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Defining the Degree of Seasonality and its Significance for Future Research

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Synopsis Seasonality describes cyclic and largely predictable fluctuations in the environment. Such variations in day length, temperature, rainfall, and resource availability are ubiquitous and can exert strong selection pressure on organisms to adapt to seasonal environments. However, seasonal variations exhibit large scale geographical divergences caused by a whole suite of factors such as solar radiation, ocean currents, extent of continents, and topography. Realizing these contributions in driving patterns of overall seasonality may help advance our understanding of the kinds of evolutionary adaptations we should expect at a global scale. Here, we introduce a new concept and provide the data describing the overall degree of seasonality, based on its two major components—amplitude and predictability. Using global terrestrial datasets on temperature, precipitation and primary productivity, we show that these important seasonal factors exhibit strong differences in their spatial patterns with notable asymmetries between the southern and the northern hemisphere. Furthermore, our analysis reveals that seasonality is highly diverse across latitudes as well as longitudinal gradients. This indicates that using a direct measure of seasonality and its components, amplitude and predictability, may yield a better understanding of how organisms are adapted to seasonal environments and provide support for predictions on the consequences of rapid environmental change.

Introduction

Seasonality is a ubiquitous feature of our planet and represents the strongest source of external variation influencing almost all natural systems (Fretwell 1972; Boyce 1979; Wingfield and Kenagy 1991). The often pervasive, but predictable, seasonal differences in the environment underpin the evolution of the earth's biodiversity as well as key biological processes such as reproduction (Bronson 2009), predator–prey interactions (Elton and Nicholson 1942), host–pathogen dynamics (Altizer et al. 2006), and the impressive annual migrations by billions of animals (Dingle 2014).

To successfully live and reproduce in seasonal habitats, organisms require a suite of morphological, physiological, and behavioral adaptations. However, seasonality varies geographically; the combined effect of the earth's tilt and rotation result in annual variations in solar radiation, with downstream implications for annual photoperiod and effects on temperature, that is greatest at the poles and less pronounced at the equator (MacArthur 1972). The necessity of an organism to adapt to seasonal environments is thus highly dependent on its location. In environments with small variation, organisms expressing one phenotype—with a set of morphological, physiological, and behavioral characteristics resulting from the interaction of its genotype with the environment—has high fitness at all times (Levins 1968). In contrast, theory predicts, that large environmental variation leads to genotypes expressing different phenotypes, each having maximum fitness at different times of the year, e.g., summer and winter (Levins 1968; Wingfield 2008). This includes phenotypic flexibility in which an individual can adjust morphology, physiology, and behavior to maximize fitness in seasonal environments. For example, snowshoe hares, *Lepus americanus*, change pelage color from brown and cryptic in summer to white and cryptic in winter (Pielou 1994). Migration is another prime example for seasonal adaptation and individuals often express high phenotypic flexibility while undergoing various life-history processes associated with the movement, reproduction and molt (e.g., Piersma and Drent 2003).

Phenotypic flexibility of individuals seems to be linked with varying seasonality and timing of seasonal life-history strategies. This flexibility may vary with latitude, but it can also vary along ecological gradients within latitude (e.g., Naya et al. 2008; Molina-Montenegro and Naya 2012). Another aspect of phenotypic flexibility addresses timing of life history stages. Individuals with more life history stages have flexibility to cope with a wide variation in environmental conditions but have less flexibility in timing those stages. Individuals with very few life history stages can tolerate less variation in environmental conditions but have greater flexibility in timing those stages (Wingfield 2008). Whereas seasonality is expressed via different climatic and biotic factors, such as temperature, precipitation, and biological productivity and while solar radiation varies strictly across latitudes, the other factors are modified by a large array of additional processes such as ocean currents, wind directions (Screen 2014), sea-ice extent (Francis et al. 2009), continental extent, and topography (Ghalambor et al. 2006). For example, most tropical habitats show high seasonal variation in precipitation pattern that require organisms to rapidly respond and time the onset of breeding to these favorable conditions (Murton and Westwood 1977).

Furthermore, global climate change has altered temperature and precipitation patterns at an unprecedented and geographically diverse rate across the globe (Burrows et al. 2011). These changes significantly altered seasonal profiles and have already generated profound impacts on ecosystem processes such as seasonal trophic interactions (Edwards and Richardson 2004; Parmesan 2006; van Gils et al. 2016).

