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1                                    **Accurate phenology analyses require bud traits and energy budgets**

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16  
17 **Keywords:** plant phenology, budburst, temperature, light, energy budget, modelling, climate warming

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22 **Spring phenology is mainly driven by temperature in extratropical ecosystems. Recent evidence**  
23 **highlighted the key role of micrometeorology and bud temperature on delaying or advancing leaf**  
24 **unfolding. Yet, phenology studies, either using ground-based or remote sensing observations,**  
25 **always substitute plant tissue temperature by air temperature. In fact, temperatures differ**  
26 **substantially between plant tissues and the air because plants absorb and lose energy. Here, we**  
27 **build on recent observations and well-established energy balance theories to discuss how solar**  
28 **radiation, wind, and bud traits might affect our interpretation of spring phenology sensitivity to**  
29 **warming. We show that air temperature might be an imprecise and biased predictor of bud**  
30 **temperature. Better characterizing the plants phenological response to warming will require new**  
31 **observations of bud traits and temperature for accurately quantifying their energy budget. Since**  
32 **consistent micrometeorology datasets are still scarce, new approaches coupling energy budget**  
33 **modelling and plant traits could help improving phenology analyses across scales.**

34

## 35 **Introduction**

36 Plant phenology, the study of the timing of life-cycle events, drives several ecosystem functions,  
37 such as plant productivity and biomass, but also local and global climates by affecting biogeochemical  
38 and biogeophysical processes, such as carbon storage and energy fluxes<sup>1,2</sup>, and the abundance and  
39 diversity of local flora and fauna, such as pollinators and herbivores<sup>3,4</sup>. Understanding the environmental  
40 controls and responses of plant phenology to climate change is thus essential for several sectors, e.g.  
41 agriculture, forestry and gardening<sup>5</sup>, but also for conservation<sup>6</sup> and public health<sup>7</sup> (e.g. allergies).

42 It is now largely assumed that bud-break is induced by warming air temperature during spring<sup>8</sup> in  
43 temperate and boreal regions, and this is the reason why phenology assessments mainly rely on critical  
44 air temperature sums preceding leaf unfolding, often referred to as the Growing Degree Day concept.  
45 Climatic warming has strongly shifted phenophases in the Northern Hemisphere in recent decades<sup>1,9-11</sup>.  
46 Rising temperatures have lengthened the annual growth cycle by advancing leaf unfolding in spring and  
47 delaying leaf fall in autumn<sup>12</sup>, albeit with variations among species<sup>13</sup> and regions<sup>14</sup>. Recent evidence,  
48 though, suggests that the sensitivity of spring phenology to warming is decreasing in northern forests<sup>15</sup>  
49 and that the rate of change in plant productivity does not match that of air temperature<sup>16</sup>. Indeed, plant  
50 phenology may be acclimated to long-term biogeographical constraints<sup>17-19</sup> and may be co-limited by  
51 several other factors, such as light<sup>20</sup>, water<sup>21-23</sup> and nutrients<sup>24</sup>. These observations suggests that warming  
52 does not have the same effect everywhere<sup>25</sup>, which has increased interest in other environmental drivers  
53 in recent decades, especially illustrated by multiple debates about the specific role of light (and  
54 photoperiodism) in spring phenology<sup>20,26-33</sup>.

55 How light affects spring phenology remains an open question. Most commonly, its effect is  
56 considered via photoperiod, often referred to as daylength. The daylength hypothesis implies that the  
57 quality and/or quantity of light is somehow directly sensed by plants through biochemical mechanisms.  
58 Some recent studies suggest that the spectral composition of light can indeed influence foliar  
59 phenology<sup>34,35</sup>. Light also plays a key role in regulating phytohormones, but the underlying mechanisms  
60 remain unknown<sup>32</sup> and clearly require more investigation. More sporadically, the effect of light has been  
61 treated as the sum of insolation over a specific period<sup>36</sup>, for which plants need a specific quatum for a  
62 phenological event to occur. The quantity and quality of light depend on plant location, which is the main  
63 reason why a response to daylength has often been proposed as a safety mechanism against frost at high  
64 latitudes and elevations. Only 35% of the woody species in the Northern Hemisphere, however, depend  
65 on daylength as a direct signal for leaf-out<sup>20</sup>, and these species are mainly at mid- to low latitudes.

66 Light effect on spring phenology is still being debated. Recent studies nonetheless suggest a  
67 complex interaction between temperature and light. Daytime and nighttime temperatures during winter

68 and spring have an asymmetrical effect on leaf unfolding<sup>37-41</sup>, with a greater weight of temperature during  
69 the day<sup>38,42,43</sup>. Whether or not plants are able to sense light, radiation has a physical impact on plants: it  
70 affects the temperatures of their tissues. Since temperature has been shown to be sensed at the bud  
71 level<sup>44,45</sup>, omitting the physical effect of radiation introduces large biases into the interpretation of spring  
72 phenological responses based on air temperature.

73 In their recent study, Vitasse et al. highlighted the strong phenological effect of bud albedo and  
74 light exposure, explaining shifts in the budburst date reaching up to 12 days<sup>44</sup>, and revealing an important  
75 role of microclimatic variation on phenology. Indeed, bud temperature ( $T_{\text{bud}}$ ) depends on its energy  
76 balance<sup>46</sup>. During the day, plant tissues absorb both shortwave (SW, visible and near-infrared) and  
77 longwave (LW, infrared) radiation from the sky but also radiation emitted and reflected by the  
78 surrounding environment (vegetation, soil) (Fig. 1a). Only a fraction ( $\alpha$ , absorptivity) of SW radiation  
79 will be absorbed depending on bud traits such as color, coating, shape and size (Fig. 1b), while most LW  
80 radiation will be absorbed by buds. According to the Stefan-Boltzmann law, buds lose energy via LW  
81 radiation emission, while they absorb LW radiation emitted from surrounding objects. Finally, a part of  
82 their energy is lost by conduction and mostly by convection<sup>47,48</sup> (e.g. due to wind) while leaves lose an  
83 important part of their energy via transpiration.  $T_{\text{bud}}$  increases when energy gains exceed losses (Fig. 2a)  
84 and vice-versa.  $T_{\text{bud}}$  can thus be lower than air temperatures ( $T_{\text{air}}$ ) on clear nights<sup>47</sup> or because of wind.  
85 On the other hand,  $T_{\text{bud}}$  can be significantly higher than  $T_{\text{air}}$  during the day. The link between  $T_{\text{bud}}$  and  
86 energy balance has been known for more than 30 years<sup>46,47</sup>. Since then, all major studies linking  
87 temperature and photoperiod to phenological changes, however, have not accounted for the true  
88 temperature of plant organs.

89 What can we expect if we account for micrometeorology and bud temperature in phenological  
90 studies? Unfortunately, the lack of *in situ* observations for bud temperature does not allow to answer  
91 directly this question. As part of the reflection, we thus applied existing well-established energy balance  
92 approaches<sup>46,47,49</sup> to explore the potential variability in temperature of an isolated bud. This situation is  
93 well representative of the conditions encountered by sun-exposed buds of a tree, and especially of  
94 deciduous species (i.e. with no or minimum shading). As commonly applied in ‘big-leaf’ models where  
95 an entire canopy is represented by a single ‘big’ leaf, discussing the microclimate effect on an isolated  
96 bud will help us to explore the variability in phenology we can expect at different spatiotemporal scales  
97 and between species.

98

99

## 100 **Results**

### 101 **Non-linear response of plant tissue temperature to microclimate**

102 As a first example, we looked at the variability in  $T_{\text{bud}}$  estimated from its energy balance and site  
103 meteorological observations for an European Beech forest<sup>52</sup>. On average,  $T_{\text{bud}}$  is expected to be higher  
104 than  $T_{\text{air}}$  during the pre-season ( $\sim 1^\circ\text{C}$  in our example; Fig. 2b). Day and night  $T_{\text{bud}}$  are higher or lower than  
105  $T_{\text{air}}$  by several degrees. The temperature of buds thus strongly depends on the diurnal radiative cycle and  
106 the spectral composition of the light (SW/LW radiation), echoing the observed asymmetrical effect of  
107 diurnal temperatures on leaf unfolding<sup>38,42,43</sup>. Applied on four other sites, this approach leads to similar  
108 results despite differences in  $T_{\text{bud}}$  profiles induced by differences in radiation along a latitudinal gradient  
109 (Fig. 3). Spring phenology does not only respond to average pre-season temperature, but mainly to the  
110 accumulated effect of temperature and its dynamics. It is often assumed that chilling and forcing  
111 temperature required for budburst are only effective over specific windows, generally between 0 and  
112  $5^\circ\text{C}$  and over  $5^\circ\text{C}$ , respectively. Daily bud temperature variability might thus be the most important  
113 factor influencing leaf unfolding, not necessarily its average temperature. We could expect that the  
114 difference in extremum temperature sensed by buds over the preceding months ( $\Delta T_{\text{min}}$  and  $\Delta T_{\text{max}}$ , Fig.  
115 2b) will inevitably affect the apparent forcing and chilling requirement for leaf unfolding.

