Macrosystems as metacoupled human and natural systems

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Macrosystems are integrated human–natural systems, in recognition of the fact that virtually every natural system on Earth influences and is influenced by human activities, even over long distances. It is therefore crucial to incorporate inherent properties of broad-scale systems, such as human–nature connectivity and feedbacks at multi-scales, into macrosystems biology studies. Here, we propose the "metacoupling" framework as a macrosystems biology approach. This framework incorporates the study of ecological and socioeconomic dimensions and their interactions within, between, and among adjacent and distant locations. We present examples highlighting that (1) human activities are increasing multi-scale interactions; (2) the increase in frequency and intensity of distant interactions reduces the importance of proximity as a dominant factor connecting systems; and (3) metacoupling generates both ecological and socioeconomic feedbacks, with profound impacts. The metacoupling framework discussed here can advance macrosystems biology, create opportunities for innovative scientific discoveries, and address global challenges.

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As early as 1942, ecosystems were depicted as multiple compartments coupled by directional fluxes of energy (Lindeman 1942). The concept of ecosystems as spatial entities with interrelated and interacting components has since been advanced as a result of work in several ecological subfields – notably landscape ecology in the 1980s (Urban *et al.* 1987) and more recently macrosystems biology (Heffernan *et al.* 2014). Macrosystems biology focuses on ecological processes occurring at scales ranging from regional to continental, and emphasizes teleconnections (ie phenomena that link geographically distant regions), macroscale feedbacks (ie amplified or diminished broad-scale feedbacks), and cross-scale interactions (ie phenomena at one temporal or spatial scale influencing another) as fundamental characteristics (Heffernan *et al.* 2014). In addition, because of the ubiquitous influence of human activities, macrosystems are inherently interconnected, complex human–natural systems (Liu *et al.* 2015a).

In a nutshell:

- Human activities influence ecological processes nearly everywhere on Earth
- Because macrosystems biology involves the study of ecological processes at broad scales, inclusion of the impact of human activities on ecological processes is necessary for a holistic view of macrosystems
- The metacoupling framework integrates human–nature interactions and feedbacks within as well as between adjacent and distant systems, and across local to global scales
- In metacoupled systems, distant interactions may be more important than adjacent ones
- The metacoupling framework can advance the conceptualization and application of macrosystems biology by identifying multi-scale connectivities

Human activities are influencing the spatiotemporal scales at which ecological processes operate (Rose *et al.* 2017). Spatially, human activities can induce processes to expand (eg larger dust storms due to reduced vegetation cover) or contract (eg anthropogenic channelization of rivers). From a temporal perspective, some processes accelerate (eg rates of sea-level rise) while others slow (eg persisting alterations in forest composition due to land-use change) (Rose *et al.* 2017). Such novel spatiotemporal combinations can result in new scaling rules for ecological processes, and can at times alter a system's resilience by pushing it closer to a threshold beyond which the system can no longer retain its essential properties (ie a tipping point; Scheffer *et al.* 2001; Peters *et al.* 2004).

Few studies have explicitly incorporated both local and distant interactions, feedbacks, and socioecological dynamics into macrosystems biology (as highlighted by Hefferman *et al.* 2014; Rose *et al.* 2017; but see Liu 2017). As a result, macrosystems research has tended to focus primarily on systems that are in close proximity or systems with exclusively long-distance teleconnections, such as those

