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Synchronized phenological dynamics of species communities

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Abstract

Phenological changes evidence that species are responding to climate change, yet the spatial variation of phenological responses at large scale is not well known. Such knowledge would be crucial for obtaining a comprehensive understanding of the consequences of climate change to species communities. By utilizing an extensive (ca. 116,000 dates) large-scale (239 localities in Russia) and long-term (1960-2014) multi-taxon (plants, birds, insects, amphibians, reptiles and fungi) database, we identified a bimodal geographical pattern in phenological responses, with some events advancing in the north but delaying in the south, whereas others advancing both in north and south. For particular events, phenological shifts were consistent among species but markedly varied among sites, suggesting a strong influence of local conditions. Variation in spring phenology was correlated with temperature for species groups other than birds, with uniform sensitivity to temperature throughout the geographical gradient. Our results notably demonstrate that phenological dynamics of multiple species can be synchronised by climate change over broad distances.

Keywords: global warming | Moran effect | synchronous community | spatial variability

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Introduction

Phenological dynamics have been recognised as one of the most reliable bio-indicators of species responses to ongoing warming conditions (Post *et al.* 2001). Together with other adaptive mechanisms, such as changes in spatial distribution and physiological adaptations, phenological plasticity is a key adaptive response for maintaining many aspects of biodiversity in a changing world (Koh *et al.* 2004; Bellard *et al.* 2012).

Many studies have documented that in the northern hemisphere spring events are becoming earlier whereas autumn events are occurring later, mostly due to raising temperatures (Parmesan & Yohe 2003; Root *et al.* 2003). Despite this broad unanimity, there is abundant evidence suggesting that there are systematic differences in phenological responses to climate change among individual species (Parmesan 2007; Both *et al.* 2009; Cook *et al.* 2012), different taxonomic groups or trophic levels (Voigt *et al.* 2003; Thackeray *et al.* 2010; Thackeray *et al.* 2016). Species-specific responses to climate change can create mismatches between species (e.g. Harrington *et al.* 1999; Visser & Both 2005) and potentially affect community persistence. Yet, up to date there has been a lack of consensus on which species are showing most, and which are showing least, changes. To realistically assess the extent to which the stability and persistence of natural systems will be hampered due to loss of phenological synchrony, we need to go beyond simply reporting correlations between temperature and dates of phenological events, and build models studying the drivers of the dynamics of populations and communities facing global change. For example, Ovaskainen *et al.* (2013) demonstrated that even if many species are shifting at different rates, synchronous species tend to shift in congruence. This result suggests that climate change may disrupt community-level synchrony less than what was assumed in earlier studies. Unfortunately, this positive finding may be only part of the story. Their study was performed using long-term data that was systematically collected on many taxonomic groups and on many kinds of weather events, but only in one locality. Climate is, however, changing in a multidimensional fashion, so it is not only shifting in time but creating unpredictable new environmental conditions that may vary with latitude (Root *et al.* 2003; Menzel *et al.* 2006b; Doi & Takahashi 2008). Few studies analysing geographically extensive datasets have observe that temporal trends in phenological response vary spatially (e.g. Root *et al.* 2003; Menzel *et al.* 2006b; Rubolini *et al.* 2007; Hurlbert & Liang 2012), yet the latitudinal trends are still unclear. For example, while Menzel *et al.* (2006b) suggested a weaker phenological responses in plant to temperature at high latitudes compared to those found in warmer countries, Root *et al.* (2003) observed the opposite patterns.

To examine to what extent the mechanisms triggering phenological events vary in time (Ovaskainen *et al.* 2013) and over space (e.g. Menzel *et al.* 2006b; Primack *et al.* 2009), a comprehensive understanding of phenological responses to climate change requires community-wide data that are both long-term and spatially extensive (Doi & Takahashi 2008). Such data are still not common and, with few exceptions (Doi & Takahashi 2008; Primack *et al.* 2009; Thackeray *et al.* 2010), the assessments of broad-scale taxonomic and geographic variations in phenological changes have generally involved meta-analyses (Root *et al.*

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2003; Ge *et al.* 2015), or analyses of large observational databases that either represent mid-latitude systems (e.g. Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003) or are characterized by low species richness (Menzel *et al.* 2006a). Therefore, the spatial variation in phenological dynamics of species communities at large scale is still not well known (Menzel *et al.* 2006a; Doi & Takahashi 2008). Yet, this information is essential for understanding how species and communities response to climate change (Roy *et al.* 2015).

The hypothesis that spatially-separated animal and plant populations may be synchronized, i.e. experiencing concurrent fluctuations over time, by climate is highly relevant because it suggests that local populations can be similarly influenced over broad distances by ongoing warming conditions (Post & Forchhammer 2002, 2004). Population synchrony has been so far mostly studied from the point of view of variations in density dependent characteristics (e.g. population abundance) within a single species or among a few interacting species (Hansen *et al.* 2013). In many systems, the strength of synchrony declines monotonically with increasing distance between populations, although more complex patterns are also possible (Ranta *et al.* 1997; Koenig 1999; Liebhold *et al.* 2004). Efforts to attribute synchronous fluctuations of contiguous populations to climate are, however, confounded by the synchronizing influences of dispersal and ecological interactions (Heino *et al.* 1997; Liebhold *et al.* 2004). Thus, the potentially synchronising role of climate may be more effectively assessed through processes that respond to climate more directly than abundance, such as phenology. As phenological events can be synchronised in the same way as population fluctuations (Ranta *et al.* 2010), assessing the spatial scale of phenological synchrony among different species (Hansen *et al.* 2013) may be crucial for predicting the large-scale consequences of climate change in ecological communities.

Our aim is to utilize a large-scale and long-term dataset to examine two major axes related with community-level spatial variation in phenological dynamics and its climatic drivers: the spatial and interspecific variability in phenological responses to climate change and the synchronizing effect of climate at the ecological community level. Specifically, we asked (*i*) whether phenological events have responded systematically to climate change over a broad geographical range, (*ii*) whether the responses are consistent among species (or higher level units of taxa) or if different species show idiosyncratic phenological trends, and (*iii*) whether spatial correlations in climate is enforcing synchronous community-level phenological responses. Based on previous studies, we hypothesize that if geographic variation in phenology reflects adaptation of the local climate, allowing species to track spatial and temporal variation of environmental conditions, we should then expect to find differences in latitudinal patterns of phenological response to changes in climatic conditions (Doi & Takahashi 2008). Even though different species may respond individualistically to climate (Cleland *et al.* 2006), synchronous species among populations may evolve similar phenological responses to environmental cues (Ovaskainen *et al.* 2013). Thus, we expect that different phenological events, even across species and higher taxa may be synchronized over long distances due to climatic conditions (Koenig 1999; Ranta *et al.* 2010; Hansen *et al.* 2013).