116 Accounting for the energy budget of buds for six common species across Europe (Extended Fig.  
117 1) we also expect a stronger interannual variability in  $T_{\text{bud}}$  than  $T_{\text{air}}$ , as well as different temporal  
118 evolutions over the last decades (Fig. 4). In our example, buds are expected to warm faster or slower than  
119 air depending on location and species, with 13 % and 7 % of the sites exhibiting an increase and a  
120 decrease in  $\Delta T$  over 1990-2015, respectively. These trends represent idealized sun-exposed conditions  
121 without site or species-specific calibration. Still, we observe that the heterogeneity in  $\Delta T$  evolution results  
122 from a complex and non-linear response to the amount of absorbed radiation and convection processes  
123 (Extended Fig. 2). Because leaf unfolding is earlier in 2015 than in 1990, the average amount of absorbed  
124 radiation during the pre-season slightly decreased over this period, while most of the interannual  
125 variability in  $\Delta T$  is driven by conduction and convection (i.e. wind). The difference in air-bud  
126 temperature and their non-linear and non-proportional relationship suggests that our current  
127 interpretation of the apparent bud sensitivity to warming needs to account for the temperature sensed by  
128 the plant.

129

### 130 **Response to warming relies on organ traits and microclimate**

131 We illustrated the role of bud energy balance through an idealized and constant representation of  
132 buds and their environment for all sites and species. Larger spatial and temporal variations are expected

133 due to the effect of topography, ground albedo (e.g. snow, understory), differences in bud traits (Fig. 1b)  
134 and micrometeorological conditions<sup>53</sup> that will affect plant tissues energy balance. By affecting the  
135 amount of radiation reaching the buds (Fig. 1a), varying ground albedo from 0.1 (~wet bare soil) to 0.9  
136 (~snow) leads to a doubling in pre-season  $\Delta T$  (Fig. 5). Since ground albedo strongly varies in space and  
137 over the pre-season (e.g. snow), we can expect substantial differences in the phenological signal at the  
138 regional scale induced by radiation, as already observed from leaf unfolding observations<sup>17</sup>.

139 Different bud colors or coating will also affect solar absorption of specific wavelengths, while  
140 shape and size will modify convection processes and the amount of intercepted radiation (Fig. 6), and  
141 hence, bud temperature. For example, Common Ash (*Fraxinus excelsior*) has black buds while sycamore  
142 (*Acer pseudoplatanus*) has green buds and mountain ash (*Sorbus aucuparia*) have dense white trichomes  
143 (i.e. hairs) on their surfaces. In our example, a difference in solar absorptivity of 0.3 leads to a doubling  
144 in  $\Delta T$  (Fig. 2a, Fig. 3a). The differences in bud traits can thus partly account for the observed interspecific  
145 differences in heat requirement and apparent sensitivity to temperature. This suggests that the  
146 phenological response of plants to warming might be more species-specific than we thought, which  
147 should be accounted for in large scale studies.

148

## 149 Discussion

150 Despite its central role at the organ level<sup>53,54</sup>, micrometeorology is rarely accounted for in  
151 phenology studies because rarely measured, or simply because it is impossible to account for its effect  
152 such as in remote sensing analysis or terrestrial biosphere modelling. Instead, phenology studies, either  
153 local or regional, often use meteorological and climate datasets with hourly to daily time resolutions. The  
154 use of a steady state energy balance is easily justified under such conditions since thermal time constants  
155 of tree buds varies between a few seconds to about ten minutes<sup>55</sup>. Accounting for average pre-season  
156 radiation and wind conditions might better explain the observed variability in plant phenology than air  
157 temperature alone. Here, we only explored spring  $T_{\text{bud}}$  variability in the case of sun-exposed buds with  
158 no shading. Accounting for the potential protecting effect of leaves or needles in evergreen species might  
159 substantially attenuate the effects of radiation and wind on intra- and bottom-canopy buds. The  
160 concomitant use of high-resolution microclimate data and transient energy budget models will be needed  
161 to quantify such effects.

162 Drivers of phenological events and light are virtually impossible to separate, because daylength  
163 and radiation are strongly correlated with the time of year. Accounting for organ energy balances is thus  
164 promising for separating the environmental drivers of phenology using a single approach and potentially  
165 for reconciling the differences observed in the field. Applying existing modelling approaches in the

166 context of sun-exposed buds suggested that air temperature might be an imprecise and biased predictor  
167 of bud temperature and more importantly of its variability over the months preceding leaf unfolding,  
168 which might introduce biases in the analysis of chilling and forcing requirement for budburst. However,  
169 we also showed that bud temperature results from a complex combination of several biotic and abiotic  
170 factors, and under certain conditions air temperature might remain a good proxy for bud temperature.  
171 The examples we have presented open new avenues to investigate and refine our interpretation of plant  
172 phenological acclimation to warming that were solely based on air temperature. For example, changes in  
173 spring radiation regimes over the last decades<sup>56,57</sup> have been hypothesized to increase discrepancies  
174 between standard air temperature and bud temperature<sup>44</sup>, which is in line with the energy budget theory  
175 described in this perspective. However, current observations do not allow such reassessment. Bud traits  
176 and *in situ* temperature observations are scarcely described in the literature. New experiments and  
177 observations are clearly needed for accurately quantifying the traits and energy budget of buds. Existing  
178 studies have mostly focused on leaves, but other organs should also be investigated. Key traits that will  
179 need to be measured to assess the interspecific variability of phenology include organ traits influencing  
180 solar absorptivity and heat storage, but organ temperatures (i.e. using thermocouples) concomitant with  
181 micrometeorological variables will also need to be directly measured. With the assumption that bud  
182 transpiration is negligible, their energy budget is simpler than for leaves. Properly calibrated, accounting  
183 for bud energy balance could improve the accuracy of phenological models that are still unable to predict  
184 the spatiotemporal variability of plant dynamics with satisfactory accuracy<sup>58</sup>. Such approach could not  
185 only improve spatiotemporal assessments of phenology (e.g. based on ground-based and remote sensing  
186 observations), but also provide new insights into ecosystem functioning such as the influence of global  
187 warming synchrony between flowers and insects, or between plant functions and climate (e.g. growth  
188 and soil moisture, signaling, etc.).

189 Finally, we stress that energy balance affects the temperature extrema sensed by plants (Fig. 2b).  
190 The lengthening of the growing season in recent decades has also been associated with an increase in  
191 environmental risks. For example, earlier leaf unfolding exposes plants to late frost<sup>59-61</sup> in spring,  
192 potentially resulting in dramatic impacts on agriculture<sup>62-64</sup> and forestry<sup>65,66</sup>. The use of energy balances  
193 to study and better predict these environmental risks can provide novel insights into the responses of  
194 plants to extreme temperatures and offer more robust predictive tools, which are essential for developing  
195 adaptation measures and reducing the ecological and economic impacts. Temperature of plant organs and  
196 their dynamics are still overlooked in both environmental studies and modeling exercises<sup>67</sup>. Energy  
197 balance thus plays a key role, not only for plant phenology but also for all other processes since plant

198 tissue temperature will govern key mechanisms such as photosynthesis and respiration and the general  
199 functioning of the plant.  
200

## 201 **Online methods**

### 202 **Description of the bud energy budget model**

203 We implemented a simplified energy budget model for buds based on Landsberg et al.<sup>47</sup>, Hamer<sup>46</sup>, as  
204 well as equations from Jones<sup>50</sup> and Muir<sup>49</sup>. We refer to Supplementary Table S1 for parameter values and  
205 units. Our implementation follows the ‘big-leaf’ concept for which the whole canopy is simplified by a  
206 single representative organ, here an isolated bud in a deciduous canopy.

207  
208 For an isolated bud, the amount of absorbed incoming radiation ( $R_{abs}$ ) is balanced by the thermal infrared  
209 radiation loss ( $LW_{bud}$ ) and the energy lost by conduction and convection, generally called the sensible  
210 heat flux ( $H$ ). The thermal time constant of buds is less than a minute<sup>55</sup>, meaning that bud temperature  
211 responds quite rapidly to local changes. Because most phenology studies use meteorological data from  
212 local stations or gridded datasets, here we simulate bud temperature by considering that the energy  
213 balance is close to equilibrium at a time scale of a few minutes, which is consistent with temporal  
214 resolution of meteorological observations from FLUXNET sites (30 min) and CRU-JRA<sup>68</sup> (6 h) and the  
215 thermal time constant of buds ranging from a few seconds to a few minutes<sup>55</sup>:

$$R_{abs} = LW_{bud} + H \quad (1)$$

216 As we consider the energy budget of the whole, two-sided bud, and not the projected area, the amount of  
217 absorbed energy by buds is the sum of incoming shortwave (SW, visible and near-infrared) and longwave  
218 (LW, infrared) radiations from the sky and the ground:

$$R_{abs} = \alpha_{sw}(1 + r)SW + \alpha_{lw}(LW_{sky} + LW_{gnd}) \quad (2)$$

219 where  $\alpha_{sw}$  is the bud absorptivity to SW;  $r$  is the fraction of SW reflected by the ground and  $\alpha_{lw}$  is the bud  
220 absorptivity to LW, which is here defined as the average of LW coming from the atmosphere  $LW_{sky}$  and  
221 coming from the ground  $LW_{gnd}$ .