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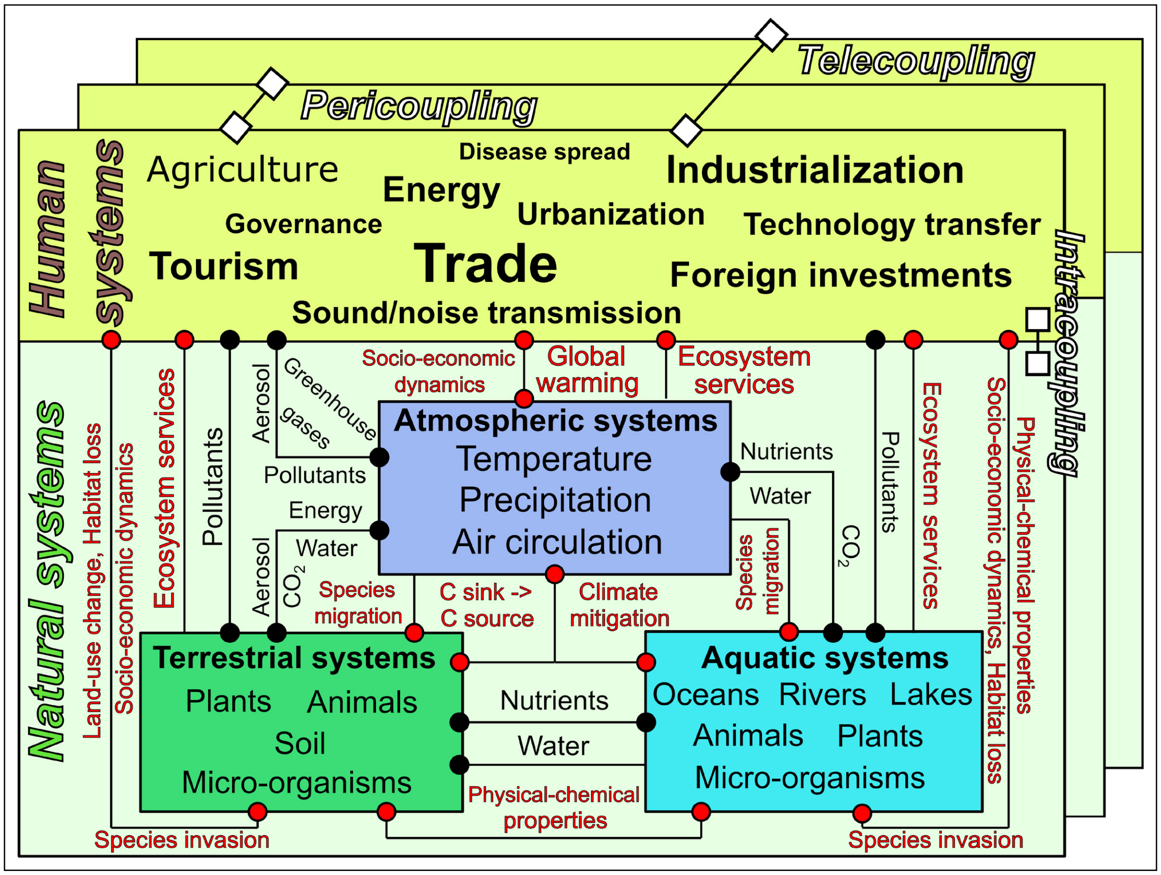

Figure 1. Conceptual framework of macrosystems metacoupling (intracoupling, pericoupling and telecoupling). Flow–fluxes are shown in black (one circle indicates unidirectional movement of material/organisms toward the circle, two circles indicate bidirectional movement), effects–feedbacks (sensu Liu 2017) are shown in red (two circles indicate an effect that is potentially capable of triggering a feedback). The three layers represent similar metacoupled human–natural systems in a gradient of connections from local to adjacent to distant systems.

responding to major changes in vegetation cover (ecoclimate teleconnections; Swann *et al.* 2018). It is, of course, difficult to conceptualize and implement multi-scale analyses that incorporate local- to continental-scale connectivities and feedbacks across different human–natural systems (Figure 1). To help overcome this challenge, Liu (2017) developed an integrated "metacoupling" framework, which provided a scheme to organize and describe interactions (also known as couplings) within ("intracoupling") and between ("intercoupling") coupled human–natural systems; note that intercoupling can be further categorized as interactions at adjacent ("pericoupling") and distant ("telecoupling") locations (refer to Table 1 for definitions). The framework has been applied to a number of important issues, including global marine fishing (fishing within and between adjacent and distant exclusive economic zones; Carlson *et al.* 2020) and sustainable development (eg impacts of trade between adjacent and distant countries on sustainable development; Xu *et al.* 2020). The framework incorporates flexibility regarding what constitutes intra-, peri-, and telecoupling, given that identification of these couplings is dependent on how a system's boundaries are defined. This flexibility emphasizes the different roles of governance and policies in defining the context in which human and natural processes can occur.

Table 1. Metacoupling framework (Liu 2017) describing the different types of connections within and among adjacent and distant human and natural systems

Types of connections		Definition
Coupling		Interactions over time and space *linking different systems or different parts within a system*, often involving fluxes of energy, materials, organisms, and/or information
Intracoupling		Coupling *within* a system
Intercoupling	Pericoupling	Coupling *among adjacent or nearby* systems
	Telecoupling	Coupling *among distant* systems
Metacoupling		Coupling *within* a system and *across different* systems; includes intracoupling and intercoupling

Reconceptualizing macrosystems biology

To advance the field of macrosystems biology, we suggest coupling prior perspectives with socioeconomic and natural components and merging interactions within as well as across adjacent and/or distant systems. We propose that the metacoupling framework serves as the foundation for this approach, not only because it incorporates and connects different approaches to macrosystems biology in a single conceptual framework, but also because it facilitates analysis of internal, adjacent, and distant interactions, feedbacks, and socioecological dynamics across multiple spatial–temporal scales. We posit that a more comprehensive understanding of human–natural systems will emerge through applications of this approach as a requisite for addressing today's large-scale ecological problems, and that this will form part of the "evolution" of the new field of macrosystems biology (Dodds *et al.* 2021; LaRue *et al.* 2021).

