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Tipping points and multiple drivers in changing aquatic ecosystems: A review of experimental studies

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Abstract

Natural ecosystems are experiencing unprecedented rates of change due to anthropogenic activities and global change, leading to either gradual changes in a given response or tipping points. While the tipping point concept has been tested in an array of habitats since the 1960s, the spatiotemporal superposition of multiple drivers in different ecosystems needs to be considered when investigating the response of species, communities, populations, and ecosystems along environmental gradients. Here, we (1) develop a historical and current perspective of tipping point studies in terrestrial, freshwater, and marine ecological systems; (2) portray the research effort in different freshwater and marine habitats; and (3) explore the results of experimental studies focusing on tipping points measured at the individual, communities, ecosystem level, as well as ecosystem functions and services in a context of single and multiple stressors. The number of studies mentioning the concept of tipping points increases every year, but very few studies have specific objective to identify them. Even fewer studies consider how the addition of another stressor into an ecosystem may alter a tipping point. In addition, many studies investigated multiple responses, but only one-fourth (7 out of 28) of them concentrate their effort on multiple biological or ecological levels of complexity. This review allowed us to identify shortcomings in this research field and propose ways to make this ecological concept anew.

Human population growth and activities trigger gradual and sudden changes in natural habitats that impose constraints on organisms (Scheffer 2009; Halpern et al. 2019). Environmental pressures arising from human activities, commonly defined as drivers (Vinebrooke et al. 2004), influence biogeochemical, hydrological, and ecological processes locally and globally (Folke et al. 2004). Impacts of human activities are ubiquitous and occur in an array of marine (e.g., coral reefs, kelp forests, and seagrass) (Hoegh-Guldberg et al. 2007; Waycott et al. 2009; Filbee-Dexter and Scheibling 2014), freshwater (e.g., lakes) (Carpenter et al. 1985; Woodward et al. 2010), and terrestrial ecosystems (Zeng et al. 1999; Yue et al. 2017; Rilling et al. 2019), leading to their degradation and even their collapse (i.e., trophic cascades leading to local extinctions) (Scheffer et al. 2001; Folke et al. 2004; Brook et al. 2008; Estes et al. 2011). The effects of temperature and turbidity on seagrass meadows or the impact of heatwaves and ocean acidification on coral reefs are two well-documented examples of how an environmental factor may lead to the collapse of key species in an ecosystem when this factor exceeds its natural range of variation and exceeds (species) tolerance levels (Hoegh-Guldberg et al. 2007; Jorda et al. 2012; Brown et al. 2013).

With the increase of human footprints on natural ecosystems, two main scenarios that are not mutually exclusive have been observed: (1) synergistic and antagonistic interactions (i.e., nonadditive effects) resulting from a spatiotemporal superposition of multiple drivers (Folt et al. 1999; Crain

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et al. 2008; Côté et al. 2016) and (2) tipping points deriving from unprecedented rates of change in terrestrial and aquatic environments (Brook et al. 2008; Steffen et al. 2011). While multiple-driver research attempts to understand and predict driver interaction (Orr et al. 2020), research on tipping points seeks to identify a point where an abrupt shift between alternative ecosystem states occurs (Dakos et al. 2019). Both scenarios, interactions and tipping points, affect responses at different biological or ecological organization levels, from physiological processes to populations, communities, ecosystem functioning (e.g., biogeochemical fluxes), and services (e.g., food security), leading to substantial environmental impacts and complexify conservation and management decisions (Forbes et al. 2017). It is now clear that identifying nonlinear responses and interacting stressors is crucial to provide guidelines for managers and conservation planning (Côté et al. 2016). Furthermore, both concepts can provide useful information on when and how acting upon a set of environmental drivers is necessary to maximize conservation efforts (Côté et al. 2016).

The theory of tipping points is integral to the idea of the theory of dynamic systems in mathematics used to describe the interaction of all kinds of processes (Scheffer 2009). In ecology, the notion of tipping points was pushed forward by pioneering works in the 1960s and 1970s and has since been applied to different aquatic ecosystems (Carpenter et al. 1985). Tipping points have been defined in various ways but can be quantified as zones of rapid change in a nonlinear relationship between an ecosystem condition and the intensity of a given driver (Selkoe et al. 2015). Increased pressure in environmental drivers in ecosystems (e.g., nutrient inputs, temperature increases, and habitat destruction) may decrease resilience and cause a linear variation in a biological response (Vitousek et al. 1997; Tilman et al. 2001), leading to smooth transitions in ecosystems states (Fig. 1a) or, on the contrary, to abrupt transitions beyond a critical level (i.e., tipping point) (Fig. 1b). Increase intensity of a given driver may also lead to a response curve that "folds" backward, implying two alternative states for the ecosystem separated by an unstable state (Fig. 1c). This unstable state marks the border between the basins of attraction (i.e., set of initial conditions that lead to a particular attractor, Scheffer 2009) of the two stable states. Tipping points or catastrophic shifts (*see* Table 1 for definitions) have been identified in many environments (empirically and theoretically). For example, when looking into bivalve aquaculture, Robert et al. (2013) used nine densities (from 0 to 1400 mussels m^{-2}) of blue mussels (*Mytilus edulis*) and their biodeposition in an in situ experiment to identify their influence on benthic infaunal assemblages and ecosystem functioning (i.e., nutrient biogeochemical fluxes). Their results identify a nonlinear response of the benthic community to increased organic loading due to biodeposition by mussels with a break in the area of 200–400 mussels m^{-2}. The authors showed the evidence for a tipping point through sediment characteristics, macrofaunal communities, benthic respiration, and biogeochemical fluxes. (Robert et al. 2013). Another well-known example is a shift from a clear water state to a state of phytoplankton dominance in the Chesapeake Bay estuary (Lenihan and Peterson 1998; Jackson et al. 2001; Scheffer 2009). This transition started with increased sedimentation and organic carbon input related to land use in the area. Gradual changes were observed, with decreased biomass of aquatic plants and an increase of phytoplankton biomass. However, the oysters present in the estuary filtered the water and avoided a transition to another state—until the collapse of the oyster fishery. In the absence of oysters, the ecosystem changed profoundly, phytoplankton biomass increased, leading to widespread anoxia (Lenihan and Peterson 1998; Jackson et al. 2001; Scheffer 2009).

