



Shifts in ecological patterns and processes under global changes

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Ecosystems around the globe are facing increased demand for ecosystem services due to the fast-expanding human population. At the same time, they are challenged by the rapidly changing climate, extensive biological invasions, and dramatic land use changes, threatening their long-term sustainability or even their sheer existence. Many studies have documented the impacts of global change on ecosystems worldwide, such as rapid losses of biodiversity, structural and compositional changes, and shifts in plant

phenology, to name a few. Given that ecosystems near or far are inherently coupled biologically (e.g., species invasions and migration) and environmentally (e.g., biogeochemical cycling), changes in one ecosystem could have strong or weak effects on the others at various scales. More importantly, the aggregating effects from within- and cross-scale interactions of these changes could lead to dramatic regime shifts in ecological patterns when certain thresholds/tipping points are crossed. Understanding regime shifts—from landscape to continental scales—is thus not only scientifically intriguing but also crucial for our efforts to effectively manage ecosystems and to develop adaptive strategies. In this collection, we show the impacts of global changes (individually or collectively) on the shifts of existing ecological patterns or the emergence of novel ecological patterns in both terrestrial and aquatic systems from landscape to global scales. Given that ecological regime shifts are inherently complex phenomena, future studies should further seek multidisciplinary solutions while taking advantage of the rapid growth of big data and advanced analytical tools to enhance our capacity to predict future ecological patterns and processes under global changes.

Ecological systems, from remote pristine rainforests to urban greenery by our doorstep, have been crucial in sustaining all human activities (Daily and Matson 2008). However, these ecological systems are now changing rapidly in response to a range of forces: climate change (Walther et al. 2002; Fei

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et al. 2017), expanding urban population (Cincotta and Gorenflo 2011), and spreading of invasive species (Simberloff et al. 2013; Fei et al. 2014), to name a few. Consequently, there is an urgent need to understand how the patterns and processes of these ecological systems shift in response to these forces. These ecological shifts sometimes can be smooth in space and slow in time, and thus in principle, easy for human society to adapt to. However, there are types of ecological shifts that feature more abrupt transitions, and non-linear self-reinforcing feedbacks that, in theory, are much less predictable and potentially more difficult to adapt to. There is a growing recognition that this class of ecological regime shifts should be better studied: what drives the change, is there a threshold, are there early warning signals, and how do we manage resilience?

These questions are and will likely remain long-standing challenges in the field of ecology and earth system sciences. Perhaps an easier question to address is “*How are ecological regime shifts perceived in the academic literature?*”.

Using the Web of Science, we constructed a word cloud of keywords that are most frequently associated with regime shift in the field of ecology (Fig. 1). In this word cloud, we can identify high-frequency keywords such as *climate change*, *resilience*, *ecosystem management*, *stable states*, and *thresholds*. However, it is from the presence of some of the less prominent keywords -- *sustainability*, *catastrophic*, *stability*, *governance*, and *vulnerability*– that we can tell clearly this research topic is not merely ecologists’ niche interest but will continue to capture the attention of multidisciplinary researchers, policymakers, and the general public.

In this special issue, we included a collection of studies spanning a wide range of research systems and approaches. In the following text, we try to place these studies within the broader context of the development trend of this emerging field.

The evolution of study systems: from simple to complex

Based on a bibliometric analysis of 1906 publications (“regime shift*” and “ecolog*” in the Web of Science), we identify a series of temporal trends of study systems (Fig. 2). We found that the study

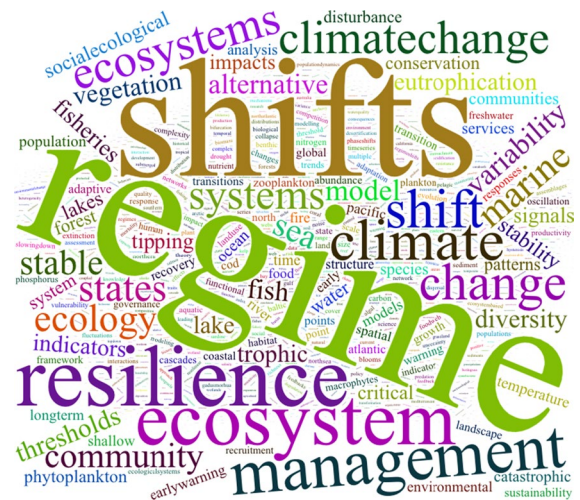


Fig. 1 Word cloud of ecological regime shifts. We compiled a database of 1906 relevant publications using search words “regime shift*” and “ecolog*” in the Web of Science database. From these publications, we extracted all keywords (including author self-identified keywords and WoS-designated keywords) to create this frequency-based word cloud (wordcloud2, R version 4.2.0)