Many ecological and social-science concepts could potentially underlie the metacoupling framework (Figure 2). For example, from the ecological perspective, the concept of the "niche" is used to define the range of environmental factors (biotic and abiotic) suitable for a given species' growth, reproduction, and movement across space and over time (Chase 2011). In the metacoupling framework, environmental factors should not be restricted to those occurring solely where the species is found, but should also include those present in adjacent and distant locations. Furthermore, biotic factors include humans and their activities. Other ecological concepts (eg biogeography, population biology [including metapopulations], community ecology [including metacommunities], large-scale ecosystems) are also relevant to metacoupled systems in various ways. For instance, a metapopulation constitutes multiple populations that interact across various locations. From a social-science perspective, human activities relating to livelihoods permit human survival but have impacts on nature at multiple scales. Scaling and feedback frameworks have been developed in both ecological and social sciences, with a focus on either ecological or social feedbacks, respectively. However, in metacoupled systems, scaling and feedbacks involve both ecological and human dimensions simultaneously.

Metacoupling includes several types of spatial couplings (Figure 2). Within focal, adjacent, and distant systems, there are intracouplings (eg harvesting, farming, hunting), although not every intracoupling appears or dominates in every system. Focal and adjacent systems are interconnected through many pericoupling processes (eg migrations, species invasions, river flows, trade, foreign investment). In contrast, focal and distant systems are linked through telecoupling processes, including climatic teleconnections. Many other types of telecoupling processes, such as trade and migration, are the same as or very similar to pericoupling processes but occur across disconnected systems and over longer distances. For example, trade and migration between focal and adjacent systems can be viewed as pericoupling processes, whereas between focal and distant systems they constitute telecoupling processes. The concept of metacoupling builds upon but differs from those previous concepts. For example, while previous concepts of connectivity are discipline-oriented (eg ecological, social, *or* economic; for instance, Peters *et al.* [2008] focused on ecological connectivity), metacoupling has an interdisciplinary orientation (eg ecological, social, *and* economic; Liu *et al.* 2013; Liu 2017).

Many hidden relationships between nature and human activities become more evident when analyzing macrosystems biology under the metacoupling framework. The distance between systems can be physical (eg Euclidean distance) but can also be determined by socioeconomic dimensions (eg two distant systems strongly interconnected through trade). Broad-scale drivers, particularly those that are human-mediated, can under certain conditions overwhelm local drivers, while in other cases local processes have the potential to produce effects over long distances (Peters *et al.* 2008). For example, two very distant countries, Brazil and China, dominated the soybean (*Glycine max*) trade market in 2019, with Brazil being an important crop producer and China being a major consumer (Herzberger *et al.* 2019), whereas little or no soybean trade occurs between many adjacent countries (Schaffer-Smith *et al.* 2018). Consequently, global market forces can drive the conversion of natural ecosystems to cropland dominated by soybeans, influencing local ecological conditions.

In general, many human activities can act as linkages between disparate ecosystems (Collins *et al.* 2011). For instance, an increase in forest cover in one country may occur at the expense of the conversion of natural vegetation in another nation because of the demand for natural resources in a third country (Lambin and Meyfroidt 2011; Viña *et al.* 2016). Human mediation can modify the linkages between natural biophysical systems, altering local versus distant connectivity and eventually creating connections (coupling) or disconnections (decoupling) between systems in a relatively short time frame. This process ultimately transforms the balance between short- and long-distance couplings over time. Changes in climate, for example, produce broad-scale effects independent of proximity to the underlying anthropogenic drivers (Marshall *et al.* 2008).

Tobler's first "law" of geography – "everything is related to everything else, but near things are more related than distant things" (Tobler 1970) – has often been a guiding generalization in ecology as well as geography. However, proximity may not always predominate in an increasingly metacoupled world because many processes can bypass one location and influence a more distant one (Reiners and Driese 2001; Xu *et al.* 2019), particularly in response to human interventions. Below, we present examples from different ecological and socioeconomic macrosystems that exhibit characteristics of metacoupled human–natural systems. Revealing such characteristics through the metacoupling framework can advance macrosystems biology by filling an existing knowledge gap in our understanding of multi-scale connectivity, and by identifying processes and feedbacks that would not be observable through a traditional macrosystems biology approach.