With the increase in occurrence and intensity of multiple drivers in terrestrial and aquatic ecosystems, adding pulses (i.e., temporary disturbances) or presses (i.e., long-term disturbances) of drivers in the system may alter tipping points (Ratajczak et al. 2017). Furthermore, multiple drivers may alter responses by acting additively or synergistically, creating an anticipated tipping point or more abrupt response curves (He et al. 2017). For instance, an increase in a given environmental driver, leading to a smooth linear variation in the ecosystem's state, may create an intensified variation in the ecosystems state with the emergence of a new driver (Fig. 1a). On the other hand, the range of conditions to which the ecosystem is sensitive may also be altered by introducing a new environmental driver (Fig. 1b). This may lead to a more extensive range of conditions to which an ecosystem can be sensitive and may also sharpen its response curve to changing conditions. Finally, for a response that "folds" backward, the appearance of a second driver in the ecosystem may lead to a larger unstable equilibrium (Fig. 1c) or to a greater backward shift to restore the ecosystem state if the conditions are reversed. Multiple drivers in a system may also create completely different responses, passing, for instance, from a smooth linear response (Fig. 1a) to a folded backward curve (Fig. 1c).

With the addition of anthropogenic to preexisting natural drivers, almost all ecosystems are now affected by cumulated drivers (Halpern et al. 2019). From experimental work to long-term monitoring, many studies have been focusing on identifying drivers' interaction and tipping points on individuals, populations and ecosystems, and functions and services (Scheffer and Carpenter 2003; Côté et al. 2016; Carrier-Belleau et al. 2021). However, very few studies have looked at whether, and if so how, additional drivers in an environment can modify specific ecosystems' thresholds and tipping points. In this review, we looked at the pervasiveness of tipping points in different natural ecosystems in the context of multiple environmental drivers. To do so, (1) we first developed a historical and current perspective on tipping point studies in terrestrial, freshwater, and marine ecological systems. In this context, we also explored how the concept of tipping points

