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New Idea

Latitudinal variation in the asynchrony of seasons: implications for higher rates of population differentiation and speciation in the tropics

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Abstract

Speciation rates for some taxa increase from the poles towards the equator, augmenting the number of species in the tropics. The causes of latitudinal variation in speciation rates are presently unknown. Here we present and discuss the Asynchrony of Seasons Hypothesis that invokes latitudinal differences in the spatial asynchrony of climate, and the corresponding phenologies of organisms, to explain increased rates of population differentiation and speciation in the tropics. At high latitudes, most organisms time their phenologies to coincide with seasonal fluctuations in solar radiation and temperature that are synchronous across broad regions. High synchrony of phenologies across high latitudes should facilitate the establishment of gametes and immigrants moving into new populations because they are likely to find themselves in the same life history stage as local individuals, with similar phenologies. In contrast, many tropical species time their phenologies to coincide with seasonal variation in precipitation, which can vary over short geographic distances due to variation in patterns of airflow and topography. Greater asynchrony in the phenologies of tropical organisms could reduce survival and reproductive success of gametes and immigrants moving between asynchronous populations, impeding gene flow and increasing rates of local adaptation and speciation.

Keywords: latitude, seasonality, synchrony of life history stages, phenological strategies, population differentiation, adaptation, ecological speciation, diversity

The latitudinal increase in taxonomic richness towards the equator is one of the broadest and strongest patterns in nature (von Humboldt 1808, Wallace 1878, Dobzhansky 1950, Fischer 1960, Pianka 1966, Rohde 1992, Gaston 2000, Schemske 2002, Willig et al. 2003, Hillebrand 2004). Higher rates of tropical speciation may be one of the mechanistic causes of this pattern (Fischer 1960, Jablonski 1993, Schemske 2002, 2009, Jablonski et al. 2006, Mittelbach et al. 2007, but see Weir and Schluter 2007). Evidence for higher rates of speciation in the tropics comes from the fossil record, molecular phylogenies, and patterns of incipient speciation (reviewed in Mittelbach et al. 2007).

While higher rates of speciation appear to augment tropical diversity at least for some taxa, we still do not know the contributions of various abiotic factors to latitudinal variation in speciation rates. Prominent hypotheses include (1) greater solar radiation or temperature in the tropics increasing rates of evolution (Rohde 1992, Allen et al. 2002, Allen et al. 2006, Wright et al. 2006), (2) reduced seasonality of temperature in the tropics increasing physiological barriers to dispersal (Janzen 1967, Ghalambor et al. 2006), (3) reduced effects of Milankovitch Oscillations (including glacial cycles) at tropical latitudes promoting spatial stability and divergence of populations (Dynesius and Jansson 2000, Jansson and Dynesius 2002), and (4) the greater importance of biotic versus abiotic selective pressures with warmer temperatures in the tropics causing greater coevolution and divergence of populations (Fischer 1960, Schemske 2002, Mittelbach et al. 2007, Schemske 2009; see also Darwin 1859, Wallace 1878, Dobzhansky 1950). Other hypotheses may also explain increased population differentiation and rates of speciation in the tropics (e.g., Connell and Orias 1964, Nettle 1998, Martin and McKay 2004, Mittelbach et al. 2007), but few of these are mutually exclusive, and no one hypothesis has yet received strong support (Mittelbach et al. 2007). Ultimately, multiple factors may contribute to greater rates of population differentiation and speciation in the tropics. If our goal is to understand the identity and measure of these factors, a balanced consideration of all potential factors will be crucial (Chamberlin 1965).

To this end, we present and discuss here a new hypothesis that could potentially explain higher rates of tropical speciation, but has received little previous attention in the literature. This hypothesis invokes latitudinal variation in the spatial asynchrony of seasons, and the corresponding phenologies of organisms, as a cause of greater rates of population differentiation and speciation in the tropics (Moore et al. 2005; hereafter the *Asynchrony of Seasons Hypothesis*). At high latitudes, the phenologies of organisms coincide with seasonal variation in temperature and solar radiation that is synchronous across vast areas. The synchrony of phenologies across populations increases the chance of successful gamete exchange (e.g., in plants) and successful dispersal and establishment of immigrants in a new population. In contrast, the phenologies of tropical organisms frequently coincide with seasonal variation in precipitation that can be asynchronous over short distances due to variation in patterns of airflow and topography (Griffiths 1972, Schwerdtfeger 1976, Takahashi 1981). Spatially asynchronous phenologies of tropical populations may act as a temporal isolating barrier by reducing the chance of successful gamete exchange and by reducing the likelihood that immigrants or hybrids can survive and reproduce after dispersing to a new population. Overall, seasonal asynchrony and locally-adapted phenologies could temporally isolate tropical populations by impeding successful dispersal, establishment, and inter-breeding among populations, effectively causing speciation through temporal or allochronic isolation (Figure 1; reviewed by Coyne and Orr 2004: 202-210).

