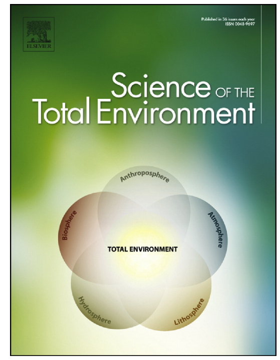

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David G. Angeler, Jani Heino, Juan Rubio-Ríos, J. Jesús Casas

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Connecting distinct realms along multiple dimensions: a meta-ecosystem resilience perspective

David G. Angeler[1,2,3,4,*], Jani Heino[5], Juan Rubio-Ríos[6,7], J. Jesús Casas[6,7,8]

[1] Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Box 7050, 750 07 Uppsala, Sweden

[2] School of Natural Resources, University of Nebraska—Lincoln, Lincoln, NE 68583, USA

[3] The Brain Capital Alliance, San Francisco, CA, USA

[4] IMPACT, The Institute for Mental and Physical Health and Clinical Translation, Deakin University, Geelong, Victoria, Australia

[5] Geography Research Unit, University of Oulu, P.O. Box 8000, FI-90014 Oulu, Finland.

[6] Department of Biology and Geology, University of Almería, 04120 Almería, Spain.

[7] Andalusian Centre for the Evaluation and Monitoring of Global Change (CAESCG), Almería, Spain.

[8] Universitary Institute of Water Research, University of Granada, 18003 Granada, Spain.

*Correspondence: david.angeler@slu.se

Abstract

Resilience research is central to confront the sustainability challenges to ecosystems and human societies in a rapidly changing world. Given that social-ecological problems span entire Earth system, there is a critical need for resilience models that account for the connectivity across intricately linked ecosystems (i.e., freshwater, marine, terrestrial, atmosphere). We present a resilience perspective of meta-ecosystems that are connected through the flow of biota, matter and energy within and across aquatic and terrestrial realms, and the atmosphere. We demonstrate ecological resilience *sensu* Holling using aquatic-terrestrial linkages and riparian ecosystems more generally. A discussion of applications in riparian ecology and meta-ecosystem research (e.g., resilience quantification, panarchy, meta-ecosystem boundary delineations, spatial regime migration and early warning indications) concludes the paper. Understanding meta-ecosystem resilience may have potential to support decision making for natural resource management (scenario planning, risk and vulnerability assessments).

Keywords: aquatic-terrestrial coupling, riparian ecosystems, meta-ecosystems, resilience, panarchy, spatial resilience, spatial regimes, scale, meta-social-ecological systems

1. Introduction

Planet Earth is facing a profound transformation in the Anthropocene, a new epoch in which human domination of Earth system processes leads to significant environmental change. The acceleration of global environmental change is causing biodiversity loss and increasing rates of species invasion, pollution, land use alterations, and climate change, among other impacts, and these may alter the structure and functioning of ecosystems and ecosystem service provisioning (Schulze & Mooney, 1993; Hooper et al., 2012; Moi et al. 2022). However, significant uncertainties remain about direct and indirect human impacts on ecosystem sustainability and resilience (Oliver et al., 2015; Wang et al., 2021).

There is a need to study environmental change impacts across different scales of space and time, not only within but also across distinct but connected ecosystems. A meta-ecosystem focus, which considers the flow of abiotic matter, organisms, and energy across spatially discrete but connected ecosystems (Loreau et al., 2003), can be useful in fundamental and applied research (Heino & Koljonen, 2022) and contribute to a better understanding of ecosystem resilience (Van Looy et al., 2019). Resilience research has taken center stage in aquatic (Pelletier et al., 2020), marine (Hughes et al. 2005) and terrestrial ecology (Nikinmaa et al., 2020), often with a focus on recovery after disturbances (Allen et al., 2019). However, knowledge of systemic resilience (i.e. ecological resilience; Holling, 1973) in meta-ecosystems is still scant (Fremier et al., 2015). Ecological resilience, which explicitly accounts for the complexity of ecosystems, can further understanding of the ecology, sustainability and resilience of meta-ecosystems.

Ecological resilience adds additional components to the many factors inherent in meta-ecosystem complexity and ecology (flows and subsidies of matter and energy, spatial connectivity, organism dispersal) (Gravel et al., 2016; Gounand et al., 2018a) (Figure 1). First, from a theoretical perspective, ecological resilience considers meta-ecosystems as an emergent phenomenon (Gunderson, 2000). Riparian ecosystems are examples of meta-ecosystems (Soininen et al., 2015; Burdon et al., 2020; Johnson et al., 2021; Osakpolor et al., 2021) constituted by atmospheric, terrestrial and aquatic components. The resilience of these meta-ecosystems emanate from the combination of the resilience of these individual constituents and would be incomplete by focusing on the resilience of either the aquatic, terrestrial or the atmospheric environments in isolation.

Second, from a more practical perspective, emergent phenomena have direct connection to non-linear often abrupt and irreversible change of ecosystems, which become of increasing conservation concern in a rapidly changing world (Sundstrom et al., 2023). Consider a shallow clear-water lake flipping to a turbid regime as a result of excessive nutrient loading (Scheffer & Jeppesen, 2007). This example demonstrates the existence of alternative regimes, shifts between these regimes, disturbance thresholds upon which these shifts become triggered and the frequently permanent stabilization of novel regimes (Suding et al., 2004; Baho et al., 2017). Ecological resilience accounts for all these facets, which is often presented in the ball-in-cup heuristic (Figure 1). Given that meta-ecosystems are affected by a range of anthropogenic disturbances such as those mentioned above, it is crucial for scientists, managers and other stakeholders to understand their vulnerability to these disturbances, their risk to be dislodged into novel (unknown), permanent regimes, and the ecology of such regimes after they have emerged in the landscape (Heino et al., 2021).

Third, directly following from the previous point, there is the need to quantify ecological resilience (Standish et al., 2014; Angeler & Allen, 2016; Dakos & Kéfi, 2022). Quantitative assessments can provide information about how to manage meta-ecosystems for keeping them in a configuration desirable for humans in terms of ecosystem service provisioning and stave off regime shifts (Biggs et al., 2009; Truchy et al., 2015). Quantitative studies may also identify vulnerability and risks of ecosystem stability and regime shifts

(Angeler et al., 2014; Gsell et al., 2016; Urrutia-Cordero et al., 2022), thereby assisting in preparing future scenarios characterized by alternative regimes relative to present-day regimes of entire social-ecological systems (Hermann et al., 2021). The earth faces the risk of the current Holocene climate shifting into a global “Hothouse Earth” (Steffen et al., 2018) with catastrophic consequences for entire systems of people and nature. This emphasizes the pressing need for resilience assessments across ecosystem types, including meta-ecosystems.

Critical for quantifying resilience is to account for hierarchical organization of complex systems of people and nature (Angeler & Allen, 2016), which operate at distinct spatiotemporal scales (Holling, 1992). These scales operate dynamically, such as aquatic insects emerging seasonally in streams (Ratif et al., 2018), and are connected in space and time. The linking of scales allows for flows of matter and energy, and information more generally (Little et al., 2022), from the highest to the lowest scales and vice versa, which is frequently portrayed in the panarchy model (Holling & Gunderson, 2002; Allen et al., 2014) and demonstrated with food webs wherein primary and secondary producers influence each other through food provisioning and consumption, respectively. In riparian ecosystems insect emergence from streams provides an example of fast cycling occurring within a few days in pool habitats (Drummond et al., 2015), relative to tree invasions changing the entire riparian landscape over longer periods (Van Oorschot et al., 2017). These processes critically influence each other through matter and energy flow across scales (Figure 1). Accounting for and identifying such scaling relationships objectively through measurement is central to depict ecological patterns and processes with highest realism and may provide a more nuance understanding of meta-ecosystem research considering scales implicitly. Also, the objective identification of key spatiotemporal scales may help to overcome inference limitations when scales are subjectively and arbitrarily defined by researchers (Angeler et al., 2016).

In this paper, we combine meta-ecosystem and resilience theories in a more inclusive, overarching perspective. We discuss aspects necessary for understanding meta-ecosystem resilience. These aspects relate to the objective assessment of dynamic, multi-scale system structure (panarchy), quantification of resilience and the identification of meta-ecosystem boundaries, and spatial regime movements. We exemplify these aspects using riparian ecosystems as a model of meta-ecosystems (e.g., Soininen et al., 2015), wherein ecological processes are connected across aquatic, terrestrial and atmospheric realms (Burdon et al., 2020; Tolkkinen et al., 2020; Johnson et al., 2021). Given that riparian ecosystems are among the systems most highly impacted by anthropogenic factors, the quantification of human influence on meta-ecosystem stability and resilience is crucial to formulate mitigation strategies (e.g., Schulz et al., 2015; Larsen et al., 2016; Dahlin et al., 2021; Manning and Sullivan, 2021). Meta-ecosystem resilience may hold potential to contribute to this information need and support management with scenario planning for potential alternative futures and risk and vulnerability assessments of meta-ecosystems to environmental change.

2. A meta-ecosystem resilience perspective

Applied and basic research needs to account for large spatial and inter-annual variation mediated by natural and anthropogenic factors operating at different scales of space and time in connected earth systems and their dynamics (Lafage et al., 2019). We suggest a framework for empirical analysis and management of meta-ecosystem resilience. This framework accounts explicitly for scaling structure envisioned in Holling's (1992) discontinuity theory. This theory has been applied in aquatic and terrestrial ecology (Nash et al., 2014), but has also been adopted for analyses in the social and social-ecological, including economic sciences (Garmestani et al., 2008a; Sundstrom et al. 2014, 2020). It has potential to unite ecological stability (recovery, robustness, variability, persistence) and vulnerability (Urrutia-

Cordero et al. 2022) aspects with complexity features (regime shifts, alternative regimes of ecosystems; Figure 1) for assessing systemic meta-ecosystem resilience.

Ecological patterns and processes often manifest as tangles resulting from the complex interaction of many system components, such as physicochemical processes (Loreau et al., 2003) and species interactions and/or dispersal between locations (Leibold et al., 2004). Such complexity is especially pronounced in meta-ecosystems such as riparian ecosystems (Gounand et al., 2018a; Qiu & Cardinale, 2020; Scherer-Lorenzen et al., 2022). This complexity includes, for instance, the relative importance and reciprocity of abiotic (dissolved nutrients, plant detritus) and biotic subsidies within riparian areas (e.g., Soininen et al., 2015). This is reflected, for example, in terrestrial invertebrates representing a large proportion (>50%) of the diet of drift-feeding fish, whereas emergent adult aquatic insects contribute a high proportion (25-100%) of energy and C to terrestrial vertebrate and invertebrate consumers (Baxter et al., 2005). Similarly, the variability of cross-ecosystem matter flows can be substantial, ranging over eight orders of magnitude (10^{-3} and 10^{5} g C m^{-2} $year^{-1}$ to recipient ecosystems; Gounand et al., 2018a). The differences in the nutritional quality of terrestrial and aquatic insects (Bartels et al., 2012; Schindler and Smits, 2017; Lafage et al., 2019) further exemplify high complexity. Furthermore, fluxes of abiotic matter and organisms across landscapes interacting with local processes – material processing, environmental filtering and biotic interactions – drive food web dynamics at different scales within a broader meta-ecosystem matrix (Polis et al., 2004). Such spatial dynamics of material and organisms, at least at intermediate intensity of between-site movements and dispersal, may have stabilizing effects of food webs, which in turn can ensure high community diversity (Moya-Laraño et al., 2014; Gravel et al., 2016). The migratory coupling of predator and prey may also influence these dynamics (Furey et al., 2018).

