

1 Ideas and perspectives: Pursuing climate change ecology

2 throughout the year

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15 **Abstract.** Changes in autumnal climate affecting ecosphere diversity and productivity are  
16 arguably as important as winter, vernal and summer conditions. Motivated by the recent calls  
17 for more research on the biological and ecological consequences of autumnal, winter and full  
18 year climate change (Gallinat et al., 2015; Williams et al., 2015; Marra et al., 2016), we  
19 present three examples of innovative biogeoscience, employing novel datasets and  
20 methodologies, which refine our ability to monitor the physiological functioning and  
21 ecosystem performance during autumn. Drawn from recent research in wildlife biology (big-  
22 game hunting), wood anatomy (tree-ring formation) and mycology (mushroom inventory),  
23 these studies provide original insights that contribute to an improved understanding of how  
24 varying environmental and climatic conditions impact the phenology, productivity and  
25 diversity of different organisms in autumn.

26 **1 Background and motivation**

27 Many organisms are mainly active during the warm season. Our understanding of seasonal-  
28 specific biological and ecological responses to intra- and inter-annual environmental changes,  
29 including climate, is therefore biased. Novel data and methods from innovative  
30 biogeosciences, however, offer the possibility for extending climate change biology and  
31 ecology throughout the year. Large-scale, long-term surveys and crowdsourcing programs are  
32 a new and valuable source of seasonal information (Newman et al., 2012; Mills et al., 2015).  
33 When posing the right questions to the right persons, and applying the correct techniques and  
34 searching for allusive signals in hitherto unknown and putatively unsuitable archives (Isaac et  
35 al., 2014), citizen science projects can reveal novel and unexpected findings (Henderson et al.,  
36 2012).

37 Here, we present timely case studies from disparate disciplines that refine our ability  
38 to monitor ecosystem responses to seasonal-specific climate conditions. These examples from  
39 wildlife population ecology, wood anatomical-oriented dendroecology, and climate change  
40 mycology are intended to illustrate how innovative and interdisciplinary research on the  
41 phenology, productivity and diversity of organisms, during periods other than when it is most  
42 convenient, or when empirical evidence is most abundant, can resolve intra-annual processes  
43 affected by climate change. The recent maturity of massive datasets, from agency surveys to  
44 citizen science, offer an unprecedented opportunity for innovative experiments to extend  
45 climate change biology and ecology throughout the year.

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47 **2 Animal migration**

48 Warming-induced range shifts along altitudinal and latitudinal gradients have been reported  
49 for many plant and animal species around the world (Parmesan and Yohe, 2003; Thomas et  
50 al., 2004; Lenoir et al., 2008; Harsch et al., 2009; Chen et al., 2011; Gottfried et al., 2012;  
51 Pauli et al., 2012). Although often complex at different spatiotemporal scales, the mobility

52 and behavioral plasticity of large animals may offer an opportunity to detect climate-induced  
53 population movements throughout different parts of the year. For example, long-term,  
54 massively replicated and geographically detailed hunting records, can supplement traditional  
55 animal tracking studies (Kays et al., 2015). Since 1991, the Swiss canton of Grisons has  
56 amassed >230,000 harvest locations of four ungulate species (Büntgen et al., 2017b). This  
57 inventory reveals year-to-year and decadal niche tracking of free-ranging ibex, chamois, red  
58 deer and roe deer populations at higher elevations, late in the year. A species-specific upward  
59 trend in the ungulates' autumnal harvest locations between 1991 and 2003 coincides with a  
60 mean September-October temperature increase of 1.3 °C during the same period, which  
61 translates into more favorable, snow-free and vegetation-rich autumnal conditions. Linear  
62 regression slopes reveal statistically significant ( $p < 0.05$ ) uphill shifts of 135, 95 and 79 m for  
63 ibex, chamois and red deer (Büntgen et al., 2017b), respectively. Such findings underscore the  
64 advantage of considering climate and its influence on environmental conditions throughout  
65 the year. By the same token, early-year census data – from which autumnal hunting quotas are  
66 derived – could be mined for resolving connections between population density, harvest  
67 intensity and climate variability. Thus, a more complete picture of the external drivers of  
68 wildlife performance, including inter-annual changes in species-specific returns to winter  
69 ranges (Rivrud et al., 2016) is obtained.