222 LW emitted by surrounding objects such as branches were considered equal to LW emitted from the  
223 ground and the sky. We set  $\alpha_{lw}$  to 0.97, which corresponds to the average absorptivity for wood and leaves  
224 <sup>50,69,70</sup>. Since no data were available in the literature, we tested two different values of  $\alpha_{sw}$ , 0.5 and 0.8,  
225 corresponding to values commonly used for broadleaves and needleleaves, respectively. We set  $r$  to 0.2,  
226 which corresponds to a reasonable value for the fraction of SW reflected by grasses. Of course,  $r$  will  
227 strongly vary according to the albedo of the ground (e.g. understory/grass, forest litter, snow, etc.), which  
228 was simplified here for our perspective paper.

229

230  $LW_{gnd}$  was computed from ground temperature following the Stefan-Boltzmann equation:

$$LW_{gnd} = \sigma \varepsilon T_{gnd}^4 \quad (3)$$

231 where  $\sigma$  is the Stefan-Boltzmann constant and  $\varepsilon$  is the bud emissivity to longwave radiations (which is  
232 equal to  $\alpha_{lw}$  since plant material tends to behave like a black body in the IR spectrum<sup>50</sup>).

233 This is important to keep in mind that ground temperature will strongly depend on soil type, vegetation  
234 and snow cover but also soil humidity.

235

236 Buds lose thermal infrared radiation proportionally to their temperature as:

$$LW_{bud} = 2\sigma \varepsilon T_{bud}^4 \quad (4)$$

237 where  $\sigma$  is the Stefan-Boltzmann constant and  $\varepsilon$  is bud emissivity to longwave radiations. As for the  
238 absorbed radiation, radiations are emitted on both sides of the bud (i.e. toward the sky and the ground).

239

240 Finally, the sensible heat flux depends on the air to bud temperature gradient and is formulated as in  
241 Muir<sup>49</sup>:

$$H = 2\rho_a c_p g_b (T_{bud} - T_{air}) \quad (5)$$

242 where  $\rho_a$  is the density of the air;  $c_p$  is the specific heat capacity of air at constant pressure and  $g_b$  is the  
243 boundary-layer conductance to heat.

$$\rho_a = \frac{P}{R_a} T_a \frac{(1 + q_a)}{\left(1 + \frac{R_w}{R_a} q_a\right)} \quad (6)$$

244 where  $P$  is the atmospheric pressure,  $R_a$  and  $R_w$  are the specific gas constant for dry air and water vapor,  
245 respectively,  $T_a$  is the temperature of the air and  $q_a$  is the specific humidity of the air.

$$g_b = \frac{D_h Nu}{d} \quad (7)$$

246 where  $Nu$  is the Nusselt number,  $D_h$  is the diffusion coefficient of heat in air and  $d$  is the bud diameter.

$$D_h = D_{h,0} \left(\frac{T}{273.15}\right)^{eT} \frac{101.3246}{P} \quad (8)$$

247  $D_h$  is function of temperature and pressure,  $D_{h,0}$  corresponds to  $D_h$  at 0°C and  $eT$  is the temperature  
248 dependence of diffusion.

249 The Nusselt number is estimated as a mixed convection such as:

$$Nu^{3.5} = Nu_{forced}^{3.5} + Nu_{free}^{3.5} \quad (9)$$

250 with

$$Nu_{forced} = e + aRe^b \quad (10)$$

251 and

$$Nu_{free} = f + cGr^d \quad (11)$$

252  $Re$  and  $Gr$  are the Reynolds and Grashof numbers, respectively;  $a$ ,  $b$ ,  $c$  and  $d$  are constants that are  
253 dependent of the flow regime.

254 In our example, we simplified bud's shape as a spherical object with a diameter of 5 mm to computes the  
255 boundary-layer conductance to heat. Please refers to Hamer<sup>46</sup> for a detailed discussion of this assumption,  
256 as well as empirical formulations for the convective heat transfer of apple buds. Condition for laminar  
257 and turbulent flows, as well as constants  $a$ ,  $b$ ,  $c$  and  $d$  for a spherical object, as well as for objects of  
258 various forms, can be found in Monteith and Unsworth<sup>71</sup>. This is a simplification to keep in mind when  
259 calculating convection processes for different species with various bud shapes and for which the close  
260 proximity of branches can modify the flow regime. Also, the evolution of turbulence and sensible heat  
261 transfer from the bud to the canopy scale (associated with aerodynamic conductance in addition to bud  
262 boundary layer one) was not considered here, and was implicitly accounted for in the form of air  
263 temperature.

264 In addition, we performed two simulations varying ground albedo from 0.1 (~wet bare soil) to 0.9  
265 (~snow) and bud diameter from 5 to 13 mm (Fig. 5 and 6)

266

267 Note that a proper calibration of species and site properties (e.g. albedo) is needed to use this model for  
268 predictions. Here, we used already existing models and assumptions for the only purpose of exploring  
269 the expected variability in bud temperature with environmental conditions and for an isolated object  
270 representative of apical buds in a tree. Model development and validation was not intended here and will  
271 require *in situ* observations of bud traits and temperature data.

272 The bud energy model simulates bud temperature in idealized conditions and at equilibrium, without  
273 distinction between species and sites and several simplifications as described above.

274 Still, we describe in the two following sections how to account for bud energy storage as well as latent  
275 heat from wet buds in rainy conditions. Both implementations were tested without significant changes in  
276 the results and the corresponding code is also implemented and available in the model.

277 **Accounting for energy storage**

278 We applied the same approach accounting for the thermal time constant of buds, which is dependent on  
279 bud traits and its associated thermal resistance. Following Jones<sup>50</sup>, the change in bud temperature with  
280 time (*t* in s) follows:

$$\frac{dT}{dt} = S/\rho^* c_p^* l^* \quad (12)$$

281 with *S* the energy stored by the bud in W m<sup>-2</sup>,  $\rho^*$  and  $c_p^*$  are the density in kg m<sup>-3</sup> and the specific heat  
282 capacity in J kg<sup>-1</sup> K<sup>-1</sup> of the bud and  $l^*$  is the volume to area ratio, corresponding to *d*/4 for a cylinder and  
283 *d*/6 for a sphere, with *d* the bud diameter in m.

284 Between two equilibrium states, this first-order differential equation gives the following bud temperature:

$$T_{bud}(t) = T_{eq}(t) - [T_{eq}(t) - T_{bud}(t_{-1})]\exp(-t/\tau) \quad (13)$$

285 with  $T_{eq}$  the bud temperature at equilibrium and  $\tau$  the thermal time constant in s (see eq. 9.8, eq. 9.9 and  
286 eq. 9.10, p. 227 in Jones<sup>50</sup>) which is function of the conditions in the boundary layer<sup>55,72</sup> (i.e. bud traits  
287 and wind):

$$\tau = \frac{\rho^* c_p^* l^*}{hA} \quad (13)$$

288 with *A* the wetted area in m<sup>2</sup> and *h* the heat transfer coefficient in W m<sup>-2</sup> K<sup>-1</sup> following:

$$h = \frac{Nu\lambda_a}{d} \quad (13)$$

289 with  $\lambda_a$  the thermal conductivity of air in W m<sup>-2</sup> K<sup>-1</sup>.

290 Michaletz & Johnson<sup>55</sup> estimated average values of  $\tau$  ranging from 8 to 30 s for 12 different species with  
291 an average value of 13 s. The effect of energy storage is thus negligible with >30 min resolution  
292 meteorological data. Using high resolution micrometeorological observations should lead to better results  
293 by accounting for rapidly changing radiation load with clouds, wind speed, bud inclination etc.

294

295 **Accounting for wet conditions**

296 We implemented an option to account for latent heat in the model in order to simulate the cooling effect  
297 of evaporation when buds are wet because of the rain or dew conditions.

298 The maximum water density ( $d_w$ ) on buds depends on bud orientation, size and hydrophilicity. Since no  
299 data were found in the literature regarding water interception from buds, we defined the maximum  
300 interception reservoir based on leaf data. In the literature,  $d_w$  for leaves varies between 0.05 and 0.2 mm<sup>73</sup>.

301 We thus arbitrary set  $d_w$  for buds to 0.15 mm. Varying  $d_w$  from 0 to 0.2 mm (kg m<sup>-2</sup>) did not change the  
302 results.