of ecological regime shifts first started in marine systems, which is relatively homogenous compared to other ecological systems (e.g., phytoplankton and coral). Similarly, studies of lake and river systems, of which knowledge derived from marine systems can be ported over, quickly arise and become one of the most popular (Fig. 2).

In this special issue, we included two studies on aquatic systems, investigating how anthropogenic stressors might lead to systematic shifts in freshwater macroinvertebrate communities. In particular, Liu et al. (2023) used hierarchical clustering analysis to classify 190 taxa into six functional groups, based on similarities of their trait combinations (Liu et al. 2023). This clustering analysis allowed them to pinpoint which functional groups were tolerant to, and which groups were most impaired by urbanization, with implications for better coordinating conservation efforts. In another study, Xiong and colleagues found corroborating evidence using fish communities across a bigger landscape area (Xiong et al. 2023). They also found that human pressure (such as urbanization) can lead to a decrease in fish diversity. However, the study also reveals a deep connection between the resilience of the aquatic system and two important geographical

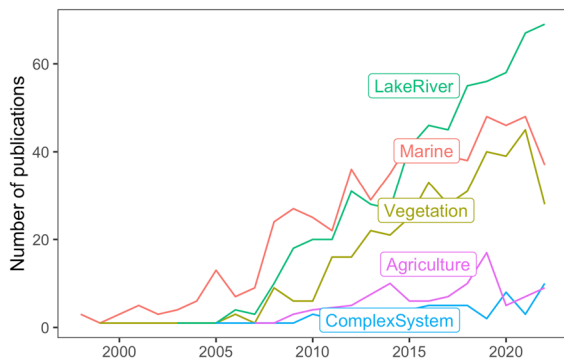


Fig. 2 Temporal trend of research systems. The early research on ecological regime shifts concentrated on marine systems (phytoplankton, coral, etc.), and later on, there was a rise of lake-river research (e.g., eutrophication) and land vegetation research. Most recently, there is a distinct rise in agricultural systems and more general studies of complex systems. Using a string detection algorithm, a paper is assigned to a study of certain systems if the abstract contains certain keywords. “Marine” is encoded when “marinelcoastalcorallreeflocan” is detected; “LakeRiver” is encoded when “lake/river” is detected; “Vegetation” is encoded when “vegetation|desert|grassland|forest|shrub|tundra” is detected; “Agriculture” is encoded when “agricultur.” is detected; and “ComplexSystem” is encoded when “complex system” is detected. The list of key terms used here is by no means exhaustive, and the frequency of key terms serves at best as a proxy. However, for the purpose of this editorial, this simplified bibliometric approach works well in revealing broad-stroke temporal patterns

factors: the presence of wetland and river-lake connectivity. Higher wetland extent and river-lake connectivity not only supports higher fish diversity but potentially makes the system more robust to human stress factors.

Terrestrial ecosystems, pristine or man-managed, are changing rapidly in response to a range of stressors, such as global warming, rising CO₂, land use, and biological invasions. For example, woodification/shrubification in grassy biomes over the past decade has become a trending topic (Myers-Smith et al. 2011; Stevens et al. 2017; García Criado et al. 2020). From the bibliometric trend analysis, we further reveal that agriculture systems are also picking up this trend, as a particular example of the coupled human-natural complex systems (Fig. 2).

