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Climate Dipoles and Their Influence on Plant and Animal Populations

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Review

Climate Dipoles as Continental Drivers of Plant and Animal Populations

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Ecological processes, such as migration and phenology, are strongly influenced by climate variability. Studying these processes often relies on associating observations of animals and plants with climate indices, such as the El Niño–Southern Oscillation (ENSO). A common characteristic of climate indices is the simultaneous emergence of opposite extremes of temperature and precipitation across continental scales, known as climate dipoles. The role of climate dipoles in shaping ecological and evolutionary processes has been largely overlooked. We review emerging evidence that climate dipoles can entrain species dynamics and offer a framework for identifying ecological dipoles using broad-scale biological data. Given future changes in climatic and atmospheric processes, climate and ecological dipoles are likely to shift in their intensity, distribution, and timing.

Highlights

Climate variability is cataloged using climate indices that ecologists rely on to study phenology, migration, and population dynamics.

Climate dipoles are a common characteristic of climate variability that emerge in terrestrial and marine systems as contrasting patterns in anomalies of temperature or precipitation appearing at two different geographic locations at the same time.

Climate dipoles have the potential to entrain continent-wide processes ranging from bird migration to plant reproduction and produce ecological dipoles.

Ecological dipoles can be identified by applying approaches of space–time analysis to biological and climatological observations collected at continental scales.

Given the altered patterns of atmospheric processes, increasing synchrony of weather, and land-use-driven changes in climate, it is likely that climate and ecological dipoles will shift dramatically in the future.

Climate Variability Mediates Ecological Processes across Time and Space

Many local ecological processes are entrained by environmental drivers operating over broad geographic scales [1–3]. **Climate variability** (see Glossary) is one such driver that influences and synchronizes a diversity of biological phenomena ranging from plant reproduction to animal migration and is distinct from the impacts of **climate change** that occur over longer time periods [4–7]. As Earth rapidly approaches a new planetary state characterized by warmer temperatures and more frequent extreme events [8–10], there is a mounting urgency to better understand the effects of climate variability on plant and animal populations across time and space. However, unpacking the biological consequences of climate variability is a challenging endeavor as it requires the study of coupled fluctuations in both climate and ecological responses over geographic extents ranging from local field studies to entire continents.

While climate change generally occurs over decades or centuries and weather varies on a daily basis, other fluctuations in temperature and precipitation operate on multiannual time scales. These regular fluctuations are a natural form of climate variability and are individually known as **modes**. Climatologists catalog only the most highly structured of these modes as **climate indices** representing a single time series that explains the largest fraction of climate variability in a particular season. These indices describe fluctuating differences in an atmospheric parameter (e.g., air pressure, air or sea temperatures, rainfall) between widely separated regions at interannual to decadal timescales. For example, the **North Atlantic Oscillation (NAO)** [11] describes a recurring alternation in sea level pressure between Iceland and the central North Atlantic. Similarly, the **ENSO** [12], in the equatorial Pacific, captures fluctuations of sea surface temperature and pressure that alternate every few years between warm (El Niño) and cool (La Niña) phases. Importantly, the NAO, the ENSO, and other indices vary over a broad range of time scales, and their fluctuations can impact global, regional, and local climate conditions.

Climate indices are an essential tool for advancing theories in migration, phenology, and population dynamics [5,6,13]. These indices are useful because they are easily obtainable,

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straightforward to interpret (with standardized values representing positive and negative phases), span multiple decades, and represent a simplified composite of weather. Ecologists associate climate indices with observations of plant and animal populations (e.g., abundance, survival, reproduction) collected over periods of time (Figure 1, Key Figure). For example, long-term records of migrating birds at a single banding station may reveal earlier spring arrival during warmer years associated with the positive phases of a specific mode of climate variability, such as the NAO [14]. The NAO and ENSO are well-documented drivers in classic examples of population cycling in snowshoe hare (*Lepus americanus*) and lynx (*Lynx canadensis*) [15,16] as well as porcupines (*Erethizon dorsatum*) [17], interactions between wolves (*Canis lupus*) and their prey [18,19], bird competition [20] and reproduction [21,22], amphibian survival rates [23], disease emergence [24,25], and flower and seed production in both temperate and tropical systems [26–28]. Likewise, in marine systems, the NAO and ENSO affect fluctuations in zooplankton numbers [29], fish growth and survival [30], and ecosystem productivity [31]. Many of these studies focus on time series of observations for a single population, often collected over decades to capture the full range of variability in the climate index and identify any time lags imposed by the direct and indirect pathways by which a species might respond to climate variability.

A distinct means by which climate variability affects multiyear ecological responses is through the synchronization of multiple populations through time and space, a phenomenon known as