To predict the response, as well as the consequences, of organisms to these changes in seasonality, there has been an increasing effort to understand the underlying ultimate and proximate mechanisms that shape an individual's success and fitness within seasonal habitats. Such research often requires the characterization of the underlying seasonality that is experienced by the organism. Given the complex integrations of a whole suite of factors on seasonality it seems important to clarify and quantify these patterns instead of using latitude as a proxy for seasonality that may limit our interpretations of seasonal mechanisms found within field studies.

The overall aim of this study is to develop global metrics of the degree of seasonality in terrestrial systems, incorporating its major components, the seasonal amplitude, and the predictability of seasonal variation (Fig. 1). The amplitude of seasonal variation is a good measure of the magnitude of seasonal differences and has been used as such in multiple studies aiming to quantify the strength of seasonality (e.g., Fan and van den Dool 2008; Wang and Dillon 2014; Lisovski et al. 2017) as well as to identify recent trends in seasonal dynamics (e.g., Vose et al. 2005; Stine et al. 2009; Burrows et al. 2011; Xu et al. 2013). Quantification of the uncertainty in seasonal dynamics—e.g., among year variation in the annual extremes of temperature and rainfall (Jetz and Rubenstein 2011), or the interactions between the within and among year variations (Wingfield et al. 1993)—are less apparent in the literature. We here aim to introduce a concept of predictability that incorporates both variation in the seasonal phenology (phase) and variation in the seasonal amplitude. Furthermore, by using an algorithm that quantifies predictability of seasonal variation based on information collected during previous annual cycles, we aim to apply a method that reflects the capabilities of organisms to foresee future seasonal dynamics, at both ultimate and proximate levels, and thereby quantify the potential strength of selection on seasonal adaptations. The seasonal amplitude and the predictability of the seasonal dynamic may by itself provide relevant measures of seasonality important for generation of hypotheses related to proximate mechanisms. However, the combination that we define as the degree of seasonality may have additional important implications to investigate proximate mechanisms by which organisms perceive environmental information and transduce it into morphological, physiological, and behavioral responses appropriate for that season. Furthermore, we aim to apply this concept to global terrestrial datasets on temperature, precipitation as well as primary productivity and discuss its suitability for future research.

Methods

Remote sensing

Data from remote sensing systems for temperature, precipitation, and vegetation index, indicative for terrestrial net primary productivity (NPP), were downloaded for 2007–2015. Global surface temperatures were obtained from the GHCN Gridded V2 dataset provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA (Fan and van den Dool 2008). The downloaded files consisted of monthly mean temperatures organized in a 0.5×0.5 degree

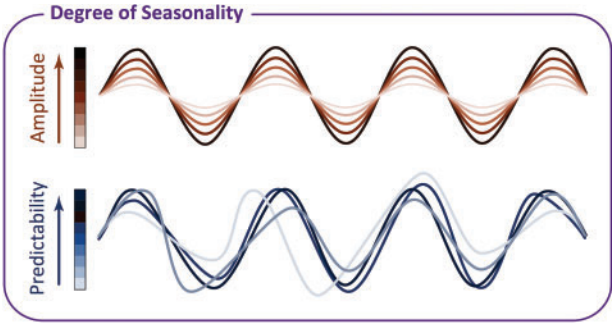

Fig. 1 The degree of seasonality, defined as a combined effect of the seasonal amplitude (magnitude of the seasonal change) and the predictability (consistency) of the seasonal variation across years. The lines exemplify different magnitudes in the amplitude and the predictability that would ultimately lead to differences in the degree of seasonality

spatial grid. Daily amounts of precipitation on a 1×1 degree grid were obtained from the NASA Global Precipitation Climatology Project (GPCP) (Huffman et al. 2001). Weekly composite (cleanest data point for each grid cell across seven consecutive images) NPP data (Running et al. 2015) with a spatial resolution of 0.1×0.1 degree were obtained from the NASA Earth Observation repository (MOD17A2_E_PSN; ftp://neoftp.sci.gsfc.nasa.gov/geotiff.float/).