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Material and methods

Phenology and climate data

The original dataset consisted of 241,225 observation dates collected in 239 localities in Russia, Ukraine, Belarus, Latvia, Lithuania and Estonia (Fig. 1) during 115-year period (from 1899 to 2014). During this period researchers intensively conducted regular observations to record dates at which a predefined list of phenological and weather-related events occurred (Table 1). Yet, in order to perform comparable analysis among the sites, we only used data from 1960 onwards (i.e. a 55-year-long time series from 1960 to 2014), which included 94% of the original number of observations. We only used the best recorded phenological events (i.e. the ones we had the longest time series over the largest geographical area) and grouped them into 14 classes (Table 1). The data used in this study consisted of 116,291 dates representing 13,094 weather-related observations and 103,197 phenological observations. Events measured for plants (trees, shrubs and grasses) include e.g. the onset days of leaf unfolding and leaf fall; for birds (both resident and migratory species) they include e.g. days for first spring and last autumn occurrences; for insects, amphibians, reptiles and fungi they include e.g. day of first occurrence in the spring. The plant data were acquired in fixed plots, and the bird data along established routes. Weather-related events were recorded as calendar dates when those events took place. We classified the weather-related events into three groups: events related to temperature (e.g. the first day when temperature crosses, for instance, -5°C), snow (e.g. the day of first winter snowfall) and ice (e.g. the first winter day with ice on ponds). The 84.6% of the phenological dates were collected by research personnel of nature protected areas and national parks, who followed a systematic protocol with sampling effort remaining nearly constant. The remaining 15.4% of the observations came from a well-established phenological network of volunteers, who notably also followed similar systematic protocol. In addition, we used three weather covariates, namely mean temperature, precipitation and snow cover, which were daily collected in a large network of meteorological stations located through Russia, Ukraine, Belarus and Kazakhstan (All-Russia Research Institute of Hydrometeorological Information - World Data Centre RIHMI-WDC). The study area has experienced an overall increase in temperature (on average +0.03°C $year^{-1}$; Fig. 1B), in precipitation (on average +0.6 mm $year^{-1}$; Supplementary Information I Fig. S1) and in snowfall (on average +0.04 cm $year^{-1}$; Supplementary Information I Fig. S1).

Additional information of the structure of the data (i.e. the representation of species and time periods across the sites) can be found in Supplementary Information I Fig. S2 and Supplementary Information II Table S1.

Statistical analyses

We used linear mixed models to study how the mean timings and long-term shifts of the phenological events and the weather events vary among the species and the sites. We built separate model for each class of phenological and weather-related events listed in Table 1. In these models, the response variable

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d_{sit} was the day when a particular event for the species i (or particular weather-event) happened in the site s in the year t. We assumed a linear mixed model, which we write with the help of fixed (F) and random (R) effects as

$$d_{sit} = L^F_{sit} + L^R_{sit} + \varepsilon_{sit}, \quad [Eq.\,1]$$

where $\varepsilon_{sit} \sim N(0, \sigma^2)$ is a normally distributed residual. The fixed effects L^F_{sit} include the linear effects of the longitude x and latitude y of the site s, the year t, and their interactions:

$$L^F_{sit} = \alpha + \beta_x x + \beta_y y + \beta_t t + \beta_{xt} xt + \beta_{yt} yt.$$

The random effects L^R_{sit} include the main effect of the site s (not explained by latitude and longitude), main effect of the species (or weather-event) i, the interaction between these two, as well as site- and species specific variation in the linear response to the year t:

$$L^R_{sit} = a_s + b_i + c_s t + d_i t + e_{si}.$$

Each random term was assumed to be normally distributed with its factor-specific variance:

$a_s \sim N(0, \sigma_A^2)$, $b_i \sim N(0, \sigma_B^2)$, $c_s \sim N(0, \sigma_C^2)$, $d_i \sim N(0, \sigma_D^2)$, $e_{si} \sim N(0, \sigma_E^2)$.

We defined *shift* as the long-term change in a phenological or weather-related event, measured by the slope of the linear regression of date explained by year. We defined *mean date* as the prediction of the model for a reference year, set here to 1990, which year approximately represents the mean year in our data. We partitioned the variation of mean dates and shifts for each event by comparing the variances for different random effects (site, species, site-species interaction) and the variance due to geographical gradient, calculated as sum of longitude and latitude effects multiplied to the variances of corresponding predictors.

We estimated the geographical gradients for the mean date and the shift for each event by considering the direction at which the values changed the most per unit distance based on the fixed effect part of the model. For graphical representation of mean dates and shifts over the study area, we used the model prediction based on both fixed and random effects, which prediction we interpolated by ordinary kriging with constant mean field and variogram of Gaussian form (Banerjee *et al.* 2004), fitted to empirical variogram of the mean dates and shifts at sites.

As the data from the Russian Far East were quite sparse (Fig. 1), we analysed the data for the eastern sites (located to the east from 70-degree meridian) separately for each location by applying the same model, but without terms related to the effect of the site s and its longitude x and latitude y.

To study how the phenological variation correlates with weather variation, we modelled the residual terms ε_{sit} further as a function of weather variables. We built three separate models, in each of which we used one of the daily measured weather covariates (mean temperature, precipitation and snow cover) as the predictor. We pre-processed the weather data to values w_{sit}

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that described the weather conditions for site s and year t at the time of the year that was relevant for the phenological event for species i. To do so, we used piecewise linear interpolation of weather data recorded at meteorological stations as the proxy for weather conditions at each site s. We then removed a linear trend of year as we aimed w_{sit} to model year-to-year variation rather than a long-term shift. We defined w_{sit} as the average the weather data over the time period $(m_{is} - d_A, m_{is} + d_B)$, where m_{is} is the mean date of the focal phenological event for site s, predicted by the Eq. 1 for year 1990, and d_A and d_B were the predefined parameters of $d_A = 60$ days and $d_B = 7$ days. To test the sensitivity of the results to these choices, we also repeated the analyses with $d_A = 15$ days and $d_B = 7$ days. In addition, we studied the effect of weather covariates at a global spatial scale. Global weather covariates were estimated by averaging daily mean observations from all meteorological stations of our study area (located to the west from 70-degree east meridian).