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Key Figure

A Framework for the Influence of Climate Dipoles on Ecological Responses

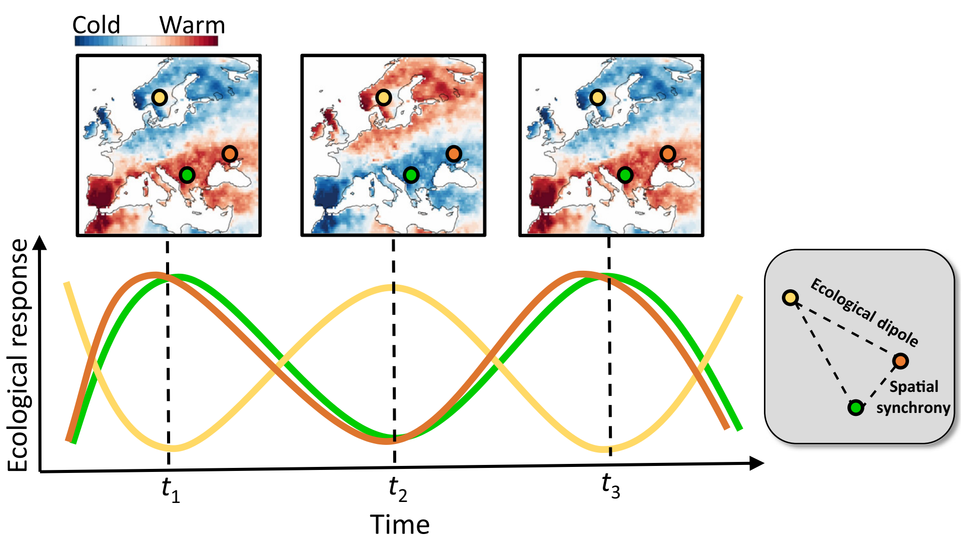

Figure 1. Under the scenario of a species that favors warm climate conditions, the species would respond favorably (increased survival, higher abundance) to warm conditions and negatively to cold conditions. Time-series models seek to capture ecological responses at single sites over time (yellow or orange or green). At multiple sites (i.e., orange and green), patterns of warm (t_1) and cold (t_2) anomalies would synchronize changes in the ecological responses among these disjunct populations (spatial synchrony). It is only by collecting data at multiple sites across continental scales (yellow, orange, and green) that we would be able to capture asynchronous patterns in species' responses to climate dipoles over time (yellow vs. orange and green).

spatial synchrony (Figure 1). Although several factors can potentially drive spatial synchrony [32], one of the most potent and pervasive is the dependence of ecological processes on climate variability [33]. Such dependence, known as the **Moran effect** [34], is invariably important as a consequence of strongly synchronized fluctuations in both rainfall and temperature across the Earth [35]. A species that prefers warm conditions, for example, is likely to show increases in abundance or survival across multiple populations when favorable regional conditions persist, and vice versa (Figure 1). Driven partially or largely by the Moran effect, synchronized changes in populations separated by hundreds to thousands of kilometers occur in plant growth and reproduction [36–38] and in insect herbivores, fishes, birds, mammals, and even human pathogens [32]. Spatial synchrony typically decays with distance, either because patterns of fluctuation become increasingly dissimilar with distance in nonperiodic populations or because of phase divergence with distance in populations that fluctuate cyclically; eventually, populations far enough apart are expected to exhibit a complete lack of spatial synchrony. At continental scales, however, climate variability can manifest itself as a **climate dipole** [39] – contrasting patterns in temperature or precipitation anomalies appearing at two different geographic locations at the same time – that has the potential to enforce negative correlations (antisynchrony) [40] between populations separated by thousands of kilometers (Figure 1). Climate dipoles play a potentially important role in forming complex geographic patterns of population synchrony that are not simply related to distance and are likely to be critical components in the geography of spatial synchrony [41].

Here, we review the concept of climate dipoles as important drivers of animal and plant populations. We introduce the concept of the '**ecological dipole**' as the relationship between an ecological process or pattern largely driven by the emergence and regularity of climate dipoles at continental scales. Our goals are to: (i) review empirical evidence on the existence of ecological dipoles; (ii) present an analytical framework for detecting dipoles; and (iii) discuss how climate change, climate variability, and widespread land-use change might alter ecological dipoles in the future.

Evidence of Climate and Ecological Dipoles

Modes of climate variability often produce **teleconnections** that reflect patterns in climatic and environmental phenomena that regularly appear in regions spanning entire hemispheres, and in some cases, the world [42,43] (Figure 2A). For example, the NAO drives changes in sea ice extent and tundra productivity across the Arctic [44] as well as the occurrence and magnitude of windstorms across Northern Europe [45,46]. El Niño promotes drought in the Amazon basin, Australia, and the Sahel, but reduces drought in eastern Africa [12,43,47]. At continental scales, the ENSO interacts with the mid-latitude storm track to produce a north–south dipole in winter precipitation across North America where positive values of the ENSO index, El Niño events, are associated with higher rainfall across the southern USA and concurrent drought conditions in the Pacific Northwest (Figure 2B); La Niña conditions produce the opposite pattern [48]. At decadal timescales, the strength and geography of this precipitation dipole can change due to interactions with other modes, such as the **Pacific Decadal Oscillation (PDO)** or **Atlantic Multidecadal Oscillation (AMO)**, with significant impacts on drought, forest fires, and snowpack [49–51].

A somewhat lesser-known example is the **Indian Ocean Dipole (IOD)**, an aperiodic pulsing of sea surface temperatures that produces warmer ocean temperatures in the western Indian Ocean and corresponding cooler waters in the east [52,53]. The IOD has far-reaching impacts on global climate [54] and is associated with a strong temperature dipole across Australia (Figure 2C) and catastrophic bushfires in the southeast [55]. Teleconnections entrain the

Glossary

Atlantic Multidecadal Oscillation (AMO): a multidecadal climate cycle with an estimated period of 60–80 years based on sea surface temperatures in the North Atlantic Ocean.
Climate change: trends in average climate that persist for several decades or longer.
Climate dipole: climatic pattern of opposite polarity appearing at two different locations at the same time that can emerge and persist over different timescales.
Climate indices: a calculated value that can be used to describe the state of and changes in the climate system, often over multiannual timescales.
Climate variability: shifts in the state or organization of the global climate at timescales ranging from seasonal to multidecadal.
Ecological dipole: fluctuations in ecological responses (e.g., abundance, survival, reproduction) of opposite polarity (antisynchronized) in populations that are separated by large geographic distances, often at continental scales.
El Niño–Southern Oscillation (ENSO): a climate pattern originating in the equatorial Pacific sector characterized by fluctuations of sea surface temperature and pressure that alternate every few years between warm (El Niño) and cool (La Niña) phases.
Empirical orthogonal function (EOF): an analytical approach used by climatologists to study possible spatial patterns of climate variability and how they change with time; similar to performing a PCA except that the EOF method finds both time series and spatial patterns.
Indian Ocean Dipole (IOD): a coupled ocean–atmosphere phenomenon based on differences in sea surface temperatures between the Arabian Sea (western pole) and the eastern Indian Ocean (eastern pole).
Macrosystems ecology: the study of diverse ecological phenomena at the scale of regions to continents and their interactions with phenomena at other scales.
Mode: a unique and identifiable form of climate variability.
Moran effect: the phenomenon whereby spatial synchrony in population fluctuations is driven by corresponding synchrony in some environmental driver.
North Atlantic Oscillation (NAO): a seesaw of sea level pressure between

magnitude and regularity of environmental phenomena across the globe, but it is at the scale of ocean basins and continents where climate dipoles and their associated ecological impacts are most conspicuous.