Quantifying scaling structure allows for disentangling such intricate ecological phenomena by assessing the distinct spatiotemporal scales at which one or more system components operate. That is, the resilience quantification builds on the postulate of ecological resilience theory that different ecological scales in single and multiple ecosystems are driven by different sets of biophysical factors (Figure 1) (Holling, 1992; Holling & Gunderson, 2002). Consider the distribution of rheophilic stream macroinvertebrates in riffles conditioned by local streamflow opposed to vast salmon home ranges spanning headwaters and marine environments determined by their reproduction ecology, or processes such as fast, local insect emergence and slowly changing riparian vegetation discussed above (Figure 1). Between these fast-local and slow-regional processes are intermediate dynamics, such as invertebrate community turnover resulting from upstream or downstream movements (Williams & Williams, 1993), leaf-litter decomposition (Tiegs et al., 2009), or downstream nutrient spiraling (Ensign & Doyle, 2006) resulting in several scale-specific phenomena. These scales are symbolized with multiple arrows connecting the aquatic and terrestrial realm within and between sites 1 and 2 in Figure 2. The different lengths of the arrows also represent a crucial aspect of meta-ecosystems; specifically, the degrees and magnitudes of connectivity in terms of matter flow and energy transfer, which can vary substantially (Tockner & Ward, 1998; Gounand et al., 2018a) and mediated by the drift paradox (Pachepsky et al., 2005). For instance, aquatic insects may play a minor role in dispersing fish-derived nutrients to riparian forests (Francis et al., 2006), while terrestrial subsidies to aquatic food webs can be substantial (Abrantes et al., 2013). These aspects will be discussed with more detail in the next section.

Critical for assessing these scaling features objectively through data are empirical analysis for which several methods are available (Stow et al., 2007). Methods widely used by ecologists (cluster analysis, classification and regression trees and their Bayesian implementations), and discontinuity analysis, based on kernel density estimation, more specifically used by resilience researchers (Barichievy et al. 2018), have potential to infer such scaling patterns by identifying independent aggregations or clusters of ecological units (sites, species) in the analyses. According to resilience theory, different aggregations arise because of the compartmentalization of ecological patterns and processes at different spatiotemporal scales (Holling, 1992; Holling & Gunderson, 2002). The number and sizes of aggregations therefore mirror wholesale scaling relationships in a system under study. Understanding overall scaling structure in a system is of applied relevance because it may provide a more nuanced picture of anthropogenic pressures affecting (riparian) ecosystem dynamics. Specifically, resilience may be more accurately evaluated through assessing at which scales in the system different forms of anthropogenic activities may be most pronounced or which scales are relatively impact free, thereby buffering against disturbances (Nash et al., 2014). Such buffering may occur through ecological dynamics at unaffected scales providing cross-scale resilience through compensation of lost functions at impacted scales. Consider subarctic and boreal lakes wherein specific groups of benthic macroinvertebrates fluctuate at decadal scales as a result of broad-scale ecological change, which is opposite to other groups of invertebrates that show temporal variation at shorter cycles where such change is not evident (Angeler et al. 2013).

These methods are useful for assessing scale when snapshot data are available. The assessment of scaling structure is also possible when monitoring data are available. For instance, time series and spatial analyses allow to identify different temporal fluctuation frequencies capturing fast to slow processes or discrete spatial extents covering small-scale to broad-scale patterns through modeling (Borcard et al. 2004; Legendre & Gauthier 2014; Baho et al. 2015). Such modeling also allows to account for directional flow of matter and energy inherent in meta-ecosystem dynamics using, for instance, canonical ordination techniques (Blanchet et al. 2011).

We propose that such methods can be applied for studying ecological patterns and processes at different scales in meta-ecosystems. For example, resilience may be assessed in a first step (Tier 1) in riparian ecosystems at the local site scale where aquatic and terrestrial habitats and the atmosphere are connected (Figure 2). It allows to objectively evaluate spatiotemporal scales at which features of these habitats such as leaf-litter fall and insect emergence are linked. For the purpose of our perspective, we consider this aquatic-terrestrial coupling as a vertical dimension of riparian ecosystems that expand up into the vegetation canopy and down into the hyporheic zone along the stream-riparian corridor (Dwire & Kauffman, 2003). In the next step, a longitudinal and lateral dimension may be included. That is, resilience may include different local sites along the stream corridor within a single riparian ecosystem to study how the aquatic, terrestrial and atmospheric components are linked longitudinally (stream flow, fish migration, insect flight) or laterally (runoff, nutrient leaching from land use, dispersal) (Figure 2). The lateral dimension can be further extended to study connectivity across different riparian ecosystems within and across watersheds connected through e.g., waterfowl migration and other abiotic and biotic processes, such as aerial transport of contaminants or dust particles from storms (Figure 3).

Assessing the scales of relevant ecosystem dynamics builds the foundation for measuring resilience. Several applications for meta-ecosystem ecology follow. Our examples are mutually inclusive and can inform each other. These examples are not exhaustive and meant to demonstrate the potential of meta-ecosystem resilience research.

3. Applications

3.1. Quantifying resilience of meta-ecosystems

The cross-scale resilience model (Peterson et al. 1998) builds on Holling's scaling ideas and allows to depict ecosystem complexity through the assessment of two resilience proxies: within-scale resilience (symbolized with the length of arrows within and between habitats in Figure 2) and cross-scale resilience (number of arrows; Figure 2). Originally, the cross-scale resilience model has a focus on biodiversity. That is, it examines the number of taxa associated with each scale and their functional traits. Determining how abundant, redundant and diverse ecological traits associated with species are within each scale provides the measure of within-scale resilience. The second resilience proxy, cross-scale resilience, derives from assessing diversity and functional redundancies (e.g., redundancy/complementarity of species within functional feeding guilds of invertebrates) across the identified scales in the system. Resilience theory posits that resilience increases with an increasing redundancy and diversity of functional attributes both within and across scales (Allen et al. 2005). This postulate can be tested for example in relation to extinction debts of species with long life-spans and turnover times in relation to ecological change (Vellend et al., 2006) and under paradoxical situations where environmental degradation (e.g., habitat fragmentation) can lead to an increase in biodiversity (Fahrig et al., 2019).

The cross-scale resilience model can be extended beyond biodiversity to include ecological variables related to organism dispersal, and the flow of matter and energy that characterize meta-ecosystems and riparian ecosystems more specifically (symbolized with arrows in Figure 3). Including such a range of variables is necessary to capture meta-ecosystem resilience as more than the sum of the resilience of its component aquatic, terrestrial and atmospheric parts. Being able to infer how abundant, redundant and diverse patterns of dispersal and matter and energy flow are, would provide insight into meta-ecosystem resilience. This is shown with a simplified example, which demonstrates meta-ecosystems with low and high resilience, respectively (Figure 4). This example inspires likely hypothetical differences between heavily anthropogenic *vs* near-pristine riparian areas demonstrated in Figure 3.

It is clear that quantifying meta-ecosystem resilience requires measuring multiple variables characterizing matter, organismal and energy flows in such ecosystems. Comprehensive data sets may, however, not be available for many, if not most, systems. This could limit management when fast protection and conservation decisions for multiple ecosystems are required. In such cases, starting with proxies of cross-ecosystem connectivity, such as pupal exuvial counts from emerged invertebrate communities (Raunio & Paasivirta, 2008; Manning & Sullivan, 2021; Roodt et al., 2022) or abiotic and biotic matter collected in pitfall or sticky traps (Herrera & Dudley, 2003; Carlson et al., 2016; Albertson et al., 2018) can be useful. Also, remote sensing of fishes and emergent insects and the application of radar techniques has shown potential to advance movement ecology and aeroecology (Stepanian et al. 2016; Hansen et al., 2020). Such proxies can be analyzed for scaling patterns imprinted in community structure (Nash et al., 2014). Community structure characterized by pupal exuviae or migration patterns obtained by remote sensing or radar may hold potential to preliminarily identify low *vs* high resilience conditions. Knowledge on resilience may be refined and improved sequentially by including more variables over time as they become available (Baho et al., 2017). This may help to gain better understanding of meta-ecosystem resilience and likely anthropogenic pressures affecting them.

3.2. Panarchy and meta-ecosystems

Panarchy theory builds on the previous point by adding explicitly dynamic system change, and connectivity across scales to spatiotemporal scaling (Holling & Gunderson, 2002). Panarchy has garnered interest across scientific disciplines (Gunderson et al., 2022), due to its recognition that there can be high uncertainty associated with system trajectories and how this uncertainty can be navigated (Allen & Holling, 2010; Sundstrom et al., 2023). Panarchy allows to envision complex systems change through their development in and movement between four distinct phases (Sundstrom & Allen, 2019) (Figure 5): ecosystem growth when the system adapts to prevailing social-ecological conditions (adaptation phase); maintenance when the ecosystem self-organizes in a specific regime (conservatism phase); system crash when its resilience is exhausted (collapse phase); and subsequent rebuilding of the system (reorganization phase). Collapse can entail the emergence of a novel system, such as when riparian forests succumb to the construction of water reservoirs.

The tenets of panarchy (hierarchical spatiotemporal scaling, dynamic system change and connectivity of scales) allow for portraying and potentially evaluating core features of meta-ecosystems (dynamic matter and energy flow, including organism dispersal, mediating ecosystems linkages). It has implication for basic understanding of meta-ecosystems. There is a potentially broad spectrum for applying panarchy to meta-ecosystem research. An exhaustive discussion is beyond the focus of this paper but a simplified example in the context of a global climate regime shift shall demonstrate this potential and the need for international collaborations beyond geopolitical frontiers.

Consider our current climate regime, the Holocene glacial-interglacial cycle, flipping into a ‘hothouse Earth regime’ (Steffen et al.; 2018), which exemplifies system collapse and reorganization at the highest level in this panarchy example. If this scenario becomes manifest, currently increasing magnitudes and frequencies of storms and droughts (Linder et al., 2010) may become a new normal in many areas of the planet. Such changes may spur long-range transport of aeolian dust from storms or smoke from wild-land fires which may affect meta-ecosystems at regional and local scales in the form of matter and nutrient input. This demonstrates cascading effects from the highest to intermediate to lowest scales in this panarchy example (Figure 5). Local and regional degradation of, for instance, riparian forests, may bolster erosion and reinforce long-range transport of matter and energy. This demonstrates cross-scale connectivity in the form of environmental effects at lower panarchy levels “percolating up” to highest levels.

