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Spring-fen habitat islands in a warming climate: Partitioning the effects of mesoclimate air and water temperature on aquatic and terrestrial biota

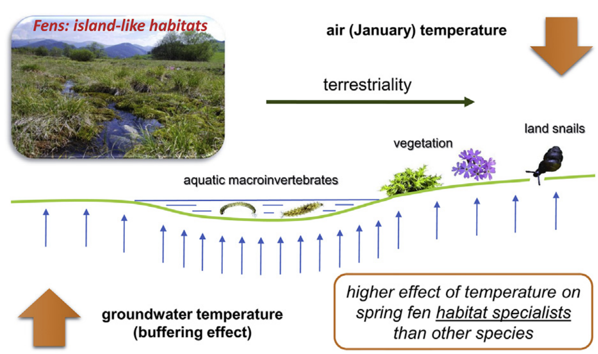
Michal Horsák *, Vendula Polášková, Marie Zhai, Jindřiška Bojková, Vít Syrovátka, Vanda Šorfová, Jana Schenková, Marek Polášek, Tomáš Peterka, Michal Hájek

Department of Botany and Zoology, Masaryk University, Kotlářská 2, CZ-61137 Brno, Czechia

HIGHLIGHTS

- Spring fen biota is strongly driven by both mesoclimate and water temperature.
- Effect of temperature is more significant for specialists than for other species.
- The importance of mesoclimate temperature increases with terrestriality.
- Aquatic and semi-aquatic spring-biota is substantially affected by water temperature.
- Biota of rare island-like spring fens can be severely threatened by climate changes.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate warming and associated environmental changes lead to compositional shifts and local extinctions in various ecosystems. Species closely associated with rare island-like habitats such as groundwater-dependent spring fens can be severely threatened by these changes due to a limited possibility to disperse. It is, however, largely unknown to what extent mesoclimate affects species composition in spring fens, where microclimate is buffered by groundwater supply. We assembled an original landscape-scale dataset on species composition of the most waterlogged parts of isolated temperate spring fens in the Western Carpathian Mountains along with continuously measured water temperature and hydrological, hydrochemical, and climatic conditions. We explored a set of hypotheses about the effects of mesoclimate air and local spring-water temperature on compositional variation of aquatic (macroinvertebrates), semi-terrestrial (plants) and terrestrial (land snails) components of spring-fen biota, categorized as habitat specialists and other species (i.e. matrix-derived). Water temperature did not show a high level of correlation with mesoclimate. For all components, fractions of compositional variation constrained to temperature were statistically significant and higher for habitat specialists than for other species. The importance of air temperature at the expense of water temperature and its fluctuation clearly increased with terrestriality, i.e. from aquatic macroinvertebrates via vegetation (bryophytes and vascular plants) to land snails, with January air temperature being the most important factor for land snails and plant specialists. Some calcareous-fen specialists with a clear distribution centre in temperate Europe showed a strong affinity to climatically cold sites in our study area and may hence be considered as threatened by climate warming. We conclude

* Corresponding author.
E-mail address: horsak@sci.muni.cz. (M. Horsák).

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that prediction models solely based on air temperature may provide biased estimates of future changes in spring fen communities, because their aquatic and semiterrestrial components are largely affected by water temperature that is modified by local hydrological and landscape settings.

1. Introduction

Climate warming and associated environmental changes lead to novel species assemblages and are expected to become a threat for global biodiversity in this century (ACIA, 2005; IPCC, 2014). Distributional shifts and range contractions of species were found among the most important results of climate change, especially in the northern hemisphere at high latitudes and elevations (e.g. Bergamini et al., 2009; Chen et al., 2011; Pauli et al., 2012). Based on current knowledge, it seems that the most threatened ecosystems are those which (i) historically developed under cold conditions and hence are composed of cold-adapted species which decline with climate warming, (ii) are low-productive because of nutrient shortage (Boeye et al., 1999), thus acting as refugia for competitively weak species which decline when decomposition of soil organic matter increases and nutrient cycling accelerates due to warming (Cornelissen et al., 2007; Friberg et al., 2009), and (iii) are distributed as scattered and isolated habitat islands hosting habitat specialists that are limited in dispersal and cannot easily migrate when climatic conditions become less favourable (e.g. Pearson and Dawson, 2005; Horsák et al., 2012). All these three main threats accumulate in high-mountain summits and temperate peatlands, the latter being potentially even more endangered than the former because at lower elevations the rate of climate change and biotic attrition are expected to be higher (Bertrand et al., 2011; Moradi et al., 2012; von Fumetti et al., 2017).