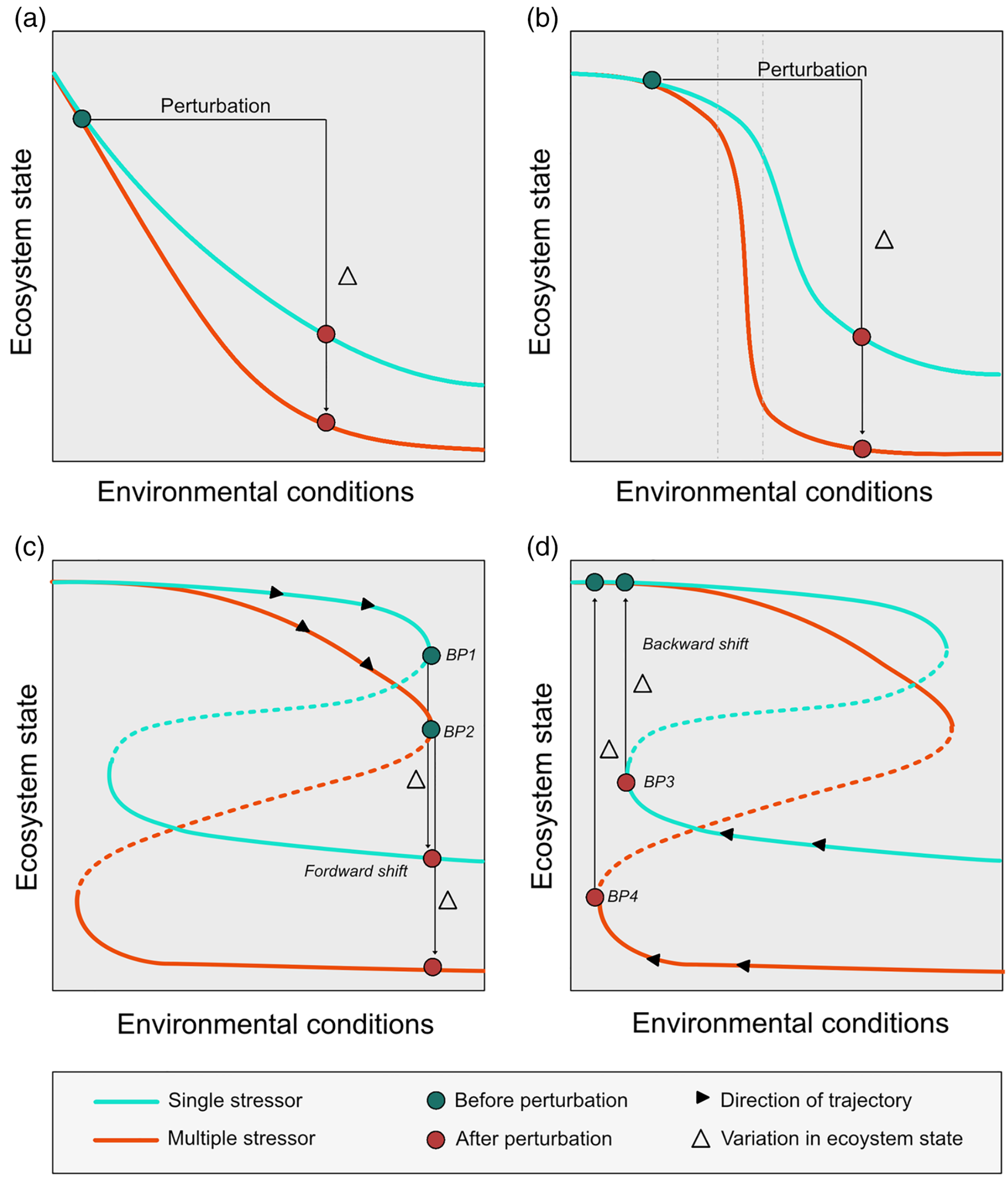

Fig. 1. Representation of different ways in which ecosystem state may vary with changes in environmental conditions in the context of single (blue) or multiple (red) drivers. (**a**) Ecosystem state may vary smoothly and almost linearly with changes in environmental conditions. This response curve may be accentuated if more than one stressor occurs in the ecosystem and result in a more substantial variation in the ecosystems state if a large external force is imposed on the system. (**b**) Ecosystems may also be sensitive to a specific range of conditions. A small perturbation or increase in environmental conditions will generate important changes in the ecosystem state for this type of response. In this sense, if a second driver is present in the ecosystem, this may generate a larger change in state for the same given perturbation. (**c**) If the ecosystem state responds so that the curve is folded backward with alternative stable states, it will strongly respond to variations in environmental conditions if the system approaches the bifurcation point (BP1, BP2). Adding a second stressor to this scenario could extend the unstable equilibria and make certain stable states inaccessible. The bifurcation point for a given environmental condition could also be at a lower or more degraded ecosystem state (BP2 vs. BP1) if there are multiple stressors in the environment and the forward shift could be more pronounced. (**d**) If stress is progressively reduced, the ecosystem may recover and show hysteresis beyond a certain point (BP3, BP4). Multiple stressors in the system may require a larger backward shift to restore the ecosystem state and a larger variation to overcome. Multiple stressors in an ecosystem could also wholly affect the way an ecosystem responds to changing conditions and could make the system shift from one response (e.g., (**a**) linear response) to another (e.g., (**b**) tipping point or (**b**) folded backward curve).

Table 1. Terminology and definitions used within the context of tipping point in marine, freshwater and terrestrial studies.

Term	Definition
Alternative stable state	Refers to the theory that predicts that ecosystems can exist under multiple nontransitory states, or stability domains. An unstable equilibria, generated by a change in external condition, marks the border between two stable states (Holling 1973; Scheffer and Carpenter 2003)
Breakpoint	Value along environmental gradient whereupon a system will move into an alternative stable state. Often used as a synonym of *threshold* (May 1977)
Driver	An environmental change (naturally or anthropogenically driven) that results in a quantifiable biological response, ranging from stress to enhancement (Boyd and Hutchins 2012)
Equilibrium	Circumstances in which the processes that affect the state and properties of a system all balance out so that the system does not change (Scheffer 2009)
Hysteresis	After a parameter returns to its original value following a perturbation, hysteresis is revealed if the system can change back to the original state at a different threshold (Beisner et al. 2003; Faassen et al. 2015)
Phase transition	Theory that states that a system can undergo strong change in its macroscopic properties if a suitable control parameter is adequately tuned. Near these critical points, the critical components (i.e., key characteristic constants) are the same for very different systems. Often used as a synonym of *critical transition* (Solé et al. 1996)
Regime shift	Sharp change from one dynamic state to a contrasting one. In the region where a regime shift occurs, a small change in pressure can cause a disproportionately large and abrupt change in system properties (i.e., single species, populations, ecosystem functioning and services) (Scheffer et al. 2001; Beisner et al. 2003; Lauerburg et al. 2020)
Stressor	An environmental change (naturally or anthropogenically driven) that decreases organismal fitness (Boyd and Hutchins 2012)
Tipping point	Thresholds of localized effects, including multiple system properties (i.e., ecological, sociocultural, and economic). Zones of rapid change in a nonlinear relationship between a response/condition and the intensity of a given driver (Selkoe et al. 2015; van Nes et al. 2016)

and related terms are used in the scientific literature. Given the prevalence of tipping point studies in aquatic ecosystems (vs. terrestrial ecosystems), we focused on the latter. Following this, (2) we separated our results among different aquatic habitats to better portray the difference in the research effort. (3) We then used a systematic approach to explore the results of experimental studies focusing on tipping points measured at the individual, communities, ecosystem level, as well as ecosystem functions and services. (4) We finally discussed our current understanding of tipping points by identifying gaps and shortcomings in this research field and possible ways forward to make this central ecological concept anew.

Methodology

Literature review

The database Web of Science (WoS, Thompson Reuters, webofknowledge.com) was used to compile all studies from 1990 to December 2020 (included). We queried the title, keywords, and abstracts of original research articles. Only primary literature (i.e., peer-reviewed literature) was included in this review.

