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EDITORIAL

Indicators of climate change adaptation from molecules to ecosystems

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Introduction

Adaptation of biological systems to current climate change is one of the leading research topics worldwide (Visser 2008; Karhu et al. 2014). Due to the hierarchy of different biological processes operative from molecules to biomes, the rate of biological adaptation is difficult to predict. While molecular and physiological processes can occur within minutes to days and months, biome-level processes typically take tens of years to even millions of years (Kowalchuk et al. 2004; Gienapp et al. 2008; Carroll et al. 2016). The crucial question is whether biological adaptation is fast enough to cope with global climate change (Stocker et al. 2013). From the human perspective, a key challenge is to adapt social systems and food security to recent rapid changes in both environment and population size; this becomes especially problematic if ecosystems fail to adapt to globally changing conditions, leading to destruction of habitats and decline of ecosystem services (Lobell et al. 2008; Kates et al. 2012; Pittelkow et al. 2015; Lesk et al. 2016).

Several studies on adaptation to environmental changes have been dedicated to the processes at molecular and genetic levels (Ehrenreich and Purugganan 2006; Gienapp et al. 2008; Moeller and Tiffin 2008; Scheffers et al. 2016) whereas a limited number of them deal with adaptation at population (Etterson and Mazer 2016) and ecosystem level (Graham et al. 2015; Urban et al. 2016; Pecl et al. 2017). Most studies of ecosystem-level adaptations have considered forest ecosystems because ongoing climate change will likely expose trees and forests to new stresses and disturbances (Littell et al. 2010; Niinemets 2010) and fewer studies have looked at adaptation of grasslands (Arnone et al. 2008) and aquatic ecosystems (Niinemets et al. 2017a; Niinemets et al. 2017b). Adaptation capacity of forests is largely unknown; however, several models have been created to predict spatial shifts of treeline and forest productivity in response to global warming (Seppälä et al. 2009; Berdanier 2010). From the practical point of view, more attention has been given to the adaptation of forestry practices to global changes (Locatelli et al. 2010).

However, there are very few comprehensive studies trying to explain adaptations to recent climate change from the molecular to ecosystem levels (Merilä and Hendry 2014). One of the reasons is the extreme complexity of pathways and causalities explaining the adaptation processes across different hierarchical levels. For instance, global change is associated with rising concentrations of atmospheric greenhouse gases, including carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O), and this is possibly responsible for elevated temperature. Both CO_2 and temperature have a profound influence on biomass production and turnover, but the relative modification of these characteristics is far from being understood (Nowak et al. 2004; Hyvönen et al. 2007; Friend 2010). In particular,

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stronger effect of temperature on organic matter turnover can result in a faster release of CO_2 from organic carbon, which can generate further rise in temperature, while elevated CO_2 enhances biomass production that reduces the rate of increase in CO_2 emissions (Mitsch et al. 2013; Niinemets et al. 2017b for a detailed analysis of such feedback loops in aquatic ecosystems). In addition, water availability increases in certain Earth locations and decreases in others further altering biomass production (Melillo et al. 1993. Major modifications in biogeochemical cycles also have large effects on productivity. Furthermore, vegetation is an important source of volatile organics (VOC) emitted constitutively and elicited during stress (Guenther et al. 2012; Guenther 2013; Niinemets et al. 2013; Copolovici and Niinemets 2016), and the VOCs lead to further important feedbacks between productivity and climate (Tunved et al. 2006; Kiendler-Scharr et al. 2009; Kulmala et al. 2013; Ehn et al. 2014). The overall response of the system is further complicated by adaptation at various time-scales at all levels of biological organization. In this special issue, Niinemets et al. (2017a) argue that a joint effort of researchers working at different levels of biological organization is crucial to understand operation of these complex biogeochemical and biological feedback loops and predict global change effects on various functional types of organisms and scale-up from physiological responses to large-scale integrated ecosystem responses in future climates.

This special issue

This special issue provides a snapshot of the research topics of ENVIRON, the Centre of Excellence in Environmental Adaptation (2011–2015) which was one of 12 centers of excellence in Estonia that served to amalgamate the expertise of different research teams to address adaptation of temperate terrestrial ecosystems to environmental alterations. ENVIRON was lead by Ülo Niinemets from the Estonian University of Life Sciences, and it involved five top teams from three major Estonian universities.

