Ideas and perspectives: Pursuing climate change ecology throughout the year

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

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

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

2 Animal migration

Warming-induced range shifts along altitudinal and latitudinal gradients have been reported for many plant and animal species around the world (Parmesan and Yohe, 2003; Thomas et al., 2004; Lenoir et al., 2008; Harsch et al., 2009; Chen et al., 2011; Gottfried et al., 2012; Pauli et al., 2012). Although often complex at different spatiotemporal scales, the mobility
and behavioral plasticity of large animals may offer an opportunity to detect climate-induced population movements throughout different parts of the year. For example, long-term, massively replicated and geographically detailed hunting records, can supplement traditional animal tracking studies (Kays et al., 2015). Since 1991, the Swiss canton of Grisons has amassed >230,000 harvest locations of four ungulate species (Büntgen et al., 2017b). This inventory reveals year-to-year and decadal niche tracking of free-ranging ibex, chamois, red deer and roe deer populations at higher elevations, late in the year. A species-specific upward trend in the ungulates’ autumnal harvest locations between 1991 and 2003 coincides with a mean September-October temperature increase of 1.3 °C during the same period, which translates into more favorable, snow-free and vegetation-rich autuminal conditions. Linear regression slopes reveal statistically significant ($p < 0.05$) uphill shifts of 135, 95 and 79 m for ibex, chamois and red deer (Büntgen et al., 2017b), respectively. Such findings underscore the advantage of considering climate and its influence on environmental conditions throughout the year. By the same token, early-year census data – from which autumnal hunting quotas are derived – could be mined for resolving connections between population density, harvest intensity and climate variability. Thus, a more complete picture of the external drivers of wildlife performance, including inter-annual changes in species-specific returns to winter ranges (Rivrud et al., 2016) is obtained.

3 Tree-ring formation

Though tree-ring formation in many extra-tropical species occurs during most of the warm season, several auxin-driven plant development processes (Vanneste and Friml, 2009), such as the thickening and lignification of xylem-cell walls, mainly occurs at the end of a growing season. Following recent advances in quantitative wood anatomy (Steppe et al., 2015), and improvements in process-based plant physiological modeling (Yang et al., 2017), our understanding of the circumstances that control the precise timing of lignification has greatly
improved. State-of-the-art studies combining high-resolution dendrometer readings with cell-level measurements have found xylem lignification of conifer species in north-eastern France to persist into late autumn/early winter (Cuny et al., 2015). The timing and duration of such processes strongly depends on the species, microenvironment, and climate. Favorable autumnal conditions can stimulate and prolong woody biomass production, leaving a fingerprint on the intra-annual course of the global carbon cycle (Piao et al., 2008). The application of wood anatomical studies, particularly in environments with strong and regular summer droughts such as the Mediterranean, could help identify moisture-controlled metabolic processes and ecophysiological reactions during the formation of tree rings, thereby enabling the separation of different development stages from anatomical traits. Consequently, our ability to connect short-term seasonal climate variations and weather extremes with intra-annual fluctuations in wood quality and quantity has dramatically increased (Battipaglia et al., 2016; De Micco et al., 2016).

4 Mushroom production

Rapid emergence, short lifespans, and non-photoperiodic constraints (Körner and Basler, 2010), make mushroom fruiting bodies ideal indicators of changes in late growing season conditions. Inter-annual and multi-decadal variations in the abundance of autumnal sporocarps (productivity), as well as the intra-annual timing of their occurrence (phenology), and species abundance (diversity), are closely related to the multifaceted interplay of biotic (mycelium and host interaction) and abiotic (environment and climate) factors (Boddy et al., 2014). Experimental findings, local observations, national inventories and their continental-scale compilations, allow seasonal- and species-specific mushroom ‘fruit body’ dynamics to be reconstructed. Despite mushrooms’ smaller economic, social and ecological importance (Büntgen et al., 2017c), in comparison to plants and animals, over seven million in situ observations of wildlife mushroom fruiting bodies, representing >10,000 fungal species from...
nine countries spanning most of the 20th century (Andrew et al., 2017), have been drawn from various scientific and citizen-science projects. In addition to providing evidence of warming-induced spatiotemporal shifts in autumn mushroom phenology – the mean annual day of fruiting has become several days to weeks later (Kauserud et al., 2012), a pan-European mycological inventory offers unique macro-ecological opportunities to assess how fungal communities interact with the environment (Büntgen and Egli, 2014), including symbiotic associations with their host vegetation (Büntgen et al., 2013). Exploring how fungal fruit body productivity and species diversity is linked to biotic and abiotic factors, such as spore maturation and dispersion (Kauserud et al., 2011; Büntgen et al., 2017a), as well as climate variation and nitrogen deposition (Boody et al., 2014; Andrew et al., 2016; Van Strien et al., 2017), respectively, will provide new biological and ecological insights throughout the year.

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

5 What’s next?

By providing timely examples of research initiatives that further a better understanding of biological and ecological responses to autumnal conditions (Gallinat et al., 2015), we hope to encourage diversity and creativity in future studies. Such attempts, for instance, should consider the biological and ecological importance of all season, including winter climate
change. Knowledge of the intensity and duration of climate variability during winter is particularly critical for higher latitude and altitude ecosystems (Williams et al., 2015), where the impacts of winter temperature and precipitation on snow cover persist through most of the year. Although varying between organisms and habitats, cold season trends and extremes may alter chilling requirements, frost injury, energy and water balance, phenology and community interactions. At the same time, winter warming generally exceeds that during other months, with implications not only on the annual temperature cycle (Duan et al., 2017) and the Earth’s carbon balance (Piao et al., 2008; Friend et al., 2014), but also by creating a temporal mismatch between the biological requirements of different ecosystem components and climate (Williams et al., 2015; Marra et al., 2016).

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

Curiosity-driven, proactive research on climate change ecology should consider the effects of changing temperature and hydroclimate (precipitation and drought) in all seasons. Emphasis should be given to investigations of the temporal synchronization of climate variability and species-specific biological demands. Future efforts should also consider mining the whole range of non-traditional, environmental inventories and metrics that exist
today, or even planned to be available in due course. Quantifying the effects of seasonal climate on those biological controls regulating yearly growth patterns can only improve the efficacy of (process-based) mechanistic models by providing valuable details of how seasonal-specific conditions and responses are inter-correlated throughout an organisms’ life cycle.

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