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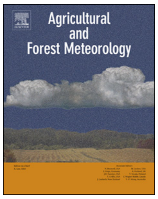

Reduced geographical variability in spring phenology of temperate trees with recent warming

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ABSTRACT

The occurrence of species-specific phenological timing among populations over broad geographical areas may have converged or diverged with recent climatic warming. The changes in spatial geographical variability of phenological timing may affect the degree of species overlap, and thus have profound ecological consequences in the context of global change. The potential converging or diverging has been little explored, although advancements of spring phenology due to climate warming have been observed worldwide in the last decades. Here we addressed this question through analyzing temporal changes in the geographical variability for 22 spring phenological events (both leaf-out and flowering phenology) of 16 temperate tree species in Europe. We found that the species-specific geographical variability of spring phenological timing decreased during 1980–2013, indicating that phenological differences among populations over a large geographical area decreased. The reduced geographical variability is mainly due to the fact that populations in cold sites had higher advancement rates and exhibited stronger responses to elevated temperature than those in warm sites. Warming-induced convergence of spring phenology in temperate trees over a large geographical area may affect the activities of other species in the food chain through trophic mismatch, and may ultimately affect the ecosystem carbon and nutrient cycles that are driven through functioning of the food chain.

1. Introduction

The last three decades is likely the warmest 30-year period during the last 1400 years in the history of the Northern Hemisphere (IPCC, 2014). Global average surface temperatures have risen by 0.2 °C per decade from 1975 to 2005 and they are predicted to continue to rise (Hansen et al., 2006). Plant phenological events, such as budburst, leaf unfolding and flowering, are important indicators of global warming (Menzel et al., 2006a). In recent decades, advances of spring phenological events with elevated temperature have been reported extensively (Cleland et al., 2007; Menzel and Fabian, 1999; Parmesan and Yohe, 2003; Root et al., 2003; Sherry et al., 2007). Furthermore, species which track climate change by adjusting phenology tend to increase their performance, as indicated by biomass, percent cover, and individual growth (Cleland et al., 2012).

Air temperature has been identified as the primary environmental factor affecting spring phenology in plants (Menzel et al., 2006a). It has a dual role in regulating the spring phenology of temperate trees (Hänninen, 2016). Long-term exposure to relatively high temperatures (‘forcing’) is required for the invisible anatomic development in the buds that leads to the visible phenological events, such as budburst. However, since the study of Coville (1920) it has been known that long-term exposure to low chilling temperatures is required in many tree species for rest break, that is, removing the growth arresting physiological conditions in the dormant buds during autumn and winter (for other references, see Hänninen (2016)). Thus, in addition to the well-known advancing of spring phenology, by reducing chilling climatic warming may have a lower impact on the advance, or sometimes even cause delayed spring phenology in temperate trees (Ford et al., 2016; Murray et al., 1989), thus complicating any inferences about the effects of climatic warming in natural conditions. Photoperiod (day length) does not change with warming climate, but it can nevertheless limit the ability of trees to respond to climate warming (Way and Montgomery, 2015). Furthermore, the photoperiodic responses of spring phenology are species-specific (Basler and Körner, 2012). A recent study even found that species from high latitudes with long winters leafed out

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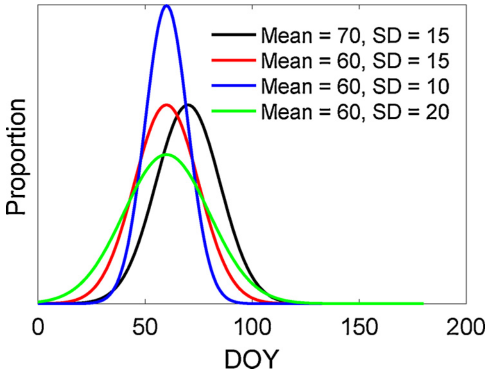

Fig. 1. A hypothetical example of the effect of climatic warming on the flowering time and its variability over a large geographical area. The vertical axis shows the proportion of populations, out of all populations in the geographical area, having their peak flowering time on the day of year (DOY) indicated by the horizontal axis. The black curve represents the current situation, and the three colored curves are three cases of advanced phenological timing caused by climatic warming. For details, see text. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

independently of photoperiod (Zohner et al., 2016).

Determined by the environmental factors and the genetic structure of the tree population, the phenological timing in a given tree species may differ significantly among populations (Beuker, 1994). Populations in warm regions are likely to have earlier phenological timing than those in cold regions. In addition, the advancement rates in response to elevated temperatures may vary among populations (Parmesan, 2007; Schwartz et al., 2006), and this may alter the degree of differences in the phenological timing among populations. In this way, climatic warming may affect not only the phenological timing at each geographical location, but also the magnitude of its variability over the large geographical area. Here we take a hypothetical example of shifted distributions of flowering time to demonstrate the potential consequences of the changes in geographical variability (Fig. 1). Under climate warming, the current flowering dates (black curve, mean DOY = 70) are assumed to be advanced by ten days, to the average DOY = 60. Despite the same average advancing by ten days, the duration of flowering season over the geographical area may be shortened (blue curve), prolonged (green curve), or it may have stayed unaltered (red curve).