70

### 71 **3 Tree-ring formation**

72 Though tree-ring formation in many extra-tropical species occurs during most of the warm  
73 season, several auxin-driven plant development processes (Vanneste and Friml, 2009), such  
74 as the thickening and lignification of xylem-cell walls, mainly occurs at the end of a growing  
75 season. Following recent advances in quantitative wood anatomy (Steppe et al., 2015), and  
76 improvements in process-based plant physiological modeling (Yang et al., 2017), our  
77 understanding of the circumstances that control the precise timing of lignification has greatly

78 improved. State-of-the-art studies combining high-resolution dendrometer readings with cell-  
79 level measurements have found xylem lignification of conifer species in north-eastern France  
80 to persist into late autumn/early winter (Cuny et al., 2015). The timing and duration of such  
81 processes strongly depends on the species, microenvironment, and climate. Favorable  
82 autumnal conditions can stimulate and prolong woody biomass production, leaving a  
83 fingerprint on the intra-annual course of the global carbon cycle (Piao et al., 2008). The  
84 application of wood anatomical studies, particularly in environments with strong and regular  
85 summer droughts such as the Mediterranean, could help identify moisture-controlled  
86 metabolic processes and ecophysiological reactions during the formation of tree rings, thereby  
87 enabling the separation of different development stages from anatomical traits. Consequently,  
88 our ability to connect short-term seasonal climate variations and weather extremes with intra-  
89 annual fluctuations in wood quality and quantity has dramatically increased (Battipaglia et al.,  
90 2016; De Micco et al., 2016).

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## 92 **4 Mushroom production**

93 Rapid emergence, short lifespans, and non-photoperiodic constraints (Körner and  
94 Basler, 2010), make mushroom fruiting bodies ideal indicators of changes in late growing  
95 season conditions. Inter-annual and multi-decadal variations in the abundance of autumnal  
96 sporocarps (productivity), as well as the intra-annual timing of their occurrence (phenology),  
97 and species abundance (diversity), are closely related to the multifaceted interplay of biotic  
98 (mycelium and host interaction) and abiotic (environment and climate) factors (Boddy et al.,  
99 2014). Experimental findings, local observations, national inventories and their continental-  
100 scale compilations, allow seasonal- and species-specific mushroom ‘fruit body’ dynamics to  
101 be reconstructed. Despite mushrooms’ smaller economic, social and ecological importance  
102 (Büntgen et al., 2017c), in comparison to plants and animals, over seven million *in situ*  
103 observations of wildlife mushroom fruiting bodies, representing >10,000 fungal species from

104 nine countries spanning most of the 20<sup>th</sup> century (Andrew et al., 2017), have been drawn from  
105 various scientific and citizen-science projects. In addition to providing evidence of warming-  
106 induced spatiotemporal shifts in autumn mushroom phenology – the mean annual day of  
107 fruiting has become several days to weeks later (Kauserud et al., 2012), a pan-European  
108 mycological inventory offers unique macro-ecological opportunities to assess how fungal  
109 communities interact with the environment (Büntgen and Egli, 2014), including symbiotic  
110 associations with their host vegetation (Büntgen et al., 2013). Exploring how fungal fruit body  
111 productivity and species diversity is linked to biotic and abiotic factors, such as spore  
112 maturation and dispersion (Kauserud et al., 2011; Büntgen et al., 2017a), as well as climate  
113 variation and nitrogen deposition (Boody et al., 2014; Andrew et al., 2016; Van Strien et al.,  
114 2017), respectively, will provide new biological and ecological insights throughout the year.