We related the residual variation in phenological timings to variation in weather conditions by the linear models

$$\varepsilon_{sit} = \hat{L}^F_{sit} + \hat{L}^R_{sit} + \hat{\varepsilon}_{sit} \quad [Eq. 2]$$

where the fixed and random parts are defined as

$$\hat{L}^F_{sit} = \hat{\alpha} + \hat{\beta}_x x + \hat{\beta}_y y + \hat{\beta}_w w_{sit} + \hat{\beta}_{xw} x w_{sit} + \hat{\beta}_{yw} y w_{sit},$$

$$L^R_{sit} = \hat{a}_s + \hat{b}_i + \hat{c}_{si} + \hat{d}_s w_{sit} + \hat{e}_i w_{sit} + \hat{f}_{si} w_{sit}.$$

As with the model of Eq. 1, each random term was assumed to be normally distributed with its factor-specific variance: $\hat{a}_s \sim N(0, \hat{\sigma}^2_A)$, $\hat{b}_i \sim N(0, \hat{\sigma}^2_B)$, $\hat{c}_{si} \sim N(0, \hat{\sigma}^2_C)$, $\hat{d}_s \sim N(0, \hat{\sigma}^2_D)$, $\hat{e}_i \sim N(0, \hat{\sigma}^2_E)$, $\hat{f}_i \sim N(0, \hat{\sigma}^2_F)$.

We used fitted results of Eq. 2 to calculate the proportion of the variance (measured as R-squared) of each phenological event explained by each weather covariate, and estimated the sensitivity (i.e. the variation of phenological response to weather covariate unit) among different species and sites for each phenological event.

Finally, to analyse spatial synchrony we computed the annual averaged residuals ε_{pst} for each phenological event p and each site s. For each pair of phenological events and each pair of sites we calculated the Pearson correlation $\rho_{s_1 s_2}$ among the residuals ε_{pst} over those $n_{s_1 s_2}$ years for which the residuals could be computed for both sites. For a given pair of events, we fitted the non-linear model

$$\rho_{s_1 s_2} = \rho_0 \exp\left(-d_{s_1 s_2}/\alpha\right) + \varepsilon_{s_1 s_2},$$

where $d_{s_1 s_2}$ is the distance between sites s_1 and s_2, and residual term $\varepsilon_{s_1 s_2} \sim N(0, \frac{\sigma^2}{n_{s_1 s_2}})$, where we assumed the error term to decrease with the number $n_{s_1 s_2}$ of years for which we had data for both

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sites. In the model fit we restricted $0 \leq \rho_0 \leq 1$ and $\alpha > 0$. To analyze how pairs of phenological events are synchronized at the zero distance we calculated the Pearson correlation coefficients among the annual averaged residuals $\varepsilon_{p_1 st}$ and $\varepsilon_{p_2 st}$ of different phenological events p_1 and p_2 within a single site s and averaged the result over the sites s.

All models were fitted in R 3.1.3 statistical software (2015), using applied Bayesian statistics methods implemented in RJAGS package (Plummer 2015). We performed our posterior sampling by 4 chains for 10^5 iterations each, with additional 10% burn-in and thinning interval of 100. The chains' convergence was checked with Gelman and Rubin's convergence diagnostic test (Gelman & Donald 1992) which score was below 1.05 level for all fitted models. The posterior sampling distribution was later used to acquire posterior mean values of parameters of interest, as well as 95% central Bayesian credibility intervals for them.

Results and Discussion

Spatial and interspecific variability in phenological responses to climate change

As elsewhere in the Northern hemisphere (Hopkins 1918; Schwartz 2013), in Russia the mean timings of phenological and weather-related events in spring generally progress from the south to the north, whereas in autumn they show the opposite spatial pattern (Fig. 1; Supplementary Information I Figs. S3 and S4). Less trivially, variation in both phenological (three out of 14 significantly; Supplementary Information II Table S2) and weather-related (one out of six significantly; Supplementary Information II Table S2) long-term shifts is also partly structured along a south-north gradient (Figs. 1-2; Supplementary Information I Figs. S3 and S4). This is especially the case for taxonomical groups other than plants and birds, for which the geographic gradient explains 31-47% of the variation in phenological trends (Fig. 2C; Supplementary Information II Table S3). Out of the ten spring and summer phenological events, six have shifted to earlier in the northern part and to later in the southern part of the study region (Fig 2A; Fig. 1D shows such a geographical pattern in the shift for the first occurrence of insects; Supplementary Information I Figs. S3 and S5 show the geographic patterns in shift for each phenological event), and four have shifted consistently to earlier throughout the study region (Fig. 2A). Out of the four events of autumn phenology, two have shifted evenly to earlier (Fig. 1F shows such a geographical pattern in the shift for onset of autumn colouring of plants) and two to later (Fig. 2A).

Our results are in line with some previous studies reporting a latitudinal effect on phenological shift. For example, the variability of the slopes for leaf colouring and leaf fall day in Japan was found to be greater at lower than at higher latitudes (Doi & Takahashi 2008). Zheng *et al.* (2006) observed an advancing trend consistently for seven spring phenophases for plants in the NE of China, and a delayed trend in the SW of China. Similarly, Ge *et al.* (2015) found that the strength of spring/summer advancement and autumn delay of woody plants in China from 1960s to 2000s was strong at high latitude, even though geographic

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factors only explained respectively the 14% and 4% of the variance in phenological changes. Root *et al.* (2003) found a stronger phenological shift in northern latitudes than in southern latitudes that was consistent among different taxonomic groups, although Menzel *et al.* (2006b) suggested the opposite. However, while earlier studies have generally reported a consistent change across different phenophases and taxonomical groups, our findings suggest that latitudinal patterns of responses among different phenological events may not necessary be consistent (Fig. 2A). The difference between our results and the earlier results may be, at least partly, explained by the fact that geographical trends in phenology variations have been generally studied for few phenological events in a single taxonomic group, mostly being either plants (e.g. Menzel *et al.* 2006b; Zheng *et al.* 2006; Doi & Takahashi 2008; Ge *et al.* 2015) or birds (e.g. Both & Visser 2001; Lukas & Marc 2003; Hurlbert & Liang 2012). These accounts attributed the discrepancy in phenological shifts in response to climate change to population - and species-specific aspects (Inouye *et al.* 2000; Both & Visser 2001; Gordo & Doi 2012). However, given the complex physiological mechanisms underlying environmentally sensitivity of different phenological events, it is perhaps not surprising that our results show that different phenological events do not respond equally along a geographical gradient (Wilczek *et al.* 2010).

Disparities in phenological responses across latitudes will certainly limit our ability to forecast future responses to warming conditions. For example, as a consequence of the patterns we documented, in the south, where some phenological events have shifted to earlier and some others have shifted to later (Fig. 2A), there is a higher potential for disruption of phenological synchrony (both among taxonomic groups and among different life-history stages) than in the north, where most events (12 out of 14 groups) have shifted to earlier. As examples of such disruptions (shown in more detail in Supplementary Information I Fig. S5), the onset of budburst in the south has shifted to later but the onset of leaf fall has shifted to earlier (Fig. 2A), shortening the length of the growing season which has been reported to be of great ecological and biogeochemical importance (e.g. Ibañez *et al.* 2010). In both south and north, birds have advanced their arrival time but delayed their autumn departure, thus prolonging the summer period everywhere and correspondingly shortening the time allocated for migration and wintering. Just as it is important to understand the relationship between phenology and organisms' life history (Forrest & Miller-Rushing 2010), understanding whether the interplay among physiology and external environmental factors controlling the timing of biological events vary along a geographical gradient is essential in order to predict phenological responses to environmental change.