There is a plethora of abiotic and biotic factors such as animal migrations, changing river flow, soil moisture, and water quality and quantity that make the patterns and processes of information flow within a meta-ecosystem panarchy even more complex. However, because panarchy allows to envision such complexity, it provides opportunities to identify management interventions for keeping meta-ecosystem panarchies as sustainable as possible. Specifically, management can be devised at scales that are amenable for interventions such as management of local riparian habitats. Panarchy allows to study how effective management outcomes at specific scales subsequently spread across scales in the entire panarchy (Angeler & Hur, 2023). Because panarchy envisions system adaptation and transformation, it allows management to consider both adaptive and transformative approaches. For instance, in riparian ecosystems a phase of collapse of a system regime undesirable for humans may be deliberately induced, followed by boosting and stabilizing the reorganization of a more desirable regime (Angeler & Allen, 2022). In the above example, revegetation of stream banks and terrestrial environments may bring about multiple desirable functional attributes such as curbing long-range matter transport and nutrient and pollution run-off from agricultural areas, provide habitat for organisms and promote biodiversity (Arimoto, 2001; Jellinek et al., 2019; Stutter et al., 2019). However, resilience-based management often targets ecosystem function and is therefore open to controversial approaches as, for instance, the use of exotic species for revegetation purposes when desirable ecosystem functions need to be managed for (Chaffin et al., 2016). Such approaches are not without risk and may lead to regime shifts with substantial ecological change and negatively affect ecosystems in the long run. The United States Superfund initiative, established by the Comprehensive

Environmental Response, Compensation, and Liability Act of 1980 (CERCLA), is a federal environmental program for ecological impact remediation that demonstrates the complexity influencing resilience-based management.

3.3. Delineating meta-ecosystem boundaries and track regime migration

There is an increasing number of resilience studies in ecology that extend the focus from single systems to the landscape scale (Cumming, 2011; Cushman & McGarigal, 2019; Rietkerk et al. 2021). Given the intricate patterns of connectivity within meta-ecosystems, it is often difficult to identify their extensions in regions and landscapes, as well as delineate them objectively. Consider riparian ecosystem along streams in agricultural areas where borders may be clearly identifiable. However, in vast floodplains with high variation of habitats and transitional gradients between them (ecotones), such borders may become blurry, complicating the identification of discrete regional and landscape-level processes mediating meta-ecosystem resilience.

The importance of landscape-level patterns and processes within and across discrete regional and landscape units has been emphasized in resilience concepts such as spatial resilience (Cumming, 2011; Allen et al., 2016) and spatial regimes (Sundstrom et al., 2017). Spatial regimes are a resilience-based conceptualization of traditionally used terms such as biomes or ecoregions (Bailey, 2009). Notably, these resilience concepts regard spatial units such as ecoregions and biomes as discrete spatial entities. Consider a temporary pond complex in a dryland agricultural environment relative to a remote waterscape of permanent lakes and streams in humid environments. Both ecosystem types differ substantially in their structure and functions resulting from land use and meteorological, climatic, and vegetation settings. They are a clear example of alternative spatial regimes. Spatial resilience and spatial regimes allow to delineate such discrete landscape units by identifying non-linear, sudden transitions that may be "hidden" in transitional gradients or ecotones (Sundstrom et al., 2017) (Figure 3). Identifying such spatial "regime shifts" can identify the extent of a meta-ecosystem. They can inform meta-ecosystem research when one set of complex tangles of physicochemical processes, species interactions and dispersal change to another set, resulting in distinct meta-ecosystem spatial regimes (riparian meta-ecosystems 1 and 2 in Figure 3). Assessing spatial meta-ecosystem regimes allows whether a meta-ecosystem (light-blue sketch in riparian ecosystem 1; Figure 3) consists of nested subunits (dark-blue sketches).

There is a vast potential of these concepts for studying meta-ecosystem resilience at the landscape scale. In addition to delineating meta-ecosystem boundaries there is potential to study how such boundaries expand, contract or move in the landscape following environmental change (Allen et al., 2022). That is, spatial regimes are not static entities in the landscape and can show non-linear, often abruptly changing boundaries and migrations at regional and continental scales due to social-ecological change, including climate warming (Roberts et al., 2019; 2022) and land-use change (Bailey, 2009; Ellis, 2021). Migrating spatial regimes are of conservation concern because once one ecosystem type (e.g., pristine riparian forest; Figure 3) becomes encroached by another type (e.g., anthropogenic landscape; Figure 3), ecological change at regional scales may become irreversible, ecological conservation costly, and protected areas unsustainable in the long run (Angeler et al. 2020).

Several tools have been recently suggested for warning of spatial transitions (Kéfi et al. 2014), including network-based indicators (Tirabassi et al., 2014), which build on a rich early warning signal literature (e.g., Scheffer et al., 2009; Dakos et al., 2015). In addition, regime boundary and migration detection (Allen et al., 2022) can be useful for assessing risks and vulnerabilities of migrating spatial regimes. These methods include spatial covariance and wombling (a method that avoids subjective, discrete classification schemes of ecological systems by estimating the probability of a given location being a spatial boundary between ecological entities). These methods have been used for studying spatial patterns and vulnerabilities to disease and invasive species spread (Carlin & Ma, 2007; Fitzpatrick et al., 2010), the spatial boundary detection of birds and butterfly communities across ecotonal gradients (Kent et al., 2013), the location of landscape barriers of gene flow and spatially distinct genotypes (Diniz-Filho et al., 2016), bird community and vegetation transitions in rangelands and grasslands (Uden et al., 2019; Roberts et al., 2022).

4. Discussion

We presented a resilience view of meta-ecosystems that, despite being preliminary and conceptual, may be broadly applied in connected systems of people and nature. A range of environmental contexts may be studied such as organic pollution (Calle-Martínez and Casas, 2006; Raunio et al., 2007), light pollution (Meyer & Sullivan, 2013), nanoparticle transport (Bundschuh et al. 2019), catchment land-use changes (Progar & Moldenke, 2009), climate warming (Greig et al., 2012; Cheney et al., 2019) and faunal-mediated spatiotemporal patterns of resource flow across aquatic-terrestrial boundaries (Bump et al., 2009) in riparian ecosystem research. This highlights the broad application potential for meta-ecosystem resilience studies, including not only biological aspects but also, for instance, ecotoxicological, hydrological, or geochemical issues pertaining to riparian ecosystems (e.g., Bundschuh et al., 2022; Roodt et al., 2022) and meta-ecosystem research more generally. We have discussed several opportunities for evaluating (spatial) meta-ecosystem resilience and presented tools for quantitative analyses.

We acknowledge that inference about meta-ecosystem resilience can be strengthened using complementary resilience-based methods that are based on power laws (Kerkhoff & Enquist, 2007; Garmestani et al., 2008a) and others that are not scale explicit (Table 1). These methods include Fisher Information (e.g., Eason et al., 2014; 2016), mathematical descriptors of non-local stability (Dakos & Kéfi, 2022), and early warning indicators of regime shifts (critical slowing down, variance, autocorrelation, skewness), although the results of the latter often need to be interpreted with care (Spanbauer et al., 2014; Dakos et al., 2015; Burthe et al., 2016). Other techniques including, for instance, dynamic factor analysis (Zuur et al., 2003), multivariate autoregressive state-space models (Taranu et al., 2018), network analyses (Mina et al. 2021), structural equation models (Andreazzi et al., 2023), and simulation studies (Albrich et al., 2020) may complement the toolbox for meta-ecosystem resilience assessments.

Resilience is perhaps best understood if scale-explicit and scale-implicit methods are combined with univariate and multivariate community structural and functional measures commonly used in ecology and indicators of ecological status used in management, including some proposed for riparian ecosystems (Burdon et al. 2020) (Table 1). For example, spatial regimes and resilience studies may consider how the synchrony of ecological patterns and processes over time weakens or strengthens resilience (Bêche et al., 2009; Walter et al., 2022). Molecular techniques increasingly complement biodiversity assessments based on morphology-based taxonomy and have potential to refine, for instance, understanding of a range of reactions to environmental change among species that contribute to the same ecosystem function (i.e. response diversity; Elmqvist et al. 2003). Scale-related assessments may help evaluating the role of terrestrial animals, such as insectivorous birds and bats, feeding on different size classes of emerged insects on meta-community resilience (Stenroth et al. 2015). Results from such studies can then be compared with other metrics such as abundance, which can be an important predictor for bat foraging in riparian forests (Fukui et al. 2006). Accounting for rare species which, due to their unique functional trait spectrum that often differs substantially from those of abundant species (Mouillot et al. 2013), can add importantly to adaptive capacity, which describes the ability of an ecosystem to respond to disturbances in ways to avoid shifts into an alternative regime (Angeler et al. 2019).

Evaluating meta-ecosystems using multiple lines of evidence in combination with increasingly powerful deep learning (artificial intelligence) algorithms, such as those already applied in a regime shift context (Bury et al., 2021), may provide robust inference mediating patterns and processes.

We conclude with highlighting that meta-ecosystems influence humans through, for example, ecosystem service provisioning (e.g., recreation, nutrient cycling) and are influenced by human activity (e.g., land-use change, pollution). This reciprocity leads to a meta-social-ecological system wherein crucial aspects of meta-ecosystem dynamics (matter, energy and information flow) are mediated by the intricate interplay of a range of factors related to human agency (Renaud et al., 2018). Integrating social factors into meta-ecosystem research would ultimately contribute to a holistic understanding of intricately linked ecosystems (Table1). For this, transdisciplinary collaborations among actors across spheres of society including scientists, politicians, managers and other private and public stakeholders is necessary. Such collaborations may broaden systems perspectives, allow for formulating and testing better hypotheses and further bolster strong inference (Gounand et al. 2018). Ultimately, research at the intersection of different knowledge domains may likely provide emerging knowledge (Johansson 2017), which can create novel ways to tailor resilience-based management schemes of riparian ecosystems and meta-ecosystems more generally. However, such an endeavor adds complexity and uncertainty, is highly resource and data demanding and currently challenged by methodological limitations (Sundstrom et al., 2023). Starting transdisciplinary work with too much or too little complexity may be susceptible to obscure relationships. The art of work at the intersection will therefore be to identify the proverbial “make things as simple as possible but not simpler” (Albert Einstein).

Accounting for such complexity is relevant in the context of current policy (e.g., European Water Framework Directive (2000/60/EC), Habitat Directive (Article 17), the

United States of America Clean Water Act, and the United Nations Sustainable Development Goals (https://sdgs.un.org/goals)). Policy and institutions are often rigid and not embracing enough the complex dynamics of nature mediating the resilience of ecological systems (Garmestani et al., 2008b; Craig, 2010). However, there is room for incorporating resilience-based thinking into policy to navigate meta-ecosystem sustainability in the fast-changing Anthropocene era (Garmestani et al., 2019). Emerging infectious diseases such as the recent Covid-19 pandemic being propagated across connected systems motivates this inclusion. Adaptive management, which is not without pitfalls, especially under low management controllability and high uncertainty (McLain & Lee, 1996), and scenario planning to envision meta-ecosystems and their ecosystem service provisioning in likely future alternative realities may be useful. Near-future environmental and ecological changes may, however, be difficult to predict, which means that multiple scenarios need to be considered for connected systems of people and nature (Hermann et al. 2021).