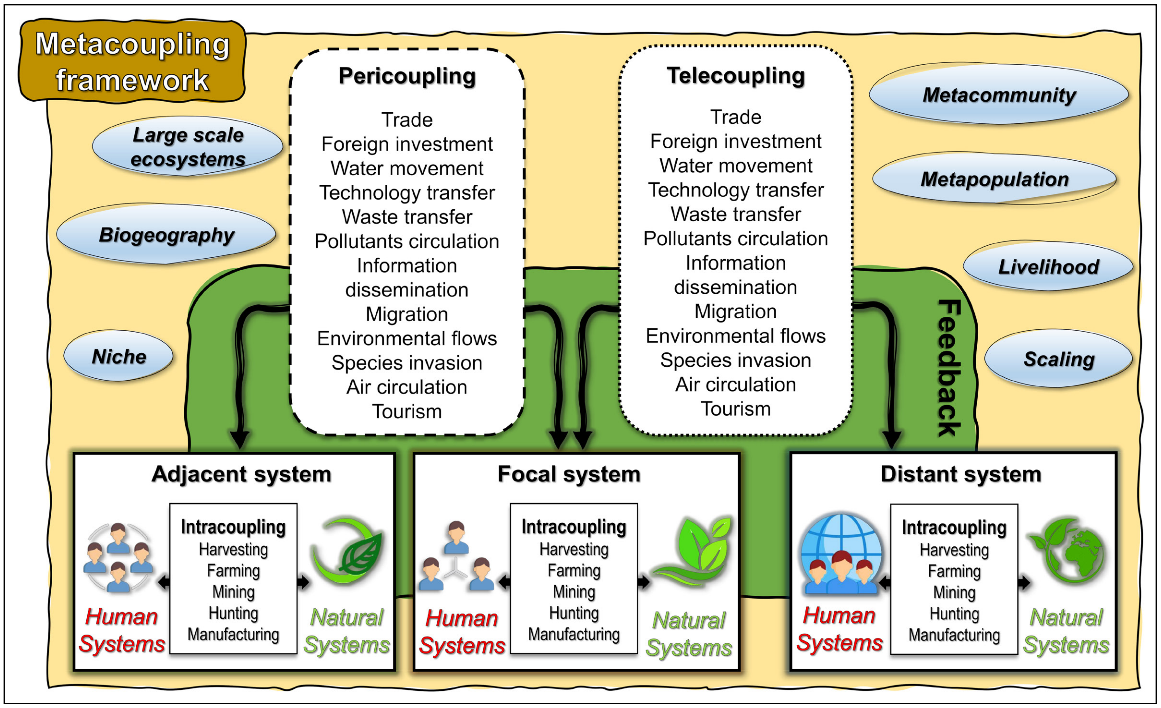

Figure 2. Schematic diagram illustrating human-driven relationships between a focal system, which includes intracoupling between its human and natural components, and an adjacent system (pericoupling) and a distant system (telecoupling). Cross-scale feedbacks (green shaded area) may occur between all systems and levels of connectivity. The metacoupling approach encompasses several ecological and socioeconomic macrosystems theories (light blue ellipses) within a single formal conceptual framework (yellow shaded area).

Characteristics of macrosystems as metacoupled human–natural systems

Macrosystems display complex behaviors that are not always predictable from mere consideration of their individual components at a specific place, because they are affected by many processes that are present locally and across adjacent and distant sites. We apply the metacoupling framework to macrosystems biology to illustrate that (1) human activities are increasing the amount and importance of multi-scale interactions in human–natural systems; (2) the increasing frequency and intensity of telecouplings renders geographic proximity insufficient as a predictor of the degree of interactions among systems; and (3) metacoupling among interconnected systems, whether adjacent or distant, produces not only ecological but also socioeconomic feedbacks, thereby altering all three types of systems (namely, systems linked by intracoupling, pericoupling, and telecoupling).

Increasing multi-scale interactions in human–natural systems

Human societies are transforming natural environments at an unprecedented rate through the consumption of natural resources, agricultural and urban expansion, and numerous other practices. The growing extent and magnitude of anthropogenic impacts has modified couplings within and among systems. Terrestrial vegetation, for instance, is a key interface between climate and terrestrial systems, through which the land surface and the atmosphere interact by exchanging water, energy, carbon (C), and aerosols. Deforestation, one of the most widely recognized types of human-driven land-use change, disrupts the rate of evapotranspiration and latent heat flux mediated by vegetation, causing rapid shifts in local temperature ranges and precipitation patterns (Lejeune *et al.* 2015). As the scale of deforestation increases, the number and intensity of interactions within (intracoupling) and between (pericoupling and telecoupling) systems also increase due to changes in atmospheric circulation resulting from the loss of vegetation. Although the effects of deforestation are generally perceived at the local scale, representation of deforestation in complex Earth system models indicates that shifts in forest cover have regional to global repercussions, leading to changes in seasonal precipitation in distant areas in both the Northern and Southern Hemispheres (Werth and Avissar 2005). Furthermore, in areas where land–atmosphere coupling is particularly robust, such as tropical forests, the intensity of this interaction can be transferred across scales, with small changes in vegetation cover producing disproportionate global effects (Lorenz and Pitman 2014).