303 The maximum surface water content  $Wc_{max}$  (in kg) intercepted by a bud was thus calculated as:

$$Wc_{max} = d_w \times S_b \quad (14)$$

304

305 With  $S_b$  the surface area of the bud in  $m^2$ .

306 Surface water content ( $Wc$ ) was estimated at each time step as the balance between water inputs from  
307 rain and dew and water outputs from evaporation. First, water coming from the rain of the previous time  
308 step is added to current  $Wc$  as:

$$Wc = \min(Wc_{max}, (Wc + rain \times S_b)) \quad (15)$$

309

310 Then, latent heat energy dissipated by evaporation or accumulated from condensing dew ( $E$ ) was  
311 calculated based on  $Wc$  following Gerlein-Safdi et al.<sup>74</sup>:

$$E = \begin{cases} \lambda_v(T_{bud}) \frac{dWc}{dt}, & \text{if } \frac{dWc}{dt} > 0 \\ \lambda_c(T_{bud}) \frac{dWc}{dt}, & \text{if } \frac{dWc}{dt} < 0 \end{cases} \quad (16)$$

312 with the latent heat of condensation  $\lambda_c$  (in  $J \text{ kg}^{-1}$ ) being equal of the latent heat of vaporization  $\lambda_v$ . The  
313 surface water content balance can be written as:

$$\frac{dWc}{dt} = 0.622 S_b \rho_a g_h \left[ \frac{e_c(T_{air}) - e_{sat}(T_{bud})}{P} \right] \quad (17)$$

314 with  $g_h$  the conductance of the boundary layer to water vapor in  $m \text{ s}^{-1}$ ,  $e_c$  the vapor pressure in Pa and  $e_{sat}$   
315 the saturating vapor pressure in Pa.

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317 Here, water does not modify the diffusion coefficient of heat in air  $D_h$ .

318 Accounting for latent heat in the energy budget did not change the results.

319

320 **Datasets and analysis**

321 Half-hourly forcing meteorological and soil temperature data (Fig. 2, 3, 5 and 6) were downloaded from  
322 the FLUXNET2015 dataset at <https://fluxnet.fluxdata.org/data/fluxnet2015-dataset/>. Historical climate  
323 data from CRU-JRA<sup>68</sup> at a spatial resolution of 0.25° and at a temporal resolution of 6 h (Fig. 4 and  
324 Extended Fig. 2) were downloaded at  
325 <https://catalogue.ceda.ac.uk/uuid/13f3635174794bb98cf8ac4b0ee8f4ed>. Soil temperature data at 0.25°  
326 were downloaded from ECMWF-ERA5<sup>75</sup> reanalysis with the ‘KrigR’ package<sup>76</sup>.

327 *In situ* leaf unfolding data (Fig. 4 and Extended Fig. 2) for Common alder (*Alnus glutinosa*), horse  
328 chestnut (*Aesculus hippocastanum*), silver birch (*Betula pendula*), European beech (*Fagus sylvatica*),  
329 European ash (*Fraxinus excelsior*) and pedunculate oak (*Quercus robur*) were downloaded from the Pan  
330 European Phenology network (<http://www.pep725.com/>). Phenological observations followed the  
331 Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie (BBCH) code, with leaf  
332 unfolding corresponding to BBCH = 11. Only sites with more than 20 years of observation over the 1990-  
333 2015 period were used, corresponding to 5050 sites\*species in total, covering 1059 sites (Extended Fig.  
334 1). Analysis and figures were generated with the R v3.5.1 software<sup>77</sup>.

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338 **Data availability**

339 FLUXNET2015 data are available at <https://fluxnet.fluxdata.org/data/fluxnet2015-dataset/>

340 CRU-JRA data are available at <https://catalogue.ceda.ac.uk/uuid/13f3635174794bb98cf8ac4b0ee8f4ed>

341 ERA5 soil temperature data are available at

342 <https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land>

343 PEP725 phenology data are available at <http://www.pep725.eu/>

344

345 **Code availability**

346 The R code of the model of energy budgets and data sets used to generate the figures and analysis of this

347 manuscript are available from Github at <https://github.com/mpeaucelle/Tbud>

348 A version of the git repository is archived on Zenodo at <https://zenodo.org/record/5897267> corresponding

349 to tag v.2.0.

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360 **Author Contributions Statement**

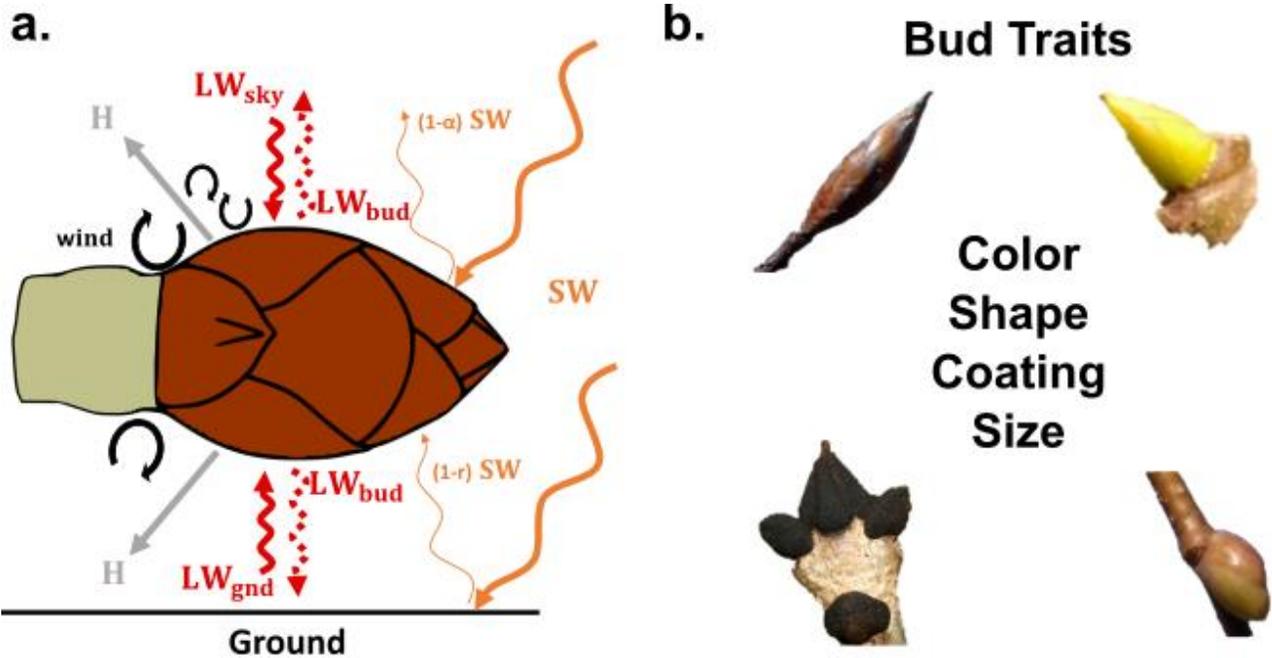
361 M.P. designed the study, performed the analysis and wrote the first version of the manuscript. J.P. and  
362 H.V. substantially contributed to the interpretation of the results and the revisions of the manuscript. All  
363 authors read and approved the final manuscript.

364

365 **Competing Interests Statement**

366 The authors declare no competing interests

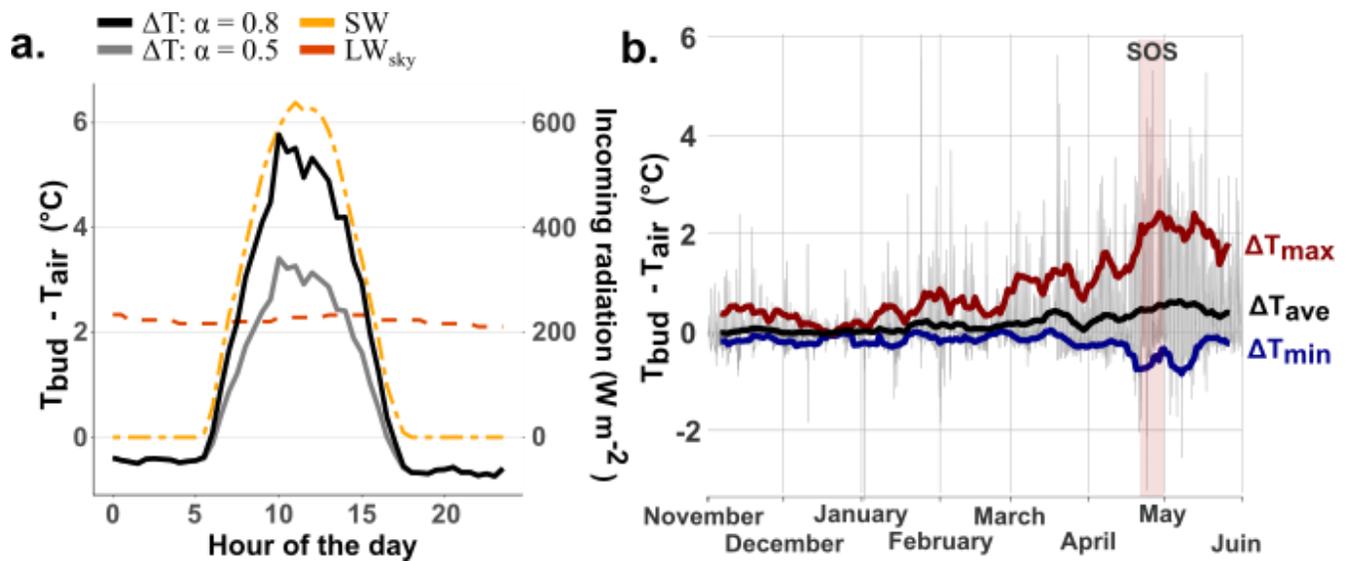
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370 **Figure 1 | Energy budget of buds and bud traits.** **a.** Buds lose energy through convection and conduction ( $H$ ). Buds absorb  
 371 incoming shortwave (visible and near-infrared,  $SW$ ) and longwave (infrared,  $LW$ ) radiation from the sky ( $LW_{sky}$ ) and the  
 372 surrounding environment (here simplified as  $LW$  radiation from the ground,  $LW_{gnd}$ ). Buds emit  $LW$  radiation as a function of  
 373 their temperature ( $LW_{bud}$ ). Only a fraction ( $\alpha$ ) of  $SW$  radiation is absorbed by buds, depending on the properties of their  
 374 surfaces. Buds also absorb a small fraction of  $SW$  reflected from the ground ( $1-r$ ). **b.** Illustration of bud traits influencing solar  
 375 absorptivity, heat conduction and convection processes, and hence, bud temperature.

