAD events in 2015, 2018 and 2022 are given.

Year	Duration (days)	Max. ± SD	Max. ± SD	Min. ± SD
1 cai	Duration (days)	Tair (°C)	VPD (kPa)	SWC (normalized)
2015	11 + 14 = 2515 + 12	26.9 ± 3.03	2.24 ± 0.4	-1.83 ± 0.20
2013	<u>= 27</u>			
2018	31 <u>32</u>	27.7 ± 2.88	2.19 ± 0.5	-1.93 ± 0.10
2022	21 22	28.3 ± 2.64	2.43 ± 0.5	-2.51 ± 0.20

3.2 Impacts of CSAD events on CO2 fluxes

All CSAD events had immediate negative impacts on ecosystem CO₂ fluxes, showing a decrease in the CO₂ fluxes compared to the long—term—means (Table 2, Figure 3a, c, e, g). Mean daily NEP, GPP, Reco and Rff tended to be lower during the CSAD events compared to the respective long-term means of the reference periods 2005-2022 (for NEP, GPP and Reco) and

2019-2021 (for Rff; Table 2), with much larger variations during CSAD events compared to those of the reference periods (except for Rff; Figure 3b, d, f, h). The lowest average NEP was recorded in the CSAD event of 2022, (minus 41%), followed by NEP in the 2018 and 2015 CSAD events, (minus 38% and minus 35%, respectively), while the lowest average GPP and Reco were found in the 2018 CSAD event (minus 28% and minus 31%, respectively). Table 2).

All cumulative CO₂ fluxes decreased during CSAD events in 2015, 2018 and 2022 compared to the long-term means (Figure 3b, d, f, h), with the only exception of Reco in 2022. The cumulative NEP during the CSAD events in 2015 and 2018 decreased by 34 μmol CO₂ m⁻² s⁻¹ and 26 μmol CO₂ m⁻² s⁻¹, respectively, compared to the respective long-term meansmean of the reference periodsperiod (2005-2022; Figure 3b). During both CSAD years 2015 and 2018, cumulative GPP and Reco decreased considerably, although cumulative GPP tended to decrease more (>40 μmol CO₂ m⁻² s⁻¹) than Reco (>30 μmol CO₂ m⁻² s⁻¹; Figure 3d, f). In contrast, during the CSAD event in 2022, cumulative NEP decreased by 27 μmol CO₂ m⁻² s⁻¹ compared to long-term mean (Figure 3b), due to a decrease in cumulative GPP (by 44 μmol CO₂ m⁻² s⁻¹) and only negligible changes in Reco (Figure 3d, f). Furthermore, Rff fluxes during the 2018 and 2022 CSAD events were lower compared to the long-term mean of the reference period (2019-2021), with 23 μmol CO₂ m⁻² s⁻¹ and 32 μmol CO₂ m⁻² s⁻¹, respectively (Figure 3h). This decrease in Rff was supported by decreasing daily mean SR rates measured in 2022 (Figure 3g).

Table 2. Daily mean CO_2 fluxes during CSAD events in 2015, 2018 and 2022 as well as their long-term means during the respective reference periods. Means and standard deviation (\pm SD) of net ecosystem production (NEP), partitioned gross primary productivity (GPP) and ecosystem respiration (Reco) as well as forest floor respiration (Rff) are given. The reference period for NEP, GPP and Reco represents all days between the 7th of July and the 23rd of August during 2005 and 2022; the reference period for Rff represents all days between the 14th of July and 23rd of August during 2019 and 2021. All fluxes are given in μ mol CO_2 m² s² in .a. = not available.

	NEP	GPP	Reco	Rff
CSAD 2015	2.09 ± 2.14	7.33 ± 2.54	5.05 ± 2.11	n.a.
CSAD 2018	1.99 ± 1.36	6.31 ± 1.44	4.23 ± 0.89	3.19 ± 0.68
CSAD 2022	1.89 ± 1.77	6.69 ± 1.33	5.73 ± 1.55	2.24 ± 0.20
Reference period	3.2 ± 0.82	8.77 ± 0.85	6.14 ± 0.65	3.81 ± 0.26

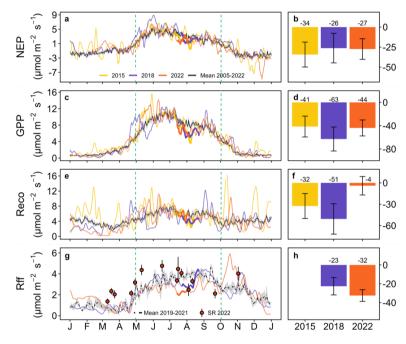


Figure 3. Comparison of daily mean (a) net ecosystem production (NEP), (bc) gross primary productivity (GPP), (ec) ecosystem respiration (Reco), and (dg) forest floor respiration (Rff) of the years when a CSAD event occurred (2015, 2018 and 2022) against the respective long-term means (a, c, e, g). The grev bands around the long-term means represent the standard error of the respective long-term mean CO2 fluxes. Soil respiration (SR) measurements are given as daily means (± SD) measured manually in 2022 only. Thicker lines represent CSAD events. The right panels (b, d, f, h) show the cumulative difference between the actual fluxes recorded during a CSAD event and the respective long-term mean fluxes (2005-2022 for NEP, GPP and Reco; 2019-2021 for Rff;); the associated error bars show the cumulative standard errors of the long-term mean CO2 fluxes for the respective CSAD event.

3.3 Drivers of NEP and Rff in 2015, 2018 and 2022

3.3.1 Comparison of drivers during the 2015, 2018, and 2022 with the long-term means

Daily mean NEP (NEP) during the growing seasons in 2015 and 2018, were mainly driven by daily mean incoming solar radiation (Rg), similar to the long-term daily mean NEP during 2005-2022 (Figure 4a). However, NEP during the 2022 growing season was more strongly driven by daily mean SWC than by Rg, as indicated by its high CVI (Figure 4a). Daily mean Tair and VPD were the second most important drivers of daily mean NEP in 2015 and 2018, with a CVI higher than the ones for the long-term mean 2005-2022. DifferentlyIn contrast to NEP, daily mean Rff during the growing seasons 2019-2021 was

mainly driven by daily mean SWC, followed by daily mean Tair_{ff} and daily mean TS (Figure 4b). We found that daily mean SWC was the main driver of daily mean Rff in 2018, with a much higher CVI compared to those of other years, followed by daily mean TS. Overall, the CVI of all variables was much lower in 2022 compared to those of the other years (Figure 4b).

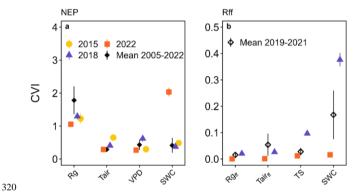
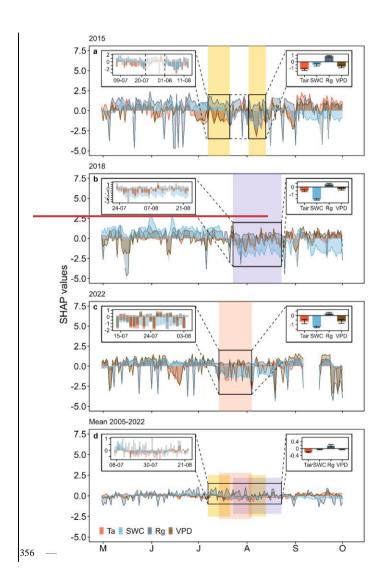


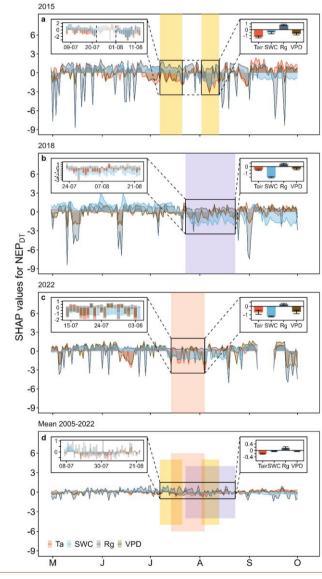
Figure 4. Driver analysis for daily mean (a) net ecosystem production (NEP) and (b) forest floor respiration (Rff) for the growing seasons 2015, 2018, 2022, compared with the long-term daily mean NEP 2005-2022 and the long-term daily mean Rff 2019-2021-long-term daily mean Rff 2019-2021-long-term daily mean Rff 2019-2021-long-term daily mean Rff 2019-2021-long-term daily mean Rff 2019-2021-long-term daily mean Rff 2019-2021-long-term daily mean Rff 2019-2021-long-term daily mean Rff 2019-2021-long-term daily mean Rff 2019-2021-long-term daily mean Rff 2019-2021-long-term daily mean Rff 2019-2021- daily mean Rff 2019-2021-long-term daily mean Rff 2019-2021-long-term daily mean Rff 2019-2021- daily mean Rff 2019-2021-

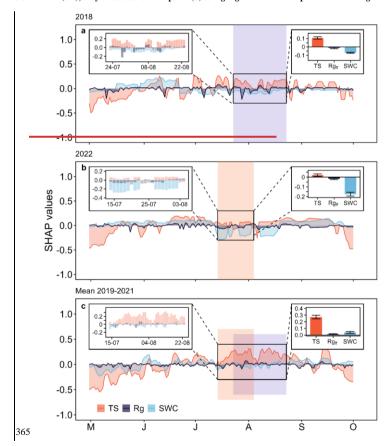
3.3.2 Temporal development of important drivers of daytime NEP and daily Rff

Testing the temporal development inof the main drivers of daytime NEP with SHAP analysis revealed that overall, SWC, VPD and Tair decreased NEP during all CSAD events (Figure 5), while Rg increased daytime NEP. During the two CSAD events in 2015, both Tair and VPD were always associated with a decrease in NEP, while SWC exhibited a less consistent pattern, increasing NEP during the first CSAD event and decreasing NEP during the second (Figure 5a). Nevertheless, the mean contributions of Tair, SWC and VPD to daytime mean NEPNEP_{DT} during the CSAD events of 2015 were negative, with Tair having the largest effect in reducing NEP (Figure 5a). As stated previously, Rg enhanced daytime mean NEPNEP_{DT} in both CSAD events of 2015, contributing positively to NEP (Figure 5a). During the CSAD event of 2018, the mean contributions of Tair, VPD and SWC to daytime mean NEPNEP_{DT} were also all negative, leading to a decrease in NEP (Figure 5b). In contrast to 2015, SWC showed the largest negative effect on daytime NEP during the 2018 CSAD event, although it had clear positive effects prior to the CSAD onset. Rg both enhanced and decreased daytime mean NEPNEP_{DT} during the CSAD event of 2018, which resulted in a small mean positive contribution (Figure 5b). As observed for 2018, the mean contributions of Tair, VPD and SWC were all negative during the CSAD event of 2022, leading to a decrease in NEP (Figure 5c). Similarly to 2018, prior to the 2022 CSAD, SWC had a positive effect on daytime NEP, but then contributed the most to the decrease in NEP during the 2022 CSAD. As observed previously, Rg increased daytime NEP also during the 2022 CSAD