Climate models based on a high greenhouse-gas emissions scenario (eg Intergovernmental Panel on Climate Change Representative Concentration Pathway 8.5) project that both the extent and intensity of land–atmosphere coupling will increase throughout most of the world (Dirmeyer *et al.* 2013). Given the role of terrestrial vegetation in regulating soil moisture, vegetation cover (or loss thereof) will therefore be even more

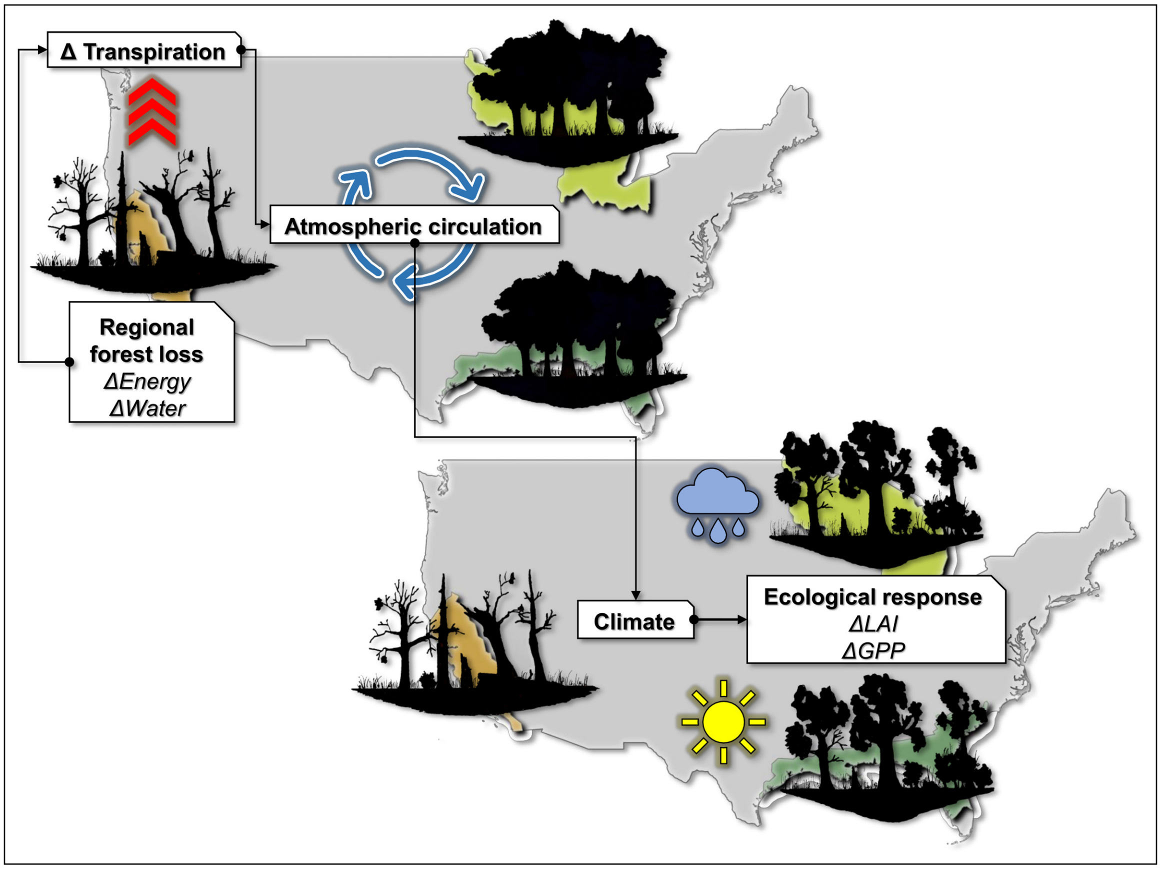

Figure 3. Illustration of an ecoclimatic teleconnection as a telecoupling process. In an Earth system model simulation, forest cover was removed from the Pacific Southwest domain of the National Ecological Observatory Network. The choice of this domain was motivated by the recent loss of tree cover in the region (an estimated ~130 million dead trees as of early 2018) in Southern California. Forest removal causes local changes in transpiration rates, influencing atmospheric circulation, which results in distant climate impacts that markedly affect leaf area index (LAI) and gross primary production (GPP) elsewhere (graphical interpretation of the model proposed by Swann *et al.* [2018]).

critical in mediating land–atmosphere feedbacks in the future. For example, it has been estimated that the complete loss of forest cover by tree die-off within the smallest of the domains of the US National Ecological Observatory Network (eg the Pacific Southwest domain, covering an area of 279,605 km^2) will alter gross primary production over the entire conterminous US by up to ±200 g C m^{-2} yr^{-1} (Figure 3; Swann *et al.* 2018). Consequently, the global effects of deforestation or other major forms of land-use/land-cover change may become more substantial than local or regional effects, which in turn could initiate cascading effects and induce new pericouplings and telecouplings among macrosystems (Wu *et al.* 2017).

Human-mediated movement of materials (eg food [Carlson *et al.* 2018], natural resources [Torres *et al.* 2017], energy [Fang *et al.* 2016], tourism [Chung *et al.* 2018]) from one location to another increases the number and intensity of metacouplings, which in turn increases the frequency of novel ecological consequences. For example, increasing occurrence of wildfires driven in part by climate change or other anthropogenic factors can produce pericouplings by transporting terrestrial particulate material directly into marine systems (Figure 4a). In 1997, high concentrations of iron deposited into adjacent seas as a result of Indonesian wildfires fertilized a red tide, leading to widespread coral die-offs in the region (Abram *et al.* 2003).