Some of the earliest evidence of dipoles influencing species and communities comes from marine systems where irregular oscillations of sea surface temperatures can occur over days to months. For example, the seesaw dynamic in sea surface temperatures associated with the IOD (Figure 3) influences the location of the Antarctic polar front – a northern boundary of cold Antarctic waters that sustains large numbers of zooplankton and fish. Positive phasing of the IOD and anomalously warm sea surface temperatures push the polar front poleward and force king penguins (*Aptenodytes patagonicus*) to travel farther and dive deeper for food, leading to reduced breeding success; an extreme positive IOD event in 1997 led to penguin population declines of over 30% [56].

In the South China Sea, a dipole of eddies (circular whirlpools of water, counter to the main current) emerges during the monsoon season that substantially constrains microbial distributions and community structure [57]; large differences in microbial diversity occur within and between this dipole of eddies due to the vertical and horizontal mixing of different water temperatures. White sharks (*Carcharodon carcharias*) in the Gulf Stream use the warm temperatures associated with the interiors of eddies to dive deeply and feed on mesopelagic prey [58]. Consequently, the warm water temperatures formed as part of these marine dipoles make prey more accessible and energetically profitable for pelagic predators, such as white sharks, by reducing the physiological costs of thermoregulation in cold water [58].

As in marine systems, dipoles of temperature and rainfall emerge across continents over years and decades with the potential to create ecological dipoles (Table 1). For example, mast seeding, or masting, is the synchronous and highly variable production of seed over time in a population of perennial plants [59–62]. For many temperate and boreal tree species, 'mast years' are dramatic, with tree branches visibly laden by reproductive structures (e.g., cones, acorns) and leading to a pulse of resources that ripples through forested ecosystems [63–65]. Temperature and rainfall are important cues for masting and can synchronize seed production for a variety of tree species across broad geographic regions [37,38,66,67]. Spatial synchrony in masting is well documented at regional scales (<2000 km) and the NAO appears to have been an important predictor of masting in beech (*Fagus sylvatica*) and spruce (*Picea abies*) in Northern Europe for the past 50+ years [68]. Understanding the role of climate dipoles on masting is challenging due to the need to collect seed production data across multiple populations spanning continental scales, but emerging evidence suggests that asynchronous masting events may occur at distances >5000 km and are closely associated with continental dipoles in summer temperatures (Box 1).

Like masting, bird migration is a visible ecological phenomenon in the natural world and is strongly influenced by climate variability [69,70]. Bird irruptions are a form of irregular migration where, in some years, large numbers of individuals appear beyond their normal wintering or breeding areas [69–72]. These irruptions are thought to be a response to resource failure (lack of seed) and fleeing adverse climate conditions [73,74]. Pine siskins (*Spinus pinus*) are one of a suite of boreal breeding species that irrupt with varying regularity across North America. Interestingly, pine siskin irruptions demonstrate dipole-like patterns spanning a north–south and west–east gradient across the continent [75] (Figure 4A). The north–south irruption dipole is characterized by large, multidecadal irruptions extending south of the boreal forest where siskins typically breed and are strongly associated with wet conditions in the boreal forest and dry conditions in the southerly Appalachians. A west–east dipole of siskin irruption (Figure 4B) exhibits biennial fluctuations between western and eastern regions of the boreal forest in response to precipitation and

Iceland and the North Atlantic High and attendant shifts in the overlying storm track that impact Europe and the eastern USA.
Pacific Decadal Oscillation (PDO): a decadal climate pattern based on anomalies of sea surface temperature in the North Pacific basin. Positive values of the PDO index correspond with cold sea surface temperatures in the central and western North Pacific and warm sea surface temperatures along the west coast of North America.
Spatial synchrony: coincident changes in the abundance or other time-varying characteristics of geographically disjunct populations.
Teleconnections: recurring, long-distance patterns of climate anomalies related to each other over large distances.