Data manipulation

If necessary, datasets were aggregated (median) to match the highest common resolution of a 1×1 degree spatial grid (restricted by precipitation data) covering the entire globe with monthly observations (restricted by temperature data). Values for grid cells located into the oceans and the Antarctic continent were discarded. For each grid cell located on land, temperature, precipitation, and NPP time series were treated in the same way and the following procedure and its algorithms were implemented into an R package called *FourSeasons* (available at: https://github.com/slisovski/FourSeasons/) also including a fine scaled temperature time series for illustration purposes (land-based NOAA weather station: Lake Yellowstone). First, a wavelet analysis was used to determine whether the time series showed significant seasonal dynamics across years; we used the wt function within R package biwavelet (Gouhier et al. 2016) with default settings, including "morlet" as the mother wavelet (for more detailed information, see description of R package FourSeasons). Test for significance was based on a regular χ^2-test, and the associated wavelet power spectrum across the time series. In case of significant seasonal periodicity, the time series was subdivided into annual cycles of 12 months centering the annual peak by fitting a cosine-curve to the data using a least-square approach. Next, predictability was quantified using a seasonally adjusted forecasting method from the R package forecast (Hyndman and Khandakar 2008); an ARIMA (autoregressive integrated moving average) model was used to decompose 4 years of the time series into its seasonal and trend components. Based on that information, predictions were made for the next year, e.g., 52 weeks. This process was applied across the time series allowing predictions for 2011–2015. These predictions were then compared with the remote sensed observations using the R^2 value as a measure of model performance and ultimately as a measure of predictability. To reduce the influence of the seasonal amplitude, quantifications of predictability were done using centered z-transformed (*scale* function in R) observations. The seasonal amplitude was simultaneously extracted for each year from 2011 to 2015 as the difference between the lower and upper 2.5 quantile of the annual variation (e.g., the 95 percentile). We deliberately ignored extreme values during the annual cycle to account for potential observational errors. Finally, the degree of seasonality was defined as the mean of the predictability and the normalized seasonal amplitude, e.g., a predictability of 0.8 and amplitude of 0.5 would lead to a 0.65 in the degree of seasonality. R code for all steps of the data manipulation and for all three data sources (temperature, precipitation, and NPP) are attached as Supplementary Material S2–S3 and can also be downloaded from https://github.com/slisovski/Lisovski-et-al.-2017-ICB.

Day length pattern

Daylight hours per day, from civil-twilight at dawn to civil-twilight at dusk, across the globe were calculated using the R package "GeoLight" and the implemented function "twilight" (Lisovski and Hahn 2012). The mean of the maximum minus the minimum in day length hours across latitudes was calculated to depict variation in day length across latitudes.

Terrestrial ecoregions

To summarize the results across major terrestrial ecoregions we used a simplified version of the elaborate classification of terrestrial ecoregions from Olson and Dinerstein (2001). See Supplementary Material S1 for detailed information on the used simplifications.

Results

Temperature

The vast majority (99.5%) of terrestrial habitat (not considering the Antarctic continent) exhibit some degree of seasonal variation of temperature. Areas lacking significant seasonality were found in northwest and central South America and small patches in equatorial regions of Africa, New Guinea, and Indonesia. In general, the degree of seasonality was highest above 30°N (~0.75), exhibits a decline toward the equator (0.2), and peaks again at ~35°S (0.58) before decreasing toward the southern tip of the land masses of South America, Africa, Australia, and New Zealand. Across latitudes, predictability was relatively higher than the normalized amplitude of the seasonal variation. Given that the predictability in the seasonal dynamic was found to be high (>0.8) in almost all environments, variation in the degree of seasonality is mainly driven by variation in the seasonal amplitude. The highest amplitude was found in north-eastern Russia in the area surrounding the Lena river (Figs. 2A and 3B).

Precipitation

The relative number of habitats that show seasonality in precipitation is considerably less (75.5%) compared with previously identified temperature patterns of seasonality. In general, the areas around the equator (20°N–20°S) show relatively high degrees of seasonality (~0.6) with the highest values in south Asia extending south of the Himalaya to northern Australia, as well as in northwestern South America. Furthermore, the Sahel zone, savannas south of the equatorial rainforest in Africa (including Madagascar) as well as central South America and central America were found to be exhibit strong seasonality in rainfall pattern. In higher latitudes, areas with moderate to low degrees of seasonality were found in the tundra/taiga regions of north-central North America and in eastern Asia (e.g., Japan, North Korea and South Korea, China, Mongolia, and the adjacent Russian Arctic). In contrast to the temperature pattern, predictability in the seasonal dynamic was generally low across the globe with a few highly predictable patches again in south Asia and toward northern Australia as well as on the Atlantic coast of western Africa (south of the Sahara Desert) and at the Amazonas river delta in South America (Figs. 2B and 3C).