Pericoupling and telecoupling can also occur with pollutants. Pesticides, fertilizers, plastics, and other domestic or industrial wastes are often released and deposited in places far beyond the source location through atmospheric fractionation. Consequently, these chemical toxicants reach remote areas of the globe, such as polar regions (Zhang *et al.* 2013) and pristine mountain areas (Hageman *et al.* 2006). For example, mercury transported in the atmosphere can be deposited in mountain lakes, where it enters the local food web and accumulates in fish tissues consumed by humans (Eagles-Smith *et al.* 2014), prompting governmental regulations and warnings about fish consumption (USACE and EPA 2015).

The cumulative effects of metacouplings brought about by the movement and deposition of pollutants are often difficult to predict. In high-latitude regions, for instance, because anthropogenic global warming enhances the volatility of organic pollutants while also accelerating melting rates, snowmelt and the melting of glaciers will likely release and reactivate pollutants with enhanced toxicity (Noyes *et al.* 2009). Shifts in ocean circulation patterns could then recirculate these toxicants, promoting their accumulation in water, soils, and organisms (Schmittner *et al.* 2008). Similarly, anthropogenic aerosol emissions can modify cloud brightness, air quality, and rain chemistry (Likens *et al.* 1996), affecting the circulation of pollutants and particulate matter between terrestrial and aquatic ecosystems.

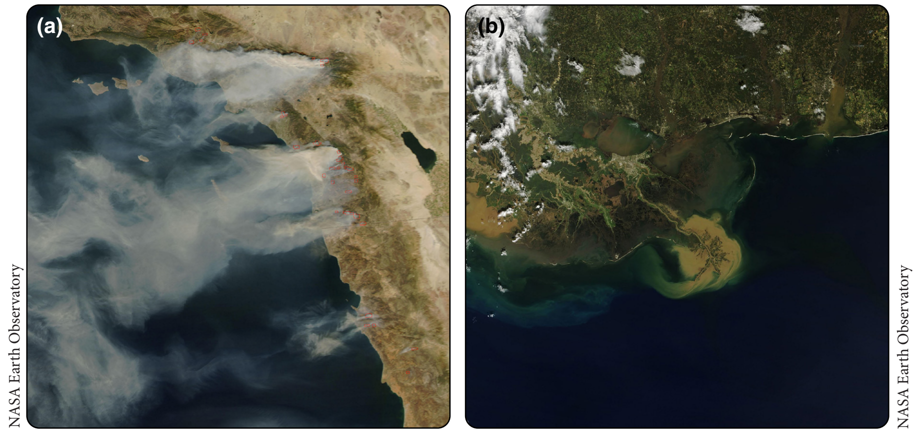

Figure 4. (a) Fires in California – from the Mexican border to north of Los Angeles in 2007, during a period of strong offshore winds – transported large amounts of particulate material to the Pacific Ocean. (b) Floods in Ohio in 2018 caused a terrestrial sediment plume in the Gulf of Mexico that covered over 300 km^2, including associated nutrients, as pericoupled by the Mississippi River.

Adjacency as an insufficient predictor of interactions among systems

As the frequency and intensity of telecouplings increase, geographic proximity becomes an insufficient predictor of the degree of interaction between systems. Here, we cite two examples in which telecoupling predominates over pericoupling, challenging Tobler's law. In non-tidally influenced rivers, gravity dictates a unidirectional water flow, and once nutrients enter the water, they are processed as they move downstream (from meters to over distances of tens to hundreds of kilometers; Figure 4b) through the watershed. Small streams form the interface between terrestrial and downstream aquatic habitats; this coupling was well-documented with a series of detailed nitrogen-15 (^{15}N)–nitrate releases in rivers across the North American continent (Mulholland *et al.* 2008). The ^{15}N–nitrate releases revealed the ways in which streams retain and release nutrients, influencing transport of terrestrial inputs to larger aquatic systems downstream and leading to nonlinear whole-system saturation dynamics that are a function of successive stream/river segments becoming saturated with upstream nutrients. The pericoupling of multiple streams within a watershed determines downstream water nutrient content, as each successive stream segment processes the materials (Helton *et al.* 2010).

Metacoupling of streamside (riparian) conditions to in-stream processes also occurs because materials become less coupled to nearby terrestrial habitats as they move downstream and more influenced by terrestrial–aquatic linkages upstream (ie "directional telecoupling"; Figure 4b). Consequently, riparian upstream conditions influence downstream characteristics, creating a type of nonlinear "shadow" effect of upstream conditions (Feijó-Lima *et al.* 2018). Riparian conditions in first-order streams explain more of the variance in water quality (eg total nitrogen, total phosphorus, pesticide concentration) at distant downstream sites than the riparian conditions of mid-size stream sites (Dodds and Oakes 2008; see Tromboni and Dodds [2017] for an exception). Surprisingly, this relationship was maintained even during seasons when many of the first-order streams were not flowing. These observations have practical implications; for example, the US Clean Water Rule (USACE and EPA 2015), which codifies linkages of small streams and wetlands through intermediate systems with larger water bodies in the US, relies on the concept of telecoupling.