341 event, shown by its positive contribution (Figure 5c). Lastly, during the reference period 2005-2022 (from 7th of July to 23rd of August), Tair, VPD and SWC affected daytime NEP negatively, although the contributions of VPD and SWC were close 342 to zero (Figure 5d). In contrast, the mean contribution of Rg to daytime mean NEPNEP or was positive, resulting in an increase 343 344 of daytime mean NEPNEPDT during the reference period 2005-2022 (Figure 5d). 345 In accordance with the previous analysis for NEP, the decrease in daily Rff during both CSAD events of 2018 and 2022 was mainly driven by negative effects of SWC (Figure 6a, b). In contrast, TS increased Rff during both CSAD events, but with 346 much larger effects during the CSAD in 2018 compared to that in 2022. This coincided with negative effects of SWC on Rff 347 348 already starting in mid-June, one month prior to the 2018 CSAD event (Figure 6a), while during the 2022 CSAD event, SWC 349 effects only became negative shortly before the 2022 event (Figure 6b). The effect of Rgff during both CSAD events in 2018 350 and 2022 was positive, but overall close to zero (Figure 6a, b). For comparison, during the reference period (from 14th of July to 23rd of August 2019-2021), TS had the largest positive effect on Rff compared to the CSAD events in 2018 and 2022, which 351 352 persisted typically until September when senescence and leaf fall set in (Figure 6c). On the other hand, the effects of Rgf and SWC varied around zero throughout all reference period summers (June, July, and August) (Figure 6c). Overall, mean 353 contributions to changes in Rff during the reference period 2019-2021 were dominated by positive effects by TS, and close to 354 355 zero contributions of Rgff and SWC (Figure 6c).







360

362

363

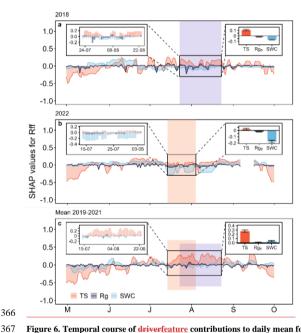


Figure 6. Temporal course of driverfeature contributions to daily mean forest floor respiration (Rff) during the growing seasons of (a) 2018, (b) 2022, and (c) the non-CSAD years 2019-2021, indicated by SHAP values for soil temperature (TS), incoming radiation at the forest floor (Rgr), and SWC. The small inserts on the left show the CSAD events (a-b) and the reference period for 2019-2021 (from 14^{th} July to 23^{rd} August) (d). The small inserts on the right show mean (\pm SD) SHAP values for TS, Rgr, and SWC during the CSAD events (a-b) and during the reference period for 2019-2021 (c). Positive SHAP values indicate a positive effect on the response variable Rff, while negative SHAP values indicate negative effects. Colour bands Coloured areas show the period in which a CSAD event occurred; they are also shown in panel (c) to highlight the reference period for 2019-2021.

3.3.3 Driver thresholds with largest effects on daytime mean NEP and daily mean Rff for the CSAD years

We derived thresholds for the drivers VPD, SWC, Tair, and TS to understandtest if the absolute values of these drivers during the CSAD events actually differed from the absolute values that showed largest effects on daytime mean NEP or daily meanNEP_{DT} or Rff (based on the maximum marginal contributions from SHAP analysis). Threshold values differed among the CSAD years, particularly for SWC_NEP_{max} and SWC_Rff_{max} which were positive in 2015 and 2018 but negative in 2022 (Table 3). VPD_NEP_{max} were relatively low for all CSAD years (between 0.7 and 0.8 kPA), while Tair_NEP_{max} increased from around 10 °C in 2015 to 13 °C in 2018 to 16 °C in 2022. For comparison, TS_Rff_{max} were around 19 °C in 2018 and 15.6 °C in 2022. Comparing measured driver values to those thresholds revealed that most daytime mean VPD values during the CSAD events were typically higher than the respective VPD_NEP_{max} threshold for each of the CSAD years, reaching values of up to 2.5 kPA (Figure 7a, d, g), only few exceptions occurred. In contrast, all daytime mean SWC values measured during

384 the CSAD events were far below the SWC_NEP_{max} thresholds in all CSAD years (Figure 7b, e, h), resulting in very negative 385 effects on daytime NEP. We also observed a decrease in SWC_NEP_{max} values from 2015 to 2022 (Figure 7b, e, h; Table 3). 386 Likewise, daytime mean Tair measured during the CSAD events was far above the Tair_NEPmax, threshold for all CSAD events (Figure 7c, f, i; Table 3). In addition, we observed an increase in Tair_NEP_{max} values from 2015 to 2022 (Figure 7c, f, i; Table 387 388 3). We also observed positive relationships between SWC_NEP_{max} and mean SWC as well as between VPD_NEP_{max} and mean 389 VPD over the different growing seasons (Figure A5). Applying the same analysis to daily mean Rff (Figure 8) revealed that daily mean TS measured during the CSAD event in 2018 varied around the TS_Rff_{max} threshold of 2018 (Figure 8a), while 390 391 measured TS values were higher than the TS_Rff_{max} threshold during the CSAD event in 2022 (Figure 8b). As observed for 392 the NEP, SWC values measured during the CSAD events of 2018 and 2022 were far below the respective SWC_Rff_{max} 393 thresholds (Figure 8b, d), with measured data as well as SWC Rff_{max} thresholds being much lower in 2022 than in 2018 (Figure 394 8b, d; Table 3).

Table 3. Absolute driver thresholds (mean \pm SE) related to the most positive effect on NEPNEPDT or Rff during the three CSAD years and the long-term means (2005-2022 for NEP and 2019-2021 for Rff). Identification was based on the maximum marginal contribution of the respective driver (VPD, SWC, Tair and TS) in the SHAP analysis for each year.

395

396 397

Year	VPD_NEP _{max} (kPa)	SWC_NEP _{max} (normalised)	Tair_NEP _{max} (°C)	TS_Rff _{max} (°C)	SWC_Rff _{max} (normalised)
2015	0.66 ± 0.04	0.40 ± 0.43	9.79 ± 0.56	n.a.	n.a.
2018	0.84 ± 0.05	0.14 ± 0.6	13.13 ± 0.30	19.15 ± 0.07	0.58 ± 0.07
2022	0.77 ± 0.06	$\text{-}0.86 \pm 0.4$	15.95 ± 0.37	15.60 ± 0.07	- 0.73 ± 0.09

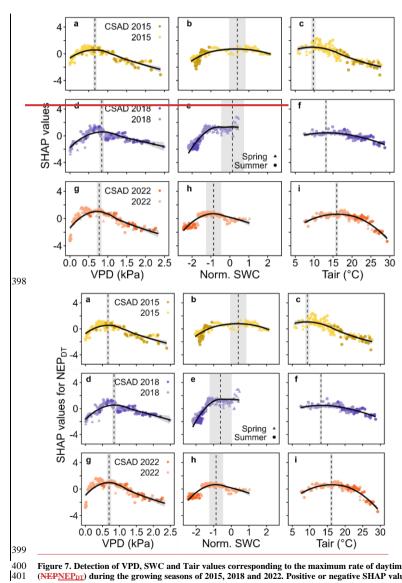
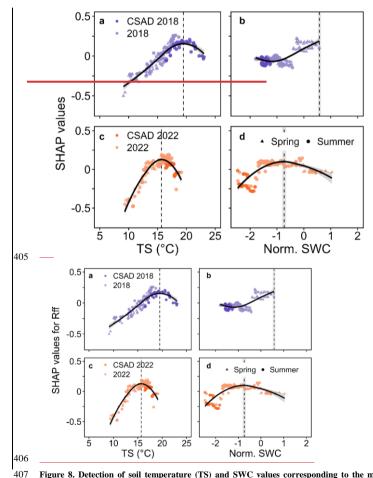


Figure 7. Detection of VPD, SWC and Tair values corresponding to the maximum rate of daytime mean net ecosystem production (NEPNEPDT) during the growing seasons of 2015, 2018 and 2022. Positive or negative SHAP values represent positive or negative



 $\begin{array}{c} 410 \\ 411 \end{array}$

Figure 8. Detection of soil temperature (TS) and SWC values corresponding to the maximum rate of daily mean forest floor respiration (Rff) in 2018 and 2022. Positive or negative SHAP values represent positive or negative effects on Rff. The vertical dashed lines and grey <u>ribbons bands</u> show TS (a, c) and SWC (b, d) and their standard deviations, corresponding to the <u>most positive largest</u> effect on Rff based on the respective maximum marginal contribution of the respective driver in the SHAP analysis for each year to Rff in 2018 and 2022.

3.4 SR responses to TS and SWC in 2022

412

413

414

416

417

418

419

420 421

422

423

424

425 426

427

428 429

430

As seen above, daily mean SR rates mirrored the responses of Rff (Figure 3), though with a much coarser time resolution. The relationships of SR with TS and SWC varied, depending if CSAD events were considered or not (Figure 9). When no CSAD 415 event was recorded, daily mean SR significantly increased with TS (R² of= 0.76, P of 0.002; linear regression). However, during the CSAD event, daily mean SR tendeddid not respond to decrease with increasing TS ($R^2 = 0.19$; Figure 9a). On the other hand, when no independent if a CSAD event was recorded, daily mean or not, SR did not respond to variation in SWC $(R^2 < 0.01)$, while daily mean SR tended to increase with SWC during the CSAD event $(R^2 \circ f \text{ and } R^2 = 0.3 \text{ respectively})$; Figure 9b).

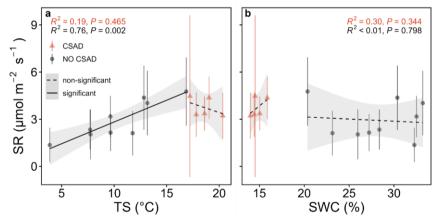


Figure 9. Linear relationships of daily mean soil respiration (SR) with (a) soil temperature (TS) and (b) soil water content (SWC) during the CSAD event 2022 and the rest of the year 2022. Two models were fitted separately for the periods with and without the CSAD event. The goodness of the fit is expressed with R^2 and p-values (P) in the respective panels according to the colour scale.