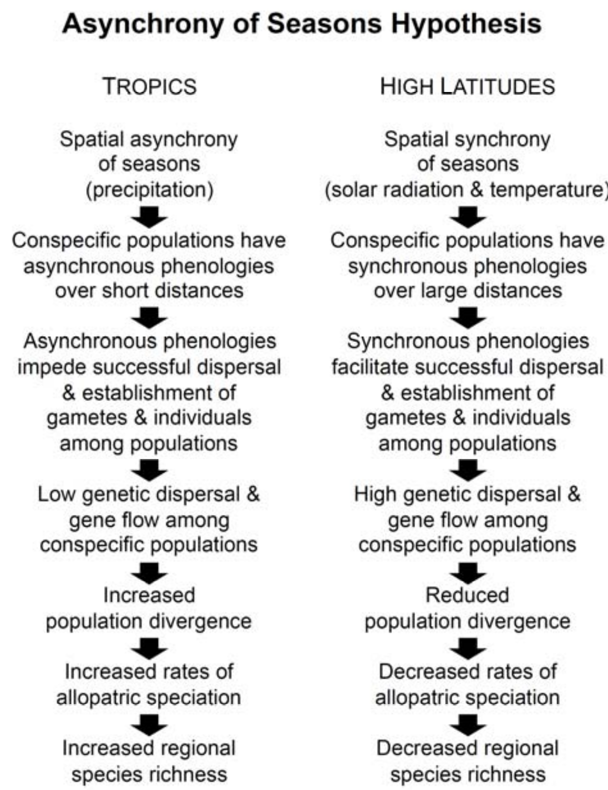

Figure 1. A flow chart of the Asynchrony of Seasons Hypothesis to explain latitudinal variation in rates of population differentiation and speciation. Phenological strategies include the seasonal timing of growth and development, reproduction, movement, and dormancy.

History of the hypothesis

The Asynchrony of Seasons Hypothesis was briefly introduced by Moore et al. (2005) when they presented evidence for asynchronous life history stages, and corresponding genetic (microsatellite) divergence, between Rufous-collared Sparrow (*Zonotrichia capensis*) populations only 25 km apart in the Ecuadorian Andes. The mechanism behind the Asynchrony of Seasons Hypothesis was also discussed by Janzen (1967: 244) who recognized that asynchronous timing of reproduction among tropical populations could act as a mechanism for reproductive isolation—the essence of the Asynchrony of Seasons Hypothesis. However, the main focus of Janzen (1967) was dampened seasonality of temperature in the tropics favoring a narrow physiological tolerance to temperature variation that increases costs to dispersal among tropical populations (see also Ghalambor et al. 2006). Reduced dispersal and gene flow among tropical populations could then promote locally-adapted traits—including local adaptation in the timing of reproduction (Janzen 1967). Janzen (1967) argued that both reduced seasonality in temperature and spatially asynchronous seasonality in precipitation may act together, at least in some cases, to cause the evolution of reproductive isolation in the tropics. We are not aware of other references to a role of asynchronous seasons as a potential cause of higher rates of speciation in the tropics. The general importance of asynchronous phenologies for population differentiation and speciation has been described previously (e.g., Smith 1988; see review in Coyne and Orr 2004).

We know of no explicit description of the Asynchrony of Seasons Hypothesis and its predictions. The link between spatial asynchrony of seasons and phenologies, and population differentiation and speciation is not discussed in most reviews and discussions of the causes of latitudinal variation in diversity (e.g., Wallace 1878, Dobzhansky 1950, Fischer 1960, Connell and Orias 1964, Simpson 1964, Pianka 1966, Stanley 1979, Rohde 1992, Palmer 1994, Rosenzweig 1995, Rohde 1999, Schemske 2002, Lomolino et al. 2006, Mittelbach et al. 2007). Here, our goal is to explicitly describe the Asynchrony of Seasons Hypothesis in the hope that this hypothesis will be included in future tests and reviews of the possible causes of high tropical speciation rates.