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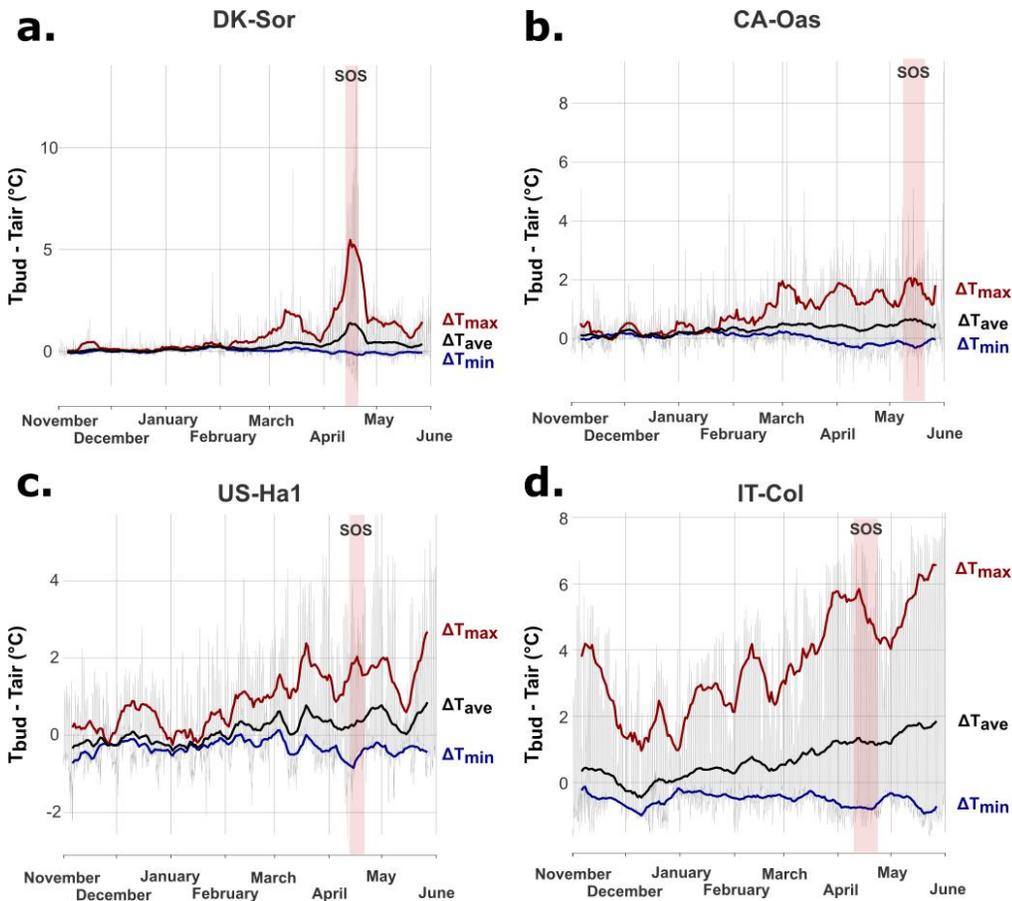
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**Figure 2 | Simulated differences in temperature between buds and the air ( $\Delta T$ ) from energy balance.** **a.** Daily variation in  $\Delta T$  for an exposed bud and a typical day in April for two solar absorptivities:  $\alpha=0.5$  (typical for broad leaves<sup>50</sup>) and  $\alpha=0.8$  (typical for needle leaves<sup>50</sup>). SW and LW<sub>sky</sub> correspond to the amount of incoming shortwave and longwave radiation from the sky. **b** Example of  $\Delta T$  simulated under idealized conditions (e.g. exposed buds in a deciduous canopy) using meteorological observations for winter and spring collected at the Hainich FLUXNET site<sup>51</sup> (temperate deciduous forest). The grey lines represent half-hourly differences in temperature simulated using an energy-budget model. The blue, black and red curves represent the 10-d rolling mean of the minimal ( $\Delta T_{\min}$ ), average ( $\Delta T_{\text{ave}}$ ) and maximal ( $\Delta T_{\max}$ ) temperature differences, respectively. Approximative Start Of growing Season (SOS) is illustrated by the light red region.



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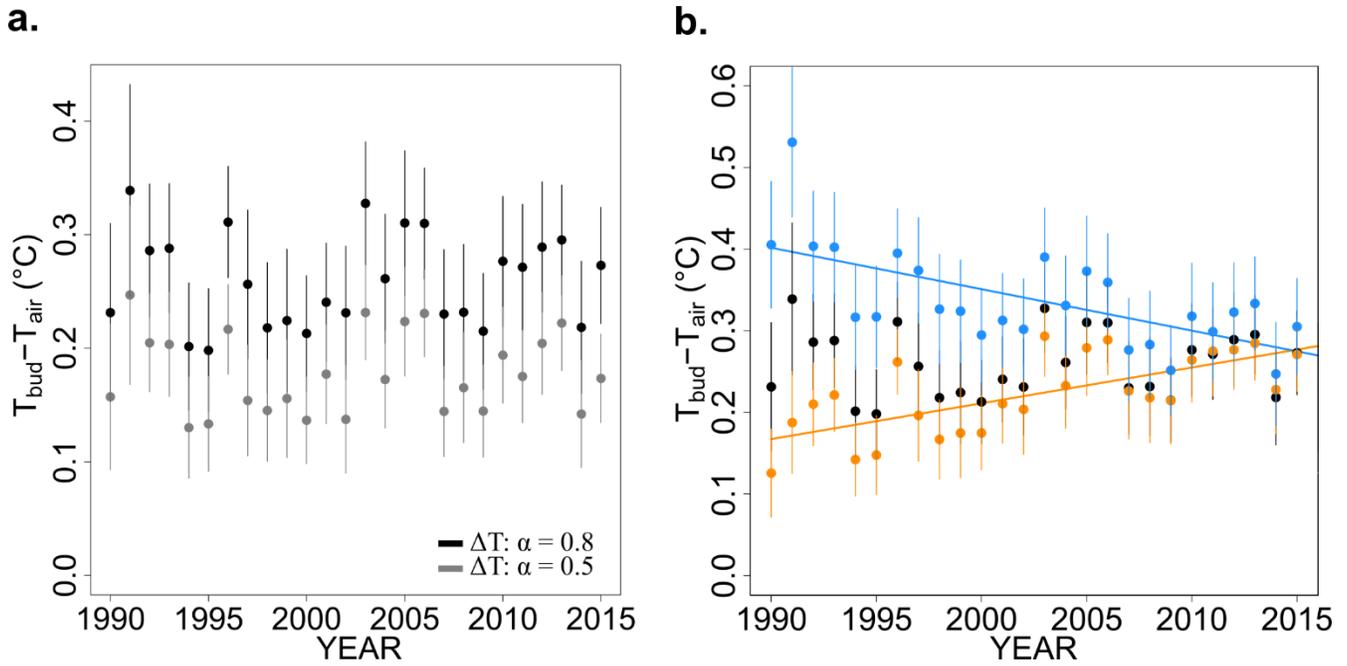
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**Figure 3 | Spatial variability in bud temperature.** Temperature difference ( $\Delta T$  in  $^{\circ}C$ ) between buds and air simulated for four different FLUXNET sites during the year 1998: DK-Sor (Deciduous Broadleaf Forest; 55.48  $^{\circ}N$ , 11.64  $^{\circ}E$ ), CA-Oas (DBF; 53.63  $^{\circ}N$ , 106.20  $^{\circ}W$ ), US-Ha1 (DBF; 42.53  $^{\circ}N$ , 72.17  $^{\circ}W$ ) and IT-Col (DBF; 41.85  $^{\circ}N$ , 13.59  $^{\circ}E$ ). The grey lines represent half-hourly differences in temperature simulated using the energy-budget model. The blue, black and red curves represent the 10-d rolling mean of the minimal ( $\Delta T_{min}$ ), average ( $\Delta T_{ave}$ ) and maximal ( $\Delta T_{max}$ ) temperature differences, respectively. Approximative Start Of growing Season (SOS) based on fluxes is illustrated by the light red region. Note that these simulations represent idealized conditions and use the same parameterization without distinction between sites and species.