NPP

The relative area of seasonal to non-seasonal habitats in primary productivity was found to be the lowest (66.5%) compared to seasonality in temperature and precipitation. Large areas that experience seasonal dynamics were found in the ranges 50°–70°N as well as 5°S–20°S. Smaller proportions were found in latitudes closer to the equator, mainly due to large vegetation free areas like the Sahara and mountains like the Himalaya, as well as in the very high northern latitudes where vegetation is limited to lichens and mosses and the landscape becomes dominated by barren rocks (Pielou 1994). Highest values of the degree of seasonality (>0.75) as well as seasonal amplitude and predictability were found in the northern hemisphere above 40°N. A slight reduction in the degree of seasonality was observed toward and south of the equator before the degree of seasonality increases again at latitudes higher than 30°S (Figs. 2C and 3D).

Global summary

The northern tundra, boreal forests/taiga as well as the temperate forests and grasslands exhibit the highest degree of seasonality in temperature and primary productivity—with the above discussed major difference in the very high Arctic where a lack of vegetation causes low or no seasonality in primary productivity while seasonality in temperature remains high. Seasonality in temperature and primary productivity was found to be intermediate (or even high) in Mediterranean, Deserts, and Xeric Scrublands. In contrast, the degree of seasonality in precipitation was found to be most pronounced in the tropical and subtropical ecoregions and generally low in the predominant ecoregions of the northern hemisphere (e.g., temperate forest, taiga, and tundra) (Fig. 2D).

Discussion

Seasonality describes fluctuations that are cyclic, largely predictable, and partitions the annual cycle of many organisms into distinct periods when life history stages such as reproduction and non-reproduction are expressed. However, while this may appear to be a simple relationship between environmental change and expression of life history stages, large scale geographical divergences in seasonal variation can significantly diversify this pattern. Thus, we find a large environmental gradient in how far seasonality may partition the annual cycle of organisms into distinct life history stages which in turn determines flexibility in timing of those stages (e.g., Wingfield 2008). Furthermore, seasonal variation can be found in many environmental factors, such as temperature, precipitation, and primary productivity,