Beforehand, a list of synonyms of tipping points or other vocabulary used within this context was established by gathering pioneer studies on the subject. This process led to form a list of 12 research terms for tipping point studies: *tipping point* (van Nes et al. 2016), *alternative stable state* (Holling 1973), *regime shift* (Lauerburg et al. 2020), *catastrophic shift* (Scheffer et al. 2001), *critical transition* (Scheffer 2009), *phase transition* (Solé et al. 1996), *fold bifurcation* (Chisholm and Filotas 2009), *bifurcation point* (Strogatz 1994), *breakpoint* (May 1977), *punctuated equilibrium* (Milkoreit et al. 2018), *ecological threshold* (Lauerburg et al. 2020), and *state shift* (Scheffer and Van Nes 2007). Although some terms are interchangeably used, we propose definitions of the main terms used throughout this article to facilitate a more consistent use of terminology (Table 1).

The terms *dose–response*, *exposure-response*, and *dose-dependent* were not purposefully included in this review. They refer to an approach that mainly focuses on characterizing cellular and organism responses as a function of exposure to a driver that is usually of chemical nature. This approach is particularly used in pharmacology and (eco)toxicology where the focus is not placed on the ecosystems. Therefore, adding these terms would have heavily skewed our research results toward chemical drivers on physiological responses. Instead, we restricted our research to environmental studies by adding the search terms *ecology*, *ecosystem*, *habitat*, *species*, *biodiversity*, *biology*, and *environment* (Dreujou et al. 2020).

We initiated our research in the literature by looking at tipping point studies in terrestrial, freshwater, and marine environments (search queries 1–3, Supplementary Table S1). We then focused on freshwater and marine ecosystems by acknowledging studies published in specific habitats within these results. Publications were grouped by the ecosystem type or habitat where the study took place by doing individual queries for these freshwater and marine habitats: *lakes*, *rivers*, *ponds*, *streams*, *wetlands*, *bogs*, *ocean*, *estuaries*, *intertidal zone*, *coastal*, *salt marsh*, *mudflats*, *seagrass meadows*, *mangroves*, *coral reefs*, *deep-sea*, *sea*, and *kelp forest* (search queries 4–24, Supplementary Table S1). Finally, the last search query was carried out by adding the terms *experiment* and *manipulation* to focus on and categorize the publications by the type of study separating; in situ manipulation experiments and laboratory experiments or bioassays (search query 25, Supplementary Table S1). We concentrated our review on experimental approaches because results are much easier to interpret than field patterns and can provide evidence for the existence of alternative attractors (Scheffer 2009). Narrowing it down to a subset of studies (experimental approaches) allowed us to proceed to an in-depth examination of the publications of the last query. We carefully read through every article to ascertain its relevance to our objectives and to identify: the type of study, the type of ecological habitat, the environmental driver(s) of interest, the biological response(s), and compartment (i.e., level of biological or ecological complexity), the term used to refer to tipping points and the statistical analyses used in the study. Here, drivers can be natural or anthropogenic processes, events, or activities that cause a change in a biological or ecological component of an ecosystem (Selkoe et al. 2015). Details of search queries and research terms are available in Supplementary Table S1.

Data analysis

Bibliographic analyses were performed using the bibliometrix R package in R studio (Aria and Cuccurullo 2017). We created the author collaboration and co-citation network in marine, freshwater, and terrestrial habitats using a "Fruchterman-Reingold" layout algorithm based on the 50 most cited papers of our dataset (Aria and Cuccurullo 2017). The keyword thematic map was performed using the co-word analyses based on the authors' keywords in all three habitats. We used the same package to show the number of publications per country and the number per authors. We assessed breakpoints in the number of studies through time using the SEGMENTED R package (Muggeo 2008; Vanacker et al. 2015). This type of analysis uses broken-line regression models to determine where a linear regression relationship changes and estimates a breakpoint.

Results and discussion

Terminology and concepts in literature

Marine, freshwater, and terrestrial studies interchangeably use multiple terms related to the concept of tipping point. We found a heterogeneous usage of terminology in this field and also patterns related to their abundance in the literature since the 1990s (Fig. 2). For example, *regime shift*, *tipping point*, and *breakpoint* were the three most mentioned terms in the literature when considering the cumulative number of publications in 2020 in terrestrial, marine, and freshwater habitats confounded. On the contrary, the terms *catastrophic shift*, *fold bifurcation*, *bifurcation point*, *punctuated equilibrium*, and *state shift* were the least used in the literature in all habitats confounded with each less than 50 cumulative number of publications in 2020.

We identified years between 1990 and 2020 where terms significantly increased in all three habitats confounded. For instance, the term *regime shift* appeared in the mid-1990s, but its usage significantly increased in 1996 and has been increasing to reach up to over 80 publications annually and near 2000 cumulative publications in 2020 (Fig. 2). While some terms have been constantly used in the scientific literature since the beginning of the 1990s, such as *phase transition*, *breakpoint*, and *critical transition*, other terms such as *tipping point* occurred later on in the literature and significantly increase in 2010 as shown by a significant breakpoint at that year.

We also found that the relative usage of terms differed among marine, freshwater, and terrestrial habitats. For example, the term *regime shift* was more often adopted in marine habitats where more than 60% of articles use this term compared to 45% in freshwater and 30% in terrestrial ecosystems (Fig. 3). On the contrary, the proportional usage of the term *tipping point* was superior in terrestrial habitats (22%), followed by freshwater (14%) and marine ecosystems (13%) (Fig. 3).