5. Conclusions

Meta-ecosystems are highly complex due to abiotic matter and energy flow, organism dispersal and migration, and connectivity patterns interacting across discrete spatial areas over time. In this paper, we provided a resilience perspective of meta-ecosystems and exemplified it with riparian ecosystems. We suggest how the evaluation of scaling structure, detection of meta-ecosystem boundaries and the movement of these ecosystems in space over time may refine basic knowledge of connected ecosystems and assist policy and management in better understanding and navigating accelerated social-ecological change in the Anthropocene.

6. References

Abrantes, K. G., Barnett, A., Marwick, T. R., & Bouillon, S. (2013). Importance of terrestrial subsidies for estuarine food webs in contrasting East African catchments. *Ecosphere*, *4*(1), 1-33.

Albertson, L. K., Ouellet, V., & Daniels, M. D. (2018). Impacts of stream riparian buffer land use on water temperature and food availability for fish. *Journal of Freshwater Ecology*, *33*(1), 195-210.

Albrich, K., Rammer, W., Turner, M. G., Ratajczak, Z., Braziunas, K. H., Hansen, W. D., & Seidl, R. (2020). Simulating forest resilience: A review. *Global Ecology and Biogeography*, *29*(12), 2082-2096.

Allen, C. R., Gunderson, L., & Johnson, A. R. (2005). The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems*, *8*(8), 958-966.

Allen, C.R., Holling, C.S. (2010). Novelty, adaptive capacity, and resilience. *Ecology and Society*, 15, 24

Allen, C. R., Angeler, D. G., Cumming, G. S., Folke, C., Twidwell, D., & Uden, D. R. (2016). Quantifying spatial resilience. *Journal of Applied Ecology*, *53*(3), 625-635.

Allen, C.R., Angeler, D.G., Chaffin, B.C., Twidwell, D. and Garmestani, A., 2019. Resilience reconciled. *Nature sustainability*, *2*(10), 898-900.

Allen, C. R., Angeler, D. G., Garmestani, A., Roberts, C. P., Sundstrom, S. M., Twidwell, D., & Uden, D. R. (2022). Applications of Spatial Regimes. In: Gunderson, L.H., Allen, C.R., Garmestani, A. (eds) *Applied Panarchy: Applications and Diffusion Across Disciplines*, pp. 94-115

Andreazzi, C. S., Martinez-Vaquero, L. A., Winck, G. R., Cardoso, T. S., Teixeira, B. R., Xavier, S. C., ... & D'Andrea, P. S. (2023). Vegetation cover and biodiversity reduce parasite infection in wild hosts across ecological levels and scales. *Ecography*, e06579.

Angeler, D. G., Allen, C. R., & Johnson, R. K. (2013). Measuring the relative resilience of subarctic lakes to global change: redundancies of functions within and across temporal scales. *Journal of Applied Ecology*, *50*(3), 572-584

Angeler, D. G., Allen, C. R., Birgé, H. E., Drakare, S., McKie, B. G., & Johnson, R. K. (2014). Assessing and managing freshwater ecosystems vulnerable to environmental change. *Ambio*, *43*, 113-125.

Angeler, D.G. and Allen, C.R., 2016. Quantifying resilience. *Journal of Applied Ecology*, *53*(3), pp.617-624.

Angeler, D. G., Allen, C. R., Barichievy, C., Eason, T., Garmestani, A. S., Graham, N. A., ... & Sundstrom, S. M. (2016). Management applications of discontinuity theory. *Journal of Applied Ecology*, *53*(3), 688-698.

Angeler, D. G., Fried-Petersen, H. B., Allen, C. R., Garmestani, A., Twidwell, D., Chuang, W. C., ... & Wonkka, C. L. (2019). Adaptive capacity in ecosystems. *Advances in Ecological Research* 60, 1-24

Angeler, D. G., Chaffin, B. C., Sundstrom, S. M., Garmestani, A., Pope, K. L., Uden, D. R., ... & Allen, C. R. (2020). Coerced regimes: management challenges in the Anthropocene. *Ecology and Society*, *25*(1), 1.

Angeler, D.G., & Allen, C.R. (2022) Scales of coercion: resilience, regimes, panarchy. In: Gunderson L, Allen CR, Garmestani A (Eds). Applied Panarchy: Applications and Diffusions Across Disciplines. Island Press; 2022. Pages: 77-93

Angeler, D. G., & Hur, R. (2023). Panarchy suggests why management mitigates rather than restores ecosystems from anthropogenic impact. *Journal of Environmental Management*, *327*, 116875.

Arimoto, R. (2001). Eolian dust and climate: relationships to sources, tropospheric chemistry, transport and deposition. *Earth-Science Reviews*, *54*(1-3), 29-42.

Baho, D. L., Futter, M. N., Johnson, R. K., & Angeler, D. G. (2015). Assessing temporal scales and patterns in time series: Comparing methods based on redundancy analysis. *Ecological Complexity*, *22*, 162-168.

Baho, D. L., Allen, C. R., Garmestani, A. S., Fried-Petersen, H. B., Renes, S. E., Gunderson, L. H. & Angeler, D.G. (2017). A quantitative framework for assessing ecological resilience. *Ecology and Society 22*(3), 17.

Bailey, R.G. (2009) Ecosystem Geography: From Ecoregions to Sites. 2nd edition. Springer.

Barichievy, C., Angeler, D. G., Eason, T., Garmestani, A. S., Nash, K. L., Stow, C. A., ... & Allen, C. R. (2018). A method to detect discontinuities in census data. *Ecology and Evolution*, *8*(19), 9614-9623.

Bartels, P., Cucherousset, J., Steger, K., Eklöv, P., Tranvik, L. J. & Hillebrand, H. (2012). Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology*, 93, 1173–1182.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. (2005). Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology*, 50(2), 201- 220.

Bêche, L. A., Connors, P. G., Resh, V. H., & Merenlender, A. M. (2009). Resilience of fishes and invertebrates to prolonged drought in two California streams. *Ecography*, 32(5), 778-788.

Biggs, R., Carpenter, S. R., & Brock, W. A. (2009). Turning back from the brink: detecting an impending regime shift in time to avert it. *Proceedings of the National Academy of Sciences*, *106*(3), 826-831.

Blanchet FG, Legendre P, Maranger R, Monti D, Pepin P. 2011. Modelling the effect of directional spatial ecological processes at different scales. *Oecologia*, 166, 357-368.

Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H. 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology*, 85, 826–1832.

Bump, J. K., Tischler, K. B., Schrank, A. J., Peterson, R. O., & Vucetich, J. A. (2009). Large herbivores and aquatic–terrestrial links in southern boreal forests. *Journal of Animal Ecology*, *78*(2), 338-345.

Bundschuh, M., Englert, D., Rosenfeldt, R. R., Bundschuh, R., Feckler, A., Lüderwald, S., ... & Schulz, R. (2019). Nanoparticles transported from aquatic to terrestrial ecosystems via emerging aquatic insects compromise subsidy quality. *Scientific Reports*, *9*(1):1567.

Bundschuh, M., Pietz, S., Roodt, A. P., & Kraus, J. M. (2022). Contaminant fluxes across ecosystems mediated by aquatic insects. *Current Opinion in Insect Science*, 50:100885.

Burdon, F. J., Ramberg, E., Sargac, J., Forio, M. A. E., De Saeyer, N., Mutinova, P. T., ... & McKie, B. G. (2020). Assessing the benefits of forested riparian zones: A qualitative index of riparian integrity is positively associated with ecological status in European streams. *Water*, *12*(4), 1178.

Burthe, S. J., Henrys, P. A., Mackay, E. B., Spears, B. M., Campbell, R., Carvalho, L., ... & Daunt, F. (2016). Do early warning indicators consistently predict nonlinear change in long-term ecological data?. *Journal of Applied Ecology*, *53*(3), 666-676.

Calle-Martínez D. & Casas J.J. (2006) Chironomid species, stream classification, and water quality assessment: The case of 2 Iberian Mediterranean mountain regions. *Journal of the North American Benthological Society*, 25, 465–476.

Carlin, B. P., & Ma, H. (2007). Bayesian multivariate areal wombling for multiple disease boundary analysis. *Bayesian Analysis*, *2*, 281-301.

Carlson, P. E., McKie, B. G., Sandin, L., & Johnson, R. K. (2016). Strong land-use effects on the dispersal patterns of adult stream insects: Implications for transfers of aquatic subsidies to terrestrial consumers. *Freshwater Biology*, *61*(6), 848-861.

Chaffin, B. C., Garmestani, A. S., Angeler, D. G., Herrmann, D. L., Stow, C. A., Nyström, M., ... & Allen, C. R. (2016). Biological invasions, ecological resilience and adaptive governance. *Journal of Environmental Management*, *183*, 399-407.

Cheney, K.N., Roy, A.H., Smith, R.F. & DeWalt, R.E. (2019). Effects of stream temperature and substrate type on emergence patterns of Plecoptera and Trichoptera from northeastern United States headwater streams. *Environ. Entomol.*, *48*(6), 1349-1359.

Craig, R. K. (2010). Stationarity is dead-long live transformation: five principles for climate change adaptation law. *Harv. Envtl. L. Rev.*, *34*, 9.

Cumming, G. S. (2011). Spatial resilience: integrating landscape ecology, resilience, and sustainability. *Landscape ecology*, *26*(7), 899-909.

Cushman, S. A., & McGarigal, K. (2019). Metrics and models for quantifying ecological resilience at landscape scales. *Frontiers in Ecology and Evolution*, *7*, 440.

Dakos, V., Carpenter, S. R., van Nes, E. H., & Scheffer, M. (2015). Resilience indicators: prospects and limitations for early warnings of regime shifts. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1659), 20130263.

Dahlin, K.M., Zarnetske, P.L.; Read, Q.D. Twardochleb, L.A., Kamoske, A.G., Cheruvelil, K.S., Soranno, P.A. (2021). Linking Terrestrial and Aquatic Biodiversity to Ecosystem Function Across Scales, Trophic Levels, and Realms. *Front. Environ. Sci*. https://doi.org/10.3389/fenvs.2021.69240.

Dakos, V., Carpenter, S. R., van Nes, E. H., & Scheffer, M. (2015). Resilience indicators: prospects and limitations for early warnings of regime shifts. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1659), 20130263.

Dakos, V., & Kéfi, S. (2022). Ecological resilience: What to measure and how. *Environmental Research Letters*, *17*(4), 043003.

Diniz-Filho, J. A. F., Soares, T. N., & de Campos Telles, M. P. (2016). Geographically weighted regression as a generalized Wombling to detect barriers to gene flow. *Genetica, 144*, 425-433.