115 Another non-traditional source of important mushroom-related data for seasonal  
116 climate change research, are governmental emergency services. Poison centers, such as the  
117 Swiss National Poisons Information Centre delivers 24-hour/7-days-a-week nationwide free  
118 medical advice (<http://toxinfo.ch>). Since its establishment in 1966, the center has registered  
119 over one million poison-related inquiries with around one percent of all cases attributed to  
120 mushrooms (Schenk-Jäger et al., 2016). Comparison between these >12,000 mushroom-  
121 related calls with survey information from the Swiss National Data Centre for Biodiversity  
122 (Senn-Irlet., 2010) demonstrates the ability of poison center data to capture spatiotemporal  
123 patterns of fungal phenology, productivity and diversity (Schenk-Jäger et al., 2016).

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## 125 **5 What's next?**

126 By providing timely examples of research initiatives that further a better understanding of  
127 biological and ecological responses to autumnal conditions (Gallinat et al., 2015), we hope to  
128 encourage diversity and creativity in future studies. Such attempts, for instance, should  
129 consider the biological and ecological importance of all season, including winter climate

130 change. Knowledge of the intensity and duration of climate variability during winter is  
131 particularly critical for higher latitude and altitude ecosystems (Williams et al., 2015), where  
132 the impacts of winter temperature and precipitation on snow cover persist through most of the  
133 year. Although varying between organisms and habitats, cold season trends and extremes may  
134 alter chilling requirements, frost injury, energy and water balance, phenology and community  
135 interactions. At the same time, winter warming generally exceeds that during other months,  
136 with implications not only on the annual temperature cycle (Duan et al., 2017) and the Earth's  
137 carbon balance (Piao et al., 2008; Friend et al., 2014), but also by creating a temporal  
138 mismatch between the biological requirements of different ecosystem components and  
139 climate (Williams et al., 2015; Marra et al., 2016).

140 In a similar vein, we cannot ignore the wide range of phenological indicators, such as  
141 the precise timing of bird migration (Jenni and Kéry, 2003), flower blossoming (Aono and  
142 Kazui, 2008), and wine harvest (Cook and Wolkovich, 2016), which have been used to obtain  
143 high-spatiotemporal-resolution data on biological and ecological responses to climatic and  
144 environmental trends and extremes throughout different seasons of the year. Moreover,  
145 aquatic organisms retain life histories in distinct seasonal increments (Cole and Fairbanks,  
146 1990; Morrongiello, et al., 2012; Black et al., 2014; Reynolds, et al., 2016). For instance, the  
147 assessment of long-lived fish, bivalve and coral species can reveal autumnal and even winter  
148 signals at high temporal resolution (Black et al., 2017). Such data might be particularly  
149 valuable for supplementing insights from terrestrial archives to draw a more complete picture  
150 of biological and ecological responses throughout the year (Piermattei et al., 2017).

151 Curiosity-driven, proactive research on climate change ecology should consider the  
152 effects of changing temperature and hydroclimate (precipitation and drought) in all seasons.  
153 Emphasis should be given to investigations of the temporal synchronization of climate  
154 variability and species-specific biological demands. Future efforts should also consider  
155 mining the whole range of non-traditional, environmental inventories and metrics that exist

156 today, or even planned to be available in due course. Quantifying the effects of seasonal  
157 climate on those biological controls regulating yearly growth patterns can only improve the  
158 efficacy of (process-based) mechanistic models by providing valuable details of how  
159 seasonal-specific conditions and responses are inter-correlated throughout an organisms' life  
160 cycle.

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173 **References**

174 Andrew, C., Heegaard, E., Halvorsen, R., Martinez-Pena, F., Egli, S., Kirk, P.M., Bässler, C.,  
175 Büntgen, U., Aldea, J., Høiland, K., Boddy, L. and Kauserud, H.: Climate impacts on  
176 fungal community and trait dynamics. *Fungal Ecol.*, 22, 17–25, 2016.

177 Andrew, C., Heegaard, E., Kirk, P., Bässler, C., Heilmann-Clausen, J., Krisai-Greilhuber, I.,  
178 Kuyper, T., Senn, B., Büntgen, U., Diez, J., Egli, S., Gange, A., Halvorsen, R., Høiland,  
179 K., Nordén, J., Rustøen, F., Boddy, L. and Kauserud, H.: Big data integration: Pan-  
180 European fungal species observations' assembly for addressing contemporary questions  
181 in ecology and global change biology. *Fungal Biol. Rev.*, 31, 88–98, 2017.