Tipping point studies in natural ecosystems: Overview and bibliometric analysis

Temporal spread of tipping point studies

A total of 2585 research articles, all habitats confounded (marine, freshwater, and terrestrial), focused on tipping points or any synonyms related to this concept stated above between 1990 and 2020. Publications were more abundant in marine, followed by freshwater and terrestrial ecosystems (Fig. 4a), with a constant increase in all three habitats since the 1990s. A steep increase in the number of publications in marine ecosystems was observed in 1999, as shown by a significant breakpoint along our timeline ($p = 0.0105$) (Fig. 4b). Significant breakpoints were also identified in 2003 for freshwater studies ($p < 0.0001$) and in 2006 for terrestrial publications ($p < 0.0001$) (Fig. 2b). When looking in more details at studies in aquatic habitats, particularly in marine habitats, we found those in the sea to be most numerous (35.0%, with a cumulative of 677 studies). This was followed by ocean (24.0%, with a cumulative of 465 studies), coastal zones, including mudflats, sandflats, rocky shore habitats and tidal pools (20.5%, with a cumulative of 396 studies), the tidal zone (4.8%, with a cumulative of 93 studies), coral reefs (4.4%, with a cumulative of 85 studies), estuaries (3.6%, with a cumulative of 69 studies), kelp forests (2.4%, with a cumulative of 47 studies), salt marshes and seagrass meadows (1.5%, with a cumulative of

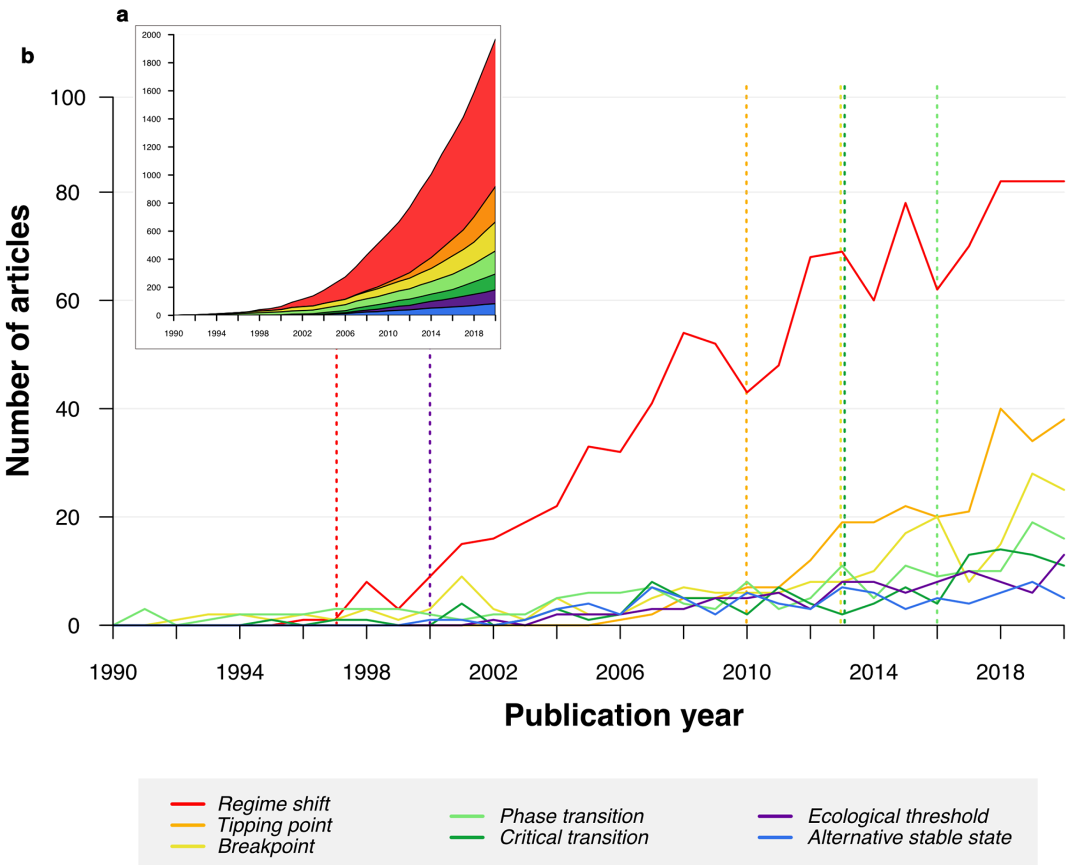

Fig. 2. Cumulative (**a**) and noncumulative (**b**) number of articles published *per* year adopting the different terms related to the concept of tipping points in marine, freshwater and terrestrial environments from 1990 to 2020. Only the seven most used terms are shown (> 50 cumulative papers). Dashed lines represent a significant ($p < 0.05$) increase in the number of studies for the terms *regime shift*, *ecological threshold*, *tipping point*, *breakpoint*, *critical transition*, and *phase transition*.

30 studies *per* habitat), and mangroves (1.3%, with a cumulative of 24 studies) followed by deep-sea research (1%, with a cumulative of 20 studies) (Fig. 5a; Supplementary Table S1). As

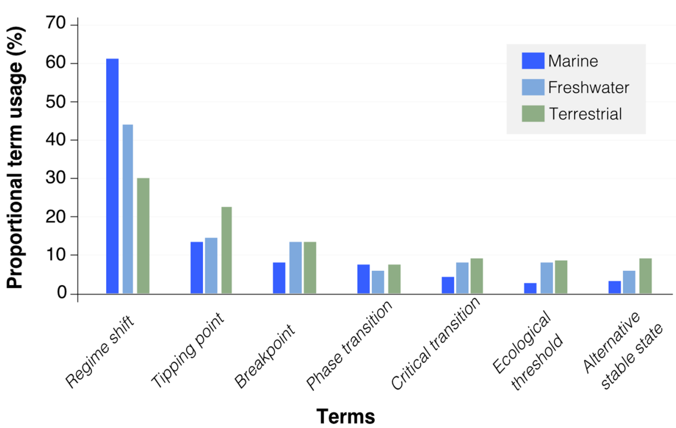

Fig. 3. Proportional usage of the seven most used terms related to the concept of tipping point in marine (dark blue), freshwater (light blue), and terrestrial (green) habitats. The bars represent the proportion of the publications using the and adds up to 100%.