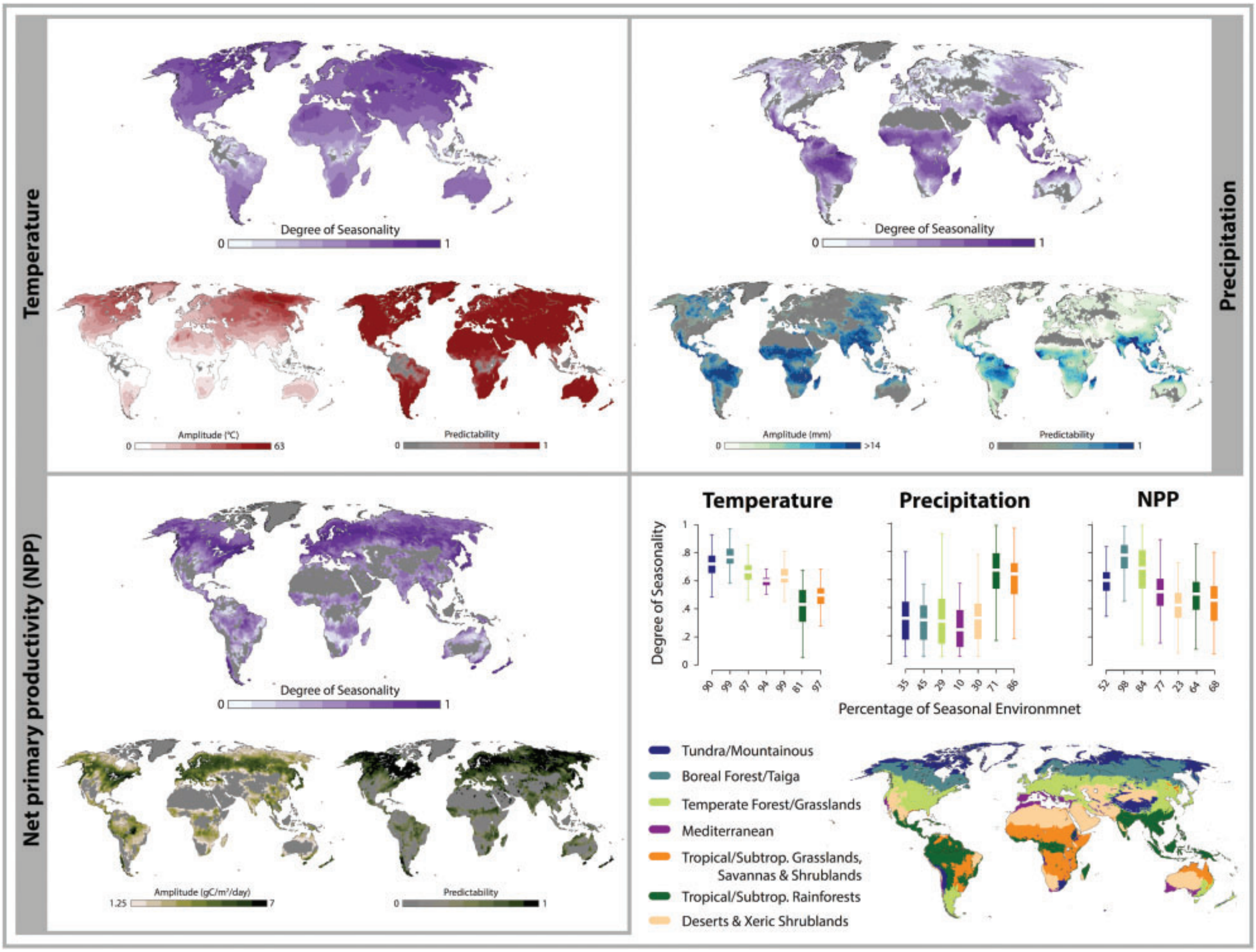

Fig. 2 Degree of seasonality in terrestrial ecosystems (purple) with its two major components, the amplitude and predictability for temperature (top left), precipitation (top right) and NPP (bottom left). All maps have a spatial resolution of 111×111 km. Areas without significant seasonal dynamics are indicated in gray. The bottom right panel shows the median and the 50 percentile (box) and the 95 percentiles (outer bars) of the degree of seasonality for all factors (e.g., temperature, precipitation, and primary productivity) across major terrestrial ecoregions. The *x*-axes indicate the relative amount (in percentage) of area that exhibits seasonal variation within each ecoregion

all exhibiting profound or slightly different patterns of seasonality. It is thus important to consider all issues that drive the patterns of overall seasonality that may provide a better understanding of the kinds of evolutionary adaptations we should expect at a global scale.

By developing a single metric reflecting the degree of seasonality that is based on its two major components—amplitude and predictability—and by applying this concept to freely available global datasets on temperature, precipitation, and NPP across all terrestrial habitats, we aimed to explore how we might investigate the concept of phenotypic flexibility in expression of life history stages and their timing. Most importantly, our analysis, and the resulting framework, provides a measure of seasonality that indirectly incorporates the effects of, e.g., the extent of land masses, ocean currents, wind directions, and topography. The results show the greater diversity of patterns of seasonality than the previously followed proxy for seasonality-latitudinal patterns of day length (Fig. 3A). In fact, the degree of seasonality and its two components, amplitude and predictability, not only show non-linear relationships across latitudes, but also substantial differences between the northern and the southern hemispheres as well as high variations across longitudinal gradients. For example, the interior lowlands and the great plains in central US exhibit similar degrees of seasonality to the north slope of Alaska situated some 30° further north with largely different photoperiods. The highest degree of seasonality in temperature measured across five recent years occurred in areas around the Lena River in central Russia (~124°E, > 55°N,) with decreasing seasonality toward both the east and the west (see similar pattern in Ghalambor et al. 2006).