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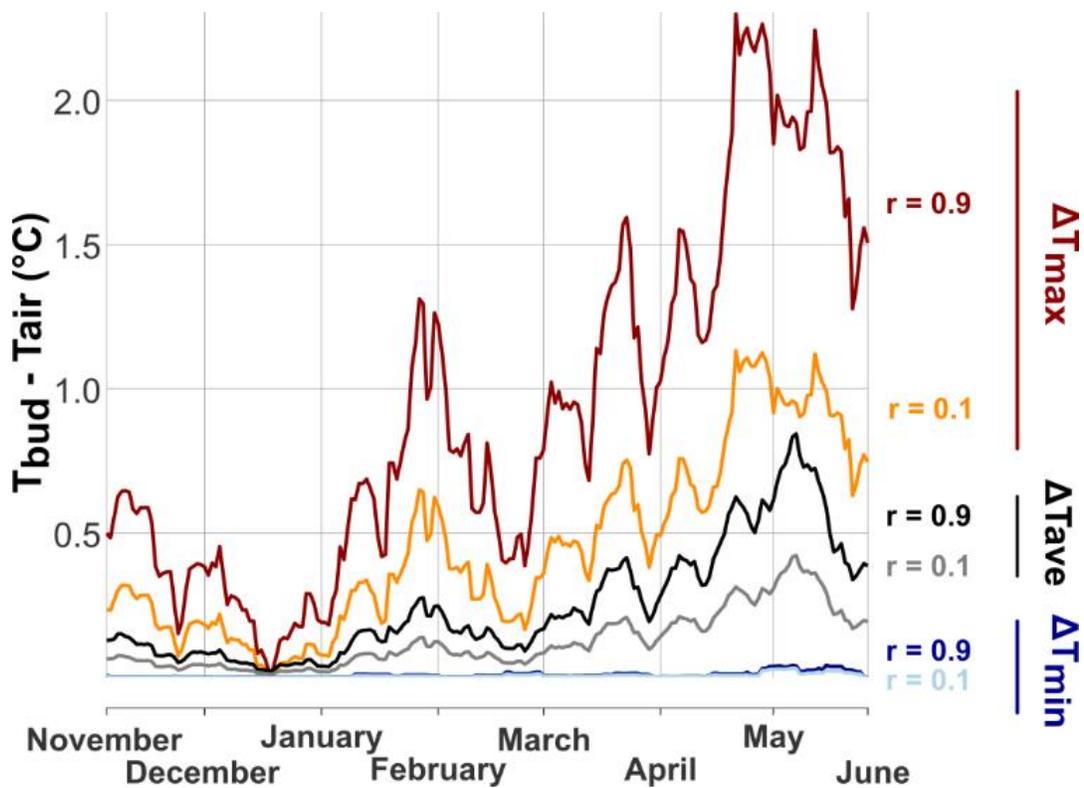
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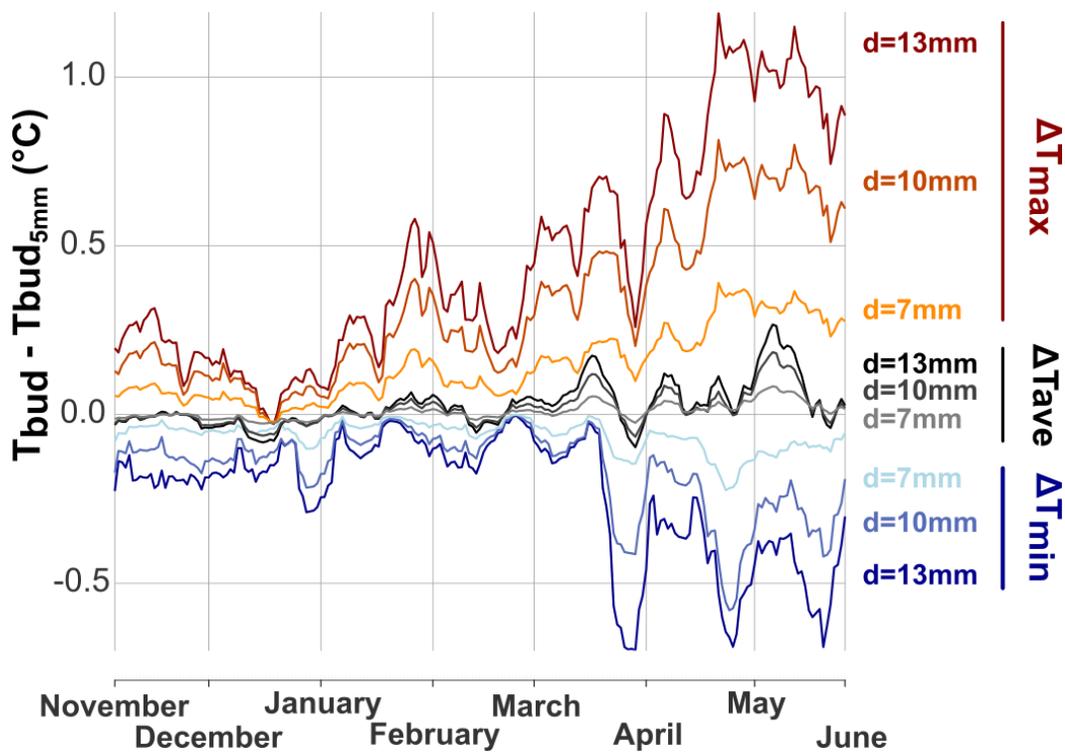
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**Figure 4 | Potential changes in  $T_{bud} - T_{air}$  over Europe. a.** Each point corresponds to the mean preseason  $\Delta T_{ave}$  (see Fig. 2) simulated for six deciduous species across Europe (1059 sites) under idealized conditions (i.e. sun-exposed buds) using field observation of budburst and global meteorological data (see Supplementary Material). All sites and species were pooled together. Two solar absorptivity values were tested, 0.5 (grey) and 0.8 (black). The error bars represent the spatial and species variability ( $\pm 1$  SD around the mean,  $n = 5050$ ). **b.** Under these conditions,  $\Delta T$  is expected to decrease (blue) over the period 1990-2015 ( $n = 375$  sites\*species, 7%) and increase ( $n = 670$  sites\*species, 13% in orange). The error bars represent the spatial and species variability ( $\pm 1$  SD around the mean). The black points correspond to all sites\*species pooled together ( $n = 5050$ ) with  $\alpha = 0.8$  as illustrated in panel a.



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**Figure 5 | Impact of ground albedo on simulated bud temperature.** Temperature difference ( $\Delta T$  in  $^{\circ}\text{C}$ ) between buds and air simulated for two different ground albedo,  $r = 0.1$  (~wet bare soil) and  $r = 0.9$  (~snow). Temperature difference was simulated using meteorological observations for winter and spring collected at the Hainich FLUXNET site (temperate deciduous forest, Germany; see Figure 2). The differences for maximum (red), average (black) and minimum (blue) temperatures are illustrated. Here, bud solar absorptivity to shortwave radiation and bud diameter were set to 0.8 and 5 mm, respectively



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**Figure 6 | Impact of bud size on simulated bud temperature.** Temperature difference ( $\Delta T$  in  $^\circ\text{C}$ ) between buds with a diameter ( $d$ ) of 7, 10 and 13mm and buds with a diameter of 5mm. Temperatures were simulated using meteorological observations for winter and spring collected at the Hainich FLUXNET site (temperate deciduous forest, Germany; see Figure 2). The differences for maximum (red), average (black) and minimum (blue) temperatures are illustrated. Big buds exhibit larger temperature variations than small buds. Here, bud solar absorptivity to shortwave radiation and ground albedo were set to 0.8 and 0.2, respectively. Please note that these results represent the average change in bud temperature with a steady state model. With a low resolution of 30 min in meteorological forcing compared to the relatively small thermal time constant of buds, big buds have the time to accumulate more energy than small buds. Using a transient model, calibrated with site data and high-resolution micrometeorological observations accounting for the sudden changes in wind and radiation might lead to different results.