far as freshwater habitats are concerned, we found that research on tipping points was dominant in lakes (38.7%, with a cumulative of 357 studies), followed by that on rivers (27.8%, with a cumulative of 257 studies), streams (16.3% with a cumulative of 150 studies), wetlands, including bogs (13.1% with a cumulative of 121 studies), ponds (4.1% with a cumulative of 38 studies), and bogs (3.1% with a cumulative of 29 studies) (Fig. 5b; Supplementary Table S1). A particular focus on tipping points in lakes was expected, since these inland waters are considered models of dynamic systems reflecting how other aquatic ecosystems might work (Scheffer 2009). Among other important research, the concept of tipping points was first suggested by Forbes (1887), in his article "The Lake as a Microcosm" and then by Scheffer (1998) in his influential book titled "Ecology of shallow lakes."

Bibliographic analysis

The concept of tipping point in marine, freshwater, and terrestrial is addressed worldwide (Fig. 6a). The majority of studies focusing on tipping points were performed in the Northern Hemisphere, with the United States, China,

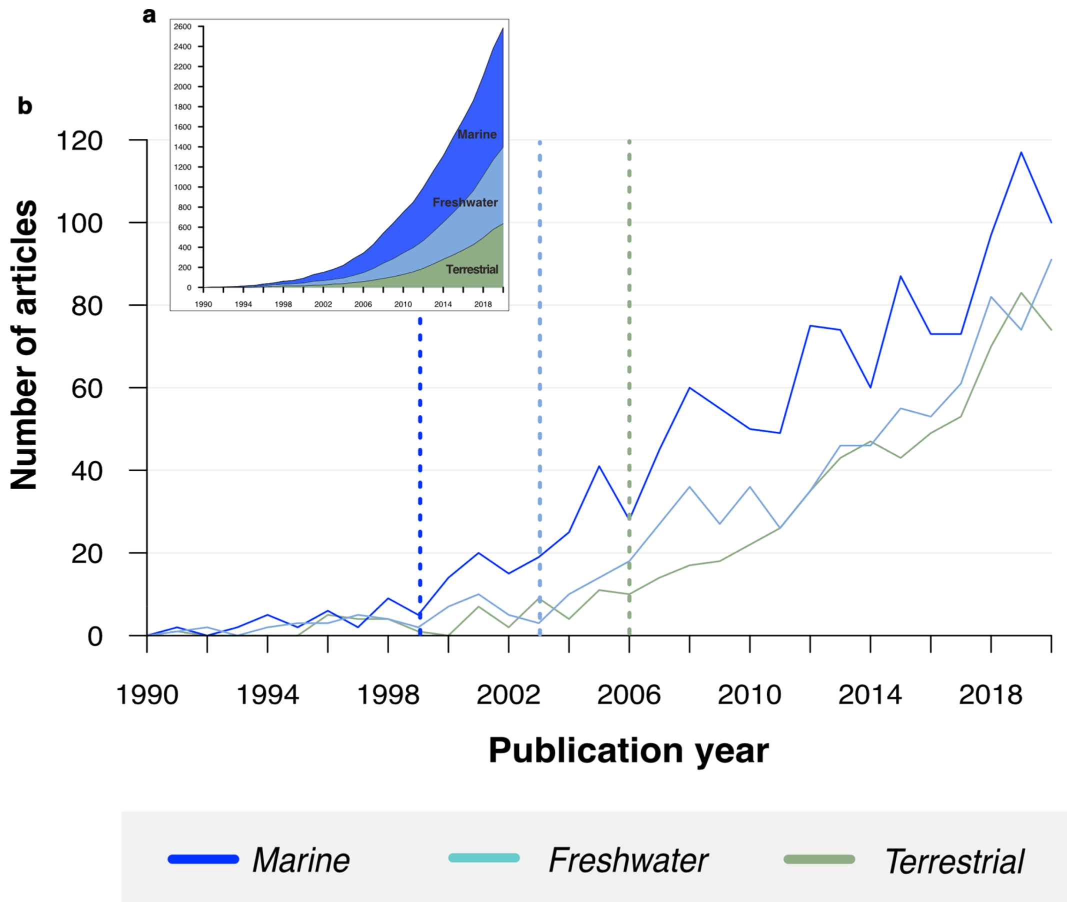

Fig. 4. Cumulative (**a**) and noncumulative (**b**) number of articles published *per* year adopting the term tipping points or a synonym in marine, freshwater, or terrestrial environments from 1990 to 2020. Dashed lines represent a significant ($p < 0.05$) increase in the number of studies in marine (dark blue), freshwater (light blue), and terrestrial (green) ecosystems.