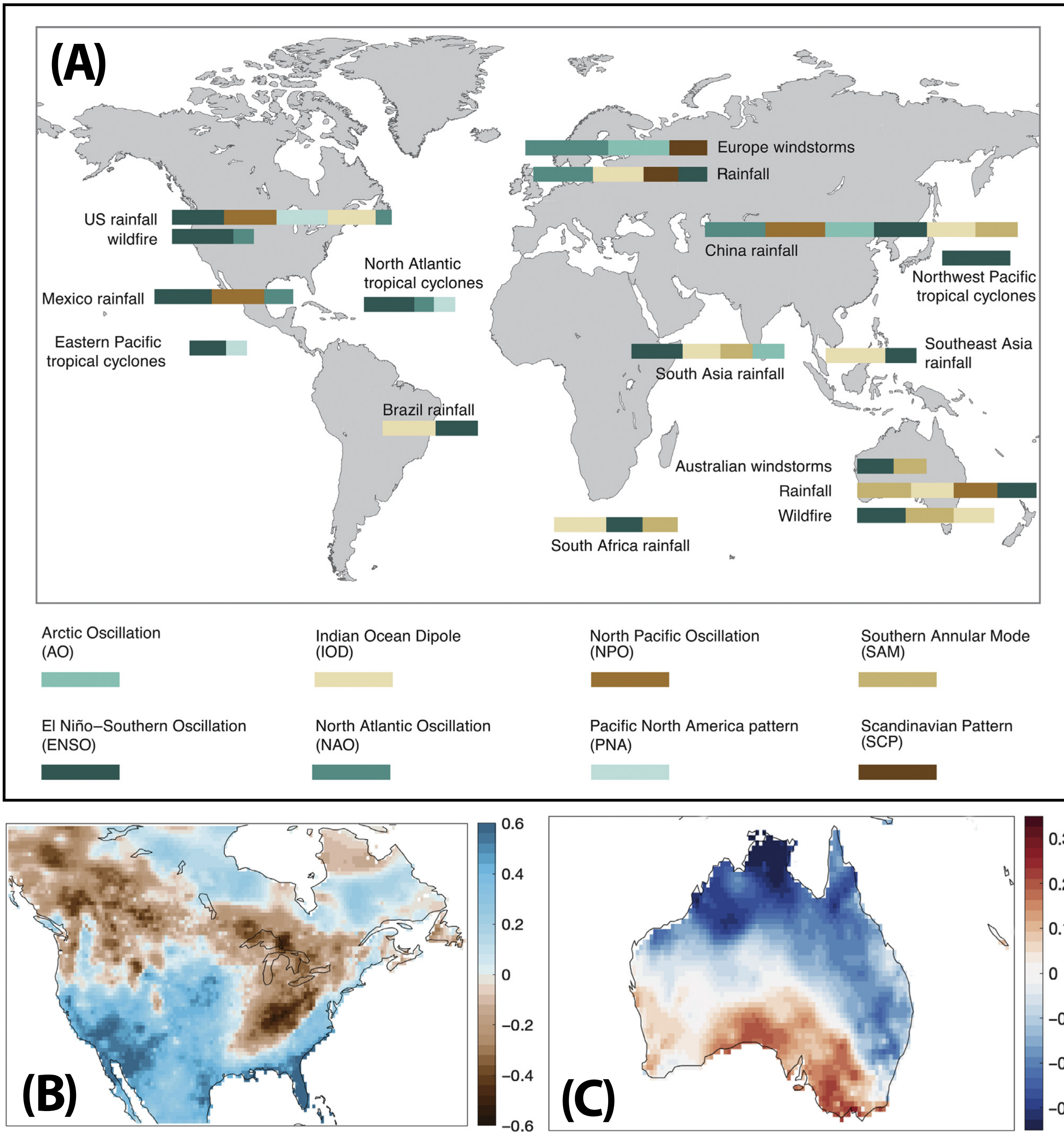

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Figure 2. Global Teleconnections and Continental Climate Dipoles. Top panel (A) shows the global distribution of regional atmospheric conditions and their associated drivers; the length of the bar is proportional to the magnitude of correlation with the mode of climate variability. Adapted from [43]. Bottom panels are examples of climate dipoles at continental scales shown by correlations between (B) gridded precipitation (January–March) and the multivariate El Niño–Southern Oscillation index and (C) gridded air temperature (January–March) and the Dipole Mode Index associated with the Indian Ocean Dipole.

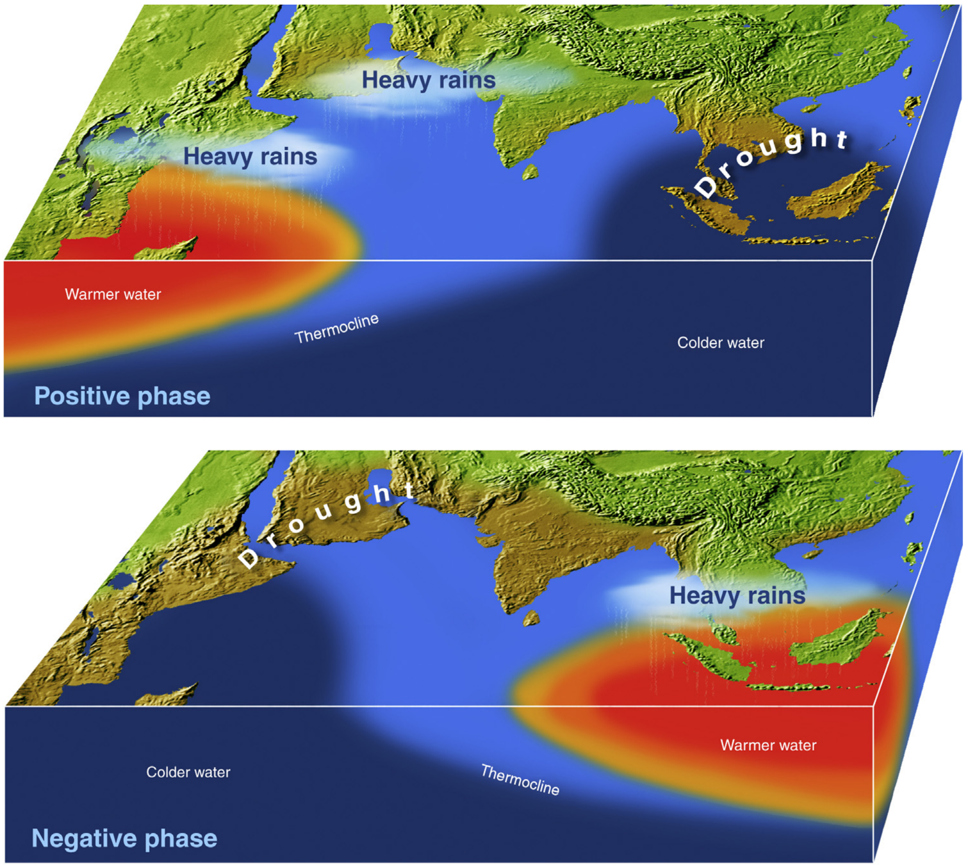

Figure 3. Indian Ocean Dipole. The Indian Ocean Dipole represents a seesaw dynamic in sea surface temperatures with wide-ranging ecological and environmental implications. During the positive phase, warmer-than-average water temperatures in the western Indian Ocean bring heavy rains to East Africa and India and colder-than-average waters bring drought to Southeast Asia. In the negative phase, ocean and monsoonal conditions reverse. Illustration by E. Paul Oberlander, with permission from the Woods Hole Oceanographic Institution.