429 **References**

- 430 1. Peñuelas, J. & Filella, I. Phenology. Responses to a warming world. *Science (New York, N.Y.)* **294**,  
431 793–795; 10.1126/science.1066860 (2001).
- 432 2. Peñuelas, J., Rutishauser, T. & Filella, I. Ecology. Phenology feedbacks on climate change. *Science*  
433 *(New York, N.Y.)* **324**, 887–888; 10.1126/science.1173004 (2009).
- 434 3. Ramos-Jiliberto, R., Moisset de Espanés, P., Franco-Cisterna, M., Petanidou, T. & Vázquez, D. P.  
435 Phenology determines the robustness of plant-pollinator networks. *Scientific reports* **8**, 14873;  
436 10.1038/s41598-018-33265-6 (2018).
- 437 4. Chuine, I. Why does phenology drive species distribution? *Philosophical transactions of the Royal*  
438 *Society of London. Series B, Biological sciences* **365**, 3149–3160; 10.1098/rstb.2010.0142 (2010).
- 439 5. Chmielewski, F.-M. Phenology in Agriculture and Horticulture. In *Phenology: An Integrative*  
440 *Environmental Science*, edited by M. D. Schwartz. 2nd ed. (Springer Netherlands; Springer e-  
441 books; Imprint: Springer, Dordrecht, 2013), pp. 539–561.
- 442 6. Morellato, L. P. C. *et al.* Linking plant phenology to conservation biology. *Biological Conservation*  
443 **195**, 60–72; 10.1016/j.biocon.2015.12.033 (2016).
- 444 7. Katelaris, C. H. & Beggs, P. J. Climate change: allergens and allergic diseases. *Internal medicine*  
445 *journal* **48**, 129–134; 10.1111/imj.13699 (2018).
- 446 8. Schwartz, M. D. (ed.). *Phenology: An Integrative Environmental Science*. 2nd ed. (Springer  
447 Netherlands; Springer e-books; Imprint: Springer, Dordrecht, 2013).
- 448 9. Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A. & SCHWARTZ, M. D. Shifting plant  
449 phenology in response to global change. *Trends in ecology & evolution* **22**, 357–365;  
450 10.1016/j.tree.2007.04.003 (2007).
- 451 10. Fu, Y. H. *et al.* Recent spring phenology shifts in western Central Europe based on multiscale  
452 observations. *Global Ecology and Biogeography* **23**, 1255–1263; 10.1111/geb.12210 (2014).
- 453 11. Jeong, S.-J., HO, C.-H., GIM, H.-J. & BROWN, M. E. Phenology shifts at start vs. end of growing  
454 season in temperate vegetation over the Northern Hemisphere for the period 1982–2008. *Global*  
455 *change biology* **17**, 2385–2399; 10.1111/j.1365-2486.2011.02397.x (2011).
- 456 12. Liu, Q. *et al.* Delayed autumn phenology in the Northern Hemisphere is related to change in both  
457 climate and spring phenology. *Global change biology* **22**, 3702–3711; 10.1111/geb.13311 (2016).
- 458 13. Vitasse, Y. *et al.* Leaf phenology sensitivity to temperature in European trees: Do within-species  
459 populations exhibit similar responses? *Agricultural and Forest Meteorology* **149**, 735–744;  
460 10.1016/j.agrformet.2008.10.019 (2009).
- 461 14. Wang, S. *et al.* Temporal Trends and Spatial Variability of Vegetation Phenology over the Northern  
462 Hemisphere during 1982–2012. *PloS one* **11**, e0157134; 10.1371/journal.pone.0157134 (2016).
- 463 15. Fu, Y. H. *et al.* Declining global warming effects on the phenology of spring leaf unfolding. *Nature*  
464 **526**, 104–107; 10.1038/nature15402 (2015).
- 465 16. Huang, M. *et al.* Velocity of change in vegetation productivity over northern high latitudes. *Nature*  
466 *ecology & evolution* **1**, 1649–1654; 10.1038/s41559-017-0328-y (2017).
- 467 17. Peaucelle, M. *et al.* Spatial variance of spring phenology in temperate deciduous forests is  
468 constrained by background climatic conditions. *Nature communications* **10**, 5388; 10.1038/s41467-  
469 019-13365-1 (2019).

- 470 18. Zohner, C. M., Mo, L., Pugh, T. A. M., Bastin, J.-F. & Crowther, T. W. Interactive climate factors  
471 restrict future increases in spring productivity of temperate and boreal trees. *Global change biology*;  
472 10.1111/gcb.15098 (2020).
- 473 19. Montgomery, R. A., Rice, K. E., Stefanski, A., Rich, R. L. & Reich, P. B. Phenological responses of  
474 temperate and boreal trees to warming depend on ambient spring temperatures, leaf habit, and  
475 geographic range. *Proceedings of the National Academy of Sciences of the United States of America*  
476 **117**, 10397–10405; 10.1073/pnas.1917508117 (2020).
- 477 20. Zohner, C. M., Benito, B. M., Svenning, J.-C. & Renner, S. S. Day length unlikely to constrain  
478 climate-driven shifts in leaf-out times of northern woody plants. *Nature Clim Change* **6**, 1120–1123;  
479 10.1038/nclimate3138 (2016).
- 480 21. Peñuelas, J. *et al.* Complex spatiotemporal phenological shifts as a response to rainfall changes.  
481 *New Phytologist* **161**, 837–846; 10.1111/j.1469-8137.2004.01003.x (2004).
- 482 22. Papagiannopoulou, C. *et al.* Vegetation anomalies caused by antecedent precipitation in most of the  
483 world. *Environ. Res. Lett.* **12**, 74016; 10.1088/1748-9326/aa7145 (2017).
- 484 23. Delpierre, N. *et al.* Modelling interannual and spatial variability of leaf senescence for three  
485 deciduous tree species in France. *Agricultural and Forest Meteorology* **149**, 938–948;  
486 10.1016/j.agrformet.2008.11.014 (2009).
- 487 24. Fu, Y. H. *et al.* Nutrient availability alters the correlation between spring leaf-out and autumn leaf  
488 senescence dates. *Tree physiology* **39**, 1277–1284; 10.1093/treephys/tpz041 (2019).
- 489 25. Seyednasrollah, B., Swenson, J. J., Domec, J.-C. & Clark, J. S. Leaf phenology paradox: Why  
490 warming matters most where it is already warm. *Remote Sensing of Environment* **209**, 446–455;  
491 10.1016/j.rse.2018.02.059 (2018).
- 492 26. Chuine, I., Morin, X. & Bugmann, H. Warming, photoperiods, and tree phenology. *Science (New*  
493 *York, N.Y.)* **329**, 277-8; author reply 278; 10.1126/science.329.5989.277-e (2010).
- 494 27. Vitasse, Y. & Basler, D. What role for photoperiod in the bud burst phenology of European beech.  
495 *Eur J Forest Res* **132**, 1–8; 10.1007/s10342-012-0661-2 (2013).
- 496 28. Way, D. A. & Montgomery, R. A. Photoperiod constraints on tree phenology, performance and  
497 migration in a warming world. *Plant, cell & environment* **38**, 1725–1736; 10.1111/pce.12431  
498 (2015).
- 499 29. Caffarra, A., Donnelly, A. & Chuine, I. Modelling the timing of *Betula pubescens* budburst. II.  
500 Integrating complex effects of photoperiod into process-based models. *Clim. Res.* **46**, 159–170;  
501 10.3354/cr00983 (2011).
- 502 30. Körner, C. & Basler, D. Plant science. Phenology under global warming. *Science (New York, N.Y.)*  
503 **327**, 1461–1462; 10.1126/science.1186473 (2010).
- 504 31. Fu, Y. H. *et al.* Daylength helps temperate deciduous trees to leaf-out at the optimal time. *Global*  
505 *change biology* **25**, 2410–2418; 10.1111/gcb.14633 (2019).
- 506 32. Singh, R. K., Svystun, T., AlDahmash, B., Jönsson, A. M. & Bhalerao, R. P. Photoperiod- and  
507 temperature-mediated control of phenology in trees - a molecular perspective. *New Phytologist* **213**,  
508 511–524; 10.1111/nph.14346 (2017).
- 509 33. Flynn, D. F. B. & Wolkovich, E. M. Temperature and photoperiod drive spring phenology across all  
510 species in a temperate forest community. *New Phytologist* **219**, 1353–1362; 10.1111/nph.15232  
511 (2018).