The patterns summarized in Fig. 2A average over variation among sites not explained by the geographical gradient (Koh *et al.* 2004). In almost all taxonomical groups, we found phenological shifts to vary markedly among sites (Fig. 2C; Supplementary Information II Table S4). This is especially the case for autumn phenological events in plants, where the random effect of site explained 51-73% of the variation (Supplementary Information II Table S3). Such phenological variation among populations is likely to reflect the potential of local populations to track the optimum timing by responding directly to the environment (i.e. phenotypic plasticity) or by natural selection increasing the frequency of alleles that

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confer a local advantage (i.e. local adaptation, Phillimore *et al.* 2012). There is ample evidence that populations within a species and even individuals from different populations experiencing different environmental conditions often differ phenotypically and genetically. As phenological traits usually show a very high level of heritability and high level of genetic variability within and among populations, they have a strong adaptive nature (Chuine 2010). As an example, Roy *et al.* (2015) provided a multi-species analysis to test the role of local adaptation in generating spatial and temporal patterns in butterfly mean flight dates. They observed that, even though all butterfly species had a plastic response to temperature, emergence dates were mostly synchronized among populations, suggesting local adaptation. As a further example, (Thuiller *et al.* 2004) showed that species growing in similar regions had developed similar phenologies. It is remarkable that, in line with these results, we found that for five out of ten spring and summer phenological events, and for three out of four autumn phenological events, the effect of site significantly explained more of the variation in the phenological shift than the combined effects of the geographic gradient and the species (Supplementary Information II Table S5), suggesting a strong contribution of local adaptation to phenology.

The patterns summarized in Fig. 2A average not only over variation in space but also over variation among species within each taxonomic group (Koh *et al.* 2004). Much of the variation in the mean timing of phenological events is explained by variation among species (Fig. 2B), which is expected to be the case as species represented in e.g. the taxonomical group of plants involves some species that bloom in early spring and other species that bloom in late spring. However, a strikingly small amount of variation in phenological shift was attributed to variation among species (Fig. 2C; Supplementary Information II Table S4 and S5). This is an important result, as it suggests that the results of Fig. 2A are highly robust in the sense that, for each particular phenological event essentially all species within an entire taxonomic group have shifted similarly. One exception is the first occurrence of reptiles, where different species showed opposite phenological shifts (Supplementary Information II Table S1). Another exception is the last occurrence of birds, where variation among bird species in phenological shift was partially explained by different migration strategies (Supplementary Information I Fig. S6). In contrast to our findings, many previous studies have reported dissimilar responses to climate change not only among taxonomical groups but also among species within a taxonomical group, an observation which has been attributed to differences in life-history parameters (Parmesan & Yohe 2003; Root *et al.* 2003; Menzel *et al.* 2006b; Zheng *et al.* 2006; Minin & Voskova 2014; Thackeray *et al.* 2016). For example, while the majority of plant species have been found to respond to warming springs with earlier flowering (Parmesan & Yohe 2003; Menzel *et al.* 2006b; Wolkovich *et al.* 2012), a consistent subset has been reported to show the opposite trend (Fitter & Fitter 2002; Menzel *et al.* 2006b), possibly related to variation among species on chilling requirements to break dormancy (Korner & Basler 2010; Yu *et al.* 2010). In our data, the shifts in plant spring phenology were outstandingly consistent among species even if the dataset consist of both early and late spring bloomers. Thus, while many earlier studies have shown consistent shifts among phenophases but contrasting shifts among species or major functional groups (Thackeray *et al.* 2010; Thackeray *et al.* 2016), our result essentially show the opposite pattern. In line with our results, a recent

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study (CaraDonna *et al.* 2014) on the flowering phenology of 121 plant species in the Colorado Rocky Mountains (USA) showed that many species exhibit an inconsistent shift in the first, peak, and last dates of this specific phenophase. Consistent with Ge *et al.* (2015), our results also suggest that a limited number of taxonomic groups may generate a biased estimates of trends.

Phenological responses to climate factors

Variation in phenological shifts can be generated by differences in environmental sensitivity among species as well variation across geographical gradients (Ge *et al.* 2015; Wang *et al.* 2015) within a species (but see Vitasse *et al.* 2009). Climatic factors driving long-term phenological shifts are expected to be correlated with climatic cues used by species to adjust their phenology to short-term variation in climatic conditions (Charmantier *et al.* 2008). These cues can be partially identified by correlating year-to-year variation in phenology with climatic variation (Koh *et al.* 2004). In line with previous studies in middle and high latitudes (Zhang *et al.* 2004; Wang *et al.* 2015), we found that variation in phenological timing in most events is highly correlated with temperature, but only moderately correlated with snow cover and precipitation (Fig. 3A; Supplementary Information II Table S6). Spring events start generally earlier in years with high temperatures, little precipitation, and early loss of snow cover (Fig. 3A). In our data, plants, insects, amphibians and reptiles show higher sensitivity to temperature (i.e. change in number of days per 1°C) than birds and fungi (Fig. 3B; Supplementary Information II Table S7). This indicates that different taxa may respond diversely to per unit change in temperature which, as recently suggested by Thackeray and colleagues (Thackeray *et al.* 2010; Thackeray *et al.* 2016), can potentially lead to temporal mismatches in trophic interactions. While we found birds to respond more strongly to short-term climate cues, plants were triggered by longer-term climatic averages (Supplementary Information I Fig. S7). Further, phenological events correlated generally more with weather variables measured at local than global spatial scales, suggesting the importance of local processes even for migratory birds (Supplementary Information I Fig. S7). In contrast to other phenological events, plant phenology in the autumn and the fruiting of fungi were only weakly correlated with any of the tested weather covariates (Fig. 3A). This result is in line with earlier research suggesting that temperature is not likely to be the dominant factor controlling autumn phenological trends (Matsumoto 2010; Gallinat *et al.* 2015).

Differences in environmental sensitivity among species as well as within species across geographical gradients may hinder the effect of latitude on phenological responses to warming (Ge *et al.* 2015). While some studies have shown that species inhabiting high latitudes are especially sensitive to thermal variation in the environment (Wang *et al.* 2015), others have shown the opposite pattern (Menzel *et al.* 2006b; Ge *et al.* 2015; Wang *et al.* 2015). The species in our study appear to adjust their phenology to temperature in a very consistent way across the entire study region (Fig. 3B). One explanation for the dissimilarity to earlier results may be the fact that our data is characterized by a high species richness covering a large geographic area compared to many earlier studies (e.g. Wang *et al.* 2015), and that the data have been acquired and analysed in a consistent way (in contrast to meta-analyses), thus increasing

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the signal to noise ratio.