4 Discussion

In this study, we identified three compound soil and atmospheric drought (CSAD) events during the last 18 years (i.e., 2015, 2018, and 2022) for a mountain mixed deciduous forest. Although they were of comparable intensity, they differed in terms of their timing. We further assessed the mainly negative impacts of these CSAD events on ecosystem CO2 fluxes (NEP, GPP, Reco) and forest floor respiration (Rff). Moreover, we quantified the temporal contribution of the main drivers to these fluxes during the CSAD events and the respective growing seasons (VPD, Tair, Rg, SWC, TS). Pronounced differences in driver impacts effects as well as their temporal development were found; for ecosystem vs. forest floor fluxes, but also among drivers and among CSAD events. In addition, we saw first signs of acclimation of NEP to such CSAD events, makingi.e., changed 432 sensitivities of NEP to its drivers, both within the same and among different growing seasons. This also suggested that

433 predictions of site-specific CSADs and their impacts might become more challenging in the future.

4.1 Compound soil and atmospheric drought (CSAD) events

434

457

461

Several recent studies have shown that Europe already did and also will experience an increase in intensity and frequency of 435 436 CSAD conditions in the future (e.g., Shekhar et al., 2023; Markonis et al., 2021). Such increased occurrence of extremes was 437 also evident during the 18 years (2005-2022) of eddy-covariance measurements at CH-Lae, with three years (2015, 2018, 2022) being characterized by CSAD events, all within the last eight years (2015-2022). Two other years, 2019 and 2020, also 438 439 characterized by atmospheric drought, albeit at lower intensity than the three years chosenidentified here (Figure 1), did not 440 show co-occurring soil drought at our forest site, and were therefore not identified as CSAD years. This nicely 441 illustrated site-specific environmental conditions playing a relevant role when discussing the impact of extreme compound events at larger spatial scales (Shekhar et al., 2023). Interestingly, even though the intensities of the CSAD events of 2015, 442 443 2018 and 2022 were comparable in terms of SWC and VPD values, the pre-conditions and the time of occurrence were 444 different. Pre-conditions (late-spring or early summer), especially in terms of soil moisture and temperature or VPD, can be 445 wet and cool, near-normal, or dry and warm. Thus, depending on these pre-conditions, the impact of any CSAD event on forest 446 performance will differ as shown here. Prior to a CSAD event, soil moisture plays a vital role in determining how well the 447 forest can resist and also recover from the stress of a CSAD event (Jiao et al., 2021). Dry and warm vs. non-limiting conditions 448 before the CSAD event can put the forest under additional water stress during the CSAD event, making it more susceptible to 449 drought and heat stress (da Costa et al., 2018). However, even prior normal soil moisture and warm conditions in spring which favour productivity, but are also accompanied by increased water demands for evapotranspiration, lead to increased soil drying, 450 and can thus amplify extreme dryness stress during summer drought as observed during the 2018 CSAD event at our mixed 451 deciduous forest site (CH-Lae) and across Central Europe (Gharun et al., 2020; Bastos et al., 2020; Shekhar et al., 2020). Thus, 452 453 CSAD events will require our full attention in the future, since their impacts will strongly differ not only depending on their 454 frequency, duration, and intensity, but also depending on the prior site-specific environmental conditions the ecosystem 455 experiences.

456 4.2 Forest CO₂ fluxes and their respective drivers

4.2.1 Net Ecosystem Productivity, NEP

The CSAD events of 2015, 2018 and 2022 resulted in a significant decrease in NEP, which was largely due to decreasing GPP4 (between 4516 and 3028%), while ecosystem respiration (Reco) either decreased or did not change compared to the long-term

460 mean at the mixed deciduous forest. Such reductions in GPP during CSAD events have been observed in earlier studies,

particularly for beech, the dominant species at our forest site (Ciais et al. 2005; Bastos et al., 2020; Dannenberg et al., 2022;

462 D'Orangeville et al., 2018; Xu et al., 2020; Gharun et al., 2020). Increased stomatal closure in response to high VPD and low

Formatted: Space After: 12 pt

464 temperatures (i.e., non-stomatal response; Buckley, 2019; Gourlez de la Motte et al., 2020) at leaf level as well as reduced 465 canopy conductance at ecosystem level (Ciais et al. 2003, Granier et al. 2007, Gharun et al. 2020) are typically associated with such CSAD events. 466 467 Our driver analysis revealed that, among the considered features, air temperature did not have an important impacthad the 468 largest effect on reducing NEPNEPDT during all threethe CSAD events, event in 2015, but not in the others suggesting that 469 stomatal responses on GPP were generally more relevant than temperature-related non-stomatal responses (Granier et al., 470 2007). Moreover, the major drivers we identified, i.e., VPD and SWC, support stomatal responses as underlying mechanisms 471 for the reduction of net CO2 uptake via GPP (Dannenberg et al., 2022; Fu et al., 2022; Petek-Petrik et al., 2023; van der Woude 472 et al., 2023) during all three-CSAD events in 2015, 2018, and 2022. However, the contributions of those dryness-related 473 variables varied among the CSAD events, suggesting that the response of the forest differed depending on the respective 474 intensity of soil dryness (SWC) and of air dryness (VPD) during the CSAD events. Also, the conditions prior to the CSAD 475 event seemed to play an important role, as SWC was more important for NEP during the 2022 CSAD event, which followed 476 upon a prevailing soil drought, compared to the 2015 and 2018 CSAD events. 477 Another line of argumentation towards dryness-related vs. temperature-related drivers of reduced NEP during CSAD events 478 is related to Reco with its two major components, i.e., plant and soil respiration. In our study, Reco was between 6-30-7-31% 479 lower during the three CSAD events vears compared to the other years, supporting the dryness- over the temperature-related 480 argumentation. While plant respiration typically increases in response to high temperatures (Schulze et al. 2019), it also 481 depends on the intensity of the event: if substrate (i.e., carbohydrate) availability is diminished during a CSAD event due to 482 reduced GPP, respiration can also decrease (Janssens et al. 2001; Ciais et al., 2005; Von Buttlar et al., 2018), albeit typically 483 less than GPP (Schwalm et al. 2010). Similarly, soil respiration decreases when substrate supply for root and microbial respiration is low (Högberg et al. 2001; Ruehr et al. 2009). Moreover, soil respiration is known to be small when soil moisture 484 is low (due to reduced microbial and root respiration) during CSAD events (-Ruehr et al. 2010; Von Buttlar et al., 2018; Wang 485 486 et al., 2014), as seen at our site in 2022. 487 In addition to the standard response of NEP (and its components GPP and Reco) to abiotic factorsdrivers (VPD, SWC and 488 Tair), NEP sensitivity to abiotic factors those drivers could change from one growing season to another, (Grossman, 2023), 489 especially during drought conditions, indicating drought acclimation of NEP (Crous et al., 2022; Aspinwall et al., 2017; 490 Sendall et al., 2015; Sperlich et al., 2019). This difference in NEP sensitivity to VPD, SWC and Tair during the 2015, 2018, 491 and 2022 growing seasons was clearly observed in our study (see response curves in Figure 7). The thresholds derived 492 from the response curves of SHAP values vs. the abiotic factorsdrivers (Figure 7) indicated drought-acclimation of NEP to higher VPD (in 2018 and 2022), and lower SWC (in 2022), as we observed a shift towards drier conditions of the VPD, and 493 SWC values corresponding to the maximum marginal contribution of the features to NEP_{DT} in CSAD years (Figure 7, A5).

soil moisture (i.e., stomatal response), reduction of photosynthesis due to reduced carboxylation rate (Rubisco activity) at high

463

Formatted: Space After: 12 pt

Such drought acclimations could be due to biophysical adjustments such as access of soil water from deeper soil layers (Brinkmann et al., 2019), changes in photosynthetic thermal acclimation and changes in stomatal sensitivity to VPD (Aspinwall et al., 2017; Smith and Dukes, 2017; Gessler et al., 2020). Such NEP acclimation to higher VPD and lower SWC will be critical in the future, enabling forests to persist (longer) during CSAD events (Kumarathunge et al., 2019).

499 4.2.2 Forest floor and soil respiration, Rff and SR

514

500 The CSAD event in 2022 resulted in a more pronounced and rapid decrease of Rff than in 2018, leading to smaller CO2 losses from the forest floor compared to 2018 CSAD and the reference period 2019-2021. We observed a similar seasonal trend of 501 502 Rff and SR, but SR was consistently higher than Rff (Figure 3d). Rff is indeed composed by soil and understory vegetation 503 respiration. At the CH-Lae site, the understory LAI (Leaf Area Index) decreased in late spring (Paul-Limoges, 2017) when 504 trees leaf- out, and light reaching the forest floor diminishes. Thus, during the growing season, most of the respiratory CO₂ 505 fluxes from below the canopy consist of SR. Yet, a small part of the SR can be offset by photosynthesis of the vegetation still 506 growing below the canopy (i.e., seedlings of Fagus sylvatica and other herbaceous plants). As we observed that GPP_{ff} was not 507 different from zero during the growing seasons (Figure A4, appendix AA6), we here assumed the effect of photosynthesis in 508 the daily Rff being negligible. European mixed forests are usually more resistant to drought than monospecific ones in terms 509 of microbial soil respiration (Gillespie et al., 2020). For example, Gillespie et al. (2020) found that CO2 emissions were not 510 decreasing under drought in natural mixed European Europ ean forests. However, a reduction of SR during drought has been 511 widely reported in other studies (e.g., Ruehr et al., 2010; Schindlbacher et al., 2012; Wang et al., 2014; Sun et al., 2019), but the interplay of intensity, duration, and biotic components can trigger different responses of the forest floor in the respective 512 ecosystems (Talmon et al., 2011; Jiao et al., 2021).

515 6) was driven by the limitation of Rff and SR by SWC. In accordance with the SR analysis, we found no effect of TS during the CSAD event in 2022 (Figure 9). Drought periods in forests can indeed diminish the temperature sensitivity of the SR 516 (Jassal et al., 2008; Ruehr et al. 2010; Sun et al., 2019; Schindlbacher et al., 2012; van Straaten et al., 2011; Wang et al., 2014). 517 518 Generally, SWC is not limiting at the CH-Lae site, but exceptions can occur during summer (Knhol Knohl et al., 2008; Ruehr 519 et al., 2010; Trabucco and Zomer, 2022). We know that SR is the sum of heterotrophic and autotrophic respiration (Ruehr and 520 Buchmann, 2009; Wang et al., 2014; Zheng et al., 2021). A large component of heterotrophic respiration is microbial activity 521 in the soil. Under drought, the microbial activity is typically reduced by the limited diffusion of soluble carbon substrate for 522 extracellular enzymes (Manzoni et al., 2012). Consequently, litter decomposition rates also decrease (Deng et al., 2021). If 523 decomposition rates decrease, soil organic matter increases in the soil, resulting in higher C and N in the soil (van der Molen et al., 2011). At the same time, drought reduces photosynthesis and so plants tend to keep non-structural carbohydrates in the leaves or roots to sustain the living tissues (Högberg et al., 2008). Thereby, root activity and production are downregulated

The decreased importance of TS during the CSAD event of 2018 and 2022 compared to the reference period 2019-2021 (Figure

Formatted: Subscript

526 (Deng et al., 2021), which can lead to a decoupling of photosynthetic and underground activities (Ruehr et al., 2009; Barba et l., 2018). Eventually, soil drought can significantly alter the N and C cycle in the ecosystem (Deng et al., 2021).