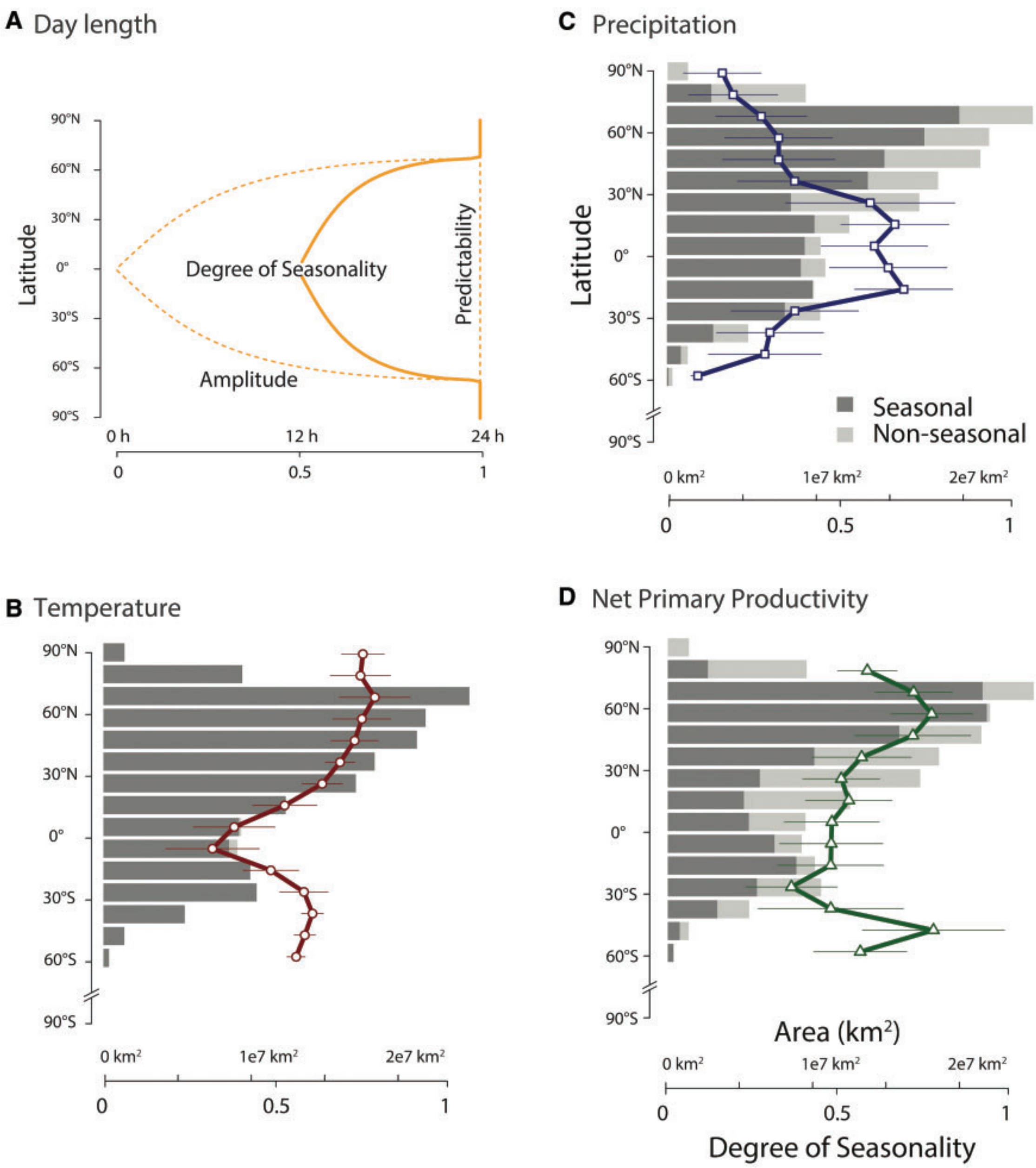

Fig. 3 The degree of seasonality across latitudes for (**A**) day length, (**B**) temperature, (**C**) precipitation, and (**D**) NPP. The thick lines and the symbols indicate the mean values for binned latitudes (error bars describe standard deviation). For day length, the amplitude has been normalized with 1 being the highest seasonal difference (e.g., 24 h). The area of terrestrial land across latitudes is shown by the bars with dark gray indicating areas exhibiting seasonal variation in the respective factors (e.g., temperature) and the light gray proportion indicates the area lacking seasonality. The Antarctic Continent has been ignored given the lack of data (e.g., no NPP data) and the very low percentage of terrestrial habitats

Looking separately at the seasonal amplitude and predictability revealed further informative patterns. For example, the highest predictability is sometimes found in areas that experience rather low intra-annual variation; seasonal rainfall patterns were highly predictable in two latitudinal bands around the equator on the African continent. Yet the highest seasonal amplitude in precipitation occurred in the areas that are highly affected by the annual monsoons such as in central-south Asia (e.g., India, Nepal, and Bangladesh), northern Australia and regions of the Amazon rainforest. Variable ENSO (El Nino-Southern Oscillation) may at least explain the lower predictability in the Australasian regions (e.g., Power et al. 1999). This example clearly shows the power of quantifying seasonality based on environmental variables that integrates, or in other words are affected by, such large-scale climatic processes.