182 Aono, Y. and Kazui, K.: Phenological data series of cherry tree flowering in Kyoto, Japan,  
183 and its application to reconstruction of springtime temperatures since the 9th century. *Int.*  
184 *J. Climatol.*, 28, 905–914, 2008.

185 Battipaglia, G., et al.: Structure and function of intra-annual density fluctuations: mind the  
186 gaps. *Front. Plant. Sci.*, 7, 595, 2016.

187 Black, B.A., Sydeman, W.J., Frank, D.C., Griffin, D., Stahle, D.W., García-Reyes, M.,  
188 Rykaczewski, R.R., Bograd, S.J. and Peterson, W.T.: Six centuries of variability and  
189 extremes in a coupled marine-terrestrial ecosystem. *Science*, 345, 1498–1502, 2014.

190 Black, B.A., Griffin, D., van der Sleen, P., Wanamaker, Jr. A.D., Speer, J.H., Frank, D.C.,  
191 Stahle, D.W., Pederson, N., Copenhaever, C.A., Trouet, V., Griffin, S. and Gillanders,  
192 B.M.: The value of crossdating to retain high-frequency variability, climate signals, and  
193 extreme events in environmental proxies. *Global Change Biol.*, 22, 2582–2595, 2016.

194 Boddy, L., Büntgen, U., Egli, S., Gange, A., Heegaard, E., Kirk, P., Mohammad, A. and  
195 Kauserud, H.: Climate variation effects on fungal fruiting. *Fungal Ecol.*, 10, 20–33, 2014.

196 Büntgen, U. and Egli, S.: Breaking new ground at the interface of dendroecology and  
197 mycology. *Trends Plant Sci.*, 19, 613–614, 2014.

198 Büntgen, U., Peter, M., Kauserud, H. and Egli, S.: Unraveling environmental drivers of a  
199 recent increase in Swiss fungi fruiting. *Glob. Change Biol.*, 19, 2785–2794, 2013.

200 Büntgen, U., et al.: New insights into the complex relationship between weight and maturity  
201 of Burgundy truffles (*Tuber aestivum*). *PLOS ONE*, 12(1), e0170375, 2017a.

202 Büntgen, U., Greuter, L., Bollmann, K., Jenny, H., Liebhold, A., Galvan, J.D., Stenseth, N.C.,  
203 Andrew, C. and Mysterud, A.: Elevational range shifts in four mountain ungulate species  
204 from the Swiss Alps. *Ecosphere*, 8(4), e01761. 10.1002/ecs2.1761, 2017b.

205 Büntgen, U., Latorre, J., Egli, S. and Martínez-Peña, F.: Socio-economic, scientific and  
206 political benefits of mycotourism. *Ecosphere*, 8(7), e01870. 10.1002/ecs2.1870, 2017c.

207 Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B. and Thomas, C.D.: Rapid range shifts of  
208 species associated with high levels of climate warming. *Science*, 333, 1024–1026, 2011.

209 Cole, J.E. and Fairbanks, R.G.: The southern oscillation recorded in the  $\delta^{18}\text{O}$  of corals from  
210 Tarawa atoll. *Paleoceanography*, 5, 669–683, 1990.

211 Cook, B.I. and Wolkovich, E.M.: Climate change decouples drought from early wine grape  
212 harvests in France. *Nature Clim.*, 6, 715–720, 2016.

213 Cuny, H.E., Rathgeber, C.B.K., Frank, D.C., Fonti, P., Mäkinen, H., Prislan, P., Rossi, S.,  
214 Martinez del Castillo, E., Campelo, F. et al.: Woody biomass production lags stem-girth  
215 increase by over one month in coniferous forests. *Nature Plants*, 1, 1–6, 2015.