Table 1. Studies of Climate Variability on Ecological Processes with the Potential for Ecological Dipoles

Region	Climate mode	Response	Scale	Refs
High Arctic	Tropical/Northern Hemisphere pattern	Survival of Sabine's gulls (*Xema sabini*)	Regional	[125]
Spain to Turkey	Climate correlation	Tree growth (*Pinus* sp.)	Regional	[126]
Kenya	IOD	Malaria risk	Regional	[127]
Western Australia	Climate correlation	Growth in blue grouper (*Achoerodus gouldii*)	Regional	[30]
North America	Climate correlation	Boreal bird irruptions	Continental	[75]
Gulf of California, Mexico	Mesoscale cyclone–anticyclone eddies	Phytoplankton	Regional	[29]
North America	Climate correlation	Masting in white spruce (*Picea glauca*)	Continental	(J.M. LaMontagne, unpublished)
Northern Europe	NAO	Masting in European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*)	Continental	[68]
North America	Climate correlation	Waterbird populations	Continental	[128]

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Box 1. Ecological Dipoles in Mast Seeding at a Continental Scale

Mast seeding is defined as the synchronous production of highly variable seed crops by a population of perennial plants over time [62]. A 'mast event' occurs when seed production is very high, often orders of magnitude greater than in other years [77]. Using data from a continental database on plant seed production [67], mast seeding in white spruce across North America displays an ecological dipole with potential connections to climatic patterns (Figure I) (J.M. LaMontagne, unpublished). It is hypothesized that anomalously warm conditions, captured as the temperature difference between the two previous summers (known as the Δ*T* model), is a strong predictor of mast seeding in some species [123].

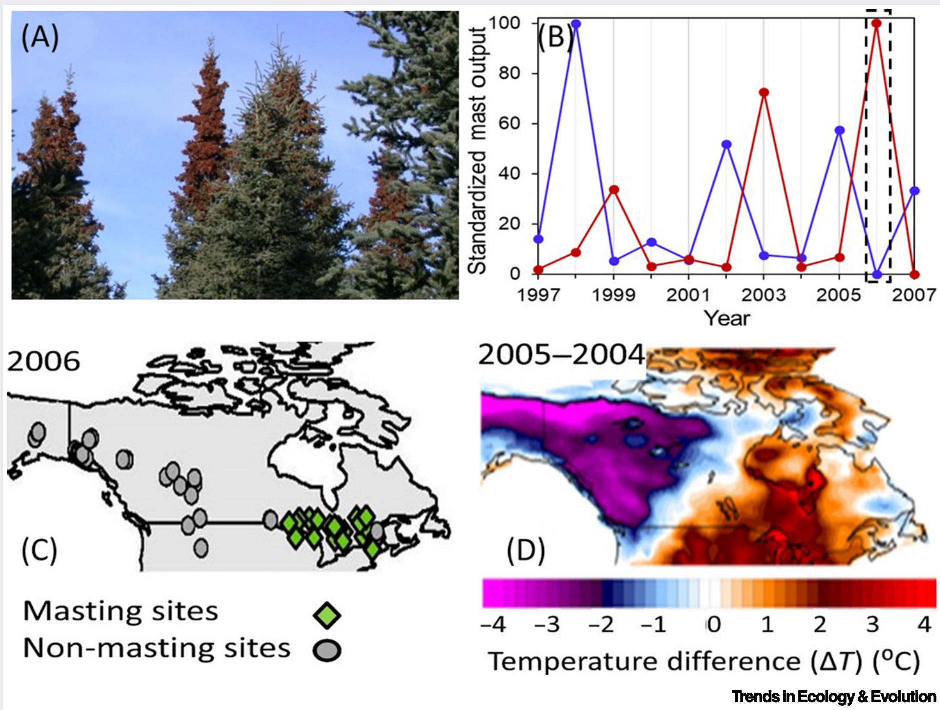

Figure I. An Ecological Dipole of Mast Seeding in White Spruce. During a mast event, the crowns of many white spruce trees in a population are covered in cones (A). At sites spanning >5200 km across North America, an ecological dipole in mast seed can be observed between populations in the east (Quebec; red line) and the west (Alaska and Yukon; blue line) (B). This dipole is apparent for 2006 (*t*), when trees in eastern North America had mast events but sites to the west did not (C). The difference in mean July temperature between the years 2005 (*t* - 1) and 2004 (*t* - 2) reveals that sites in eastern North America were much warmer in 2005 than in 2004 (D), leading to the observed widespread 2006 mast events in the east.

temperature anomalies at multiyear time lags (Figure 4C,D). These time lags indicate a recurring climate-induced failure of food resources, presumably the boom and bust of conifer masting (Box 1) [76,77]. Importantly, these irruptions represent an ecological dipole where the direct and indirect effects of climate dipoles pushed and pulled irruptive bird movements across the continent at biennial to decadal scales.