The special issue includes both concept papers as well as case studies with a major emphasis on northern hemisphere boreal and temperate ecosystems. In the first two review papers, Niinemets et al. (2017a, b) analyze the interactions of environmental and chemical stresses under a global change in aquatic ecosystems as well as discuss the role of chemical stressors in the environmental feedbacks in aquatic ecosystems. Their analysis highlights major variations in tolerance of different environmental stresses and in extent and speed of acclimation and adaptation to various environmental drivers within and among species groups at different trophic levels. Specifically, new stresses and novel combinations of the severity of stresses cause modifications in species composition and diversity and can lead to asynchronous peak activities of organisms. All these effects can importantly alter aquatic ecosystem productivity, resilience, and adaptation capacity and can ultimately lead to modified global feedbacks between ecosystem-level processes and environmental drivers (Niinemets et al. 2017a). On the other hand, raising temperatures alter the capacity of aquatic ecosystems for carbon sequestration and greenhouse gas release, modifying the bioavailability of pollutants deposited in the past, and increasing the probability for their uptake by aquatic organisms. Greater temperatures can also enhance eutrophication and deposition of pollutants in organic sediments, further speeding up productivity and eutrophication, with the overall net effects depending on the balance between different processes. Overall, this analysis demonstrates that global change and human impacts can generate novel feedback loops among organisms and environment, e.g., feedbacks due to pollution stress. These feedbacks must be incorporated in models predicting the carbon balance of aquatic ecosystems under globally changing environmental conditions (Niinemets et al. 2017b).

The paper by Hallik et al. (2017) focuses on relationships between leaf pigment contents and spectral vegetation indices using a chemically and structurally large dataset sampled in Mallorca, Balearic Islands. The dataset covers plants from mesic environments as well as from highly stressed environments supporting plants with unique leaf optical properties. The target audience of this manuscript is the remote sensing community that looks at how key vegetation properties can be gauged from a distance. In addition, this work also targets ecophysiologists and plant canopy researchers who study the efficiency of light harvesting and interaction of light with plant canopies. The study provides a review of all available vegetation spectral indices and develops a series of new, and presumably more general, indices that will certainly be of use in remote sensing in stressful environments where standard remote sensing indices currently in use seem not to perform well. As a novel practical aspect, the authors suggest that chlorophylls absorbing light at longer wavelengths than 700 nm can be useful for future remote sensing studies on climate-warming induced reactions of vegetation.

The rest of the papers in this special issue considers forest ecosystem responses to climate change. Napa et al. (2017) analyze heavy metals that have been accumulated in the soil organic horizon of coniferous forests during the peak of oil-shale usage period from 1960 to 1990 in the Baltic region. The study demonstrated that heavy metal concentrations in the soil organic horizon and fine roots were strongly correlated, and thus, fine roots and their associated mycelia in the soil retain heavy metals in forest biogeochemical cycle for unexpectedly long periods. This might indicate potentially higher release of contaminants or shift in translocation processes in boreal coniferous forests in response to climate change.

Staudt et al. (2017) analyzed direct and indirect effects of climate warming and drought on isoprenoid emissions from

Mediterranean oaks. Their results demonstrated how complex the plant responses to climate change can potentially be. Elevated temperature treatments significantly enhanced isoprenoid emissions whereas reduced precipitation tended to decrease them. However, leaf biomass at plant and community levels was not affected by the treatments but was strongly reduced by the presence of herbaceous competitors. Thus, temperature, drought and competition, and their interactions can alter volatile emissions, suggesting that predicting the future evolution of isoprenoid emissions in Mediterranean oak forests are much more complicated than current model efforts have assumed.

Papers by Sellin et al. (2017), Kupper et al. (2017), Kangur et al. (2017), and Rohula et al. (2017) are based on the results of long-term experimental studies in the free-air humidity manipulation (FAHM) station located in Rõka-Järvselja, South-East Estonia (Fig. 1). FAHM was one of ENVIRON's activities and has by now operated for 10 years. It is so far the only experimental facility in the world to study possible impacts of elevated humidity.