Drummond, L. R., McIntosh, A. R., & Larned, S. T. (2015). Invertebrate community dynamics and insect emergence in response to pool drying in a temporary river. *Freshwater Biology*, *60*(8), 1596-1612.

Dwire, K. A., & Kauffman, J. B. (2003). Fire and riparian ecosystems in landscapes of the western USA. *Forest Ecology and Management*, *178*(1-2), 61-74.

Eason, T., Garmestani, A. S., & Cabezas, H. (2014). Managing for resilience: early detection of regime shifts in complex systems. *Clean Technologies and Environmental Policy*, *16*(4), 773-783.

Eason, T., Garmestani, A. S., Stow, C. A., Rojo, C., Alvarez-Cobelas, M., & Cabezas, H. (2016). Managing for resilience: an information theory-based approach to assessing ecosystems. *Journal of Applied Ecology*, 656-665.

Ellis, E.C. 2021. Land Use and Ecological Change: A 12,000-Year History. *Annual Review of Environment and Resources*, 46, 1-33.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., & Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, *1*(9), 488-494.

Ensign, S. H., & Doyle, M. W. (2006). Nutrient spiraling in streams and river networks. *Journal of Geophysical Research: Biogeosciences*, *111*(G4).

Fahrig, L., Arroyo-Rodríguez, V., Bennett, J. R., Boucher-Lalonde, V., Cazetta, E., Currie, D. J., ... & Watling, J. I. (2019). Is habitat fragmentation bad for biodiversity?. *Biological Conservation*, *230*, 179-186.

Fitzpatrick, M. C., Preisser, E. L., Porter, A., Elkinton, J., Waller, L. A., Carlin, B. P., & Ellison, A. M. (2010). Ecological boundary detection using Bayesian areal wombling. *Ecology*, *91*(12), 3448-3455.

Francis, T. B., Schindler, D. E., & Moore, J. W. (2006). Aquatic insects play a minor role in dispersing salmon-derived nutrients into riparian forests in southwestern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(11), 2543-2552.

Fremier, A. K., Kiparsky, M., Gmur, S., Aycrigg, J., Craig, R. K., Svancara, L. K., ... & Scott, J. M. (2015). A riparian conservation network for ecological resilience. *Biological Conservation*, *191*, 29-37.

Fukui, D. A. I., Murakami, M., Nakano, S., & Aoi, T. (2006). Effect of emergent aquatic insects on bat foraging in a riparian forest. *Journal of Animal Ecology*, *75*(6), 1252-1258.

Furey, N. B., Armstrong, J. B., Beauchamp, D. A., & Hinch, S. G. (2018). Migratory coupling between predators and prey. *Nature Ecology & Evolution*, *2*(12), 1846-1853.

Garmestani, A. S., Allen, C. R., & Gallagher, C. M. (2008a). Power laws, discontinuities and regional city size distributions. *Journal of Economic Behavior & Organization*, *68*(1), 209-216.

Garmestani, A. S., Allen, C. R., & Cabezas, H. (2008b). Panarchy, adaptive management and governance: policy options for building resilience. *Neb. L. Rev.*, *87*, 1036.

Garmestani, A., Ruhl, J. B., Chaffin, B. C., Craig, R. K., van Rijswick, H. F., ... & Allen, C. R. (2019). Untapped capacity for resilience in environmental law. *Proceedings of the National Academy of Sciences*, *116*(40), 19899-19904.

Gounand, I., Harvey, E., Little, C. J., & Altermatt, F. (2018a). Meta-ecosystems 2.0: rooting the theory into the field. *Trends in Ecology & Evolution*, *33*(1), 36-46.

Gounand, I., Harvey, E., Little, C. J., & Altermatt, F. (2018b). On embedding meta-ecosystems into a socioecological framework: a reply to Renaud et al. *Trends in Ecology & Evolution*, *33*(7), 484-486.

Gravel, D., Massol, F., & Leibold, M. A. (2016). Stability and complexity in model meta-ecosystems. *Nature Communications*, *7*(1), 1-8.

Greig, H.S., P. Kratina, P.L. Thompson, W.J. Palen, J.S. Richardson, and J.B. Shurin. 2012. Warming, eutrophication, and predator loss amplify subsidies between aquatic and terrestrial ecosystems. *Global Change Biology*, 18, 504–514.

Gsell, A. S., Scharfenberger, U., Özkundakci, D., Walters, A., Hansson, L. A., Janssen, A. B., ... & Adrian, R. (2016). Evaluating early-warning indicators of critical transitions in natural aquatic ecosystems. *Proceedings of the National Academy of Sciences*, *113*(50), E8089-E8095.

Gunderson, L. H. (2000). Ecological resilience--in theory and application. *Annual Review of Ecology and Systematics*, 31, 425-439.

Gunderson, L. H., Allen, C. R., & Garmestani, A. (Eds.). (2022). *Applied panarchy: applications and diffusion across disciplines*. Island Press.

Heino, J., Alahuhta, J., Bini, L. M., Cai, Y., Heiskanen, A. S., Hellsten, S., ... & Angeler, D. G. (2021). Lakes in the era of global change: moving beyond single-lake thinking in maintaining biodiversity and ecosystem services. *Biological Reviews*, *96*(1), 89-106.

Heino, J. & Koljonen, S. (2022) A roadmap for sustaining biodiversity and ecosystem services through joint conservation and restoration of northern drainage basins. *Ecological Solutions and Evidence*, 3, e12142.

Herrera, A. M., & Dudley, T. L. (2003). Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (Arundo donax) invasion. *Biological Invasions*, *5*(3), 167.

Herrmann, D., Schwarz, K., Allen, C., Angeler, D., Eason, T. and Garmestani, A., 2021. Iterative scenarios for social-ecological systems. *Ecology and Society*, *26(4)*, 8

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4, 1-23.

Holling, C. S. (1992). Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs*, *62*(4), 447-502.

Holling, C. S., & Gunderson, L. H. (2002). *Panarchy: understanding transformations in human and natural systems*. Washington, DC: Island Press.

Hooper, D.U. E.C. Adair, B.C. Cardinale, J.E.K. Byrnes, B.A. Hungate, K.L. Matulich, A. Gonzalez, J.E. Duffy, L. Gamfeldt, M.I. O'Connor (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, 486, 105-108.

Hughes, T. P., Bellwood, D. R., Folke, C., Steneck, R. S., & Wilson, J. (2005). New paradigms for supporting the resilience of marine ecosystems. *Trends in Ecology & Evolution*, *20*(7), 380-386.

Jellinek, S., Wilson, K. A., Hagger, V., Mumaw, L., Cooke, B., Guerrero, A. M., ... & Standish, R. J. (2019). Integrating diverse social and ecological motivations to achieve landscape restoration. *Journal of Applied Ecology*, *56*(1), 246-252.

Johansson, F. (2017). *The Medici Effect, with a new preface and discussion guide: what elephants and epidemics can teach us about innovation*. Harvard Business Review Press.

Johnson, R. K., Carlson, P., & McKie, B. G. (2021). Contrasting responses of terrestrial and aquatic consumers in riparian–stream networks to local and landscape level drivers of environmental change. *Basic and Applied Ecology*, *57*, 115-128.

Kéfi, S., Guttal, V., Brock, W. A., Carpenter, S. R., Ellison, A. M., Livina, V. N., ... & Dakos, V. (2014). Early warning signals of ecological transitions: methods for spatial patterns. *PloS one*, *9*(3), e92097.

Kent, R., Levanoni, O., Banker, E., Pe'er, G., & Kark, S. (2013). Comparing the response of birds and butterflies to vegetation-based mountain ecotones using boundary detection approaches. *PLoS One*, *8*(3), e58229.

Kerkhoff, A.J. and Enquist, B.J., 2007. The implications of scaling approaches for understanding resilience and reorganization in ecosystems. *Bioscience*, *57*(6), pp.489-499.

Lafage, D., E. Bergman, R. L. Eckstein, E. M. Osterling, J. P. Sadler, and J. J. Piccolo. 2019. Local and landscape drivers of aquatic-to-terrestrial subsidies in riparian ecosystems: a worldwide meta-analysis. *Ecosphere*, 10, e02697

Larsen, S., Muehlbauer, J. D., & Marti, E. (2016). Resource subsidies between stream and terrestrial ecosystems under global change. *Global Change Biology*, 22, 2489–2504. https://doi.org/10.1111/gcb.13182

Legendre, P., & Gauthier, O. (2014). Statistical methods for temporal and space–time analysis of community composition data. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1778), 20132728.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., ... & Gonzalez, A. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology letters*, *7*(7), 601-613.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., ... & Marchetti, M. (2010). Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management*, *259*(4), 698-709.

Little, C. J., Rizzuto, M., Luhring, T. M., Monk, J. D., Nowicki, R. J., Paseka, R. E., ... & Yen, J. D. (2022). Movement with meaning: integrating information into meta-ecology. *Oikos*, *2022*(8), e08892.

Loreau, M., Mouquet, N., & Holt, R. D. (2003). Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecology Letters*, *6*(8), 673-679.

Manning, D. W., & Sullivan, S. M. P. (2021). Conservation across aquatic-terrestrial boundaries: Linking continental-scale water quality to emergent aquatic insects and declining aerial insectivorous birds. *Frontiers in Ecology and Evolution*, *9*, 633160.

McLain, R. J., & Lee, R. G. (1996). Adaptive management: promises and pitfalls. *Environmental Management*, *20*, 437-448.

Meyer, L. A., & Sullivan, S. M. P. (2013). Bright lights, big city: Influences of ecological light pollution on reciprocal stream–riparian invertebrate fluxes. *Ecological Applications*, 23, 1322– 1330.

Mina, M., Messier, C., Duveneck, M., Fortin, M. J., & Aquilué, N. (2021). Network analysis can guide resilience-based management in forest landscapes under global change. *Ecological Applications*, *31*(1), e2221.

Moi, D.A., Lansac-Tôha, F.M., Romero, G.Q., Sobral-Souza, T., Cardinale, B.C., Kratina, P., Perkins, D.M., de Mello, F.T., Jeppesen, E., Heino, J., Lansac-Tôha, F.A. & Mormul, R.P. (2022) Human pressure drives biodiversity–multifunctionality relationships in large Neotropical wetlands. *Nature Ecology and Evolution*, *6*(9), 1279-1289.

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., ... & Thuiller, W. (2013). Rare species support vulnerable functions in high-diversity ecosystems. *PLoS biology*, *11*(5), e1001569.

Moya-Laraño J, Bilbao-Castro JR, Barrionuevo G, Ruiz-Lupión D, Casado LG, Montserrat M, Melián CJ, Magalhães S. 2014. Eco-evolutionary spatial dynamics: rapid evolution and isolation explain food web persistence. In: Moya-Laraño J, Rowntree J, Woodward G, Eds. Advances in ecological research, Vol. 50. Oxford: Academic Press. p 75–143.