In this special issue, we included a number of studies that focus on terrestrial ecosystems. Potter et al. (2023) examined the potential of Hawaii tropical forests undergoing regime shift by analyzing the prevalence of non-native species across age

structures, i.e., seedling, sapling, and canopy tree (Potter et al. 2023). Their findings revealed a delayed prevalence of non-native species in higher age classes, suggesting a potential canopy shift in the near future. The authors however, noted categorical differences in forest dynamics as a function of land ownership: forests on reserved land, public lands, and fenced localities were less impacted by non-native species.

In another study, Zheng and Lv studied the vegetation transition between mixed evergreen forests and Moso bamboo stands (Zheng and Lv 2023), a quite unique landscape pattern/process that remains poorly understood. Using a combination of remote sensing and boots-on-the-ground field sampling, the investigators identified a “non-random” bamboo strategy to encroach into forest patches. This across-scale study suggested Moso bamboo might have a system of strategies they deploy that enables their expansion, an understanding that is important for the predictions of future bamboo distributions across disturbed landscapes in southern China.

Forested wetlands represent another poorly-understood terrestrial ecosystem. In this collection, Wells et al. (2023) explored the potential driving factors of interannual variability (IAV) of net ecosystem exchange (NEE) in forested wetlands using the Total Ecosystem (TECO) model based on long-term ecological data from three loblolly pine plantations and a bottomland hardwood forest of contrasting stand age in wetland areas of the lower coastal plain of North Carolina. Their findings suggested that anomaly correlation between IAV of NEE and ecological processes served as a useful tool for assessing the specific drivers of annual variability in ecosystem-level carbon exchange, and incorporating dynamic ecological responses could help improve the models.

With our meteoric rise in engineering power, human civilization can instate regime shifts through ecological engineering across a short time scale over vast areas of land. In this special issue, we included a number of studies that focused on human-engineered ecosystems.

Shirkey et al. (2023) examined the effects of land cover, land use change, and land management on landscape carbon production in an agroecosystem using a cause-effect path analysis of socioecological latent variables, and found that anthropogenic processes contributed more to net primary production than environmental processes. In another study, Li

et al. (2023a) analyzed the impacts of ecological engineering on carbon uptake in northeastern China. They found that while both climate change and eco-engineering increased land greenness and carbon uptake, the impacts of ecological engineering overpowered the effects of climate change (e.g., warming and CO₂ fertilization). Other than carbon benefits, managed forest can greatly impact water quality in surrounding areas. Qiu et al. (2023) synthesized studies that looked into water quality as a function of forest cover and forest landscape patterns. Particularly interesting, they identify that mixed/natural forests are better than planted monoculture in improving water quality.

While excelling in productivity and providing a range of ecological benefits, human-instated vegetation shifts have historically suffered in system stability. From the Great Plains Shelterbelt Project after the 1930s Dust Bowl in the United States to the still ongoing Three-North Afforestation Program in northern China, protective forests are highly dependent on artificial regeneration and have problems with natural reproduction, with the result that most eco-engineered forests degrade once human efforts become absent (Zhu and Song 2021). Qi et al. (2023) tackled this very puzzle of regeneration bottleneck. They revealed that while existing trees had no problem producing cones or seeds, germination and sapling establishment proved to be a bottleneck step for tree regeneration largely due to high afforestation density.

Along this theme of system stability, Li et al. (2023b) investigated the relationship between biodiversity and stability through a forest-grassland transitional zone. While the biodiversity-stability relationship is an old topic, what is crucial and underexplored is the potential dependence of this relationship on the grain size of observation (Wu and Levin 1994; Wu and Loucks 1995). The insights gained from this research can potentially help researchers better scale up local understandings and practices to broader landscapes.

The evolution of methods: the age of data

Based on the same bibliometric analysis, we identified a series of temporal trends of methodology that are quite revealing. First of all, early studies of ecological

regime shifts tended to have modeling components (theoretical and/or computational), while early empirical work mainly relied on paleo-reconstruct approaches to study past regime shifts (e.g., the use of sediments). However, in the most recent decade (since 2010), studies that relied on dataset approach and remote sensing rose steeply (Fig. 3). We saw a similar trend in the collection of articles from this special issue: the dominant research methodology was based on remote sensing and datasets.