Large scale analyses that are global in extent come with obvious caveats. Global datasets, and notably remote sensing data, are often indirect measures of abiotic or biotic factors. For example, we used the MODIS NPP dataset which is mainly based on the fraction of photosynthetically active radiation and the leaf area index from another MODIS system. Although it better reflects the NPP, it is highly correlated with the commonly used NDVI (Normalized Differenced Vegetation Index) dataset that has been shown to also indicate primary productivity pattern in many different habitats (e.g., Zhang et al. 2003; Soudani et al. 2006). However, such measures are not always linear across habitats (Hmimina et al. 2013). Furthermore, climate and notably cloud cover creates noise in remote sensed data and often leads to non-informative pixels (Hmimina et al. 2013). While new raw-data processing methods deal with many of these issues (e.g., Kanamitsu et al. 2002; Hird and McDermid 2009) it often results in a decrease in spatial and temporal resolution that hamper our ability to perform seasonal analysis requiring more than a few data points across the annual cycle. In our analyses, we aggregated the time-series into monthly measures, matching the lowest temporal resolution of the used datasets. While monthly observations, or aggregated monthly means, might be enough to derive measures of amplitude (some studies used four or even two measures per year to quantify seasonal variation and variability; e.g., Burrows et al. 2011; Jetz and Rubenstein 2011); it is arguably a course resolution for the quantification of predictability or certain phenological measures like the start of the season, where changes, trends, and variation occur within short time periods (e.g., days and weeks) have biological significance (e.g., Sheriff et al. 2015; van Gils et al. 2016). Spatial resolution is another factor that needs to be accounted for in the interpretation of the results presented here. Despite a high temporal resolution in the NPP and the dataset we used for surface temperature (monthly means), the spatial resolution of the precipitation dataset restricted our analysis to a 1×1 degree grid that is rather low compared to a 0.1×0.1 degree resolution of the NPP dataset. Arguably, a resolution of 1×1 degree only allows for inferences on large scale pattern. Thus, our results provide an overall geographic pattern on the underlying seasonality that might not reflect the exact seasonality individuals experience within their (micro-) habitat.

Nevertheless, and despite the above cautionary caveats, our results reveal interesting patterns and can have multiple applications for future research. For example, does variation in degree of seasonality predict phenotypic flexibility and how organisms perceive environmental cues that indicate future conditions for breeding and other life history stages (i.e., perception–transduction–response, Wingfield and Mukai 2009)? Furthermore, our results and numerous previous analyses have demonstrated the strong hemispheric asymmetry in climatic conditions (e.g., Addo-Bediako et al. 2000; Ghalambor et al. 2006); yet, the use of latitude remains a major proxy for the magnitude of seasonal variation. The dominance of continents in the north (80% of the land masses if we ignore the separated Antarctic continent) and the extensive oceans in the south have demonstrable effects on the climatic conditions (Bonan 2002). The resulting hemispheric differences in seasonality have led to very different physiological adaptions in organisms between the two hemispheres. For example, differences have been found in frost tolerance and proportion of deciduous tree species (Korner and Paulsen 2004). In animals, the lower predictability of the inter-annual variation is thought to be responsible for the generally lower metabolic rates of terrestrial mammals of most of the southern continents than in northern counterparts (Lovegrove 2000). Furthermore, low-temperature related diapause is virtually absent in southern insect species (Convey 1996). Also, the combination of more unpredictable and low-amplitude seasonality in the south has led to relatively more species showing erratic and nomadic movements compared to the highly predictable and directed migrations of many bird species breeding in the northern hemisphere (Dingle 2014). While there is an increasing body of literature revealing these fundamental differences in seasonal adaptations between the hemispheres (reviewed in Chown et al. 2004), our results suggest that even the northern hemisphere experiences large geographical differences that should be taken into consideration.

We hope that the concept of the degree of seasonality as well as its two components, predictability and amplitude, and the results in forms of data-layers (supplementary material), may guide future research. Additionally, the R package and the code provided can be used on both fine- and broad-scale climate datasets, providing the same metrics for different spatial scales. While this may help to pin down degree of seasonality at specific localities and allow direct correlation of traits with the underlying environment, we also hope that the results can help to generate hypotheses and allow precise predictions to be made that can be pursued with experimental approaches.

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Supplementary Data

Supplementary Data available at *ICB* online.

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