Seasonality in climate and timing of phenologies

Seasonality at higher latitudes is dominated by variation in solar energy and temperature that cycle annually with the rotation of the tilted earth about the sun (Figure 2, right panels). This rotation of the earth about the sun creates hemisphere-wide synchrony in seasons that are generally coincident over large geographic distances at the same latitude (Figure 2). For example, periods of maximal sunlight and temperature occur in the months of June and July across most of the arctic, from North America through northern Eurasia (Orvig 1970, Wallen 1970, Bryson 1974, Lydolph 1977). Most phenological strategies of organisms at higher latitudes are closely matched to seasonal variation in solar energy and temperature, resulting in waves of migration, territorial establishment, flowering, growth, breeding, molt, diapause, hibernation, and other annual events (Stonehouse 1989, Thomas and Fogg 2008). The synchrony of phenologies at high latitudes increases the chance of successful gene flow among populations; gene flow among populations impedes population differentiation, local adaptation, and speciation.

In contrast, seasonality in the tropics is dominated by variation in precipitation (Wallace 1878, Janzen 1967, Griffiths 1972, Schwerdtfeger 1976, Takahashi 1981; Figure 2, right panels), with many tropical species timing their phenologies to match seasonal patterns of rainfall (Wallace 1878, Dobzhansky 1950, Janzen 1967, Wolda 1988, Stutchbury and Morton 2001, Scheuerlein and Gwinner 2002). Unlike seasonal variation in solar radiation and temperature at high latitudes, seasonal variation in precipitation can vary over short geographic distances due to variation in the influence of airflow and topography (Griffiths 1972, Schwerdtfeger 1976, Takahashi 1981). However, even if tropical populations timed their phenologies to correspond to subtle variation in solar radiation and temperature (e.g., some tropical insects; Tauber and Tauber 1976, Denlinger 1986, Tauber et al. 1986), we also find greater spatial asynchrony of these cues in the tropics (Figure 2a,b) because of the influences of variation in topography, precipitation, and cloud cover on solar radiation and temperature at low latitudes. Thus, we find spatial asynchrony in solar radiation, temperature, and precipitation in the tropics (Figure 2), potentially impeding gene flow among tropical populations and promoting local adaptation and speciation.

If the mechanism underlying the Asynchrony of Seasons Hypothesis contributed to current latitudinal variation in species richness, then the same variation in patterns of seasonal asynchrony observed today (Figure 2) should have been present in historical times, when present species were in the process of speciation. The seasonal synchrony in solar radiation and temperature at high latitudes is a consequence of the axial tilt of the earth as it rotates around the sun that has characterized the earth's climate throughout history. Similarly, dampened seasonal variation in temperature in the tropics compared with high latitudes has been documented over millions of years (e.g., Bralower et al. 1995), increasing the potential importance of seasonal variation in precipitation in determining the timing of phenologies of tropical organisms over long periods of time. Given that seasonal variation in precipitation is influenced by local patterns of topography and air currents, we expect that the latitudinal gradient in the asynchrony of seasonal variation in climate has influenced organisms throughout history.

Central assumptions and predictions of the hypothesis

The Asynchrony of Seasons Hypothesis relies on several key assumptions, and makes several predictions that can be tested:

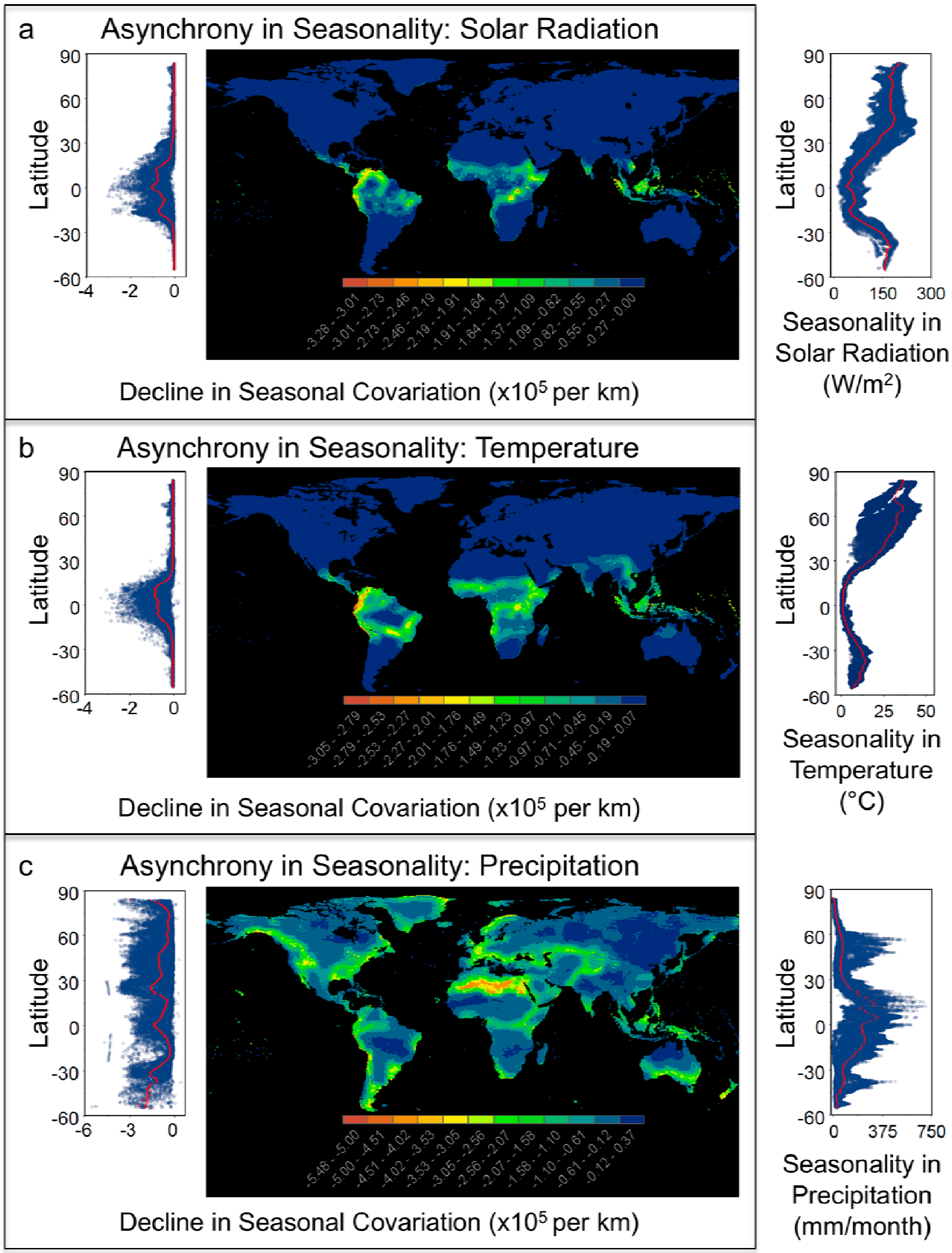

Figure 2. Geographic variation in the asynchrony of seasons for (a) solar radiation (W/m^2), (b) temperature (˚C), and (c) precipitation (mm/day). Color map shows geographic variation in the slope of decline in covariation of seasonality in climate (r^2) with increasing distance from a point ($x10^5$ per km). Higher negative values (red) indicate areas of high asynchrony (rapidly declining r^2 values with increasing distance). Left panels illustrate the same dataset (blue points) with mean values (red line) for each 0.5° latitude. Right panels illustrate seasonality in climate (maximum monthly value - minimum monthly value) for comparison. Note that variation in spatial asynchrony of seasonality in climate (left and center panels) did not reflect the magnitude of changes in climate (right panels). Data come from New et al. (1999) for all panels except seasonality in temperature and precipitation, where data are from New et al. (2002). All datasets provide 30-year mean monthly values from 1961-1990 (New et al. 1999, 2002). High latitude species commonly time their phenologies to coincide with variation in solar radiation (a) and temperature (b). In contrast, many tropical organisms time their phenologies to coincide with seasonal changes in precipitation (c). See further details in Appendix 1.

(1) Tropical populations exhibit seasonality in their life history stages.

(2) Tropical populations show greater spatial asynchrony in the timing of life history stages as compared with higher latitude populations.

(3) Plasticity in the timing of life history stages is limited in tropical organisms, such that dispersing individuals (or gametes) will often be unable to adjust their phenologies to match that of a new population.