Both advances in mean phenological timing and changes in its geographical variability may affect the degree of species overlap in phenological timing over geographical areas. This may have profound consequences on ecological processes. The convergence or divergence of phenological events in one species is not only critical for its own growth and reproduction, but it may also affect the survival of other species in the food web (Post and Forchhammer, 2008; Saino et al., 2011; Thomas et al., 2004) through both direct and indirect interactions (Ma and Kazanci, 2013). A trophic mismatch related to these changes has been reported in all major ecosystems of the world (Edwards and Richardson, 2004; Memmott et al., 2007). For example, temporal mismatches between plants and their pollinators could reduce seed set in plants and reduce food availability to the pollinators. Ultimately, this may lead to the extinction of both the pollinator and the plant species involved in the interaction (Memmott et al., 2007). The changes in geographical variability, through affecting the temporal overlap between species, may aggravate the trophic mismatch (Hegland et al., 2009; Rafferty et al., 2015), and thus affect the carbon cycles and nutrient cycles that rely on the transfer of mass and energy through the food chain (Edwards and Richardson, 2004; Richardson et al., 2010). Therefore, it is critical to better understand how and to what extent the geographical variability in plant phenology may change under climate warming.

Previous research has mainly focused on the overall advancement of the spring phenological timing, but less on the potential changes in its geographical variability. Although there are a few related studies (Menzel et al., 2006b; Post et al., 2008), no agreement on the changes in geographical variability has been reached yet and the reasons for the altered variability remain poorly understood. In recent decades, there has been growing evidence that high altitudes and latitudes (cold areas) experience more rapid warming than low altitudes and latitudes (IPCC, 2014; Pepin et al., 2015). The uneven warming may cause more dramatic advances of spring phenology in cold than in warm areas. Additionally, Fu et al. (2015) recently showed that spring phenological response of trees to temperature rise has declined during the last three decades. This decline in sensitivity of spring phenology is probably partly due to reduced chilling in warm years, although the possible constraining effect of photoperiod cannot be excluded (Fu et al., 2015). Similarly, the reduced chilling may also restrict the further advance of already early phenological timings in warm areas. We expect to retrieve this pattern of decreasing sensitivity from cold to warm regions, which may ultimately shorten the difference between late phenological timing in cold regions and early timing in warm areas. Thus, we hypothesize that the advances of spring phenological timing over time have been accompanied by the decrease in its geographical variability.

To address this hypothesis, we examined comprehensive long-term phenological records across Europe provided by the Pan European Phenology (PEP) network (www.pep725.eu) (Templ et al., 2018). Our aim was to examine the changes in geographical variability in spring phenology during the period 1980–2013, which is characterized by the strongest warming being recorded until today. To further explore the underlying mechanisms behind varying geographical variability in phenology, we investigated how the changes in preseason temperature, phenological timing, and chilling accumulation varied among sites representing different temperature conditions.

2. Materials and methods

2.1. Phenological data and climate data

The phenology dataset used in the study was obtained from the Pan European Phenology network (PEP, www.pep725.eu), which provides an open access to *in situ* phenology records across Europe (Templ et al., 2018). The PEP phenology dataset, contributed by both researchers and citizen scientists, includes multiple phenophases for a variety of plant species. The phenological timing was recorded as the day of year (DOY). Selection of the data was based on the following criteria: (i) The selected sites cover at minimum 25 years' observations during 1980–2013. Selecting sites with long-term phenological records guaranteed that there were a similar number of sites each year and the geographical distribution of the sites did not vary significantly among years. Fig. S1 shows that the geographical distribution of sites where first flowering dates for *Tilia platyphyllos* were recorded was similar over the years. The yearly distributions of the sites for each of the other 21 phenophases were also similar during the studied period, but are not shown due to the large number of figures involved. (ii) The selected phenological events include at least 100 observation sites. This ensured there was enough data each year to compute the geographical variability. The locations of all 1415 selected phenological observation sites are shown in Fig. 2. The geographical distribution of observation sites for each phenological event is provided in Fig. S2. Most of the phenological sites are located in Germany. A total of 22 phenological events (5 phenophases in 16 temperate tree species) were included in the study. There are 3 conifer and 13 broadleaf species (3 ring-, 1 semi-ring- and 9 diffuse-porous species), and 8 wind- and 8 insect-pollinated species included in the study. Summary statistics of the phenological events are provided in Table 1. In total, 510,506 phenological observations were included in this study.