Although ecological dipoles may be a common, albeit understudied, characteristic of contemporary plant and animal dynamics, climate dipoles can persist over millennia with the potential to influence evolutionary processes and the maintenance of entire biomes [78–80]. Glacial–interglacial variability is characterized by robust cooling and warming of the Earth's climate and, in many cases, the formation of stable climate dipoles. For example, the north–south winter precipitation dipole of western North America discussed earlier (Figure 2B) can persist across multidecadal to century timescales, but also switched signs and geography during the last deglaciation [81]. Similarly, in tropical South America, Quaternary climate change produced an east–west precipitation

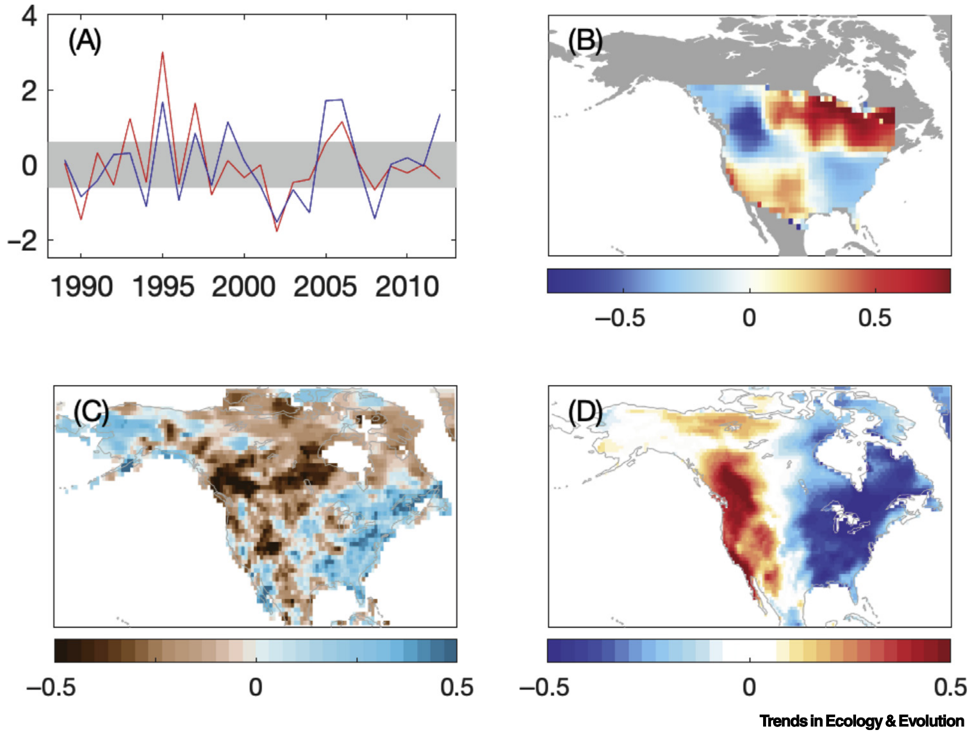

Figure 4. Ecological Dipoles and Climate Drivers of Boreal Bird Irruptions. West–east irruption mode of pine siskin irruption and associated climate drivers. (A) West–east irruption mode (red line) is the time series of pine siskin counts over the period of record (1989–2012). The blue line is a statistical model of the west–east irruption mode constructed from climate indices. (B) Spatial pattern of the west–east irruption mode of pine siskin counts with red areas showing high counts and blue areas low counts. Correlation of west–east irruption mode with (C) summer (June through August) precipitation anomalies and (D) temperature anomalies from 2 years prior to irruption. Adapted from [75]; copyright 2015 National Academy of Sciences.

dipole associated with Earth's orbital cycles (~20 000-year cyclicity) that resulted in periods of high precipitation that persisted for centuries to millennia [78].

Over the past 250 000 years, the South American monsoon (SAM) and the ENSO have interacted to produce a dipole in rainfall between western (wetter) and eastern (drier) Amazonia; this dipole is thought to be essential to the stability of regions serving as tropical refugia for species during periods of rapid climate change and maintaining patterns of biodiversity [78]. Similar to the push and pull of contemporary climate dipoles, many of the teleconnections we have discussed may have provided opportunities for human migration and evolution. For example, shifts in the NAO and associated droughts may have contributed to punctuated periods of human migration, conflict, and the eventual collapse of the Roman Empire [82]. Over thousands of years, there is compelling evidence that early populations of *Homo sapiens* were similarly influenced by continent-wide dipoles in rainfall that created alternating opportunities for human migration out of Africa [83]. Because patterns of climate variability persist across decades and centuries, the seesaw of climate dipoles offers the potential to affect evolutionary dynamics and patterns of biodiversity.

Approaches for Uncovering Ecological Dipoles

Identification of ecological dipoles relies on a suite of analytical tools rarely employed by ecologists. As ecological networks [e.g., the National Ecological Observatory Network (NEON)] [84] and citizen science databases (e.g., eBird) [85] become more established and spatially distributed, their structural organization enables the use of statistical approaches that are well developed for space–time discovery in atmospheric and oceanic data. There are a suite of recent methods for assessing the geography of spatial synchrony, such as spectral methods [86], synchrony networks [41], spatial regression [87], and orthogonal functions (see later) that are amenable for coupled pattern discovery. A shared characteristic of these approaches is the decomposition of ecological data and synchronized climate drivers, over space and time. Importantly, instead of depending on existing climate indices developed to explain atmospheric or oceanic variability, ecologists can use these methods to find prominent patterns in ecological time series over geographic scales and then seek the climate drivers that explain maximal ecological variance (Box 2).

A common approach used by climatologists to detect space–time modes of variability and climate dipoles is **empirical orthogonal function (EOF)** analysis [88]. In this application, a set of climatological observations at m sites, each with record length n, are assembled into a ($n \times m$) matrix and the EOFs are the eigenvectors of the associated ($m \times m$) spatial covariance or correlation matrix. The EOFs are thus spatial 'loading' patterns onto which the data are projected to define a set of orthogonal time series ordered to successively maximize variance. EOF analysis has a rich application history in ecology and geography, although it is most often

Box 2. A Method for Dipole Discovery

The climate science community diagnoses modes of variability from gridded climate data (time series at multiple grid points) using methods like EOF analysis [88,89]. EOF analysis yields a climate mode's spatial pattern (the eigenvector of the spatial covariance matrix) and time series index (the projection of the data onto the eigenvector) as illustrated in Figure IA–C.