216 De Micco, V., Campelo, F., De Luis, M., Bräuning, A., Grabner, M., Battipaglia, G. and  
217 Cherubini, P. Intra-annual density fluctuations in tree rings: how, when, where, and why?  
218 *IAWA Journal*, 37, 232–259, 2016.

219 Duan, J., Esper, J., Büntgen, U., Li, L., Xoplaki, E., Zhang, H., Wang, L., Fang, Y. and  
220 Luterbacher, J.: Weakening of annual temperature cycle over the Tibetan Plateau since  
221 the 1870s. *Nature Com.*, 8, 14008, 2017.

222 Friend, A.D., Lucht, W., Rademacher, T.T., Keribin, R., Betts, R., Cadule, P., Ciais, P., Clark,  
223 D.B., Dankers, R., Falloon, P.D. et al.: Carbon residence time dominates uncertainty in  
224 terrestrial vegetation responses to future climate and atmospheric CO<sub>2</sub>. *Proc. Natl. Acad.*  
225 *Sci. USA*, 111, 3280–3285, 2014.

226 Gallinat, A.S., Primack, R.B. and Wagner, D.L.: Autumn, the neglected season in climate  
227 change research. *Trends Ecol. Evol.*, 30, 169–176, 2015.

228 Gottfried, M., et al.: Continent-wide response of mountain vegetation to climate change.  
229 *Nature Clim. Change*, 2, 111–115. 2012.

230 Harsch, M.A., Hulme, P.E., McGlone, M.S. and R. P. Duncane, R.P.: Are treelines  
231 advancing? A global meta-analysis of treeline response to climate warming. *Ecol. Lett.*,  
232 12, 1040–1049, 2009.

233 Henderson, S.: Citizen science comes of age. *Frontiers Ecol. Environ.*, 10(6), 283–283, 2012.

234 Isaac, N.J., Strien, A.J., August, T.A., Zeeuw, M.P. and Roy, D.B.: Statistics for citizen  
235 science: extracting signals of change from noisy ecological data. *Methods Ecol. Evo.*, 5,  
236 1052–1060, 2014.

237 Jenni, L. and Kéry, M.: Timing of autumn bird migration underclimate change: advances in  
238 long-distance migrants, delays in short-distance migrants. *Proc. R. Soc. Lond. B*, 270,  
239 1467–1471, 2003.

240 Kauserud, H., Heegaard, E., Halvorsen, R., Boddy, L., Høiland, K. and Stenseth, N.C.:  
241 Mushroom's spore size and time of fruiting are strongly related: is moisture important?  
242 *Biol. Lett.*, 7, 273–276, 2011.

243 Kauserud, H., Heegaard, E., Büntgen, U., Halvorsen, R., Egli, S., Boddy, L., Senn-Irlet, B.,  
244 Greilhuber, I., Dämon, W., Sparks, T., Nordén, J., Høiland, K., Kirk, P., Semenov, M.  
245 and Stenseth, N.C.: Warming-induced shift in European mushroom fruiting phenology.  
246 *Natl. Acad. Sci. USA*, 109, 14488–14493, 2012.

247 Kays, R., Crofoot, M.C., Jetz, W. and Wikelski, M.: Terrestrial animal tracking as an eye on  
248 life and planet. *Science*, 343, 24781–24788, 2015.

249 Körner, C. and Basler, D.: Phenology under global warming. *Science*, 327, 1461–1462, 2010.

250 Lenoir, J., Gégout, J.C., Marquet, P.A., de Ruffray, P. and Brisse, H.: A significant upward  
251 shift in plant species optimum elevation during the 20th century. *Science*, 320, 1768–  
252 1771, 2008.

253 Marra, P.P., Cohen, E.B., Loss, S.R., Rutter, J.E. and Tonra, C.M.: A call for full annual cycle  
254 research in animal ecology. *Biol. Lett.*, 11, 20150552, 2016.

255 Mills, J.A., et al.: Archiving primarydata: solutions for long-termstudies. *Trends Ecol. Evo.*,  
256 30(10), 581–589, 2015.