Using 20 years of continuous satellite observational data (Moderate Resolution Imaging Spectroradiometer, MODIS), Wang et al. (2023) discovered increasing savannization in Mainland Southeast Asia. The African savanna ecosystem has been a classical example of regime shifts, where forests and savanna hang in a subtle balance and exist as alternative stable states (Sankaran et al. 2005; Staver et al. 2011). What is less known, however, is that savanna as a biome can be observed across many continents. This study not only shed light on this previously overlooked area

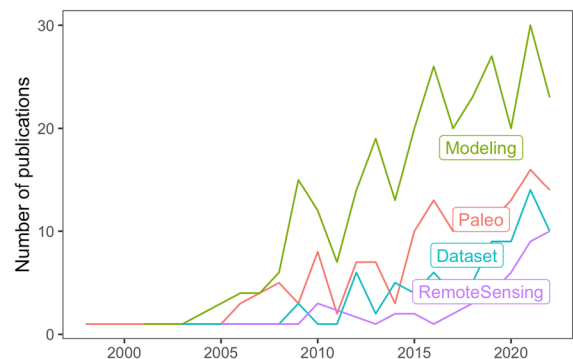


Fig. 3 Temporal trend of methodology in the study of ecological regime shifts. Early studies are predominantly theoretical modeling work, dominant until today. There is plenty of research using sediment records to paleo-reconstruct past regime shifts. More recently, there has been a steep rise in studies using database approaches and remote sensing approaches. A paper is assigned to be using a certain approach if the abstract contains certain keywords. “Modeling” is encoded when “mathematical modelmodelingsimulation|theoretical analysis|computational model|conceptual framework” is detected; “RemoteSensing” is encoded when “remote sensing|satellitelimagery” is detected; “Paleo” is encoded when “sediment” is detected; and “Dataset” is encoded when “dataset|meta-analysis|database” is detected. The list of key terms used here is by no means exhaustive, and the frequency of key terms serves at best as a proxy. However, for the purpose of this editorial, this simplified bibliometric approach works well in revealing broad-stroke temporal patterns

of Mainland Southeast Asia, but also further examined the differential driving force of savannization before and after 2009. The findings from this work served as a testament to the power of remote sensing. Indeed, the previously mentioned study by Li et al. (2023a) used the same MODIS imagery to tease out the impacts of eco-engineering with the effects of climate change on vegetation greenness and gross primary production.

Despite the strength of the remote sensing approach, integration of remote sensing with other complementary approaches can help overcome the limitations of remote sensing and prove to be quite fruitful. In this special issue, Jin et al. (2023) combined the strength of the MODIS products with a statistical model built for understanding land surface energy balance (SEBAL). They were able to elucidate how urbanization impacted the ecohydrological processes (focusing on evapotranspiration) at the watershed scale in southern China. By the same token, Zheng and Lv (2023) combined the strength of Landsat imagery with boot-on-the-ground surveys of microscale plant traits in their bamboo-forest boundary study, as mentioned earlier. The researchers set up transects and sampled bamboo stems, rhizomes, and fine roots to analyze their nutrient and carbon economy, something remote sensing could not reach.

Parallel to the exploding availability of remote-sensing products, we have witnessed a rapid increase in global datasets: homogenized, standardized, often organized by international teams, and fueled by the open-source culture. This rapid increase in datasets also comes with challenges. It can be overwhelming for new researchers to navigate the complex landscapes of datasets, let alone to select and use the suitable datasets to address the right ecological questions. In this special issue, Fusco et al. (2023) surveyed the landscape of datasets on invasive plant species, with the aim of enhancing “data literacy” and fascinating future research.

Advancements in data naturally necessities the development of more powerful statistical models. Lots of studies have attempted to use ecological models to make predictions for different ecological patterns and processes under global changes (Yates et al. 2018). However, modeling studies using empirical data may be biased to an unknown degree by lack of knowledge on the true ecological responses (Bouchet et al. 2019). Simulations with known ecological

patterns or processes provide a useful tool for better understanding and evaluating model predictions in various ecological scenarios. In this special issue, Song et al. (2023) examined historical climate-phenology coupling and assessed phenological mismatch under climate change using four simulation experiments fused with empirical data of plant flowering phenology in the eastern United States and bird reproductive phenology in Finland. Their findings suggested that the prediction-based approach effectively quantified different types of phenological mismatch, demonstrating a comparable and generalizable measure of phenological mismatch across ecological systems or scales.