An ecological time series of interest (e.g., bird observations from citizen scientists) may be correlated with such a climate index, but not optimally (Figure ID). With the evolution of citizen science and ecological observatory networks collecting biological data over multiple sites across time, the analysis approach can be inverted to first discover the ecological pattern of interest via EOF analysis or PCA (Figure IE–G). Correlating the time-series index of the ecological response with a gridded climate time series yields a 'heterogeneous correlation map' informing a simple climate index (e.g., mean red-region temperature minus mean blue-region temperature), which may be better correlated with the ecological response (Figure IH,I).

Climate and ecological dipoles can be more directly discovered via methods combining the two data sets, simultaneously yielding the pair of patterns (maps and time series) that optimize correlation or covariance. Examples of this class of methods include combined PCA, canonical correlation analysis, and maximum covariance analysis [124]. An advantage of such an approach is using the ecological data to identify unknown climate dipoles given that existing climate indices may be inadequate for explaining the ecological pattern. Like any climate–ecological correlation, one needs to be careful about assuming causation, and the discovery of an ecological dipole should be followed by a more in-depth exploration of plausibility and mechanisms.

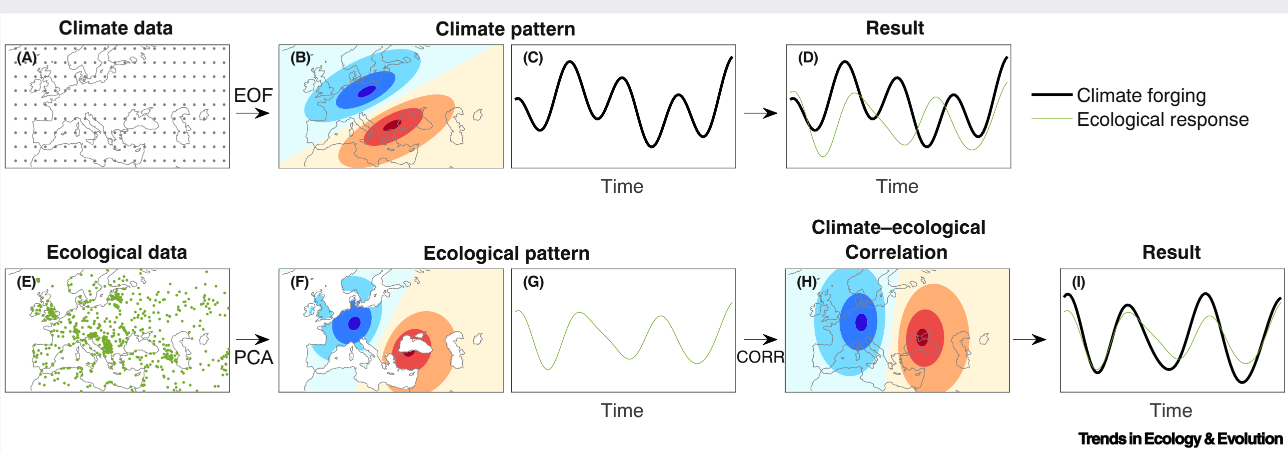

Figure I. Schematic of Process for Detecting Climate and Ecological Dipoles. Empirical orthogonal function (EOF) analysis yields a climate pattern (A–C), which is then correlated with an ecological response (D). Alternatively, the ecological pattern can first be found via principal component analysis (PCA) (E–G) and then its correlation with climate (H) can yield a more refined view of the atmospheric driver (I).

applied in a different manner from that described earlier and is also referred to as principal component analysis (PCA) [89]. In a conventional PCA, ecologists use sampling locations as the data elements and a suite of highly correlated fields or descriptors as the variables. A climate science-style EOF approach inverts this concept, such that the data elements are sampling times and the variables are ecological response (e.g., species occurrence, abundance, survival) measured at multiple sites. While this PCA variant is commonplace in climate science, its application for ecological analysis is rare. Organized patterns, like dipoles, emerge from EOF analysis because the linear combinations of variables that maximize variance naturally exploit the substantial spatial autocorrelation present in environmental fields. It is possible to also incorporate temporal autocorrelation explicitly with extended EOF methods [90] such as Hilbert empirical orthogonal function analysis [91] that are useful for detecting modes that propagate over time and space [92].

Once dipoles in ecological observations are detected, there are two main approaches to find the associated climate drivers: (i) map the correlation between the ecological response and gridded climate time series; or (ii) leverage more advanced techniques for coupled pattern discovery involving simultaneous analysis of the ecological and climate data (Box 2). In the first approach, sometimes called single-field PCA [93], one can assess the temporal correlation between each ecological principal component time series and an atmospheric or oceanic space–time array over multiple time lags. Multiple climate arrays can be incorporated, including precipitation, wind, and sea surface temperature. The resulting correlations can be tested for local and 'field' statistical significance [94] and evaluated for their plausibility as drivers of ecological variability. Simple indices can then be developed based on the correlation maps and described as ecological dipoles, analogous to how the pressure difference between stations in Iceland and Portugal is used to define an index of the NAO. This comprehensive and brute-force approach yields results that are generally straightforward to interpret, and we have found it fruitful for uncovering climate drivers of a broad array of phenomena ranging from lake temperatures to bird migration and frost timing [75,95,96].

The second approach, analyzing the climate and ecological data simultaneously, draws on methods for coupled pattern discovery [97]. The question here is no longer what mode explains the most variance in either ecology or climate, but rather what mode explains the most covariation between ecological responses and climate. Typically the two data sets are processed so that each has the same record length n, but they are measured at different numbers of sites, m and p. As one example of this approach, maximum covariance analysis uses a singular value decomposition of the associated $m \times p$ covariance matrix to identify the two patterns (one from each field) that are most strongly correlated (or covarying). Both of the approaches can be deployed by ecologists to identify ecological dipoles.