The synchronizing effect of climate at the ecological community level

Many interspecific interactions depend upon the synchrony of phenological events, and thus decoupling of phenological synchrony may have major consequences on community structure and functioning (Gilman *et al.* 2010). Synchrony among phenological timing among species can be expected either if the species respond to common environmental drivers or if the species have tight ecological interactions (Liebhold *et al.* 2004). We found that synchrony was high among phenological events that were highly correlated with temperature (e.g. spring phenological events of plants, amphibians, insects and reptiles; Fig. 4A), lending support to the former view. In contrast, synchrony among birds, fungi and autumn phenological events was generally low (Fig. 4A), which is in line with the fact that these groups were weakly correlated with temperature and the other measured weather covariates (Fig. 3). For example, autumn phenological events in plants are known to be modulated by multiple mechanisms, including leaf structural constraints on longevity, several plant hormones and programmed cell death (Keenan & Richardson 2015). Some previous studies have reported a relationship between irregularities in timing of spring phenology and the leaf senescence, suggesting that the influence of temperature on leaf fall may be offset by the influence of an earlier spring (Keenan & Richardson 2015). Yet, the influence of some other less predictable factors on autumn phenology, such as soil humidity and wind (Gallinat *et al.* 2015), may hinder the synchrony between spring and autumn timing in plants.

We found a negative relationship between phenological synchrony and distance, as has been found also in previous studies (Koenig 1999). The spatial synchrony in spring plant phenology was high at short distances (Fig. 4C), suggesting that the environmental factors driving phenological events in plants show a more localized spatial autocorrelation. Further, the spatial synchrony in the arrival of birds was somewhat lower at short distances but spanned over a larger spatial scale (Fig. 4D), likely due to the fact that the breeding populations overlap in their wintering grounds and that migration is partly controlled by photoperiod (Ramenofsky 2012). Interestingly, the level of spatial synchrony in birds drops considerably from the onset of their arrival to the start of singing and display flights (Fig. 4D), suggesting that the latter events are controlled by some idiosyncratic factors not considered here. Amphibians, insects and reptiles also showed substantial spatial synchrony (Fig. 4E), whereas fungi and autumn phenological events showed very little – consistent with the weaker responses of these groups to temperature (Fig. 3). Variation in temperature was synchronized over much larger distances than variation in phenological events (Fig. 4B), suggesting that the other factors that control phenological dynamics are less correlated in space than temperature.

Many phenological events are closely associated with population growth (Post 2003; Ranta *et al.* 2010). For example, the timing of flowering affects the success of fruit maturation, the quality of progeny and the success of pollination (for review see Levin 2006). Thus the spatial scales of phenological synchrony

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reported here can be expected to be related to the spatial scale of synchrony in population fluctuations as well. Several authors have emphasized the need for understanding the drivers of the dynamics of populations and communities facing global change rather than just reporting whether some phenological events are advancing, delaying, or not changing through time (Heino *et al.* 1997; Ranta *et al.* 1997). We have taken first steps in this direction by utilizing long-term and spatially extensive data to analyse the community-level spatial synchrony in phenological dynamics and its climatic drivers.

Supplementary Material

Supplementary Information I

Supplementary Information II

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Tables

Table 1. Summary of phenological and weather-related events recorded. For each event, values shown are the total number of observations (no), the number of locations (Locations), the total number of species (Species) or climatic events, and the mean number of observations per location (no/Location). The bars represent the timings of the events, ranging from the minimum to the maximum mean dates (mean date is represented by the circle).

	Events	no	Locations	Species	no/Location
BIRDS	1st occurrence	19008	174	195	110
	1st song	9214	176	88	53
	Last occurrence	1789	14	36	128
PLANTS	Onset of budburst	4269	16	117	267
	Onset of leaf unfolding	13872	206	153	68
	Onset of blooming	42798	220	505	195
	1st ripe fruit or berries	10361	29	225	358
	Onset of autumn colouring	10513	161	133	66
	Onset of leaf fall	6768	55	127	124
	Leaf fall end	9407	192	110	49
INSECTS	1st occurrence	5844	27	60	217
AMPHIBIANS	1st occurrence	863	18	10	48
REPTILES	1st occurrence	1051	21	11	51
FUNGI	1st occurrence	1848	22	24	84
CLIMATIC	Temperature (spring/autumn)	5663/ 3825	27/24	30/14	210/160
	Snow (spring/autumn)	3706/ 2181	26/25	49/14	143/88
	Ice (spring/autumn)	1260/ 1130	23/20	21/19	55/57