528 The TS and SWC at which Rff_{max} was observed varied from growing season to growing season, as we saw for 2018 and 2022 529 (Figure 8). The SWC recorded during the CSAD events was clearly below-than the SWC Rffmax, but the TS recorded during 530 the CSAD events was observed to be in the range of TS Rff_{max} in 2018. The interplay and the seasonal trends of TS and SWC 531 can thus determine at which abiotic conditions the highest respiration rate is found. Even though SR is projected to increase 532 under global warming (Schindlbacher et al., 2012), the more frequent occurrence of droughts (Grillakis, 2019) could partially 533 offset those emissions (Zheng et al., 2021), as we observed in the decrease of Rff during CSAD events. However, the decrease in CO2 emissions can be compensated by CO2 bursts from rain events occurring after drought periods (Lee et al., 2002) as we 534 535 observed in after the CSAD event in 2022 (Figure 3d). In general, a recovery of SR is expected if the soil moisture quickly 536 returns to normal conditions (Yao et al., 2023). Yet, biotic factors like fine roots are crucial for treestree recovery after drought (Netzer et al., 2016; Hikino et al., 2021; Hikino et al., 2022). For example, it is well known that the fine roots of Fagus sylvatica 537 538 can grow to deeper soil depths during drought, but only if the drought is not too severe, then when they can be shed 539 (Hildebrandt, et al., 2020). Indeed, Nickel et al., (2017) found a progressive decrease in vital fine roots after repeated drought 540 in a mixed deciduous forest in Europe. Hence, the pre-and post-conditions, the timing, the intensity, and the duration of a 541 CSAD are very important to predict the consequences in terms of respiratory CO₂ emissions (Wang et al., 2014).

542 5 Conclusions

543 In this study For our mixed deciduous forest, we found first signs of forest's NEP to acclimate acclimation to more extreme soil (low SWC) and atmospheric drought (high VPD) conditions when comparing sensitivities of NEP to these drivers during the 544 545 same growing season, which will be fundamental for drought resistance in the future. Nevertheless, we expect to witness a 546 larger reduction of GPP with more extreme CSAD events in the future, even if complemented by a reduction in Reco. Hence 547 responses to CSAD events might lead to a reduction of the CO2 sink capacity of the forest in the future. The study also 548 highlighted a decoupling between the drivers and the different behaviours of the responses of the above-canopy and the forest 549 floor CO2 fluxes during CSAD events. With further global warming in Europe, we expect an increase in Rff, but with more 550 extreme droughts and more intense precipitation events, we assume a higher variability of the CO₂ emissions from forest soils 551 and thus uncertain consequences for the respective soil carbon stocks. Ultimately, the consequences of such CSAD events will 552 influence the annual carbon budget of a forest, and thus jeopardising many restoration/reforestation projects or nature-based 553 solutions as proposed in the Paris Agreement.

554 Appendix A

$555 \quad \textbf{Table A1. List of instruments, models and manufacturers used in this study.}$

	Instrument	Model	Manufacturer
l	Infrared gas analyser (IRGA)1	LI-7500 (2004-2015)	LI-COR Inc., Lincoln, NE, USA
	Infrared gas analyser (IRGA)1	LI-7200 (2016-2022)	LI-COR Inc., Lincoln, NE, USA
l	3-D Sonic anemometer ¹	HS-50	Gill Instruments Ltd., Lymington, UK
	Air temperature and relative humidity ²	Rotronic MP 101 A	Rotronic AG, Bassersdorf, Switzerland
	Incoming radiation ²	BF2_BF2116	Delta-T Devices Ltd, Cambridge, UK
l	Infrared gas analyser (IRGA) ³	LI-7500	LI-COR Inc., Lincoln, NE, USA
l	3-D Sonic anemometer ³	R-350	Gill Instruments Ltd., Lymington, UK
	Air temperature and relative humidiy ⁴	CS215_E16511	Campbell Scientific Ltd., UG, USA
	Soil temperature and water content ⁵	Decagon ECH2O EC-20 probes (2004-2020)	Pullman, WA, USA
	Soil temperature and water content ⁵	TEROS 12_00007171 (2020-2022)	METER Group AG, NE, USA
	Incoming radiation ⁴	LI190SB-L	LI-COR Inc., Lincoln, NE, USA
	Infrared gas analyser (IRGA) ⁶	LI-8100	LI-COR Inc., Lincoln, NE, USA
l	Soil temperature ⁶	GTH 175 PT	GHM Messtechnik GmbH, Regenstauf, Germany
	Soil water content ⁶	HH2 Moisture Meter	Delta-T Devices, Cambridge, United Kingdom

Formatted: Font color: Auto

³Below-canopy EC system (1.5 m height) ⁴Below-canopy meteorological station (2 m height)

⁵Forest floor meteorological station (profile measurements up-toat 5, 10, 20, 30, 50 cm depth)

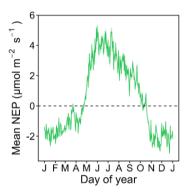


Figure A1. Long-term (2005-2022) daily mean and standard deviation of net ecosystem productivity (NEP) of CH-Lae. The zero-line highlights whether the daily NEP is positive or negative. The growing season—(GS) was identified as the period in which daily NEP was positive (1st May to 31st September).

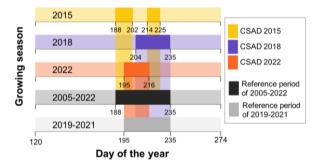
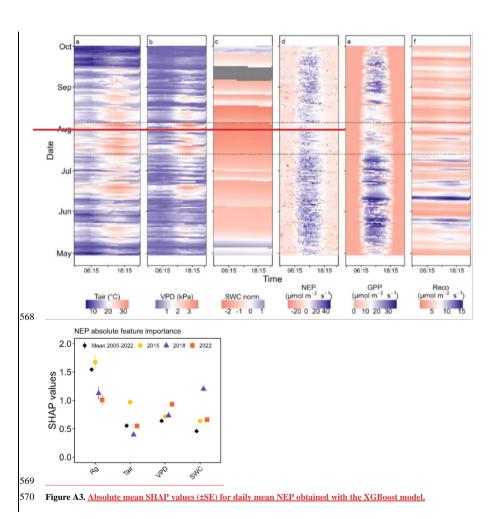


Figure A2. Graphical definition of reference periods. The five horizontal bendsbars display the three growing seasons in which a CSAD event occurred, and the two long term means used as areference periods for comparison-period (2005-2022 for ecosystem level measurements and 2019-2021 for forest floor measurements). The CSAD periods are marked for each growing season in the CSAD years. The reference period of the mean 2005-2022 used in the analysisour analyses corresponds to the interval of time between day 188 (7th July) and day 235 (23rd of August), while the one of the mean 2019-2021 corresponds to the interval of time between day 195 (14th July) and day 235 (23rd of August).



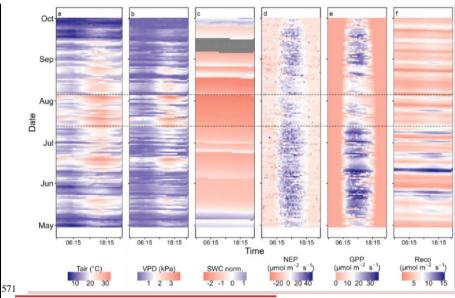
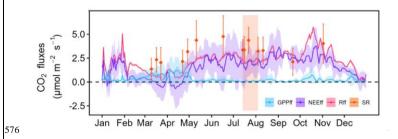


Figure A4. Diurnal (x-axis) and intra-annual (y-axis) variation of (a) air temperature (Tair), (b) VPD, (c) normalized soil water content (SWC at 20 cm depth) (d) net ecosystem production (NEP), (e) gross primary productivity (GPP), and (f) ecosystem respiration (Reco) induring the 2022 growing season. 30 min averages are plotted in all panels. The two black dashed lines extending from 14 H July 2022 to and 4 A August 2022 mark the compound soil and atmospheric drought (CSAD) event of summer 2022.



Formatted: Superscript

Formatted: Superscript

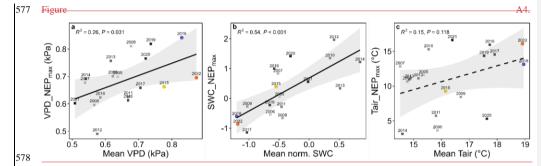


Figure A5. Linear regressions of mean VPD, SWC, and Tair values during the growing season of a given year against maximum marginal contributions of VPD, SWC and Tair (here abbreviated as feature_NEP_{max}) to daytime NEP. SWC values were normalized. The grey bands around the regression lines indicate the 95% confidence interval. R² and p-values are given as well.

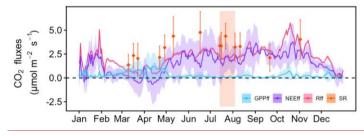


Figure A6. Forest floor CO₂ fluxes in 2022. The continuous lines show gap-filled and partitioned daily mean fluxes and standard deviations (coloured ribbons) of the forest floor-bands). 30 min averages are plotted. The diamonds represent daily means of manual soil respiration measurements, standard deviations are given as well. The area colored in orange-bend represents the CSAD event of 2022.

587 Code availability

579

580

582 583

584

585

586

590

588 The R scripts used for the data analysis and plots are available.

589 The R scripts used for data analyses and plots are available in the Git repository with the following link

https://github.com/lscapucci/Compound-soil-and-atmospheric-drought-events-and-CO2-fluxes-of-a-mixed-deciduous-forest.

Author contribution

- 592 LS, AS, MG, NB conceptualization of the study, LS, AS, SAB, AB field campaigns, LS, AS, LH data processing and
- 593 management, LS, AS data analyses-and; LS, AS, NB manuscript writing, and all-the authors revision and editing of the
- 594 manuscript.

595 Competing interests

596 The contact author has declared that none of the authors has any competing interests.

597 Acknowledgements

- 598 Authors acknowledge funding from the ETH Zürich project FEVER (ETH-27 19-1), and the SNF funded projects COCO
- 599 (200021_197357), ICOS-CH Phase 3 (20F120_198227), and EcoDrive (IZCOZ0_198094), and the great support of the
- 600 Grassland Sciences group members, especially Anna Katarina Gilgen, Luana Krebs, Julia Hauri, Franziska Richter, Yi Wang,
- 601 Fabio Turco, Ruikun Gou, Roland Anton Werner, and Davide Andreatta.