A Future of Shifting Dipoles

Atmospheric circulation patterns are changing due to modern climate change. There have been documented changes in spring and summer rainfall and dipole precipitation patterns across North America [98], poleward shifts in mid-latitude jet streams and storm tracks [99–101], alternations in the origination and magnitude of El Niño from the eastern to the western Pacific [102], and changes in the position and strength of the Arctic polar vortex [103]. Importantly, climate dipoles and associated ecological dipoles reflect teleconnections in coupled atmospheric and oceanic processes occurring throughout the world. For example, climate dipoles arising in North America result from atmospheric waves that can be traced to the tropical Pacific or Indian Ocean [104] and even westward around the hemisphere to the North Atlantic [105]. Consequently, increases in oceanic warming are important for climate dipoles on land [106] and warming within the tropics can trigger atmospheric wave propagation [107] that can alter ecological dipoles across mid-latitudes.

In addition to shifting modes of climate variability, surface temperatures are now more geographically coherent than they have been at any time during the past 2000 years [108], with significant implications for ecological processes [109]. Enhanced spatial synchrony in weather patterns is a global phenomenon resulting in record-breaking monthly temperatures globally [110]. Intensifying and more synchronized patterns of climate variability are associated with increased spatial synchrony of tree growth patterns in conifer forests of central Siberia and Spain [111], changes in the abundance of wintering bird populations across North America [112], and outbreaks of gypsy moth (*Lymantria dispar*) defoliations [113]. The synchronization of temperature changes is predicted to rise over the next century, but this will be strongly regional [114], and the contrast between wet and dry regions of the Earth will only increase in magnitude and intensity [115].

Adding complexity to the dynamics of climate change, widespread changes in land use through agricultural expansion, reforestation, and urbanization can directly alter patterns of atmospheric circulation at continental scales [116]. For example, the conversion of North American grasslands to forests via afforestation is expected to shift the Intertropical Convergence Zone (ITCZ) by creating an energy imbalance between the Northern and Southern Hemispheres [117]. This shift in the ITCZ promotes drying over the southern Amazon and a subsequent decrease in productivity and possible change in forest structure in locations far removed from the original land-cover change. Given the altered patterns of climate variability, increasing synchrony of weather, and land-use-driven changes in climate, it is likely that the strength and directionality of ecological dipoles will change in the future. Understanding and predicting the consequences of climate and land-use change on these ecological dipoles will be challenging.

Concluding Remarks and Future Perspectives

Climate variability is a critical driver of ecological and environmental processes over time and space. Here, we present emerging evidence that the ubiquity of climate dipoles is an important component of climate variability with the potential to push and pull population and ecosystem dynamics in terrestrial and marine systems. We present methods to detect ecological dipoles – and their associated climate drivers – in an effort to open new avenues of exploration in the study of plant and animal communities (see Outstanding Questions).

Although studies on ecological dipoles are rare, climate dipoles can influence a wide range of ecological processes, such as shifts in migratory or foraging behavior, disease emergence, primary production in terrestrial and marine systems, and altered population and evolutionary dynamics. Fusing continent-wide observations from citizen science and observatory networks with temperature and precipitation time series accentuate the value of sustained and synoptic biological observations that match the scales at which climate dipoles are manifested and will undoubtedly uncover additional ecological consequences. Unfortunately, the observational scales of most current ecological studies are generally narrow due to conventional field-based approaches; most ecological observations are collected across spatial extents of less than 100 km^2, are unreplicated or infrequently repeated, and are collected for only a few years [118]. Because these limitations have persisted for the past several decades, an expansive gulf remains between the scales at which ecological dipoles arise and the scope of ecological observation.

Current technological advances and the growth of citizen science are contributing to the kinds of long-term, macrogeographic data required to address the questions we highlight here. The former include advances in remote sensing and climate models while the latter includes modern

Outstanding Questions

Are there are other drivers, beyond climate variability, that could result in the appearance of ecological dipoles?

Assuming a more comprehensive catalog of existing climate dipoles than currently available, and an understanding of their stabilities in time and space, what is the full range and significance of associated ecological dipoles in both the marine and the terrestrial realm?

How might climate dipoles drive evolutionary processes and the persistence of biogeographic gradients and biome boundaries?

What are the underlying mechanisms and characteristics of species (e.g., dispersal capabilities, density dependence, distribution) and ecosystems that are most likely to demonstrate dipole patterns?

Dipole detection depends on ecological time series collected over broad geographic and temporal extents. What are the dimensions (e.g., number of years, sample size) of the biological data sets needed to detect ecological dipoles?

How will climate and land-use change either disrupt or introduce climate and ecological dipoles in the future and what might be the ecological, environmental, and societal consequences?

initiatives such as eBird, iNaturalist [119], the Map of Life [120], the National Phenology Network [121], and camera trap networks [122] that successfully enlist large numbers of people into a geographically widespread and interconnected monitoring network that can then be coupled with climate data. These monitoring networks will be essential for collecting broad-scale data on population dynamics (e.g., abundance, occurrence, reproduction, disease prevalence) and ecosystem functioning (e.g., primary productivity, eddy-covariance flux measurements) that are potentially sensitive to climate dipoles. New theoretical fields of ecology, such as **macrosystems ecology** [2], set the stage for investigations of the role of climate variability on ecological and environmental processes over broad geographic scales. Together, these advances offer new avenues to further uncover the roles that climate dipoles, teleconnections, and other large-scale climatic phenomena play in driving ecological processes. Because climate dipoles are a likely broad-scale driver in the geography and periodicity of ecological dipoles at continental scales, shifting climate variability is likely to have wide-ranging impacts on species and ecosystems in the future.

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