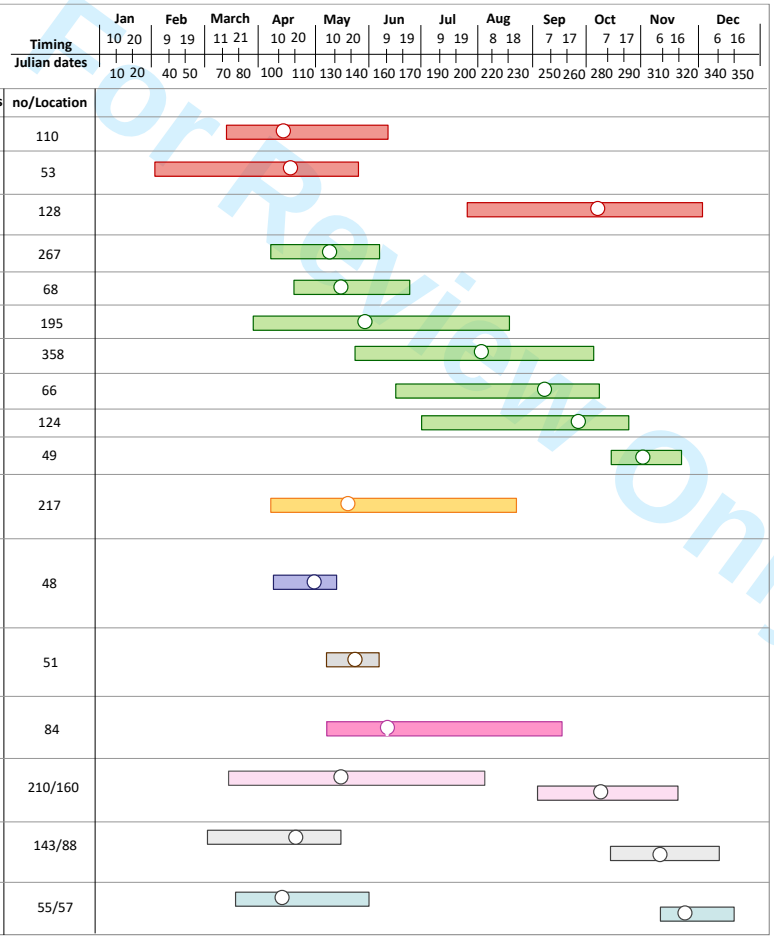

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Figure legends

Figure 1. Examples of spatio-temporal patterns in climatic and phenological data. Panel **A** shows mean temperature over the study period 1960-2010, panel **B** the shift in mean temperature per decade, panels **CD** the relative mean day (centred on calendar day 125) and shift for the first occurrence of insects, and panels **EF** the relative mean day (centred on calendar day 244) and shift for the onset of autumn colouring of plants from 1960 to 2014 (Supplementary Figure 2 displays relative mean day and shift for each phenological and weather-related events analysed). The locations of the data sources are shown by the squares (black if a particular event was recorded, grey otherwise) and dots (meteorological stations). Stars on the latitude axis mark the selected latitudes of South (red) and North (blue) analysed in Fig. 2. Phenological mean dates and shift are interpolated over the western part of the study area with high density of observed locations and depicted for local neighbourhoods of sparse locations in the east.

Figure 2. Spatio-temporal patterns in weather-related and phenological data. In panel **A** each event is located based on its shifts observed in the Northern and Southern parts of the study area (indicated by the stars in Fig. 1). Red and blue lines over the symbols of weather-related events indicate spring and autumn events respectively. Panels **BC** partition variation in mean timing (**B**) and shift (**C**) of phenological and weather-related events. The partitions have the following meaning: average shift (red and blue bars represent shift to earlier and later dates), variation due to species (orange) or weather-related group (brown), variation due to major linear geographic gradient (black), variation due to location (green) and the variation related to the interaction between species and location (white). Red, green and blue bars below the histogram represent respectively spring, summer and autumn phenological and weather-related events.

Figure 3. Year-to-year variation in phenological timing explained by climatic factors. In panel **A** the solid bars show the Pearson correlation coefficient of phenological timing and local weather covariates, the latter averaged over the period from 60 days before to 7 days after the onset of phenological events. The edge of extended semi-transparent bar represents the square root of the R-squared for the corresponding hierarchical model. Dark and light colours respectively correspond to negative and positive correlations. Panel **B** partitions variation in response of phenological timing to temperature: average response (red and blue indicating negative or positive effects respectively), variation explained by species (orange), by geographic gradient (black), location (green) and the interaction between species and location(white). Red, green and blue bars in the bottom of the figure represent respectively spring, summer and autumn phenological events.

Figure 4. Spatial synchrony among phenological and climatic events. Panel **A** shows the level of synchrony between events within the same locality with width of connecting curves representing the proportion between the number of localities where two corresponding events were synchronized and the number of localities where the two corresponding events were observed. Red, green and blue colours correspond to the mean timing of event: spring, summer and autumn, respectively. Panel **B** shows the synchrony of temperature (red) and precipitation (blue), averaged over Mar-Apr (solid) and Sep-Oct (dashed). Panels **CDE** show within-event phenological synchronies

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as a function of distance between localities for events related to plants (C), birds (D), and other phenological events (E). Solid lines stand for spring events, dotted for summer and dashed for autumn.