Nash, K. L., Allen, C. R., Angeler, D. G., Barichievy, C., Eason, T., Garmestani, A. S., ... & Sundstrom, S. M. (2014). Discontinuities, cross-scale patterns, and the organization of ecosystems. *Ecology*, *95*(3), 654-667

Nikinmaa, L., Lindner, M., Cantarello, E., Jump, A. S., Seidl, R., Winkel, G., & Muys, B. (2020). Reviewing the use of resilience concepts in forest sciences. *Current Forestry Reports, 6*, 61-80.

Oliver, T.H., Isaac, N.J.B., August, T.A., Woodcock, B.A., Roy, D.B. & Bullock, J.M. (2015). Declining resilience of ecosystem functions under biodiversity loss. *Nat. Commun*., 6, 10122.

Osakpolor, S. E., Kattwinkel, M., Schirmel, J., Feckler, A., Manfrin, A., & Schäfer, R. B. (2021). Mini-review of process-based food web models and their application in aquatic-terrestrial meta-ecosystems. *Ecological Modelling*, *458*, 109710.

Pachepsky, E., Lutscher, F., Nisbet, R. M., & Lewis, M. A. (2005). Persistence, spread and the drift paradox. *Theoretical Population Biology*, *67*(1), 61-73.

Pelletier, M.C., Ebersole, J., Mulvaney, K., Rashleigh, B., Gutierrez, M.N., Chintala, M., Kuhn, A., Molina, M., Bagley, M. and Lane, C., (2020). Resilience of aquatic systems: review and management implications. *Aquatic Sciences, 82*, 44.

Peterson, G., Allen, C. R., & Holling, C. S. (1998). Ecological resilience, biodiversity, and scale. *Ecosystems*, *1*(1), 6-18.

Polis, G. A., M. Power, and G. R. Huxel, editors. 2004. Food webs at the landscape level. University of Chicago Press, Chicago, Illinois, USA.

Progar, R., and A. R. Moldenke. 2009. Aquatic insect emergence from headwater streams flowing through regeneration and mature forests in western Oregon. *Journal of Freshwater Ecology*, 24, 53–66.

Qiu, J., and B. J. Cardinale. 2020. Scaling up biodiversity–ecosystem function relationships across space and over time. *Ecology*, 101(11), e03166. 10.1002/ecy.3166

Raitif, J., Plantegenest, M., Agator, O., Piscart, C., & Roussel, J. M. (2018). Seasonal and spatial variations of stream insect emergence in an intensive agricultural landscape. *Science of the Total Environment*, *644*, 594-601.

Raunio, J., Paavola, R., & Muotka, T. (2007). Effects of emergence phenology, taxa tolerances and taxonomic resolution on the use of the Chironomid Pupal Exuvial Technique in river biomonitoring. *Freshwater Biology*, 52, 165–176.

Raunio, J., & Paasivirta, L. (2008). Emergence patterns of lotic Chironomidae (Diptera: Nematocera) in southern Finland and the use of their pupal exuviae in river biomonitoring. *Fundamental and Applied limnology* 170(4): 291-301.

Renaud, P. C., Roque, F. D. O., Souza, F. L., Pays, O., Laurent, F., Fritz, H., ... & Fabricius, C. (2018). Towards a meta-social-ecological system perspective: a response to Gounand et al. *Trends in Ecology & Evolution*, *33*(7), 481-482.

Rietkerk, M., Bastiaansen, R., Banerjee, S., van de Koppel, J., Baudena, M., & Doelman, A. (2021). Evasion of tipping in complex systems through spatial pattern formation. *Science*, *374*(6564), eabj0359.

Roberts, C. P., Allen, C. R., Angeler, D. G., & Twidwell, D. (2019). Shifting avian spatial regimes in a changing climate. *Nature Climate Change*, *9*(7), 562-566.

Roberts, C. P., Uden, D. R., Allen, C. R., Angeler, D. G., Powell, L. A., Allred, B. W., ... & Twidwell, D. (2022). Tracking spatial regimes in animal communities: Implications for resilience-based management. *Ecological Indicators*, *136*, 108567.

Roodt, A. P., Röder, N., Pietz, S., Kolbenschlag, S., Manfrin, A., Schwenk, K., ... & Schulz, R. (2022). Emerging Midges Transport Pesticides from Aquatic to Terrestrial Ecosystems: Importance of Compound-and Organism-Specific Parameters. *Environmental Science & Technology*, *56*(9), 5478-5488.

Scheffer, M., & Jeppesen, E. (2007). Regime shifts in shallow lakes. *Ecosystems*, *10*(1), 1-3.

Scheffer, M., Bascompte, J., Brock, W. A., Brovkin, V., Carpenter, S. R., Dakos, V., ... & Sugihara, G. (2009). Early-warning signals for critical transitions. *Nature*, *461*(7260), 53-59.

Scherer-Lorenzen, M., Gessner, M. O., Beisner, B. E., Messier, C., Paquette, A., Petermann, J. S., Soininen, J., & Nock, C. A. (2022). Pathways for cross-boundary effects of biodiversity on ecosystem functioning. *Trends in Ecology and Evolution*, 37, 454–467.

Schindler DE, Smits AP. 2017. Subsidies of aquatic resources in terrestrial ecosystems. *Ecosystems*, 20(1), 78–93.

Schulze, E. D., & Mooney, H. A. (1993). Biodiversity and Ecosystem Function. Berlin: Springer-Verlag.

Schulz R, Bundschuh M, Gergs R et al. (2015) Review on environmental alterations propagating from aquatic to terrestrial ecosystems. *Science of The Total Environment*, 538, 246–261.

Soininen, J., Bartels, P., Heino, J., Luoto, M. & Hillebrand, H. (2015) Toward more integrated ecosystem research in aquatic and terrestrial environments. *BioScience*, 65, 174-182.

Spanbauer, T. L., Allen, C. R., Angeler, D. G., Eason, T., Fritz, S. C., Garmestani, A. S., ... & Stone, J. R. (2014). Prolonged instability prior to a regime shift. *PLoS One*, *9*(10), e108936.

Standish, R. J., Hobbs, R. J., Mayfield, M. M., Bestelmeyer, B. T., Suding, K. N., Battaglia, L. L., ... & Thomas, P. A. (2014). Resilience in ecology: Abstraction, distraction, or where the action is?. *Biological Conservation*, *177*, 43-51.

Steffen, W., Rockström, J., Richardson, K., Lenton, T. M., Folke, C., Liverman, D., ... & Schellnhuber, H. J. (2018). Trajectories of the Earth System in the Anthropocene. *Proceedings of the National Academy of Sciences, 115*(33), 8252-8259.

Stenroth, K., Polvi, L. E., Fältström, E., & Jonsson, M. (2015). Land-use effects on terrestrial consumers through changed size structure of aquatic insects. *Freshwater Biology*, *60*(1), 136-149.

Stow, C., Allen, C. R., & Garmestani, A. S. (2007). Evaluating discontinuities in complex systems: toward quantitative measures of resilience. *Ecology and Society*, *12*(1).

Stutter, M., Kronvang, B., Ó hUallacháin, D., & Rozemeijer, J. (2019). Current insights into the effectiveness of riparian management, attainment of multiple benefits, and potential technical enhancements. *Journal of Environmental Quality*, *48*(2), 236-247.

Suding, K. N., Gross, K. L., & Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution*, *19*(1), 46-53.

Sundstrom, S. M., Angeler, D. G., Garmestani, A. S., García, J. H., & Allen, C. R. (2014). Transdisciplinary application of cross-scale resilience. *Sustainability*, *6*(10), 6925-6948.

Sundstrom, S. M., Eason, T., Nelson, R. J., Angeler, D. G., Barichievy, C., Garmestani, A. S., ... & Allen, C. R. (2017). Detecting spatial regimes in ecosystems. *Ecology Letters*, *20*(1), 19-32.

Sundstrom, S. M., & Allen, C. R. (2019). The adaptive cycle: More than a metaphor. *Ecological Complexity*, *39*, 100767.

Sundstrom, S. M., Allen, C. R., & Angeler, D. G. (2020). Scaling and discontinuities in the global economy. *Journal of Evolutionary Economics*, *30*(2), 319-345.

Sundstrom, S.M., Angeler, D.G., Bell, J., Hayes, M., Hodbod, J., Jalalzadeh-Fard, B., Mahmood, R., VanWormer, E. & Allen, C.R. Panarchy theory for convergence. *Sustainability Science,* https://doi.org/10.1007/s11625-023-01299-z

Taranu, Z. E., Carpenter, S. R., Frossard, V., Jenny, J. P., Thomas, Z., Vermaire, J. C., & Perga, M. E. (2018). Can we detect ecosystem critical transitions and signals of changing resilience from paleo-ecological records?. *Ecosphere*, *9*(10), e02438.

Tiegs, S. D., Akinwole, P. O., & Gessner, M. O. (2009). Litter decomposition across multiple spatial scales in stream networks. *Oecologia*, *161*, 343-351.

Tirabassi, G., Viebahn, J., Dakos, V., Dijkstra, H. A., Masoller, C., Rietkerk, M., & Dekker, S. C. (2014). Interaction network based early-warning indicators of vegetation transitions. *Ecological Complexity*, *19*, 148-157.

Tockner, K., & Ward, J. V. (1999). Biodiversity along riparian corridors. *Large rivers*, *11*(3), 293-310.

Tolkkinen, M., Heino, J., Ahonen, H.K.A., Lehosmaa, K. & Mykrä, H. (2020) Streams and riparian forests depend on each other: a review with a special focus on microbes. Forest Ecology and Management 462: 117962.

Truchy, A., Angeler, D.G., Sponseller, R. A., Johnson, R. K., & McKie, B. G. (2015). Linking biodiversity, ecosystem functioning and services, and ecological resilience: towards an integrative framework for improved management. *Advances in Ecological Research* 53, 55-96).

Uden, D. R., Twidwell, D., Allen, C. R., Jones, M. O., Naugle, D. E., Maestas, J. D., & Allred, B. W. (2019). Spatial imaging and screening for regime shifts. *Frontiers in Ecology and Evolution*, *7*, 407.

Urrutia-Cordero, P., Langenheder, S., Striebel, M., ... & Hillebrand, H. (2022). Integrating multiple dimensions of ecological stability into a vulnerability framework. *Journal of Ecology*, *110*(2), 374-386.

Van Looy, K., Tonkin, J.D., Floury, M., Leigh, C., Soininen, J., Larsen, S., Heino, J., Poff, N.L., Delong, M., Jähnig, S.C., Datry, T., Bonada, N., Rosebery, J., Jamoneau, A., Ormerod, S.J., Collier, K.J. & Wolter, C. (2019) The three Rs of river resilience: Resources, Refugia and Recruitment. *River Research and Applications*, 35, 107-120.

Van Oorschot, M., Kleinhans, M. G., Geerling, G. W., Egger, G., Leuven, R. S. E. W., & Middelkoop, H. (2017). Modeling invasive alien plant species in river systems: Interaction with native ecosystem engineers and effects on hydro-morphodynamic processes. *Water Resources Research*, *53*(8), 6945-6969.

Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., & Hermy, M. (2006). Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology*, *87*(3), 542-548.

Walter, J. A., Castorani, M. C., Bell, T. W., Sheppard, L. W., Cavanaugh, K. C., & Reuman, D. C. (2022). Tail-dependent spatial synchrony arises from nonlinear driver–response relationships. *Ecology Letters*, 25(5), 1189-1201.

Wang, S., Isbell, F., Deng, W., Hong, P., Dee, L. E., Thompson, P., & Loreau, M. (2021). How complementarity and selection affect the relationship between ecosystem functioning and stability. *Ecology*, 102(6), e03347.

Williams, D. D., & Williams, N. E. (1993). The upstream/downstream movement paradox of lotic invertebrates: quantitative evidence from a Welsh mountain stream. *Freshwater Biology*, *30*(2), 199-218.

Zuur, A. F., Tuck, I. D., & Bailey, N. (2003). Dynamic factor analysis to estimate common trends in fisheries time series. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(5), 542-552.

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Conflict of Interest

The authors declare that no conflicts of interest exist.

Data availability

No data were used for this study

Author contribution

DGA conceived the study and wrote the paper. All authors contributed to idea development and the writing.

Table 1: Overview summarizing aspects of and approaches for studying meta-ecosystem resilience integrating resilience and meta-ecosystem research (riparian ecology) considering streams, rivers, lakes and wetlands from local to regional scales.

Aspect	Measurements	Proxies	Approaches/Tools	Application
From water to land	Aquatic invertebrates with terrestrial stage	Exuvial counts, emerged communities Taxonomic structure and functional traits analyses (redundancy, diversity, abundance), fatty acids, stoichiometry, stable isotopes	Emergence traps, sticky tapes, aquatic habitat sampling, matter/energy flow (Meta)community ecology, biodiversity research, spatial resilience and regimes (spatial synchrony, non-stationary change)	Management, indicator development, assessment of human pressures (climate change, agriculture, pesticides, pollution, biodiversity loss, dams, channelization)
From land to water	Egg deposition combined with DNA-based identification, (in)organic matter deposition, terrestrial species (e.g. spiders) subsidizing aquatic food webs,	Resilience assessments: *Scale explicit* (Within-scale resilience, cross-scale resilience); *Scale implicit*	Time series modeling, discontinuity analysis (Gap rarity index, Cluster analysis, BCART), Fisher Information, Wombling, mathematical descriptors, early warning signals	Implications for alternative regimes, thresholds, adaptive capacity, regime shifts, early warning (risk) indication, ecosystem vulnerability

From water to land and back	Life cycles and biotic interactions within and across the aquatic-terrestrial interface, waterfowl and fish migration	Assessments of multiple aquatic and terrestrial communities	Network analyses, metacommunity analysis, hydrological and geomorphological modeling	Spatial connectivity, habitat fragmentation, nutrient transport
Social-ecological factors	Human agency, landuse decisions, ecosystem service provisioning	Economic models, societal transformation, technology development, digitalization	Environmental policy (Water Framework Directive, Habitat Directive), Sustainable Development Goals, stakeholder and public engagement, environmental education and awareness	

Figure legends

Figure 1 Ecological resilience presented with the ball-in-cup heuristic, which demonstrates core features such as alternative regimes (different cups), regime shifts (the ball rolling from one cup to the next) and adaptive capacity (ecological processes and memory which allows the system to stay in the same regime after disturbances; symbolized with dotted arrows). Spatiotemporal scaling explicit in ecological resilience is demonstrated with scale-specific examples pertaining to meta-ecosystems (these examples are not exhaustive) and the panarchy heuristic portraying dynamic change at each scale and interconnectedness of scales.

Figure 2: Merging ecological resilience and meta-ecosystem research. The model shows the compartmentalization of ecological patterns and processes at distinct spatiotemporal scales at local sites within a riparian ecosystem (e.g., aquatic-terrestrial coupling) (symbolized with dark blue and purple arrows, respectively). These sites exemplify areas with different land use and hypothetical resilience patterns (low (site 2) *vs* high (site 1)). It also shows how compartmentalized ecological patterns and processes across sites may influence meta-ecosystem resilience regionally (e.g. connectivity, dispersal, nutrient runoff, riparian species invasions). The model emphasizes a “vertical dimension” (vertical arrows) and a “horizontal dimension” (horizontal arrows) which allow for a two-tier assessment of resilience (see text).

Figure 3: Schematic of two spatial regimes delineating two (riparian) meta-ecosystems, in near-pristine and anthropogenic settings, respectively, with contrasting ecological organization (patterns of connectivity, resource and organism flows). Such regimes can be assessed with spatial resilience analysis. They allow for finding sudden change in spatial ecological configurations in ecotonal gradients. They also allow assessing for hierarchical

structuring (dark-blue meta-ecosystem subunits nested in the light-blue “overall” meta-ecosystem). The schematic also presents the influence of atmospheric processes resulting from long-range transport of industrial contaminants and particles from storms.

Figure 4: Examples demonstrating high and low meta-ecosystem resilience. The high-resilience case exemplifies redundant selected meta-ecosystem attributes within and across scales. The low-resilience case shows the lack of and limited redundancy of attributes.

Figure 5: Schematic of a meta-ecosystem panarchy connecting local, regional and global scales. The model is demonstrated with a potential climate regime shift altering matter and energy flow across these scales. Selected examples of meta-ecosystem alterations are shown for each scale. The figure is a modified version adapted from Angeler and Allen (2022).

Figure 1

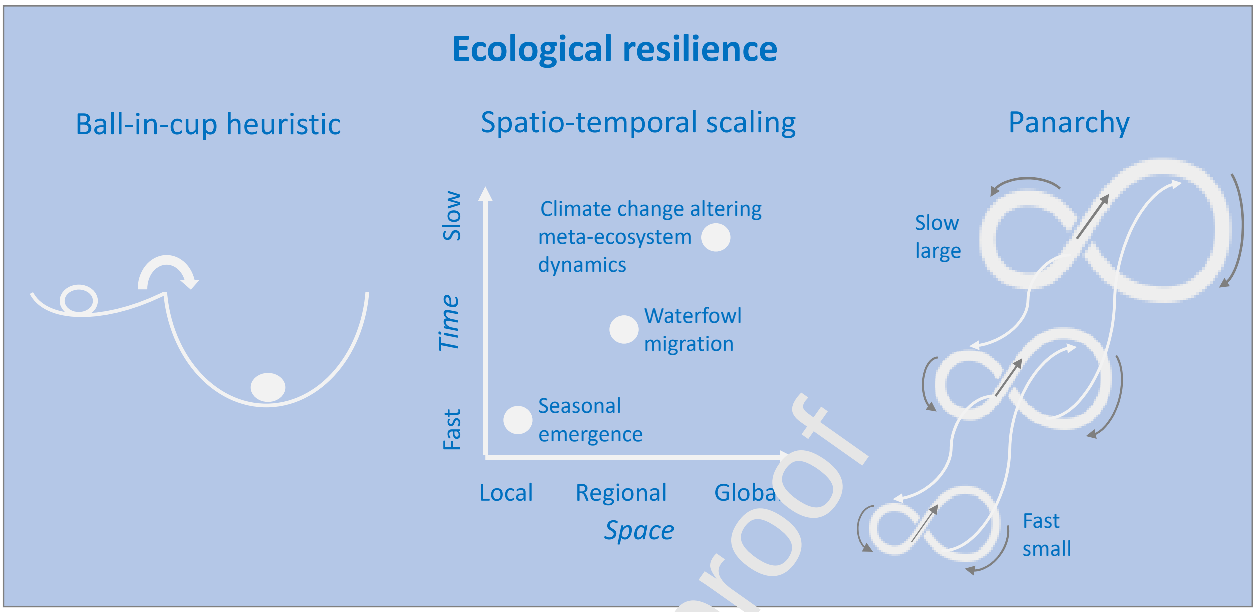

Ecological resilience
Ball-in-cup heuristic
Spatio-temporal scaling
Panarchy
Slow
Time
Fast
Climate change altering meta-ecosystem dynamics
Waterfowl migration
Seasonal emergence
Local
Regional
Globa
Space
Slow large
Fast small

Figure 2

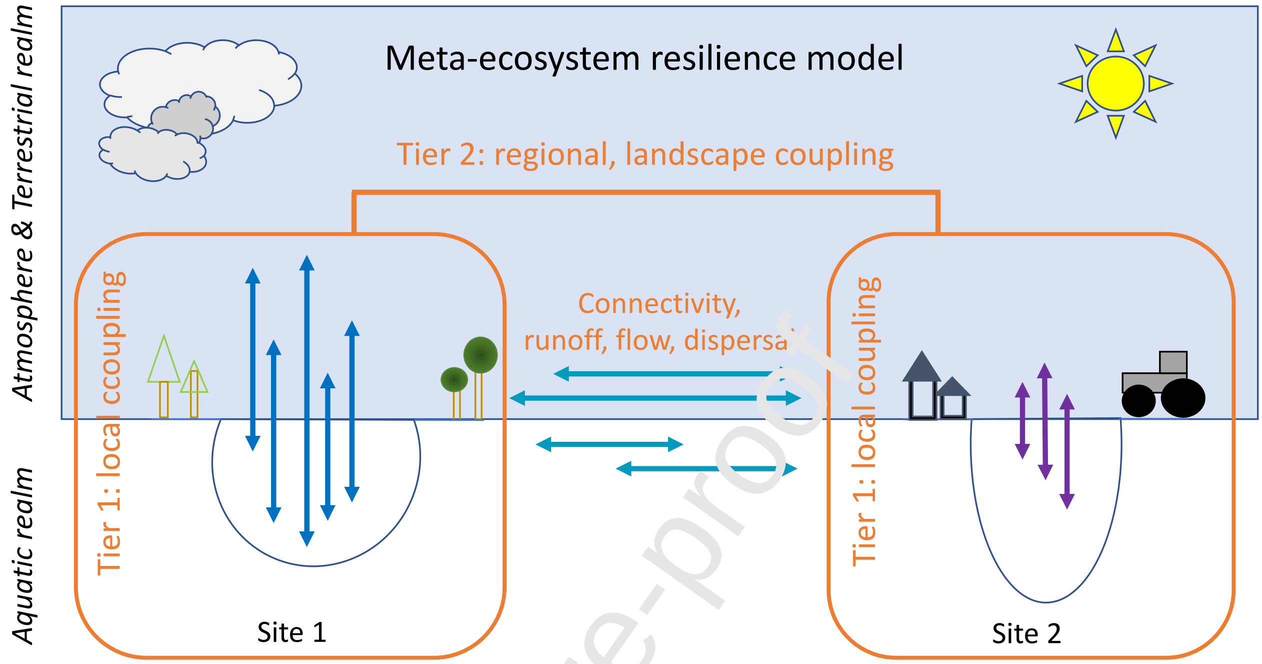

Atmosphere & Terrestrial realm
Aquatic realm
Meta-ecosystem resilience model
Tier 2: regional, landscape coupling
Tier 1: local ccoupling
Connectivity,
runoff, flow, dispersal
Tier 1: local coupling
Site 1
Site 2