Wang and Jackson (2023) compared seven commonly used species distribution modeling (SDM) approaches using simulated and empirical data: *linear discriminant analysis*, *multiple logistic regression*, *generalized additive models*, *boosted regression trees*, *random forests*, *artificial neural networks*, and *maximum entropy (MaxEnt) models*. These SDMs formed a spectrum ranging from traditional models that require more domain-knowledge assumptions to more recently developed approaches that are more data-hungry while agnostic of underlying mechanisms (e.g., *neural networks* and *MaxEnt*). This study demonstrated that the optimal choice of modeling approach lies in the balance of sample size and a range of other factors.

Wang and Jackson’s work offered a way to enhance the robustness of model predictions. By employing different suitable models for the same data, one can derive an ensemble of model understanding, potentially mitigating the limitations of using a single specific modeling approach. Other than cross-comparing among multiple model predictions, researchers can combine other approaches to obtain an integrative understanding of ecological regime shifts. For instance, using presence data from the literature, Liao et al. (2023) developed *MaxEnt* models to predict warming-induced shifts of ant distributions across the Tibetan Plateau. Given the lack of knowledge on model mechanisms and the propensity to over-fitting for *MaxEnt* approach (Wang and Jackson 2023), Liao et al. (2023) calibrated the macroscale *MaxEnt* predictions using in-situ ants observations from a long-term manipulation experiment.

Conclusions and future directions

Complexity and integration

Ecological regime shifts are inherently complex phenomena (Scheffer 2010) as the focal ecological systems are often coupled with other complex systems, being natural or socio-economical (Tromboni et al. 2021). The complex nature of regime shifts thus demands multidisciplinary perspectives and deep integration of various approaches. Empirical approaches, such as field sampling (Zheng and Lv 2023), traits measurement (Liu et al. 2023), periodic forest surveys (Potter et al. 2023), and manipulative experiments (Liao et al. 2023) are advantageous for gaining in-depth, mechanistic, local understanding. However, these approaches are often limited to site-specific studies due to logistic and time constraints. At the other end of the spectrum, big data approaches (e.g., Qiu et al. 2023) take advantage of existing knowledge (e.g., data-mining and database compiling) and excel in statistical sophistication. These approaches often can generate regional to global insights due to the scope, but are confined to what empirical evidence is already in place and may lack sufficient details. Remote sensing approaches (LaRue et al. 2023) can acquire new information across large areas with relatively high resolution and reasonably low cost, complementary to both the empirical and the big data approaches. For future research in this avenue, we argue that the integration of perspectives and approaches is essential to generate “well-rounded” insights into ecological patterns and processes.

Landscape scale as a bridge

A key feature of ecological complexity is the hierarchy of nested spatial and temporal scales involved (Levin 1992). At one end of the spectrum, we study micro-scale processes at a relatively short time scale to gain mechanistic understanding. For instance, investigation of photosynthetic response to warming in lab settings, measurement of root traits using minirhizotron, and fish growth response to urban-origin toxins, to name a few. At the other end of the spectrum, we deeply care about global-scale consequences and planetary impacts that happen at a much longer time scale, such as land carbon sinks

as a consequence of greening, global biogeochemical cycling of nitrogen pumped via plant roots, and global fish biodiversity as a function of land use practices. In between these two ends, we consider landscape ecological processes as a bridge of time and spatial scales. Landscape ecology deals with ecological patterns and processes across a range of tens to hundreds of kilometers (Wu 2000). We thus call for future research on ecological regime shifts to use the landscape scale as a bridge to link micro-scale understanding (e.g., physiological knowledge, traits, manipulation experiments, and lab experiments) with our planetary quest (land carbon sinks, climate extremes, etc.). We envision the advances through such efforts would enable us to more effectively predict future patterns or processes under global changes, and in turn, prepare us to better adapt in a rapidly changing world.

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