England, Germany, Australia, and Canada being in combination responsible for more than 50% of all publications, with the majority of publications carried out by single countries (Fig. 6a,b). Even though the field of research is widely spread, with over 9042 contributing authors, some authors have contributed abundantly to the field (Fig. 6c). While authors mainly contribute to either marine, freshwater, or terrestrial studies, others have combined different habitats to their research. The author collaboration network for marine, freshwater, and terrestrial habitats confounded unveiled three main groups of interlinked authors (in blue, purple and green) as well as multiple smaller collaborations among few authors (Fig. 6d). The three main clusters seem to reflect work done in different research spheres; in blue, we find authors related to studies in freshwater environments (e.g., Pace, Carpenter); in purple are researchers focusing on mathematical models (e.g., Van Nes, Scheffer, Dakos); in green authors working mainly in marine habitats (e.g., Edwards, Beaugrand, Tian). The co-citation network revealed three author groups based on nine main publications (in bold) (Fig. 6e). These publications are recognized as pioneer works in the field of tipping points and alternative stable states (Holling 1973; Scheffer et al. 2001; Scheffer and Carpenter 2003; Folke et al. 2004; Scheffer 2009).

The most frequently used terms regarding the concept of tipping points in marine, freshwater, and terrestrial habitats are represented through a thematic network of keywords and a keyword co-occurrence analysis (Fig. 7). The thematic network represents clusters that are considered as different themes (Fig. 7a,c,e) (Cobo et al. 2011). Keywords in the upper-left quadrat are developed and very specialized themes and differ between marine (e.g., global warming), freshwater (e.g., climate variability), and terrestrial habitats (e.g., land use). Themes in the upper-right quadrat represent motor themes that are well developed and important for structuring the research field. No common terms were found between all three habitats for this theme. Themes in the bottom-left quadrat are both weakly developed and marginal and represent either emerging, or disappearing themes (Cobo et al. 2011). For instance, in terrestrial habitats, themes such as *resilience*, *wildfire*, or *ecosystem services* may need development due to the research field growing toward them (Lam-Gordillo et al. 2020).

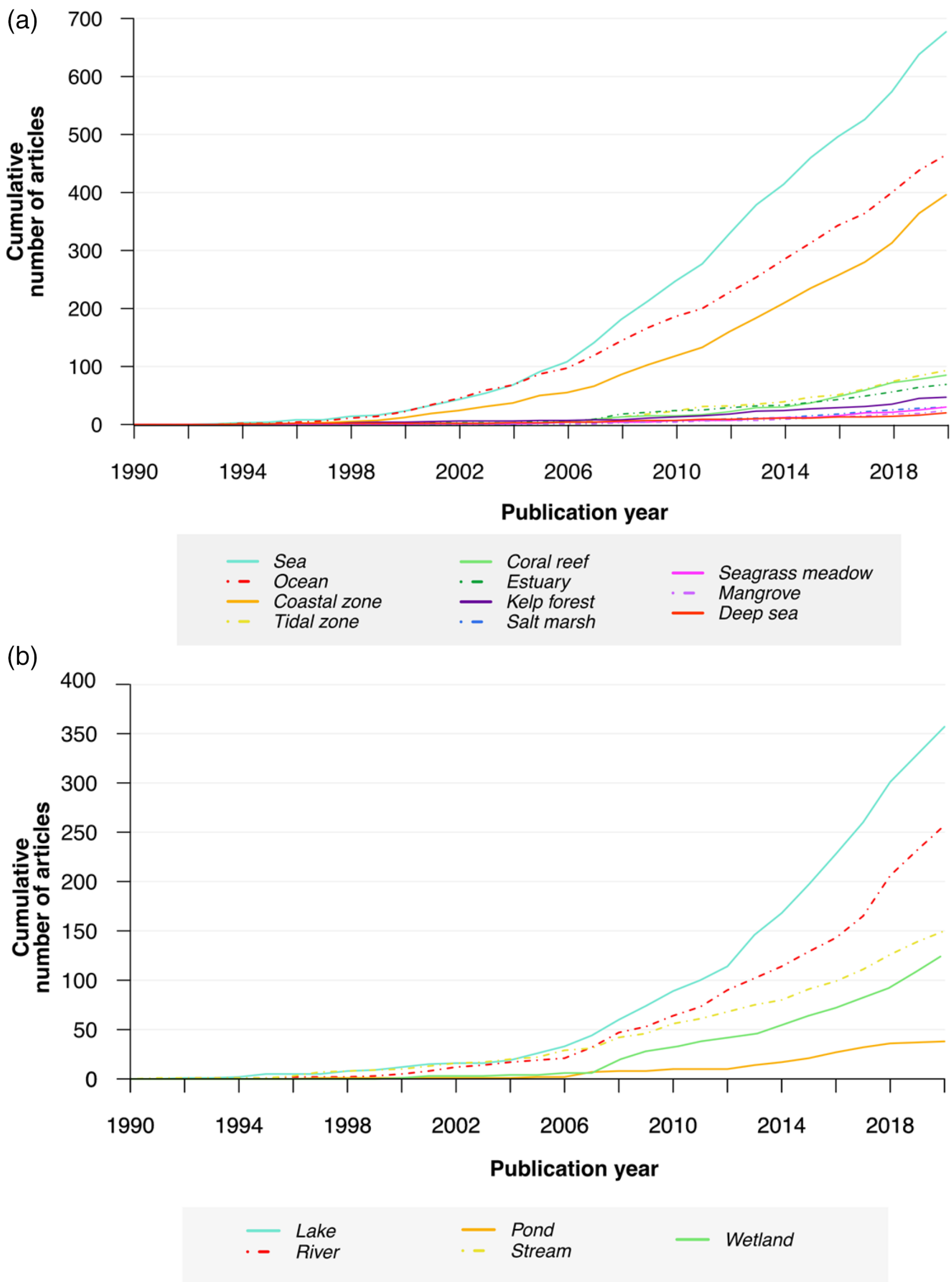

Fig. 5. Cumulative number of scientific articles from 1990 to 2020 referring to tipping points in (**a**) marine and (**b**) freshwater ecosystems divided by habitats. Marine habitats include oceans, seas (enclosed by land), estuaries, coastal zones, tidal zones (including mudflats, sandflats, rocky shores, tidal pools, and salt marshes), seagrass meadows, mangroves, coral reefs, kelp forests, and deep seas. Freshwater habitats include lakes, rivers, ponds, streams, and wetlands (including bogs).