602 References

- Anderegg, W. R. L., Wu, C., Acil, N., Carvalhais, N., Pugh, T. A. M., Sadler, J. P., and Seidl, R.: A climate risk analysis of
- Earth's forests in the 21st century, Science, 377, 1099-1103, 10.1126/science.abp 9723, 2022.
- 605 Aspinwall, M. J., Vårhammar, A., Blackman, C. J., Tjoelker, M. G., Ahrens, C., Byrne, M., Tissue, D. T., and Rymer, P. D.:
- Adaptation and acclimation both influence photosynthetic and respiratory temperature responses in, Tree Physiology, 37,
- 607 1095-1112, 10.1093/treephys/tpx047, 2017.
- 608 Aubinet, M., Vesala, T., and Papale, D.: Eddy covariance: a practical guide to measurement and data analysis, Springer Science
- 609 & Business Media2012.
- 610 Barba, J., Lloret, F., Poyatos, R., Molowny-Horas, R., and Yuste, J. C.: Multi-temporal influence of vegetation on soil
- 611 respiration in a drought-affected forest, Iforest-Biogeosciences and Forestry, 11, 189-198, 10.3832/ifor2448-011, 2018.
- 612 Bastos, A., Ciais, P., Friedlingstein, P., Sitch, S., Pongratz, J., Fan, L., Wigneron, J. P., Weber, U., Reichstein, M., Fu, Z.,
- Anthoni, P., Arneth, A., Haverd, V., Jain, A. K., Joetzjer, E., Knauer, J., Lienert, S., Loughran, T., McGuire, P. C., Tian,
- 614 H., Viovy, N., and Zaehle, S.: Direct and seasonal legacy effects of the 2018 heat wave and drought on European ecosystem
- productivity, Science Advances, 6, ARTN eaba2724, 10.1126/sciadv.aba2724, 2020.
- 616 Bates, D., Mächler, M., Bolker, B. M., and Walker, S. C.: Fitting Linear Mixed Effects Models Using Ime4, Journal of
- 617 Statistical Software, 67, 1-48, DOI 10.18637/jss.v067.i01, 2015.

- 618 Birami, B., Gattmann, M., Heyer, A. G., Grote, R., Arneth, A., and Ruehr, N. K.: Heat Waves Alter Carbon Allocation and
- 619 Increase Mortality of Aleppo Pine Under Dry Conditions, Frontiers in Forests and Global Change, 1, ARTN 8,
- 620 10.3389/ffgc.2018.00008, 2018.
- 621 Bogati, K. and Walczak, M.: The Impact of Drought Stress on Soil Microbial Community, Enzyme Activities and Plants,
- 622 Agronomy-Basel, 12, ARTN 189, 10.3390/agronomy12010189, 2022.
- 623 Breiman, L.: Random forests, Machine Learning, 45, 5-32, Doi 10.1023/A:1010933404324, 2001.
- 624 Brinkmann, N., Eugster, W., Buchmann, N., and Kahmen, A.: Species-specific differences in water uptake depth of mature
- temperate trees vary with water availability in the soil, Plant Biology, 21, 71-81, 10.1111/plb.12907, 2019.
- Buckley, T. N.: How do stomata respond to water status?, New Phytologist, 224, 21-36, 10.1111/nph.15899, 2019.
- 627 Chen, T. and Guestrin, C.: XGBoost: A Scalable Tree Boosting System, Proceedings of the 22nd ACM SIGKDD International
 - Conference on Knowledge Discovery and Data Mining, San Francisco, California, USA, 10.1145/2939672.2939785, 2016.
- 629 Chi, J. S., Zhao, P., Klosterhalfen, A., Jocher, G., Kljun, N., Nilsson, M. B., and Peichl, M.: Forest floor fluxes drive differences
- in the carbon balance of contrasting boreal forest stands, Agricultural and Forest Meteorology, 306, ARTN 108454,
- 631 10.1016/j.agrformet.2021.108454, 2021.
- 632 Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A.,
 - Chevallier, F., De Noblet, N., Friend, A. D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner,
- 634 G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J. M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G.,
- Soussana, J. F., Sanz, M. J., Schulze, E. D., Vesala, T., and Valentini, R.: Europe-wide reduction in primary productivity
- caused by the heat and drought in 2003, Nature, 437, 529-533, 10.1038/nature03972, 2005.
- 637 Copernicus Climate Change Service: European State of the Climate 2019, 2019.https://climate.copernicus.eu/ESOTC/2019,
- 638 2019.

633

- 639 Copernicus Climate Change Service (C3S): European State of the Climate 2022,
- 640 <u>2023.https://climate.copernicus.eu/esotc/2022, 2023.</u>
- 641 Crous, K. Y., Uddling, J., and De Kauwe, M. G.: Temperature responses of photosynthesis and respiration in evergreen trees
- from boreal to tropical latitudes, New Phytologist, 234, 353-374, 10.1111/nph.17951, 2022.
- da Costa, A. C. L., Rowland, L., Oliveira, R. S., Oliveira, A. A. R., Binks, O. J., Salmon, Y., Vasconcelos, S. S., Junior, J. A.
- 644 S., Ferreira, L. V., Poyatos, R., Mencuccini, M., and Meir, P.: Stand dynamics modulate water cycling and mortality risk
- 645 in droughted tropical forest, Global Change Biology, 24, 249-258, 10.1111/gcb.13851, 2018.
- Dannenberg, M. P., Yan, D., Barnes, M. L., Smith, W. K., Johnston, M. R., Scott, R. L., Biederman, J. A., Knowles, J. F.,
- Wang, X., Duman, T., Litvak, M. E., Kimball, J. S., Williams, A. P., and Zhang, Y.: Exceptional heat and atmospheric
- dryness amplified losses of primary production during the 2020 U.S. Southwest hot drought, Glob Chang Biol, 28, 4794-
- 649 4806, 10.1111/gcb.16214, 2022.
- de la Motte, L. G., Beauclaire, Q., Heinesch, B., Cuntz, M., Foltynová, L., Sigut, L., Kowalska, N., Manca, G., Ballarin, I. G.,
- 651 Vincke, C., Roland, M., Ibrom, A., Lousteau, D., Siebicke, L., Neiryink, J., and Longdoz, B.: Non-stomatal processes

- reduce gross primary productivity in temperate forest ecosystems during severe edaphic drought, Philosophical
- Transactions of the Royal Society B-Biological Sciences, 375, ARTN 20190527, 10.1098/rstb.2019.0527, 2020.
- 654 Deng, L., Peng, C. H., Kim, D. G., Li, J. W., Liu, Y. L., Hai, X. Y., Liu, Q. Y., Huang, C. B., Shangguan, Z. P., and Kuzyakov,
- 655 Y.: Drought effects on soil carbon and nitrogen dynamics in global natural ecosystems, Earth-Science Reviews, 214, ARTN
- 656 10350, 10.1016/j.earscirev.2020.103501, 2021.
- 657 Dirmeyer, P. A., Balsamo, G., Blyth, E. M., Morrison, R., and Cooper, H. M.: Land-Atmosphere Interactions Exacerbated-
- 658 <u>atmosphere interactions exacerbated</u> the <u>Droughtdrought</u> and <u>Heatwave Over Northernheatwave over northern</u> Europe
- 659 During Summerduring summer 2018, AguAGU Advances, 2, ARTN-e2020AV000283, 10.1029/2020AV000283, 2021.
- 660 D'Orangeville, L., Maxwell, J., Kneeshaw, D., Pederson, N., Duchesne, L., Logan, T., Houle, D., Arseneault, D., Beier, C. M.,
- 661 Bishop, D. A., Druckenbrod, D., Fraver, S., Girard, F., Halman, J., Hansen, C., Hart, J. L., Hartmann, H., Kaye, M.,
- 662 Leblanc, D., Manzoni, S., Ouimet, R., Rayback, S., Rollinson, C. R., and Phillips, R. P.: Drought timing and local climate
- determine the sensitivity of eastern temperate forests to drought, Global Change Biology, 24, 2339-2351,
- 664 10.1111/gcb.14096, 2018.
- 665 Etzold, S., Buchmann, N., and Eugster, W.: Contribution of advection to the carbon budget measured by eddy covariance at a
- steep mountain slope forest in Switzerland, Biogeosciences, 7, 2461-2475, 10.5194/bg-7-2461-2010, 2010.
- 667 Etzold, S., Ruehr, N. K., Zweifel, R., Dobbertin, M., Zingg, A., Pluess, P., Häsler, R., Eugster, W., and Buchmann, N.: The
- 668 Carbon Balance of Two Contrasting Mountain Forest Ecosystems in Switzerland: Similar Annual Trends, but Seasonal
- 669 Differences, Ecosystems, 14, 1289-1309, 10.1007/s10021-011-9481-3, 2011.
- 670 Fan, S. M., Wofsy, S. C., Bakwin, P. S., Jacob, D. J., and Fitzjarrald, D. R.: Atmosphere-Biosphere Exchangebiosphere
- exchange of Go2CO₂ and O₃ in the Central-Amazon-Forest, Journal of Geophysical Research-Atmospheres, 95, 16851-
- 672 16864. DOI 10.1029/JD095iD10p16851. 1990.
- 673 Foken, T., Göockede, M., Mauder, M., Mahrt, L., Amiro, B., and Munger, W.: Post-field data quality control, in: Handbook
- 674 of micrometeorology; a guide for surface flux measurement and analysis, Springer, 181-208, 2004.
- 675 Fratini, G., Ibrom, A., Arriga, N., Burba, G., and Papale, D.: Relative humidity effects on water vapour fluxes measured with
- 676 closed-path eddy-covariance systems with short sampling lines (vol 165, pg 53, 2012), Agricultural and Forest
- Meteorology, 166, 234-234, 10.1016/j.agrformet.2012.10.013, 2012.
- 678 Gazol, A. and Camarero, J. J.: Compound climate events increase tree drought mortality across European forests, Science of
- 679 the Total Environment, 816, ARTN 151604, 10.1016/j.scitotenv.2021.151604, 2022.
- 680 George, J. P., Bürkner, P. C., Sanders, T. G. M., Neumann, M., Cammalleri, C., Vogt, J. V., and Lang, M.: Long-term forest
- monitoring reveals constant mortality rise in European forests, Plant Biology, 24, 1108-1119, 10.1111/plb.13469, 2022.
- 682 Gessler, A., Bottero, A., Marshall, J., and Arend, M.: The way back: recovery of trees from drought and its implication for
- 683 acclimation, New Phytologist, 228, 1704-1709, 10.1111/nph.16703, 2020.
- 684 Gharun, M., Hörtnagl, L., Paul-Limoges, E., Ghiasi, S., Feigenwinter, I., Burri, S., Marquardt, K., Etzold, S., Zweifel, R.,
- 685 Eugster, W., and Buchmann, N.: Physiological response of Swiss ecosystems to 2018 drought across plant types and