A second example of adjacency as an insufficient predictor of the interaction strength relates to globalization and increased international trade. As humans migrate or travel across and between continents, they may intentionally or accidentally transport animals, plants, and microorganisms (Zhang *et al.* 2018). Increasing global trade over the past several decades has intensified the movement of organisms to unprecedented levels (Meyerson and Mooney 2007), resulting in changes in biodiversity patterns (Carrasco *et al.* 2017), as well as the composition and structure of ecological communities and their C or nutrient cycles (Ehrenfeld and Yu 2012). The 2020 outbreak of severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) is a recent example demonstrating the speed at which a local disease can become ubiquitous in a very short time due to human movement, creating new global socioeconomic and environmental dynamics, as well as ways in which humans have increased coupling of animal diseases to human health.

The homogenization of ecological communities is one of the most common consequences of telecoupling systems through the displacement of organisms. For instance, homogenization of freshwater fish communities occurs worldwide (Toussaint *et al.* 2016), and this trend is expected to increase as human pressures intensify, despite regulations to limit species movement across regions. As another example, populations of species in close proximity are expected to be more genetically similar than distant ones because adjacent populations should experience more natural genetic flow by dispersal. However, in Lake Michigan, distant populations of the invasive round goby (*Neogobius melanostomus*; Jude *et al.* 1992) connected by frequent ship transport are more similar genetically to each other than to their adjacent populations (LaRue *et al.* 2011).

Globalization and the redistribution of crops, pollinators, farm animals, pet species, exotic animals, and aquatic plants are all major causes behind the coupling of distant systems (López-Hoffman *et al*. 2010). The flow of nonnative organisms often generates ecological impacts that propagate along food webs and can eventually alter ecosystem properties and functioning of the receiving systems (Fei *et al*. 2014). Such impacts occur as a direct consequence of the introduction of nonnative species, or as a secondary consequence through cascading effects within an ecosystem. However, the strength and duration of the resulting telecoupling through organism displacement remains highly dependent on a species' ability to adapt to new abiotic conditions and to develop new competitive, symbiotic, or multitrophic interactions (Kueffer 2017).

Ecological–socioeconomic feedbacks

Connections across macrosystems produce feedbacks that in turn can affect pericoupling and telecoupling. Ecological feedbacks, such as those that occur between terrestrial environments and the atmosphere, have been investigated by ecologists and climatologists for decades, particularly in relation to the contribution that terrestrial vegetation provides in mitigating the climate warming driven by increased carbon dioxide (CO_2) emissions (Zeng *et al*. 2017). For example, the response of climatic systems to deforestation at the global scale may not always be cumulative, suggesting the existence of negative feedbacks at the land–atmosphere interface (Avissar and Werth 2005). Deforestation generally leads to higher temperatures and lower precipitation (Devaraju *et al*. 2015), and the active use of fires to clear large forested areas results in abrupt releases of CO_2 into the atmosphere (van der Werf *et al*. 2009). However, plants can respond to reduced water availability and rising CO_2 concentrations by increasing their water-use efficiency, which limits the effects of climatic changes on terrestrial vegetation (Keenan *et al*. 2013). In addition, ecoclimatic teleconnections often generate profound socioeconomic feedbacks, and therefore can be viewed as examples of telecoupling (Liu *et al*. 2019). Changes in crop and forest harvesting practices resulting from remote vegetation-driven climate change in turn create feedbacks locally and through ecoclimatic teleconnections on the coupled vegetation–climate–socioeconomic system (Ewers 2006).

Animal migrations between breeding and wintering sites, often spanning thousands of kilometers, also produce feedbacks. As the number of migrants moving from breeding sites to wintering sites increases, the number of individuals returning from wintering sites to breeding sites usually also increases, generating a positive feedback that hinges on the population's success in each location (Hulina *et al*. 2017). Furthermore, the numbers of migrants in both wintering and breeding sites are often affected by human activities, such as land use and hunting (intracouplings).

Humans act across much broader spatial scales than any other organism in ecological systems. In an increasingly metacoupled world, human activities have the potential to increase the number of feedbacks between local and distant places. Human-mediated feedbacks emerge as a consequence of international trade, foreign direct investments, tourism, policies, and regulations, such as payment for ecosystem services, among many others (Yang *et al*. 2018). For instance, China loans giant pandas (*Ailuropoda melanoleuca*) to zoos in both nearby (eg Japan) and distant (eg the US) countries for US$1 million per panda per year. One feedback resulting from this practice is that some revenues generated by loaning pandas to foreign zoos have been invested in efforts to conserve and restore panda habitat across their geographic range in China (Liu *et al*. 2015b). Thus, a potential benefit of applying the metacoupling framework to macrosystems biology is to offer a new means for placing feedbacks within broader socioeconomic and ecological contexts, and for predicting when or where a feedback may become strong enough to exhibit multi-scale effects.