(4) Organisms that disperse among asynchronous populations show reduced survival or reproductive success compared with organisms that disperse among synchronous populations, independent of latitude.

(5) Greater spatial asynchrony of seasons (i.e., seasonal variation in climate) coincides with increased population differentiation and reproductive isolation, independent of latitude.

While these five assumptions and predictions are testable, adequate tests are currently difficult due to the paucity of information on tropical populations.

Further considerations of the hypothesis

The Asynchrony of Seasons Hypothesis proposes that the high asynchrony in climate (notably rainfall) in the tropics acts as an isolating barrier that should be particularly prominent in regions of high topographic relief where population differentiation and speciation are believed to be at their highest (Fjeldså 1994, Rahbek and Graves 2001, Phillimore et al. 2007). Could the same hypotheses contribute to higher rates of speciation in tropical marine and freshwater environments? Tropical marine environments show seasonal changes in climatic conditions and phenologies of organisms, and these seasonal changes may be influenced by local weather, topography, patterns of nutrient runoff, and water currents (Parsons and Takahashi 1973, Mathieson and Nienhuis 1991). These local influences on seasonality create the potential for spatial asynchrony of seasons in tropical marine systems, at least in coastal environments.

Overall, the Asynchrony of Seasons Hypothesis presents a plausible mechanism to explain geographic variation in rates of population differentiation and speciation. While the hypothesis has not received broad attention in the literature, it has the potential to explain important variation in rates of population divergence and evolution, and deserves consideration in future discussions of the causes of latitudinal variation in diversity.

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Appendix 1. Methods for mapping asynchrony in seasonal variation in solar radiation, temperature, and precipitation (Figure 2).

We mapped global variation in spatial asynchrony in seasonality for the following three variables: (a) solar radiation (W/m^2), (b) mean temperature (^oC), and (c) mean precipitation (mm/day). To map spatial asynchrony in seasonality, we used observed, global, terrestrial weather data calculated from 12,000-19,000 weather stations (depending on the climatic variable) and fit to a 0.5°-latitude x 0.5°-longitude grid of the earth (excluding Antarctica) using thin-plate splines as a function of latitude, longitude, and elevation (New et al. 1999). For each variable, we used 30-year monthly mean values to examine temporal correlations through the year at five distances. Specifically, for each 0.5° x 0.5° cell, we calculated the mean square of the Pearson correlation coefficient (r^2) over a 12 month period for (1) all neighboring cells 0.5° away (first ring, 8 cells), (2) cells 1.0° away (second ring, 16 cells), (3) cells 1.5° away (third ring, 24 cells), (4) cells 2.0° away (fourth ring, 32 cells), and (5) cells 2.5° away (fifth ring, 40 cells). We also measured mean distance (km) of all cells for which r^2 values were calculated (fifth ring corresponded to a maximum of 276 km distance), allowing us to calculate the slope of the decline in covariation (r^2 values) per kilometer for each point in the 0.5° x 0.5° grid of the earth. A high slope of decline characterizes points that show relatively high spatial asynchrony in seasonality with respect to the abiotic variable of interest (solar radiation, temperature, precipitation). For cells that were not completely surrounded by other cells (e.g., coastal sites), we calculated mean covariance (r^2) and mean distance for all cells containing data. We measured asynchrony of climate for points that ranged from 36 km (first ring) to 276 km (fifth ring) away because most estimates of long-distance dispersal in vagile, terrestrial organisms are less than 300 km (Paradis et al. 1998, Sutherland et al. 2000, Kinlan and Gaines 2003). Latitudinal patterns of variation in asynchrony did not appear to be influenced by variation in the distance between longitudinal degrees (Supporting Figure 1). We plotted the slope of the decline in spatial covariation of seasons for each point in the 0.5° x 0.5° grid of the earth, allowing us to examine geographic variation in the spatial asynchrony of seasons for each of the three abiotic variables.

Our estimates of spatial asynchrony in climate could be underestimated in regions of few weather stations (e.g., northern North America, Greenland, northern and central Asia, Saharan Africa, the Amazon basin, and west-central Australia; New et al. 1999: Figures 1, 2 for map of weather stations). Poor spatial sampling in some regions should not alter our general results because sampling intensity was sufficient to show high asynchrony in poorly-sampled regions (e.g., Figure 2c, Saharan Africa).