Formatted: Indent: Left: 0 cm, Hanging: 0.5 cm

Formatted: Subscript

- elevation, Philosophical Transactions of the Royal Society B-Biological Sciences, 375, ARTN 20190521,
- 687 10.1098/rstb.2019.0521, 2020.
- 688 Gillespie, L. M., Fromin, N., Milcu, A., Buatois, B., Pontoizeau, C., and Hättenschwiler, S.: Higher tree diversity increases
- soil microbial resistance to drought, Communications Biologybiology, 3, ARTN-377, 10.1038/s42003-020-1112-0, 2020.
- 690 10.1038/s42003-020-1112-0, 2020.
- 691 Gillespie, L. M., Fromin, N., Milcu, A., Buatois, B., Pontoizeau, C., and Hättenschwiler, S.: Higher tree diversity increases
- 692 soil microbial resistance to drought, Communications Biology, 3, ARTN 377
- 693 10.1038/s42003 020 1112 0, 2020.
- 694 Greco, S. and Baldocchi, D. D.: Seasonal variations of CO₂ and water vapour exchange rates over a temperate deciduous forest,
- 695 Global Change Biology, 2, 183-197, 10.1111/j.1365-2486.1996.tb00071.x, 1996.
- 696 Grillakis, M. G.: Increase in severe and extreme soil moisture droughts for Europe under climate change, Science of the The
- 697 Total Environment, 660, 1245-1255, 10.1016/j.scitotenv.2019.01.001, 2019.
- 698 Grossiord, C., Buckley, T. N., Cernusak, L. A., Novick, K. A., Poulter, B., Siegwolf, R. T. W., Sperry, J. S., and McDowell,
 - N. G.: Plant responses to rising vapor pressure deficit, New Phytologist, 226, 1550-1566, 10.1111/nph.16485, 2020.
- 700 Grossiord, C., Sevanto, S., Borrego, I., Chan, A. M., Collins, A. D., Dickman, L. T., Hudson, P. J., McBranch, N., Michaletz,
 - S. T., Pockman, W. T., Ryan, M., Vilagrosa, A., and McDowell, N. G.: Tree water dynamics in a drying and warming
- 702 world, Plant Cell and Environment, 40, 1861-1873, 10.1111/pce.12991, 2017.
- 703 Grossman, J. J.: Phenological physiology: seasonal patterns of plant stress tolerance in a changing climate, New Phytologist,
- 704 <u>237, 1508-1524, 2023.</u>

701

712

- Haberstroh, S., Werner, C., Grün, M., Kreuzwieser, J., Seifert, T., Schindler, D., and Christen, A.: Central European 2018 hot
- drought shifts scots pine forest to its tipping point, Plant Biology, 24, 1186-1197, 10.1111/plb.13455, 2022.
- 707 Harris, N. L., Gibbs, D. A., Baccini, A., Birdsey, R. A., de Bruin, S., Farina, M., Fatoyinbo, L., Hansen, M. C., Herold, M.,
- Houghton, R. A., Potapov, P. V., Suarez, D. R., Roman-Cuesta, R. M., Saatchi, S. S., Slay, C. M., Turubanova, S. A., and
- 709 Tyukavina, A.: Global maps of twenty-first century forest carbon fluxes, Nature Climate Change, 11, 10.1038/s41558-020-
- 710 00976-6, 2021.
- Hermann, M., Röthlisberger, M., Gessler, A., Rigling, A., Senf, C., Wohlgemuth, T., and Wernli, H.: Meteorological history
 - of low-forest-greenness events in Europe in 2002-2022, Biogeosciences, 20, 1155-1180, 10.5194/bg-20-1155-2023, 2023.
- 1713 Hikino, K., Danzberger, J., Riedel, V. P., Rehschuh, R., Ruehr, N. K., Hesse, B. D., Lehmann, M. M., Buegger, F., Weikl, F.,
- 714 Pritsch, K., and Grams, T. E. E.: High resilience of carbon transport in long-term drought-stressed mature Norway spruce
- 715 trees within 2 weeks after drought release, Global Change Biology, 28, 2095-2110, 10.1111/gcb.16051, 2022.
- 716 Hikino, K., Danzberger, J., Riedel, V. P., Hesse, B. D., Hafner, B. D., Gebhardt, T., Rehschuh, R., Ruehr, N. K., Brunn, M.,
- 717 Bauerle, T. L., Landhäusser, S. M., Lehmann, M. M., Rötzer, T., Pretzsch, H., Buegger, F., Weikl, F., Pritsch, K., and
- 718 Grams, T. E. E.: Dynamics of initial carbon allocation after drought release in mature Norway spruce-Increased

Formatted: Indent: Left: 0 cm, Hanging: 0.5 cm

- $719 \qquad \text{below ground allocation of current photoassimilates covers only half of the carbon used for fine-root growth, Global Change} \\$
- 720 Biology, 28, 6889-6905, 10.1111/gcb.16388, 2022.
- 721 Hildebrandt, A.: Root-Water Relationswater relations and Interactions in Mixed Forest Settingsmixed forest
- 722 <u>settings</u>, Forest-Water Interactions, 240, 319-348, 10.1007/978-3-030-26086-6_14, 2020.
- 723 Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., Nyberg, G., Ottosson-Löfvenius, M.,
- 724 and Read, D. J.: Large-scale forest girdling shows that current photosynthesis drives soil respiration, Nature, 411, 789-792,
- 725 Doi 10.1038/35081058, 2001.

- Högberg, P., Högberg, M. N., Göttlicher, S. G., Betson, N. R., Keel, S. G., Metcalfe, D. B., Campbell, C., Schindlbacher, A.,
 - Hurry, V., Lundmark, T., Linder, S., and Näsholm, T.: High temporal resolution tracing of photosynthate carbon from the
- 728 tree canopy to forest soil microorganisms, New Phytologist, 177, 220-228, 10.1111/j.1469-8137.2007.02238.x, 2008.
- Horst, T. W.: A simple formula for attenuation of eddy fluxes measured with first-order-response scalar sensors, Boundary-
- 730 Layer Meteorology, 82, 219-233, Doi 10.1023/A:1000229130034, 1997.
- 731 Hothorn, T., Hornik, K., and Zeileis, A.: Unbiased recursive partitioning: A conditional inference framework, Journal of
- 732 Computational and Graphical Statistics, 15, 651-674, 10.1198/106186006x133933, 2006.
- 733 Intergovernmental Panel on Climate, C.: Climate Change 2022 Impacts, Adaptation and Vulnerability: Working Group II
- 734 Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University
- 735 Press, Cambridge, DOI: 10.1017/9781009325844, 2023.
- 736 Ionita, M., Dima, M., Nagavciuc, V., Scholz, P., and Lohmann, G.: Past megadroughts in central Europe were longer, more
- 737 severe and less warm than modern droughts, Communications Earth & Environment, 2, ARTN 61
- 738 10.1038/s43247-021-00130-w, 2021.
- 739 Ionita, M., Tallaksen, L. M., Kingston, D. G., Stagge, J. H., Laaha, G., Van Lanen, H. A. J., Scholz, P., Chelcea, S. M., and
- 740 Haslinger, K.: The European 2015 drought from a climatological perspective, Hydrology and Earth System Sciences, 21,
- 741 1397-1419, 10.5194/hess-21-1397-2017, 2017.
- Janssens, I. A., Lankreijer, H., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz,
- 743 B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E. J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev,
- 744 S., Clement, R., Gudmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen,
- 745 N. O., Vesala, T., Granier, A., Schulze, E. D., Lindroth, A., Dolman, A. J., Jarvis, P. G., Ceulemans, R., and Valentini, R.:
- 746 Productivity overshadows temperature in determining soil and ecosystem respiration across European forests, Global
- 747 Change Biology, 7, 269-278, DOI 10.1046/j.1365-2486.2001.00412.x, 2001.
- 748 Jassal, R. S., Black, T. A., Novak, M. D., Gaumont-Guay, D., and Nesic, Z.: Effect of soil water stress on soil respiration and
- 749 its temperature sensitivity in an 18-year-old temperate Douglas-fir stand, Global Change Biology, 14, 1305-1318,
- 750 10.1111/j.1365-2486.2008.01573.x, 2008.

- 751 Jiao, T., Williams, C. A., De Kauwe, M. G., Schwalm, C. R., and Medlyn, B. E.: Patterns of post-drought recovery are strongly
- 752 influenced by drought duration, frequency, post-drought wetness, and bioclimatic setting, Global Change Biology, 27,
- 753 4630-4643, 10.1111/gcb.15788, 2021.
- 754 Kim, J. B., So, J. M., and Bae, D. H.: Global Warming Impacts on Severe Drought Characteristicssevere drought
- 755 characteristics in Asia Monsoon Regionmonsoon region, Water, 12, ARTN 1360
- 756 10.3390/w12051360, 2020.
- 757 Kittler, F., Eugster, W., Foken, T., Heimann, M., Kolle, O., and Göckede, M.: High-quality eddy-covariance CO
- 758 CO₂ budgets under cold climate conditions, Journal of Geophysical Research-Biogeosciences, 122, 2064-2084.
- 759 10.1002/2017jg003830, 2017.
- 760 Knohl, A., Soe, A. R. B., Kutsch, W. L., Göckede, M., and Buchmann, N.: Representative estimates of soil and ecosystem 761
 - respiration in an old beech forest, Plant and Soil, 302, 189-202, 10.1007/s11104-007-9467-2, 2008.
- 762 Körner, C., Möhl, P., and Hiltbrunner, E.: Four ways to define the growing season, Ecology Letters, 10.1111/ele.14260, 2023.
- 763 Kumarathunge, D. P., Medlyn, B. E., Drake, J. E., Tjoelker, M. G., Aspinwall, M. J., Battaglia, M., Cano, F. J., Carter, K. R.,
- 764 Cavaleri, M. A., Cernusak, L. A., Chambers, J. Q., Crous, K. Y., De Kauwe, M. G., Dillaway, D. N., Dreyer, E., Ellsworth,
- 765 D. S., Ghannoum, O., Han, O. M., Hikosaka, K., Jensen, A. M., Kelly, J. W. G., Kruger, E. L., Mercado, L. M., Onoda,
- 766 Y., Reich, P. B., Rogers, A., Slot, M., Smith, N. G., Tarvainen, L., Tissue, D. T., Togashi, H. F., Tribuzy, E. S., Uddling,
- 767 J., Vårhammar, A., Wallin, G., Warren, J. M., and Way, D. A.: Acclimation and adaptation components of the temperature
- 768 dependence of plant photosynthesis at the global scale, New Phytologist, 222, 768-784, 10.1111/nph.15668, 2019.
- Lal, P., Shekhar, A., Gharun, M., and Das, N. N.: Spatiotemporal evolution of global long-term patterns of soil moisture, 769
- 770 Science of the Total Environment, 867, ARTN 161470, 10.1016/j.scitotenv.2023.161470, 2023.
- 771 Lasslop, G., Reichstein, M., Papale, D., Richardson, A. D., Arneth, A., Barr, A., Stoy, P., and Wohlfahrt, G.: Separation of net
- 772 ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global
- 773 evaluation, Global Change Biology, 16, 187-208, 10.1111/j.1365-2486.2009.02041.x, 2010.
- 774 Lee, M.S.-s., Nakane, K., Nakatsubo, T., Mo, W.H.h., and Koizumi, H.: Effects of rainfall events on soil €02€0 2 flux in a
- cool temperate deciduous broad-leaved forest, Ecological Research, 17, 401-409, UNSP ere_498.sgm10.1046/j.1440-775
- 776 1703.2002.00498.x, 2002.
- 777 DOI 10.1046/j.1440-1703.2002.00498.x, 2002.
- 778 Lloyd, J. and Taylor, J. A.: On the Temperature Dependence temperature-dependence of Soil Respirationsoil respiration,
- 779 Functional Ecology, 8, 315-323, Doi 10.2307/2389824, 1994.
- 780 Lu, R. Y., Xu, K., Chen, R. D., Chen, W., Li, F., and Lv, C. Y.: Heat waves in summer 2022 and increasing concern regarding
- 781 heat waves in general, Atmospheric and Oceanic Science Letters, 16, ARTN 100290, 10.1016/j.aosl.2022.100290, 2023.
- 782 Lundberg, S. M. and Lee, S. I.: A Unified Approach to Interpreting Model Predictions, Advances interpreting model
- 783 predictions, advances in Neural Information Processing Systems 30 (Nips 2017), neural information processing systems,
- 784 30, 2017.