Research opportunities and future directions

The world is increasingly connected through the movements of people, organisms, goods, and services (Liu *et al*. 2013), with human influence reaching even the most remote locations. We have altered the fundamental scaling properties of the natural world. As a result, the world is facing a moment unique in Earth's history, in which human activities have the potential to push ecosystems past tipping points and severely imperil ecosystem services (Dodds 2008). Macrosystems biology represents a promising area of research for advancing knowledge and developing sustainable solutions to these pressing global environmental challenges, and is particularly relevant to the large spatial scales at which humans affect natural environments. However, more research is needed to understand multi-scale connectivities. The examples discussed here highlight the fact that phenomena occurring at one location can have consequences at locations far from the source. Earlier conceptualizations (Heffernan *et al*. 2014; Rose *et al*. 2017) included the notion that macrosystems approaches should incorporate teleconnections and socioecological dynamics. The metacoupling framework presented here can be used to advance the field of macrosystems biology because it addresses a missing key component of human interactions within as well as between adjacent and distant systems. Our examples illustrate cases where sequential coupling and multi-scale system interactions are increasingly important due to the pervasive nature of human activities. They are, at times, exceptions to Tobler's first law, where proximity in space does not strengthen relationships, supporting the need for approaches that facilitate assessment of both local and distant interactions.

Although rapidly becoming more widespread within the subfield of macrosystems biology, research on metacoupled systems is still limited. However, macrosystems biology is only in the initial stages of incorporating metacouplings into predictive ecological science, and as such, gaps in knowledge of multi-scale connectivities – especially with respect to feedbacks that relate to spatially distant telecouplings – remain. Feedbacks are more difficult to identify and characterize than unidirectional fluxes, although feedbacks are at the heart of metacouplings, yielding unexpected ecological and socioeconomic outcomes. Research examining feedbacks and the array of drivers affecting different phenomena at regional to continental scales is therefore needed for this subfield to achieve maximum impact and relevance. In particular, we advocate for more quantitative, comparative, and integrative efforts to systematically analyze the agents, flows, feedbacks, causes, and effects across various metacoupled systems around the world.

To expand these research opportunities, we suggest combining theoretical exploration, modeling, observations, and experiments to promote conceptual advances while testing theoretical predictions against observations. To date, telecoupling has been quantified primarily through modeling, but model predictions still require field observations to determine if they can be differentiated from background noise. Identification of the most influential and sensitive metacoupling processes will provide a more integrative understanding of metacoupled systems across the globe, advancing scientific discoveries and facilitating effective solutions for global challenges. For example, a need exists from local to global scales to understand impacts of metacoupling on C dynamics in order to coordinate C management among all nations. It is important to work with relevant stakeholders to produce knowledge for advancing metacoupling science and to build a strong foundation for developing effective management plans.

An increasing number of funding agencies are promoting integrated human–environment programs and new international scientific networks are being developed to promote research on large-scale human–environment interactions. It is our hope that a deeper understanding of metacoupled systems will emerge from such interdisciplinary collaborations. These and other relevant efforts can further advance macrosystems biology to address global challenges and improve human well-being while promoting ecological sustainability worldwide.

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FrontiersEcoPics

Needle deformation in longleaf pines

Longleaf pine (*Pinus palustris*) is a fire-dependent conifer endemic to the southeastern US. Historically extending across 37 million hectares, the species' current range has declined by 97% since 1930. This contraction was largely due to extensive logging and urban development, as well as fire suppression, which further prevented natural regeneration. In the past few decades, federal agencies have subsidized landowner restoration of longleaf pine forests to promote biodiversity and conservation values. Longleaf pine ecosystems provide habitat to numerous endangered species and, as compared to ecosystems dominated by other southern pines, are more resilient to pests, pathogens, and extreme weather events.

Needles of this species are distinctly long, straight, and nestled in a fascicle. However, malformed needles, with an unusual zigzag appearance, have been documented in a few longleaf pine plantations. Recently, we observed this phenomenon in a 13-year-old longleaf pine plantation in Wilcox County, Georgia, at a site where natural longleaf pine had previously grown. No signs of insects or pathogens were detected on the needles, nor was there any other evidence of stress or damage on the trees.

The cause behind these malformations is unknown. Is it possible that the presence of such needles is indicative of a soil nutrient imbalance, altered water availability, or other site-specific characteristics (abiotic or biotic)? Most importantly, could this phenomenon adversely affect individual tree growth and possibly hinder critical ongoing restoration efforts of longleaf pine ecosystems?

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