Contrary to high-mountain summits (e.g. Pauli et al., 2012) and ombrotrophic peatlands (e.g. Jassey et al., 2013), groundwater-dependent temperate peatlands (i.e. percolations and spring fens) have been less frequently explored in terms of species composition sensitivity to climate change, although they harbour many relict species and habitat-specific ecotypes (Williams, 1991; Hájková et al., 2008; Hájek et al., 2011a). Climate change has been assumed as a dominant cause of the vegetation succession in a revisiting study of Swiss fen vegetation (Moradi et al., 2012). Essl et al. (2012) predicted a future loss of fen habitats in Austria by habitat distribution models based on both current species distributions and climatic conditions. This approach is in line with most of the existing studies from various ecosystems which were conducted based on air temperature models operating on regional (i.e. mesoclimate) scale. However, a remarkable heterogeneity in the currently observed distributional shifts suggests that species are not moving in response to regional temperature alone (McLaughlin et al., 2017). The principal effect of mesoclimatic conditions can be further modified by topography and also mediated by small-scale environmental factors and vegetation cover (Geiger et al., 2009). Locally obtained thermal data are hence crucial for any prediction about the impact of climatically-induced warming, especially in azonal ecosystems which only secondarily depend on regional climate, being mainly driven by local edaphic factors (Breckle, 2002).

The fact that biota of groundwater-fed fens is largely affected by many environmental parameters such as water chemistry, hydrology and nutrient loading has been demonstrated by many studies (e.g. Sjörs, 1952; Malmer, 1986; Glazier, 1991; Zoltai and Vitt, 1995; Almendinger and Leete, 1998; Wheeler and Proctor, 2000; Hájek et al., 2006; van Diggelen et al., 2006; Horsák and Cernohorsky, 2008; Horsáková et al., 2018). However, only few studies have attempted to determine the effect of climatic conditions (Gignac et al., 1991; Virtanen et al., 2009; Hájek et al., 2011b; Sekulová et al., 2013; Jyväsjärvi et al., 2015), and even less is known about the real impact of water temperature on the variation of spring biota (Kløve et al., 2014; but see Jyväsjärvi et al., 2015 and von Fumetti et al., 2017). Only recently has it been directly documented by continuous in situ measurements that the groundwater supply on spring fens buffers surface and soil temperatures and thus causes high climate resilience of spring fens (Fernández-Pascual et al., 2015). Spring fens may hence act as climatic “microrefugia” supporting populations of species when the surrounding climate is unsuitable for their occurrence (Rull, 2009) as for many species with boreal distribution (e.g. Grootjans and van Tooren, 1984). Thermal buffering can, however, be alleviated by climate warming and this reduction increases as the aquifer size decreases (van der Kamp, 1995; Taylor et al., 2013).

Despite the fact that in the boreal zone numerous spring and fen habitats are distributed continuously (Sjörs et al., 1965; Joosten et al., 2017), the diversity of aquatic cold-stenotherm spring specialists in Fennoscandia has been significantly declining over the last few decades due to climate warming (Jyväsjärvi et al., 2015). In the temperate zone spring fen habitats are often highly isolated and fragmented both naturally and due to human-made changes (e.g. Rybníček, 1974; Soomers et al., 2013), and therefore there is a higher risk of local extinctions and a lower chance for recolonization once the source populations are scattered and remote, which especially applies for short-life-span organisms (Horsák et al., 2012). However, up to now, there has been no study testing the effect of continuously in situ measured spring-water temperature on both aquatic and terrestrial biota of groundwater-dependent ecosystems in the temperate zone. Because of the absence of any long-term historical monitoring data on spring fen communities, exploring climatically promoted variation in biotic communities is only possible via correlative studies. Our study is therefore based on an analysis of species composition variation along a continuous climatic gradient in an area that harbours climatic late-glacial plant and snail relicts (Hájek et al., 2011a). As local environmental conditions change in time along with the climate, both independently or in response to climate changes, it is mostly difficult to identify a pure effect of climate change on variation in biotic communities. In this study we therefore paid attention to precisely described main environmental drives of species composition variation to separate environment-related and temperature-related patterns in the system.

We specifically explored the following hypotheses: (1) Water temperature will not significantly correlate with mesoclimate because of different, mesoclimate-independent intensity of thermal buffer of the groundwater; (2) The importance of water temperature in expense of mesoclimate air temperature (and hence the importance of the thermal buffer) will decrease with terrestriality, i.e. from aquatic via semiterrestrial to terrestrial biotic assemblages; (3) The effects of temperature, specifically mesoclimate air or water temperature and its fluctuations, will be higher for specialists than for matrix-derived species (i.e. species colonizing fens from adjacent matrix; these are mostly represented by generalists), which are limited more by local environment than mesoclimate; (4) Temperature conditions, however, will also be significant for matrix-derived species, due to the climatically driven increase of resource availability related to higher decomposition rates.

2. Materials and methods

2.1. Study area and sites

The studied sites were sloping treeless spring fens, mostly of small area and evenly distributed across the Western Carpathian Mountains (Fig. 1). For the study we carefully selected 30 reference sites out of