Formatted: Indent: Left: 0 cm, Hanging: 0.5 cm

Formatted: Indent: Left: 0 cm, Hanging: 0.5 cm

- Lundberg, S. M., Erion, G., Chen, H., DeGrave, A., Prutkin, J. M., Nair, B., Katz, R., Himmelfarb, J., Bansal, N., and Lee, S.
- 786 I.: From local explanations to global understanding with explainable AI for trees, Nature Machine Intelligence, 2, 56-67,
- 787 10.1038/s42256-019-0138-9, 2020.
- 788 Manzoni, S., Schimel, J. P., and Porporato, A.: Responses of soil microbial communities to water stress: results from a meta-
- 789 analysis, Ecology, 93, 930-938, Doi 10.1890/11-0026.1, 2012.
- 790 Markonis, Y., Kumar, R., Hanel, M., Rakovec, O., Máca, P., and AghaKouchak, A.: The rise of compound warm-season
- 791 droughts in Europe, Science Advances, 7, ARTN eabb9668, 10.1126/sciadv.abb9668, 2021.
- 792 Martinez-Garcia, E., Nilsson, M. B., Laudon, H., Lundmark, T., Fransson, J. E. S., Wallerman, J., and Peichl, M.: Overstory
- dynamics regulate the spatial variability in forest-floor CO₂ fluxes across a managed boreal forest landscape, Agricultural
- 794 and Forest Meteorology, 318, ARTN 108916, 10.1016/j.agrformet.2022.108916, 2022.
- 795 Mauder, M. and Foken, T.: Impact of post-field data processing on eddy covariance flux estimates and energy balance closure,
- 796 <u>Meteorologische Zeitschrift, 15, 597-610, 2006.</u>
- 797 MeteoSvizzera. (2023). Rapporto sul clima 2022.
- 798 Miralles, D. G., Gentine, P., Seneviratne, S. I., and Teuling, A. J.: Land-atmospheric feedbacks during droughts and heatwaves:
- 799 state of the science and current challenges, Annals of the New York Academy of Sciences, 1436, 19-35,
- 800 10.1111/nyas.13912, 2019.
- 801 Moncrieff, J., Clement, R., Finnigan, J., and Meyers, T.: Averaging, detrending, and filtering of eddy covariance time series,
- in: Handbook of micrometeorology: A guide for surface flux measurement and analysis, Springer, 7-31, 2004.
- 803 Moravec, V., Markonis, Y., Rakovec, O., Svoboda, M., Trnka, M., Kumar, R., and Hanel, M.: Europe under multi-year
- 804 droughts; how severe was the 2014-2018 drought period?, Environmental Research Letters, 16, ARTN
- 805 0340621010.1088/1748-9326/abe828, 2021.
- 806 Netzer, F., Thöm, C., Celepirovic, N., Ivankovic, M., Alfarraj, S., Dounavi, A., Simon, J., Herschbach, C., and Rennenberg,
- 807 H.: Drought effects on C, N, and P nutrition and the antioxidative system of beech seedlings depend on geographic origin,
- 808 Journal of Plant Nutrition and Soil Science, 179, 136-150, 10.1002/jpln.201500461, 2016.
- 809 Nickel, U. T., Weikl, F., Kerner, R., Schäfer, C., Kallenbach, C., Munch, J. C., and Pritsch, K.: Quantitative losses vs.
- qualitative stability of ectomycorrhizal community responses to 3 years of experimental summer drought in a beech-spruce
- forest, Global Change Biology, 24, E560-E576, 10.1111/gcb.13957, 2018.
- 812 Obladen, N., Dechering, P., Skiadaresis, G., Tegel, W., Kessler, J., Höllerl, S., Kaps, S., Hertel, M., Dulamsuren, C., Seifert,
 - T., Hirsch, M., and Seim, A.: Tree mortality of European beech and Norway spruce induced by 2018-2019 hot droughts in
- central Germany, Agricultural and Forest Meteorology, 307, ARTN-10.1016/j.agrformet.2021.108482, 2021.
- 815 10.1016/j.agrformet.2021.108482, 2021.
- 816 Orth, R.: When the Land Surface Shifts Gears, Aguland surface shifts gears, AGU Advances, 2, ARTN e2021AV000414.
- 817 10.1029/2021AV000414, 2021.

Formatted: Subscript

Formatted: Indent: Left: 0 cm, Hanging: 0.5 cm

Formatted: Indent: Left: 0.5 cm

```
818 Paul-Limoges, E., Wolf, S., Eugster, W., Hörtnagl, L., and Buchmann, N.: Below-canopy contributions to ecosystem CO<sub>2</sub>
```

- fluxes in a temperate mixed forest in Switzerland, Agricultural and Forest Meteorology, 247, 582-596,
- 820 10.1016/j.agrformet.2017.08.011, 2017.
- Paul-Limoges, E., Wolf, S., Schneider, F. D., Longo, M., Moorcroft, P., Gharun, M., and Damm, A.: Partitioning
- 822 evapotranspiration with concurrent eddy covariance measurements in a mixed forest, Agricultural and Forest
- 823 Meteorology, 280, ARTN 1077861010.1016/j.agrformet.2019.107786, 2020.
- 824 Pei, F. S., Li, X., Liu, X. P., and Lao, C. H.: Assessing the impacts of droughts on net primary productivity in China, Journal
- of Environmental Management, 114, 362-371, 10.1016/j.jenvman.2012.10.031, 2013.
- 826 Petek-Petrik, A., Húdoková, H., Fleischer, P., Jamnická, G., Kurjak, D., Sliacka Konôpková, A., and Petrík, P.: The
- 827 combined effect of branch position, temperature, and VPD on gas exchange and water-use efficiency of Norway spruce,
- 828 Biologia plantarum, 67, 136, 2023.
- 829 Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T.,
- 830 Granier, A., Grünwald, T., Havránková, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D.,
- Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J. M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen,
- 832 J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., and Valentini, R.: On the separation of net ecosystem exchange into
- assimilation and ecosystem respiration:: review and improved algorithm, Global Change Biology, 11, 1424-1439,
- 834 10.1111/j.1365-2486.2005.001002.x, 2005.
- 835 Ruehr, N. K. and Buchmann, N.: Soil respiration fluxes in a temperate mixed forest: seasonality and temperature sensitivities
 - differ among microbial and root-rhizosphere respiration, Tree Physiology, 30, 165-176, 10.1093/treephys/tpp106, 2010.
- 837 Ruehr, N. K., Knohl, A., and Buchmann, N.: Environmental variables controlling soil respiration on diurnal, seasonal and
- annual time-scales in a mixed mountain forest in Switzerland, Biogeochemistry, 98, 153-170, 10.1007/s10533-009-9383-
- 839 z, 2010.

- 840 Ruehr, N. K., Offermann, C. A., Gessler, A., Winkler, J. B., Ferrio, J. P., Buchmann, N., and Barnard, R. L.: Drought effects
- on allocation of recent carbon: from beech leaves to soil CO₂ efflux, New Phytologist, 184, 950-961, 10.1111/j.1469-
- 842 8137.2009.03044.x, 2009.
- Rukh, S., Sanders, T. G. M., Krüger, I., Schad, T., and Bolte, A.: Distinct Responses of European Beech (responses of
- European beech (L.) to drought intensity and length A review of the impacts of the 2003 and 2018-2019 drought events
- in central Europe, Forests, 14, 10,3390/f14020248, 2023.
- 846 L.) to Drought Intensity and Length A Review of the Impacts of the 2003 and 2018 2019 Drought Events in Central Europe,
- 847 Forests, 14, ARTN 24810.3390/f14020248, 2023.
- 848 Sabbatini, S., Mammarella, I., Arriga, N., Fratini, G., Graf, A., Hörtriagl, L., Ibrom, A., Longdoz, B., Mauder, M., Merbold,
- 849 L., Metzger, S., Montagnani, L., Pitacco, A., Rebmann, C., Sedlák, P., Sigut, L., Vitale, D., and Papale, D.: Eddy covariance
- raw data processing for CO₂ and energy fluxes calculation at ICOS ecosystem stations, International Agrophysics, 32, 495-
- 851 +, 10.1515/intag-2017-0043, 2018.

Formatted: Left, Indent: Left: 0 cm, Hanging: 0.5 cm

Formatted: Left, Indent: Left: 0 cm, Hanging: 0.5 cm

Formatted: Left, Indent: Left: 0 cm, Hanging: 0.5 cm

- 852 Schindlbacher, A., Wunderlich, S., Borken, W., Kitzler, B., Zechmeister-Boltenstern, S., and Jandl, R.: Soil respiration under
- 853 climate change: prolonged summer drought offsets soil warming effects, Global Change Biology, 18, 2270-2279,
- 854 10.1111/i.1365-2486.2012.02696.x. 2012.
- 855 Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T. E. E., Hauck, M., Hajek,
- P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübbe, T., Nelson, D. B.,
- 857 Rammig, A., Rigling, A., Rose, L., Ruehr, N. K., Schumann, K., Weiser, F., Werner, C., Wohlgemuth, T., Zang, C. S., and
- 858 Kahmen, A.: A first assessment of the impact of the extreme 2018 summer drought on Central European forests, Basic and
- 859 Applied Ecology, 45, 86-103, 10.1016/j.baae.2020.04.003, 2020.
- 860 Schulze ED, B. E., Buchmann N, Clemens S, Müller-Hohenstein K, Scherer-Lorenzen M Springer (Ed.): Plant Ecology, 2,
- 861 928 pp._2019.