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1 Fig. 1

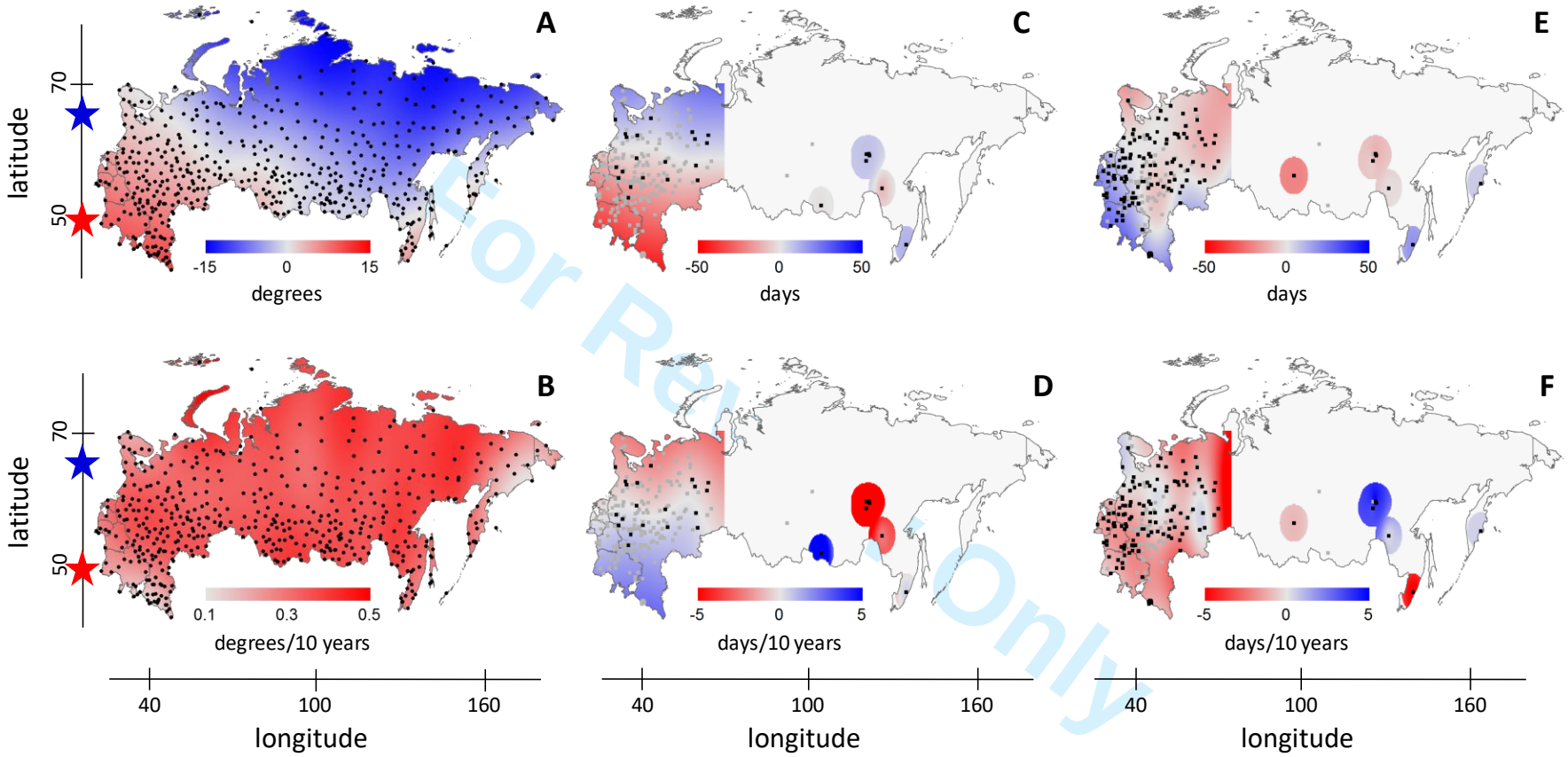

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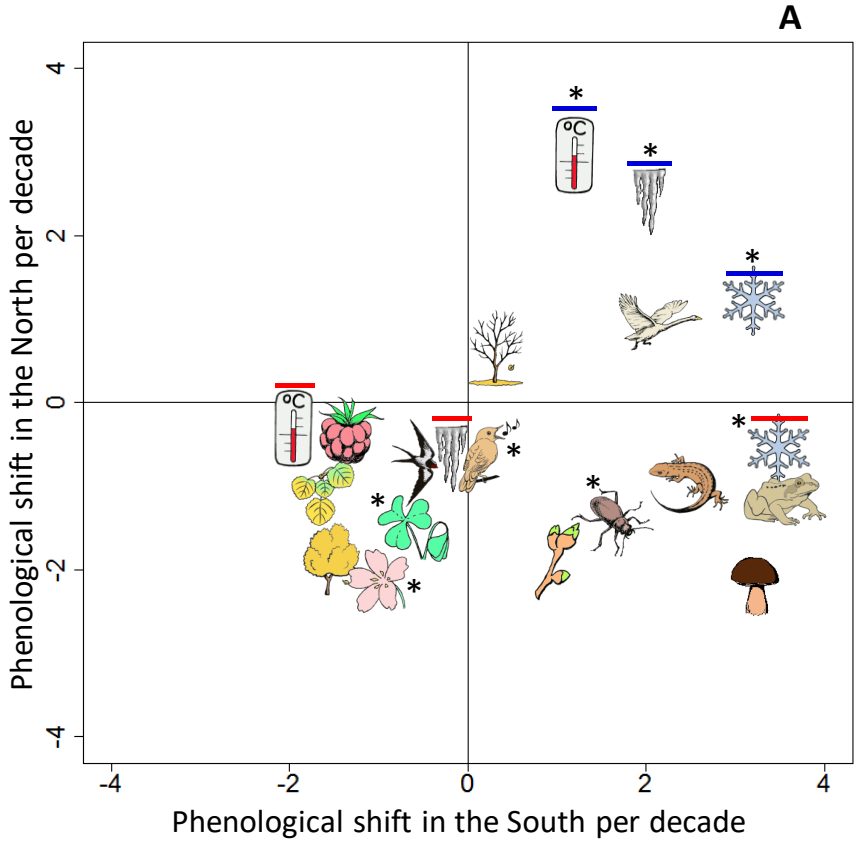
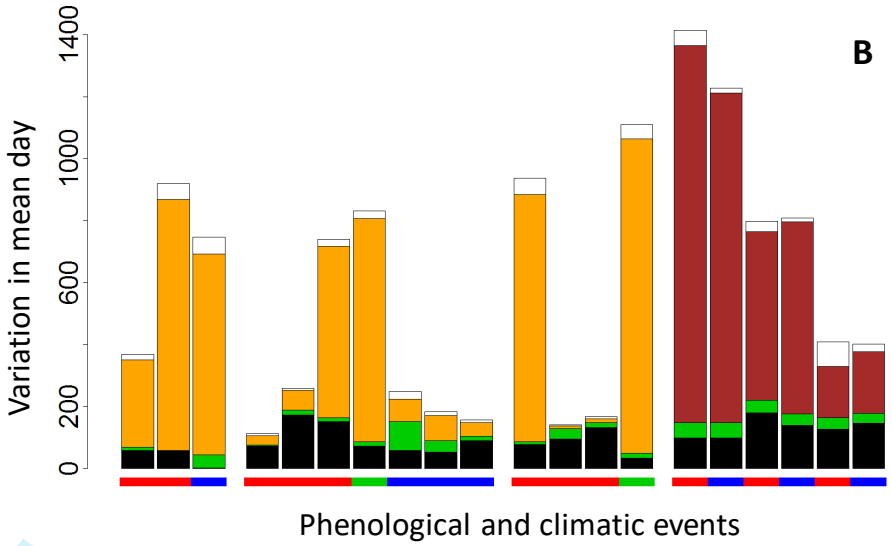
Fig. 2


A
Phenological shift in the North per decade
Phenological shift in the South per decade
-4
-2
0
2
4