257 Morrongiello, J.R., Thresher, R.E. and Smith, D.C.: Aquatic biochronologies and climate  
258 change. *Nature Clim. Change*, 2, 849 – 857, 2012.

259 Newman, G., Wiggins, A., Crall, A., Graham, E., Newman, S. and Crowston, K.: The future  
260 of citizen science: emerging technologies and shifting paradigms. *Frontiers Ecol.*  
261 *Environ.*, 10(6), 298–304, 2012.

262 Parmesan, C. and Yohe, G.: A globally coherent fingerprint of climate change impacts across  
263 natural systems. *Nature*, 421, 37–42, 2003.

264 Pauli, H., et al.: Recent plant diversity changes on Europe's mountain summits. *Science*, 336,  
265 353–355, 2012.

266 Piao, S., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luyssaert, S., Margolis, H.,  
267 Fang, J., Barr, A. et al.: Net carbon dioxide losses of northern ecosystems in response to  
268 autumn warming. *Nature*, 451, 49–52, 2008.

269 Piermattei, A., Urbinati, C., Tonelli, E., Eggertsson, Ó., Levanic, T., Kaczka, R., Andrew, C.,  
270 Schöne, B.R. and Büntgen, U.: Potential and limitation of combining terrestrial and  
271 marine proxy archives from Iceland. *Glob. Planet. Change*, 155, 213–224, 2017.

272 Reynolds, D.J., Scourse, J.D., Halloran, P.R., Nederbragt, A.J., Wanamaker, A.D., Butler,  
273 P.G., Richardson, C.A., Heinemeier, J., Eiriksson, J., Knudsen, K.L. and Hall, I.R.:  
274 Annually resolved North Atlantic marine climate over the last millennium. *Nature Com.*,  
275 7, 13502, 2016.

276 Rivrud, I.M., Bischof, R., Meisingset, E.L., Zimmermann, B., Egil Loe, L. and Mysterud, A.:  
277 Leave before it's too late: anthropogenic and environmental triggers of autumn migration  
278 in a hunted ungulate population. *Ecol.*, 97, 1058–1068, 2016.

279 Schenk-Jäger, K.M., Egli, S., Hanimann, D., Senn-Irlet, B., Kupferschmidt, H. and Büntgen,  
280 U.: Introducing mushroom fruiting patterns from the Swiss National Poisons Information  
281 Centre. *PLOS ONE*, 11(9), e0162314, 2016.

282 Senn-Irlet, B.: The use of a database for conservation–case studies with macrofungi. *Mycol.*  
283 *Balcanica*, 7, 59–66, 2010.

284 Steppe, K., Sterck, F. and Deslauriers, A.: Diel growth dynamics in tree stems: linking  
285 anatomy and ecophysiology. *Trends Plant Sci.*, 20, 335–343, 2015.

286 Thomas, C.D., et al.: Extinction risk from climate change. *Nature*, 427, 145–148, 2004.

287 Vanneste, S. and Friml, J.: Auxin: A trigger for change in plant development. *Cell*, 136 1005–  
288 1016, 2009.

289 Van Strien, A.J., Boomsluiter, M., Noordeloos, M.E., Verweij, R.J.T. and Kuyper, T.W.:  
290 Woodland ectomycorrhizal fungi benefit from large-scale reduction in nitrogen  
291 deposition in the Netherlands. *J. Ecol.*, doi:10.1111/1365-2664.12944, 2017.

292 Williams, C.M., Henry, H.A.L. and Sinclair, B.J.: Cold truths: how winter drives responses of  
293 terrestrial organisms to climate change. *Biol. Rev.*, 90, 214–235, 2015.

294 Yang, B., He, M., Shishov, V., Tychkov, I., Vaganov, E., Rossi, S., Ljungqvist, F.C.,  
295 Bräuning, A. and Grießinger, J.: New perspective on spring vegetation phenology and  
296 global climate change based on Tibetan Plateau tree-ring data. *Proc. Natl. Acad. Sci.*  
297 USA, doi/10.1073/pnas.1616608114, 2017.