Sellin et al. (2017) discus possible mechanisms behind the growth retardation of northern deciduous trees under increasing atmospheric humidity at the FAHM experimental station. Increasing atmospheric humidity reduces water flux through vegetation and causes a reduction in tree growth rate. Based on the results obtained from the long-term experiment, the authors highlight several mechanisms to explain this phenomenon: (1) diminished nutrient uptake leads to lower leaf nutritional status and to an unbalanced foliar phosphorus/nitrogen ratio, resulting in a decline in leaf photosynthetic capacity; (2) readjustment of foliar metabolism causes disturbed N metabolism, accumulation of starch, and changes in secondary metabolite contents which impair both photosynthetic performance and growth; (3) increased carbohydrate content in the leaves leads to reduced sink strength of trees due to feedback effects of elevated carbohydrate content on photosynthetic capacity; (4) high humidity itself constitutes a stress that hinders foliar development; (5) an increase in the proportion of living parenchyma cells in relation to dead xylem elements in sapwood additionally enhances respiration costs; (6) disproportionate changes in hydraulic versus stomatal conductance become a critical factor in the case of weather extremes; (7) elevated humidity results in favorable conditions for development of pathogens, in particular, increased frequency of fungal damage. The study provides evidence for several of these hypotheses, but important year-to-year and rotation-to-rotation differences have also been observed, indicating that long-term data are needed to gain insight into the cause-effect relationships.

Kangur et al. (2017), Kupper et al. (2017), and Rohula et al. (2017) focused on night-time water regime in hybrid aspen ((*Populus tremula* L. × *P. tremuloides* Michx.) and silver birch (*Betula pendula* Roth.) grown at ambient and elevated air humidity. In particular, Kangur et al. (2017) demonstrated that increasing atmospheric humidity does not affect the magnitude of predawn disequilibrium between soil and leaves of hybrid aspen, whereas nocturnal transpiration and water loss from the foliage is still possible through the open stomata at

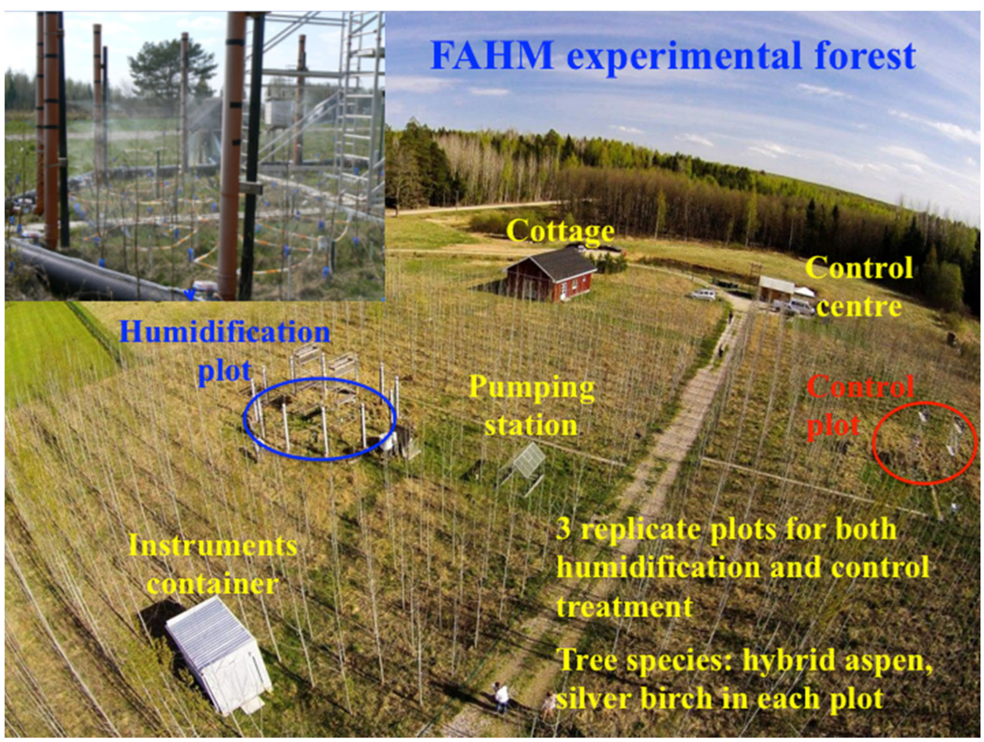

Fig. 1 Aerial view (April 2017) of the free-air humidity management (FAHM) experimental forest area in Järvselja-Rõka, Estonia. Photo by Priit Kupper

night. On the other hand, Rohula et al. (2017) showed that endogenous increase in predawn water flux associated with decreased growth rate of hybrid aspen grown at elevated air humidity. In contrast, Kupper et al. (2017) found that elevated daytime atmospheric humidity increases the potential for night-time water flux in silver birch, and might also facilitate uptake of mineral nutrients. Thus, regional changes in air humidity can differently impact night-time water relations, nutrient uptake, and tree growth in fast-growing tree species, implying that multi-species studies are needed to understand the effects of elevated humidity on boreal and temperate forests.

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