- 512 34. Brelsford, C. C., Nybakken, L., Kotilainen, T. K. & Robson, T. M. The influence of spectral  
513 composition on spring and autumn phenology in trees. *Tree physiology* **39**, 925–950;  
514 10.1093/treephys/tpz026 (2019).
- 515 35. Strømme, C. B. *et al.* UV-B and temperature enhancement affect spring and autumn phenology in  
516 *Populus tremula*. *Plant, cell & environment* **38**, 867–877; 10.1111/pce.12338 (2015).
- 517 36. Fu, Y. H. *et al.* Increased heat requirement for leaf flushing in temperate woody species over 1980-  
518 2012: effects of chilling, precipitation and insolation. *Global change biology* **21**, 2687–2697;  
519 10.1111/gcb.12863 (2015).
- 520 37. Huang, Y., Jiang, N., Shen, M. & Guo, L. Effect of pre-season diurnal temperature range on the start  
521 of vegetation growing season in the Northern Hemisphere. *Ecological Indicators* **112**, 106161;  
522 10.1016/j.ecolind.2020.106161 (2020).
- 523 38. Meng, F. *et al.* Opposite effects of winter day and night temperature changes on early phenophases.  
524 *Ecology* **100**, e02775; 10.1002/ecy.2775 (2019).
- 525 39. Zhang, S., Isabel, N., Huang, J.-G., Ren, H. & Rossi, S. Responses of bud-break phenology to  
526 daily-asymmetric warming: daytime warming intensifies the advancement of bud break.  
527 *International journal of biometeorology* **63**, 1631–1640; 10.1007/s00484-019-01776-0 (2019).
- 528 40. Meng, L. *et al.* Divergent responses of spring phenology to daytime and nighttime warming.  
529 *Agricultural and Forest Meteorology* **281**, 107832; 10.1016/j.agrformet.2019.107832 (2020).
- 530 41. Bigler, C. & Vitasse, Y. Daily Maximum Temperatures Induce Lagged Effects on Leaf Unfolding in  
531 Temperate Woody Species Across Large Elevational Gradients. *Frontiers in plant science* **10**, 398;  
532 10.3389/fpls.2019.00398 (2019).
- 533 42. Fu, Y. H. *et al.* Three times greater weight of daytime than of night-time temperature on leaf  
534 unfolding phenology in temperate trees. *The New phytologist* **212**, 590–597; 10.1111/nph.14073  
535 (2016).
- 536 43. Piao, S. *et al.* Leaf onset in the northern hemisphere triggered by daytime temperature. *Nature*  
537 *communications* **6**, 6911; 10.1038/ncomms7911 (2015).
- 538 44. Vitasse, Y. *et al.* Impact of microclimatic conditions and resource availability on spring and autumn  
539 phenology of temperate tree seedlings. *New Phytologist*; 10.1111/nph.17606 (2021).
- 540 45. Azeez, A. *et al.* EARLY BUD-BREAK 1 and EARLY BUD-BREAK 3 control resumption of  
541 poplar growth after winter dormancy. *Nature communications* **12**, 1123; 10.1038/s41467-021-  
542 21449-0 (2021).
- 543 46. HAMER, P. The heat balance of apple buds and blossoms. Part I. Heat transfer in the outdoor  
544 environment. *Agricultural and Forest Meteorology* **35**, 339–352; 10.1016/0168-1923(85)90094-2  
545 (1985).
- 546 47. Landsberg, J. J., Butler, D. R. & Thorpe, M. R. Apple bud and blossom temperatures. *Journal of*  
547 *Horticultural Science* **49**, 227–239; 10.1080/00221589.1974.11514574 (1974).
- 548 48. Grace, J. The temperature of buds may be higher than you thought. *New Phytologist* **170**, 1–3;  
549 10.1111/j.1469-8137.2006.01675.x (2006).
- 550 49. Muir, C. D. tealeaves: an R package for modelling leaf temperature using energy budgets. *AoB*  
551 *PLANTS* **11**, plz054; 10.1093/aobpla/plz054 (2019).
- 552 50. Jones, H. G. *Plants and microclimate. A quantitative approach to environmental plant physiology*  
553 (Cambridge university press, Cambridge, 2013).

- 554 51. Knohl, A., Schulze, E.-D., Kolle, O. & Buchmann, N. Large carbon uptake by an unmanaged 250-  
555 year-old deciduous forest in Central Germany. *Agricultural and Forest Meteorology* **118**, 151–167;  
556 10.1016/S0168-1923(03)00115-1 (2003).
- 557 52. Granier, A., Bréda, N., Longdoz, B., Gross, P. & Ngao, J. Ten years of fluxes and stand growth in a  
558 young beech forest at Hesse, North-eastern France. *Ann. For. Sci.* **65**, 704; 10.1051/forest:2008052  
559 (2008).
- 560 53. Zellweger, F. *et al.* Forest microclimate dynamics drive plant responses to warming. *Science (New*  
561 *York, N.Y.)* **368**, 772–775; 10.1126/science.aba6880 (2020).
- 562 54. Bailey, B. N., Stoll, R., Pardyjak, E. R. & Miller, N. E. A new three-dimensional energy balance  
563 model for complex plant canopy geometries: Model development and improved validation  
564 strategies. *Agricultural and Forest Meteorology* **218-219**, 146–160;  
565 10.1016/j.agrformet.2015.11.021 (2016).
- 566 55. Michaletz, S. T. & Johnson, E. A. A heat transfer model of crown scorch in forest fires. *Can. J. For.*  
567 *Res.* **36**, 2839–2851; 10.1139/x06-158 (2006).
- 568 56. Sanchez-Lorenzo, A. *et al.* Reassessment and update of long-term trends in downward surface  
569 shortwave radiation over Europe (1939–2012). *J. Geophys. Res. Atmos.* **120**, 9555–9569;  
570 10.1002/2015JD023321 (2015).
- 571 57. Pfeifroth, U., Sanchez-Lorenzo, A., Manara, V., Trentmann, J. & Hollmann, R. Trends and  
572 Variability of Surface Solar Radiation in Europe Based On Surface- and Satellite-Based Data  
573 Records. *J. Geophys. Res. Atmos.* **123**, 1735–1754; 10.1002/2017JD027418 (2018).
- 574 58. Richardson, A. D. *et al.* Terrestrial biosphere models need better representation of vegetation  
575 phenology: results from the North American Carbon Program Site Synthesis. *Glob Change Biol* **18**,  
576 566–584; 10.1111/j.1365-2486.2011.02562.x (2012).
- 577 59. Liu, Q. *et al.* Extension of the growing season increases vegetation exposure to frost. *Nature*  
578 *communications* **9**, 426; 10.1038/s41467-017-02690-y (2018).
- 579 60. Ma, Q., Huang, J.-G., Hänninen, H. & Berninger, F. Divergent trends in the risk of spring frost  
580 damage to trees in Europe with recent warming. *Global change biology* **25**, 351–360;  
581 10.1111/gcb.14479 (2019).
- 582 61. Zohner, C. M. *et al.* Late-spring frost risk between 1959 and 2017 decreased in North America but  
583 increased in Europe and Asia. *Proceedings of the National Academy of Sciences of the United States*  
584 *of America*; 10.1073/pnas.1920816117 (2020).
- 585 62. Xiao, L. *et al.* Estimating spring frost and its impact on yield across winter wheat in China.  
586 *Agricultural and Forest Meteorology* **260-261**, 154–164; 10.1016/j.agrformet.2018.06.006 (2018).
- 587 63. Unterberger, C. *et al.* Spring frost risk for regional apple production under a warmer climate. *PloS*  
588 *one* **13**, e0200201; 10.1371/journal.pone.0200201 (2018).
- 589 64. Leolini, L. *et al.* Late spring frost impacts on future grapevine distribution in Europe. *Field Crops*  
590 *Research* **222**, 197–208; 10.1016/j.fcr.2017.11.018 (2018).
- 591 65. Greco, S. *et al.* Late Spring Frost in Mediterranean Beech Forests: Extended Crown Dieback and  
592 Short-Term Effects on Moth Communities. *Forests* **9**, 388; 10.3390/f9070388 (2018).
- 593 66. Augspurger, C. K. Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate  
594 deciduous forest. *Functional Ecology* **23**, 1031–1039; 10.1111/j.1365-2435.2009.01587.x (2009).

- 595 67. Dong, N., Prentice, I. C., Harrison, S. P., Song, Q. H. & Zhang, Y. P. Biophysical homeostasis of  
596 leaf temperature: A neglected process for vegetation and land-surface modelling. *Global Ecol*  
597 *Biogeogr* **26**, 998–1007; 10.1111/geb.12614 (2017).
- 598 68. University Of East Anglia Climatic Research Unit (CRU) & Harris, I. C. CRU JRA v1.1: A forcings  
599 dataset of gridded land surface blend of Climatic Research Unit (CRU) and Japanese reanalysis  
600 (JRA) data; Jan.1901 - Dec.2017, 2019.
- 601 69. Dupleix, A., Sousa Meneses, D. de, Hughes, M. & Marchal, R. Mid-infrared absorption properties  
602 of green wood. *Wood Sci Technol* **47**, 1231–1241; 10.1007/s00226-013-0572-5 (2013).
- 603 70. Howard, R. & Stull, R. IR Radiation from Trees to a Ski Run: A Case Study. *Journal of Applied*  
604 *Meteorology and Climatology* **52**, 1525–1539; 10.1175/JAMC-D-12-0222.1 (2013).
- 605 71. Monteith, J. L. & Unsworth, M. H. *Principles of environmental physics. Plants, animals, and the*  
606 *atmosphere*. 4th ed. (Elsevier/Academic Press, Amsterdam, Boston, 2013).
- 607 72. Bergman, T. L., Incropera, F. P. & Lavine, A. S. *Fundamentals of heat and mass transfer* (J. Wiley  
608 & Sons, Hoboken (N.J.), 2011).
- 609 73. Jacobs, A., Heusinkveld, B. G. & Kessel, G. Simulating of leaf wetness duration within a potato  
610 canopy. *NJAS - Wageningen Journal of Life Sciences* **53**, 151–166; 10.1016/S1573-5214(05)80003-  
611 X (2005).
- 612 74. Gerlein-Safdi, C. *et al.* Dew deposition suppresses transpiration and carbon uptake in leaves.  
613 *Agricultural and Forest Meteorology* **259**, 305–316; 10.1016/j.agrformet.2018.05.015 (2018).
- 614 75. Muñoz Sabater, J. Copernicus Climate Change Service: ERA5-Land hourly data from 1981 to  
615 present, 2019.
- 616 76. Kusch, E. & Davy, R. KrigR -- A tool for downloading and statistically downscaling climate  
617 reanalysis data, 04/06/2021.
- 618 77. R Core Team. *R: A Language and Environment for Statistical Computing*. Available at  
619 <https://www.R-project.org/> (Vienna, Austria, 2018).