B
Variation in mean day
0
200
600
1000
1400
Phenological and climatic events

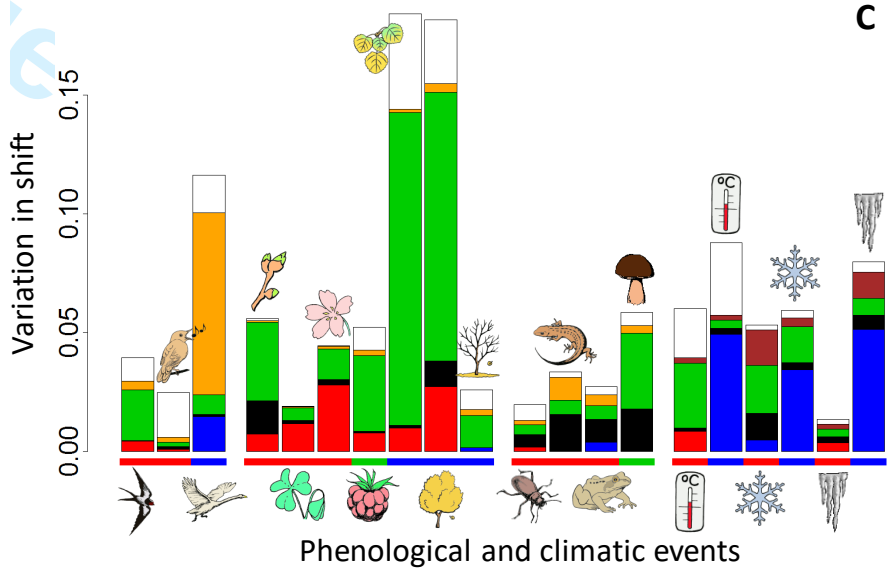

C
Variation in shift
0.00
0.05
0.10
0.15
Phenological and climatic events

Fig. 3

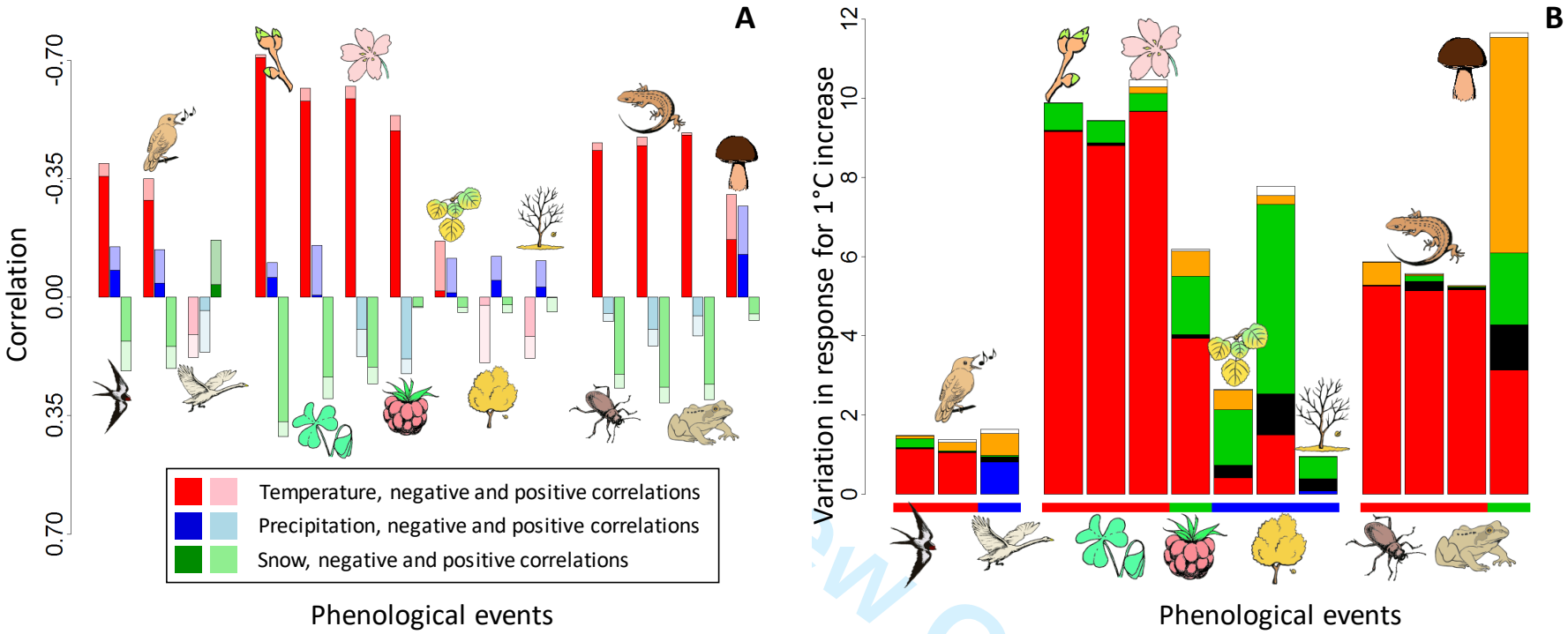


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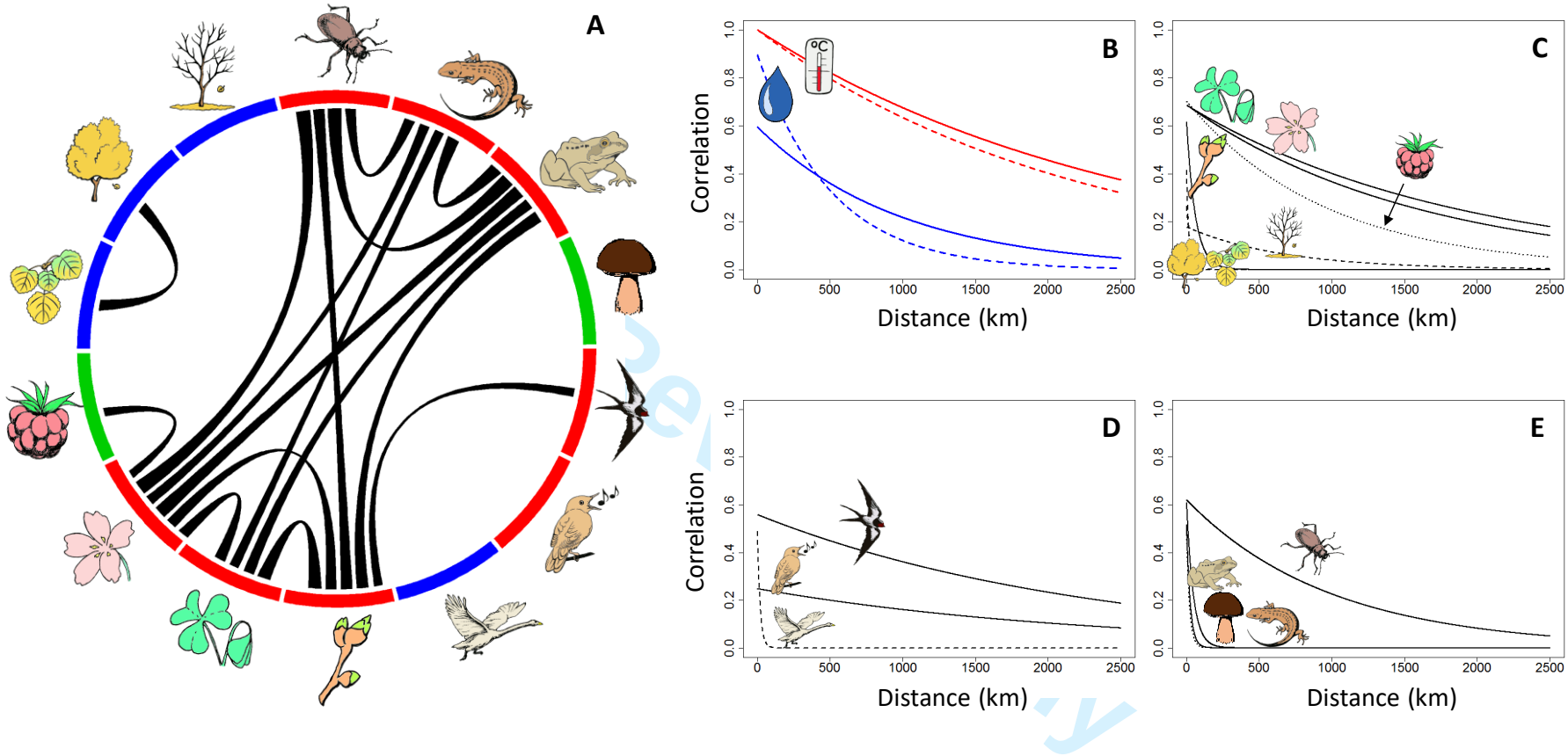
Fig. 4


A
B
C
D
E
Correlation
Distance (km)
0
500
1000
1500
2000
2500
0.0
0.2
0.4
0.6
0.8
1.0
°C