Variation in spatial asynchrony of seasonality in climate did not reflect the magnitude of changes in climate (cf. asynchrony versus seasonality, Figure 2). For example, seasonal changes in temperature near the equator are relatively small (Figure 2b; Wallace 1878, Janzen 1967, Griffiths 1972, Schwerdtfeger 1976, Takahashi 1981, Ghalambor et al. 2006), and these small changes underlie the high asynchrony in seasonality of temperature in the tropics (Figure 2b). Thus, it is possible that the high spatial asynchrony in temperature near the equator may be relatively unimportant to the species that occur there. Alternatively, tropical organisms that experience dampened variation in temperature may be more sensitive to small changes in temperature, and these small changes may influence fitness (Deutsch et al. 2008) and drive variation in the timing of life history traits (Denlinger 1986). Data on the importance of seasonal variation in temperature for tropical organisms are lacking, although evidence that tropical phenologies often coincide with seasonal changes in rainfall (e.g., Wallace 1878, Wolda 1988, Stutchbury and Morton 2001, Scheuerlein and Gwinner 2002) supports the idea that variation in precipitation may be a more important selective influence on phenology in the tropics.

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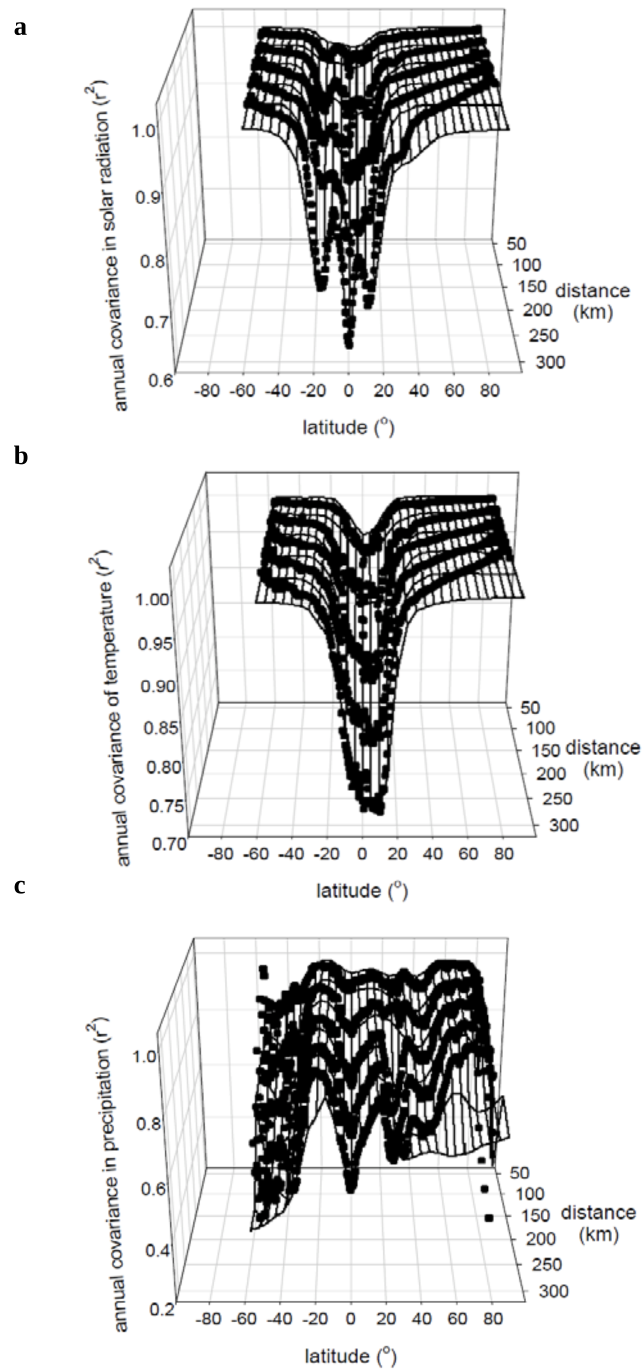

Supporting Figure 1. Latitudinal variation in the covariation of (a) solar radiation (W/m^2), (b) temperature (˚C), and (c) precipitation (mm/day) at increasing distances from a point. Covariation among points was measured by correlating monthly variation in the abiotic factor of interest, generating an r^2 value that declines with increasing asynchrony (Appendix 1). Climate data are from a 0.5˚-latitude x 0.5˚-longitude grid of the earth (excluding Antarctica) (New et al. 1999).