Figure 3

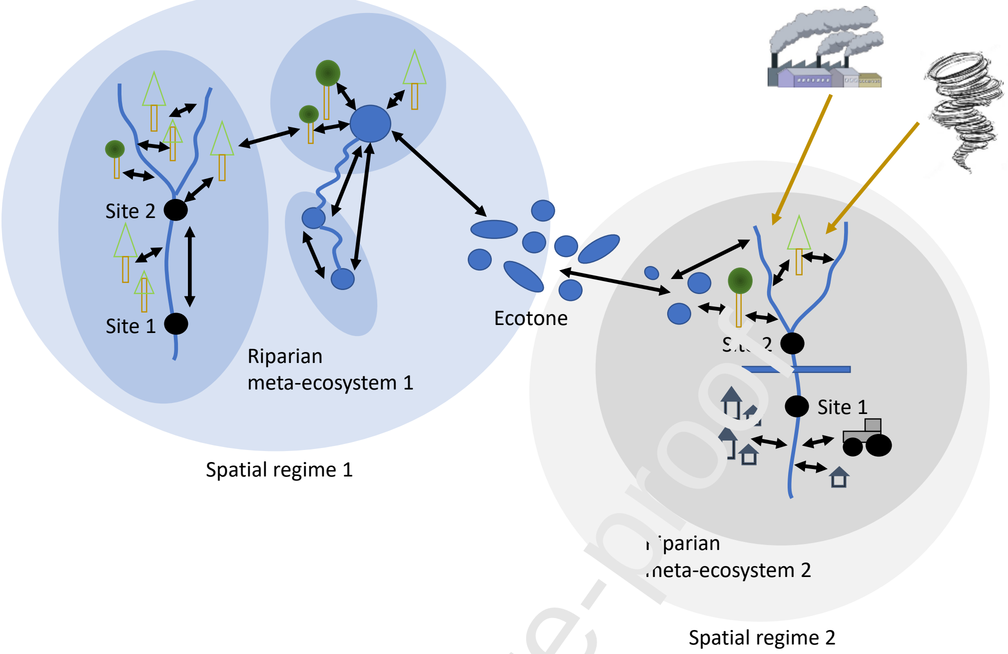

Site 2
Site 1
Riparian
meta-ecosystem 1
Spatial regime 1
Ecotone
Site 2
Site 1
Riparian
meta-ecosystem 2
Spatial regime 2

Figure 4

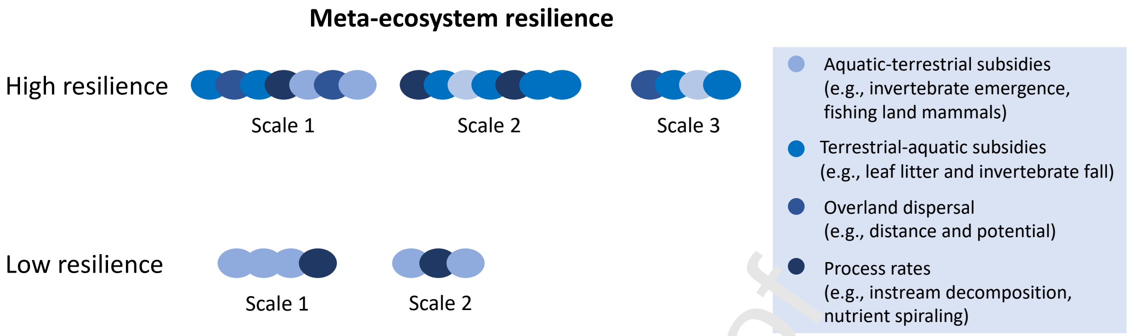
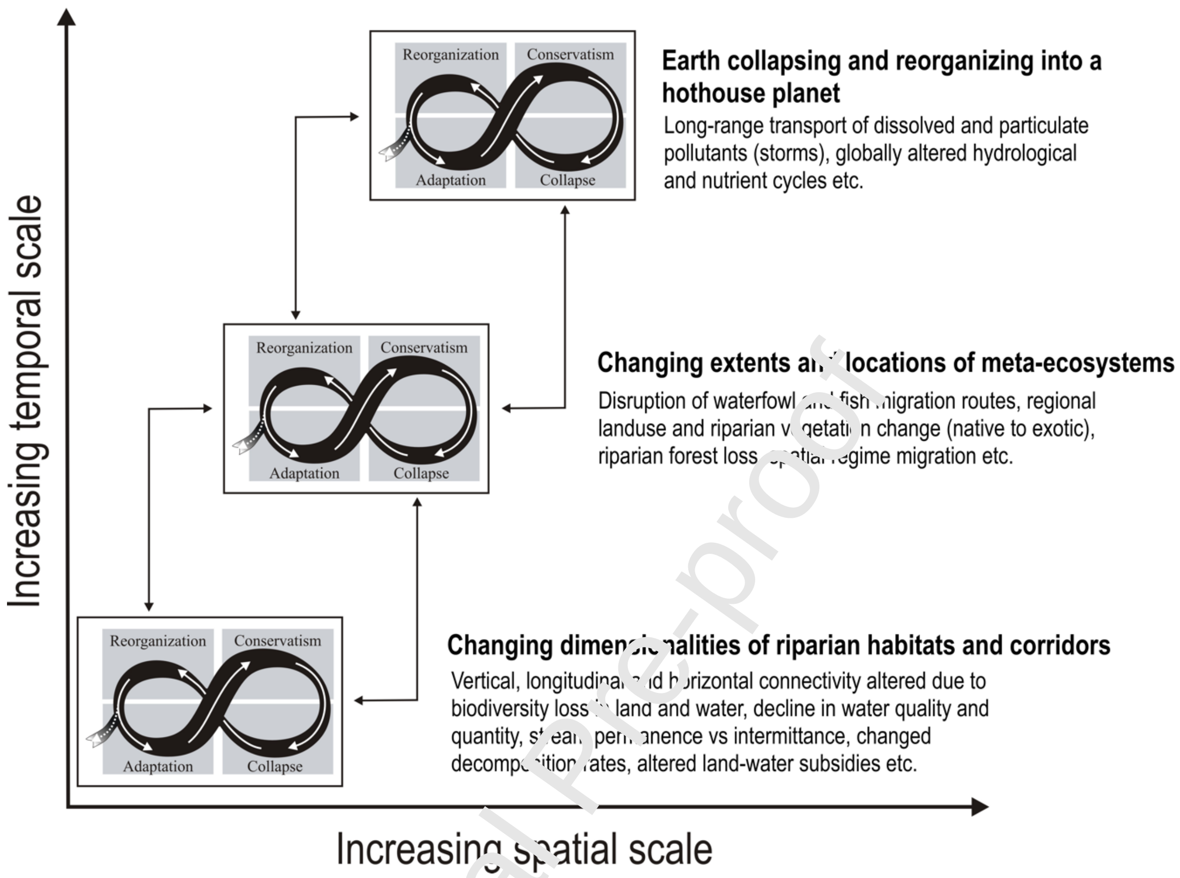

Meta-ecosystem resilience
High resilience
Scale 1
Scale 2
Scale 3
Low resilience
Scale 1
Scale 2
Aquatic-terrestrial subsidies
(e.g., invertebrate emergence, fishing land mammals)
Terrestrial-aquatic subsidies
(e.g., leaf litter and invertebrate fall)
Overland dispersal
(e.g., distance and potential)
Process rates
(e.g., instream decomposition, nutrient spiraling)

Figure 5

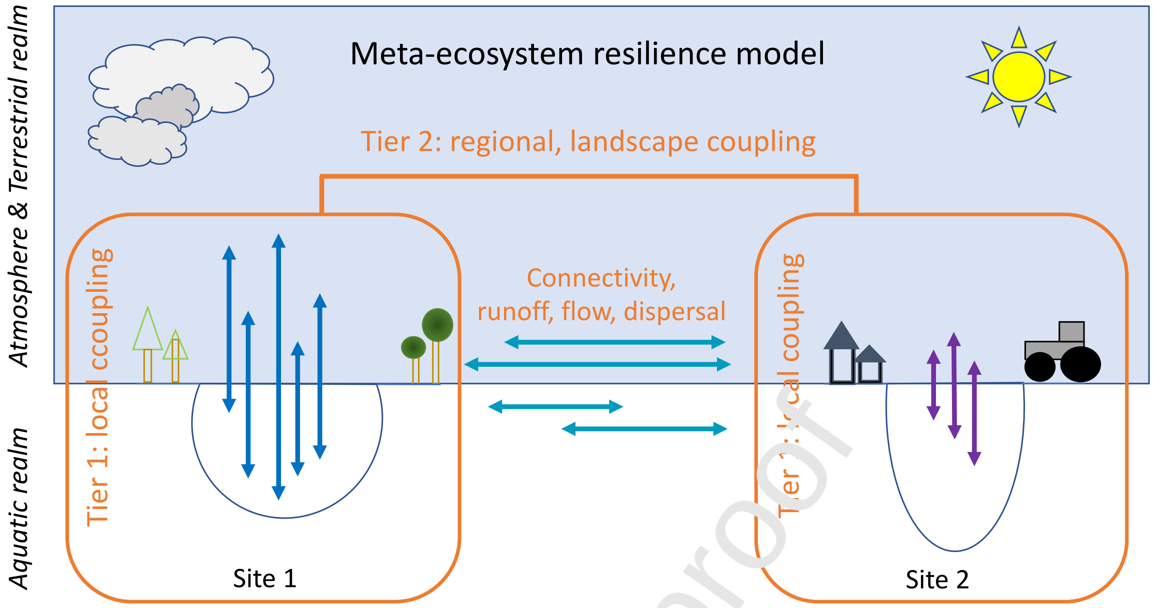

Reorganization
Conservatism
Adaptation
Collapse
Earth collapsing and reorganizing into a hothouse planet
Long-range transport of dissolved and particulate pollutants (storms), globally altered hydrological and nutrient cycles etc.
Changing extents ar locations of meta-ecosystems
Disruption of waterfowl fish migration routes, regional
landuse and riparian v getati n change (native to exotic),
riparian forest loss egime migration etc.
Changing dimen nalities of riparian habitats and corridors
Vertical, longitudina d h rizontal connectivity altered due to
biodiversity loss land and water, decline in water quality and
quantity, st ea per anence vs intermittance, changed
decomp ition ates, altered land-water subsidies etc.
Increasing temporal scale
Increasing spatial scale

Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Graphical abstract



A meta-ecosystem resilience model showing biotic and abiotic linkages across distinct spatiotemporal scales

Highlights

- A novel resilience perspective of meta-ecosystems is presented
- The model builds on ecological resilience
- Applications include resilience quantification, panarchy, meta-ecosystem boundary delineations, spatial regime migration and early warning indications