870

- 862 Schwalm, C. R., Williams, C. A., Schaefer, K., Arneth, A., Bonal, D., Buchmann, N., Chen, J. Q., Law, B. E., Lindroth, A.,
- 863 Luyssaert, S., Reichstein, M., and Richardson, A. D.: Assimilation exceeds respiration sensitivity to drought: A FLUXNET
- 864 synthesis, Global Change Biology, 16, 657-670, 10.1111/j.1365-2486.2009.01991.x, 2010.
- 865 Sendall, K. M., Reich, P. B., Zhao, C. M., Hou, J. H., Wei, X. R., Stefanski, A., Rice, K., Rich, R. L., and Montgomery, R. A.:
- 866 Acclimation of photosynthetic temperature optima of temperate and boreal tree species in response to experimental forest
 - warming, Global Change Biology, 21, 1342-1357, 10.1111/gcb.12781, 2015.
- 868 Shapley, L. S.: Stochastic Games, P Natl Acad Sci USA, 39, 1095-1100, DOI 10.1073/pnas.39.10.1095, 1953.
- 869 Shekhar, A., Humphrey, V., Buchmann, N., and Gharun, M.: More than three-fold increase of extreme dryness across Europe
 - by end of 21st century, 10.21203/rs.3.rs-3143908/v2, 2023.
- 871 Shekhar, A., Chen, J., Bhattacharjee, S., Buras, A., Castro, A. O., Zang, C. S., and Rammig, A.: Capturing the Impactimpact
- of the 2018 European Droughtdrought and Heatheat across Different Vegetation Types Using different vegetation types
- 873 using OCO-2 Solar-Induced Fluorescence, Remote Sensing, 12, ARTN 3249, 10.3390/rs12193249, 2020.
- 874 Shekhar, A., Hörtnagl, L., Paul-Limoges, E., Etzold, S., Zweifel, R., Buchmann, N., and Gharun, M.: Contrasting impact of
- 875 extreme soil and atmospheric dryness on the functioning of trees and forests, Science of The Total Environment,
- 876 10.1016/j.scitotenv.2024.169931, 2024.
- 877 Smith, N. G. and Dukes, J. S.: Short-term acclimation to warmer temperatures accelerates leaf carbon exchange processes
- 878 across plant types, Global Change Biology, 23, 4840-4853, 10.1111/gcb.13735, 2017.
- 879 Sperlich, D., Chang, C. T., Peñuelas, J., and Sabaté, S.: Responses of photosynthesis and component processes to drought and
- temperature stress: are Mediterranean trees fit for climate change?, Tree Physiology, 39, 1783-1805,
- 881 10.1093/treephys/tpz089, 2019.
- 882 Spinoni, J., Vogt, J. V., Naumann, G., Barbosa, P., and Dosio, A.: Will drought events become more frequent and severe in
- 883 Europe?, International Journal of Climatology, 38, 1718-1736, 10.1002/joc.5291, 2018.
- 884 Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T., and Zeileis, A.: Conditional variable importance for random forests,
- 885 BMC bioinformatics, 9, 1-11, 2008.

Formatted: Indent: Left: 0 cm, Hanging: 0.5 cm

Formatted: Superscript

- 886 Sun, S. Q., Lei, H. Q., and Chang, S. X.: Drought differentially affects autotrophic and heterotrophic soil respiration rates and
- their temperature sensitivity, Biology and Fertility of Soils, 55, 275-283, 10.1007/s00374-019-01347-w, 2019.
- 888 Talmon, Y., Sternberg, M., and Grünzweig, J. M.: Impact of rainfall manipulations and biotic controls on soil respiration in
- Mediterranean and desert ecosystems along an aridity gradient, Global Change Biology, 17, 1108-1118, 10.1111/j.1365-
- 890 2486.2010.02285.x, 2011.
- 891 Team, R. C.: R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing, (No
- 892 Title), 2021.
- 893 Trabucco, A.: Global aridity index and potential evapotranspiration (ET0) climate database v2, CGIAR Consort Spat Inf, 2019.
- 894 Tripathy, K. P. and Mishra, A. K.: How Unusual Is the 2022 European Compound Drought and Heatwave Event?, Geophysical
- 895 Research Letters, 50, ARTN e2023GL105453, 10.1029/2023GL105453, 2023.
- van der Molen, M. K., Dolman, A. J., Ciais, P., Eglin, T., Gobron, N., Law, B. E., Meir, P., Peters, W., Phillips, O. L.,
- 897 Reichstein, M., Chen, T., Dekker, S. C., Doubkova, M., Friedl, M. A., Jung, M., van den Hurk, B. J. J. M., de Jeu, R. A.
- 898 M., Kruijt, B., Ohta, T., Rebel, K. T., Plummer, S., Seneviratne, S. I., Sitch, S., Teuling, A. J., van der Werf, G. R., and
- 899 Wang, G.: Drought and ecosystem carbon cycling, Agricultural and Forest Meteorology, 151, 765-773,
- 900 10.1016/j.agrformet.2011.01.018, 2011.
- 901 van der Woude, A. M., Peters, W., Joetzjer, E., Lafont, S., Koren, G., Ciais, P., Ramonet, M., Xu, Y. D., Bastos, A., Botia, S.,
- 902 Sitch, S., de Kok, R., Kneuer, T., Kubistin, D., Jacotot, A., Loubet, B., Herig-Coimbra, P. H., Loustau, D., and Luijkx, I.
- 903 T.: Temperature extremes of 2022 reduced carbon uptake by forests in Europe, Nature Communications, 14, ARTN 6218,
- 904 10.1038/s41467-023-41851-0, 2023.
- 905 van Straaten, O., Veldkamp, E., and Corre, M. D.: Simulated drought reduces soil CO2 efflux and production in a tropical
- 906 forest in Sulawesi, Indonesia, Ecosphere, 2, Artn 119, 10.1890/Es11-00079.1, 2011.
- 907 von Buttlar, J., Zscheischler, J., Rammig, A., Sippel, S., Reichstein, M., Knohl, A., Jung, M., Menzer, O., Arain, M. A.,
- 908 Buchmann, N., Cescatti, A., Gianelle, D., Kiely, G., Law, B. E., Magliulo, V., Margolis, H., McCaughey, H., Merbold, L.,
- 909 Migliavacca, M., Montagnani, L., Oechel, W., Pavelka, M., Peichl, M., Rambal, S., Raschi, A., Scott, R. L., Vaccari, F. P.,
- 910 van Gorsel, E., Varlagin, A., Wohlfahrt, G., and Mahecha, M. D.: Impacts of droughts and extreme-temperature events on
- 911 gross primary production and ecosystem respiration: a systematic assessment across ecosystems and climate zones,
- 912 Biogeosciences, 15, 1293-1318, 10.5194/bg-15-1293-2018, 2018.
- 913 Wang, Y. F., Hao, Y. B., Cui, X. Y., Zhao, H. T., Xu, C. Y., Zhou, X. Q., and Xu, Z. H.: Responses of soil respiration and its
- 914 components to drought stress, Journal of Soils and Sediments, 14, 99-109, 10.1007/s11368-013-0799-7, 2014.
- 915 Wang, H., Yan, S. J., Ciais, P., Wigneron, J. P., Liu, L. B., Li, Y., Fu, Z., Ma, H. L., Liang, Z., Wei, F. L., Wang, Y. Y., and
- 916 Li, S. C.: Exploring complex water stress-gross primary production relationships: Impact of climatic drivers, main effects,
- 917 and interactive effects, Global Change Biology, 28, 4110-4123, 10.1111/gcb.16201, 2022.

- 918 Wang, H., Yan, S. J., Ciais Ciaiss, P., Wigneron, J. P., Liu, L. B., Li, Y., Fu, Z., Ma, H. L., Liang, Z., Wei, F. L., Wang, Y. Y.,
- 919 and Li, S. C.: Exploring complex water stress-gross primary production relationships: Impact of climatic drivers, main
- effects, and interactive effects, Global Change Biology, 28, 4110-4123, 10.1111/gcb.16201, 2022.
- 921 Webb, E. K., Pearman, G. I., and Leuning, R.: Correction of Flux Measurements for Density Effects Due to Heat and Water-
- 922 Vapor Transfer, Quarterly Journal of the Royal Meteorological Society, 106, 85-100, DOI 10.1002/qj.49710644707, 1980.
- 923 Wutzler, T., Lucas-Moffat, A., Migliavacca, M., Knauer, J., Sickel, K., Sigut, L., Menzer, O., and Reichstein, M.: Basic and
- 924 extensible post processing of eddy covariance flux data with REddyProc, Biogeosciences, 15, 5015-5030, 10.5194/bg 15-
- 925 5015-2018, 2018.

- 926 Xu, B., Arain, M. A., Black, T. A., Law, B. E., Pastorello, G. Z., and Chu, H. S.: Seasonal variability of forest sensitivity to
- 927 heat and drought stresses: A synthesis based on carbon fluxes from North American forest ecosystems, Global Change
 - Biology, 26, 901-918, 10.1111/gcb.14843, 2020.
- 929 Yao, Y., Liu, Y. X., Zhou, S., Song, J. X., and Fu, B. J.: Soil moisture determines the recovery time of ecosystems from
- 930 drought, Global Change Biology, 29, 3562-3574, 10.1111/gcb.16620, 2023.
- 931 Zheng, P. F., Wang, D. D., Yu, X. X., Jia, G. D., Liu, Z. Q., Wang, Y. S., and Zhang, Y. G.: Effects of drought and rainfall
- 932 events on soil autotrophic respiration and heterotrophic respiration, Agriculture Ecosystems & Environment, 308, ARTN
- 933 107267, 10.1016/j.agee.2020.107267, 2021.
- 934 Zhou, S., Williams, A. P., Berg, A. M., Cook, B. I., Zhang, Y., Hagemann, S., Lorenz, R., Seneviratne, S. I., and Gentine, P.:
- 935 Land-atmosphere feedbacks exacerbate concurrent soil drought and atmospheric aridity, Proceedings of the National
- Academy of Sciences of the United States of America, 116, 18848-18853, 10.1073/pnas.1904955116, 2019.