Finally, themes in the bottom-right quadrat are basic themes. While they are essential for the research field, they are not developed. Interestingly, the themes *regime shift* and *alternative stable state* occurred for all three habitats.

For freshwater and terrestrial habitats, three clusters of keywords (represented in green, blue, and red) were identified whereas two clusters were associated with marine habitats (Fig. 7b,d,f). Those clusters represent themes that are usually used

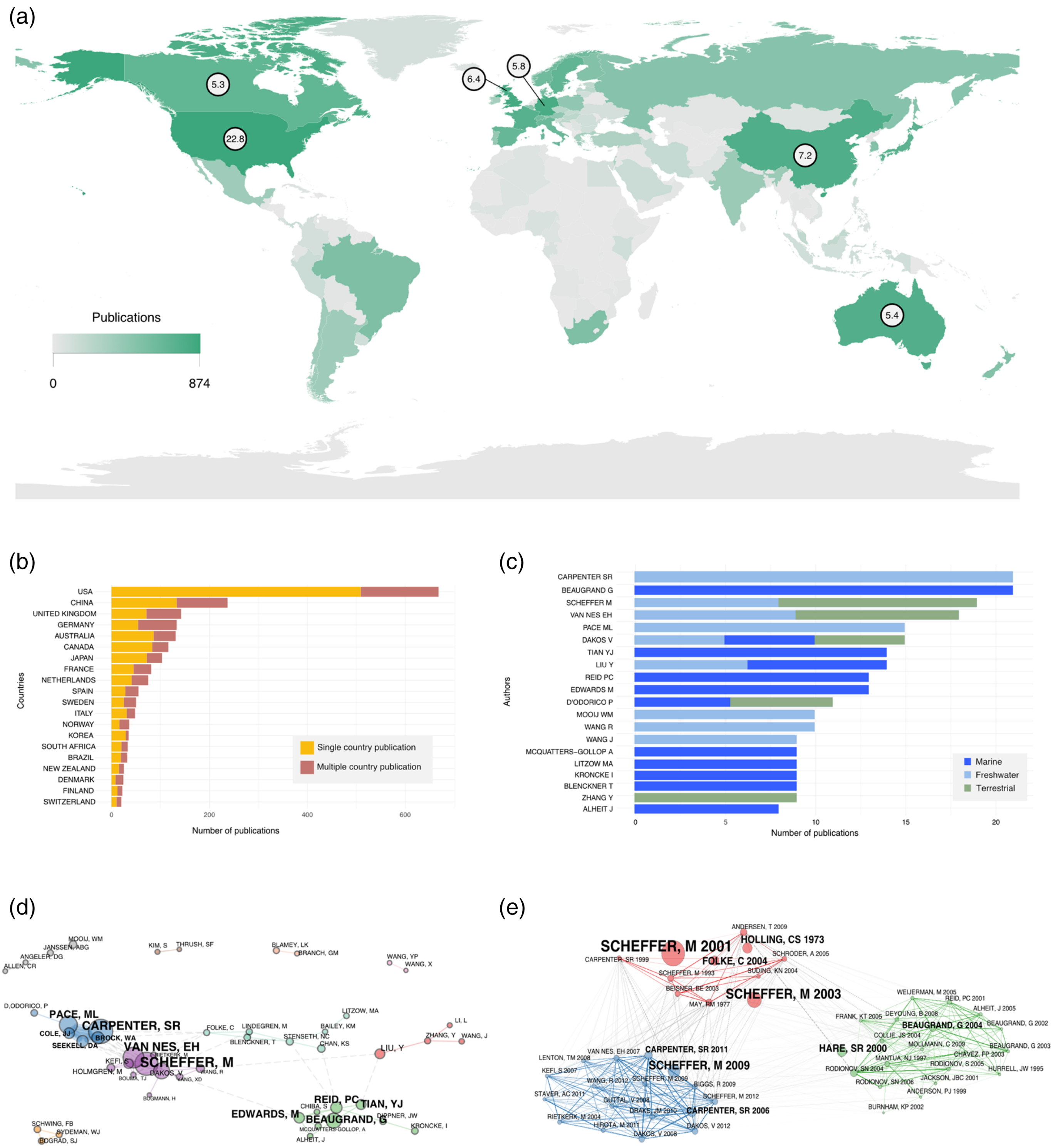

Fig. 6. Studies focusing on the concept of tipping point in marine, freshwater, and terrestrial habitats. (**a**) Geographical distribution of the included publications in the literature review. The color intensity represents the number of publications affiliated with a given country (all authors) and the circled number represents the proportion of publications (%) associated with the top six productive countries. (**b**) The top 20 most productive countries with single country publications (yellow) and multiple country publications (brown). (**c**) The top 20 most productive authors. The colors represent the habitat in which the work of the author has mainly been carried out: marine (dark blue), freshwater (light blue), and/or terrestrial (green). (**d**) Author collaboration network. Nodes represent relations between the authors of the 50 most cited papers of the dataset; lines represent at least one co-authorship; node and font size are proportional to the number of publications; node colors represent different networks of authors. (**e**) Co-citation network. Nodes represent relations between the 50 most cited papers of the dataset; node and font size are proportional to the number of citations of the article; node colors represent different networks of citations.

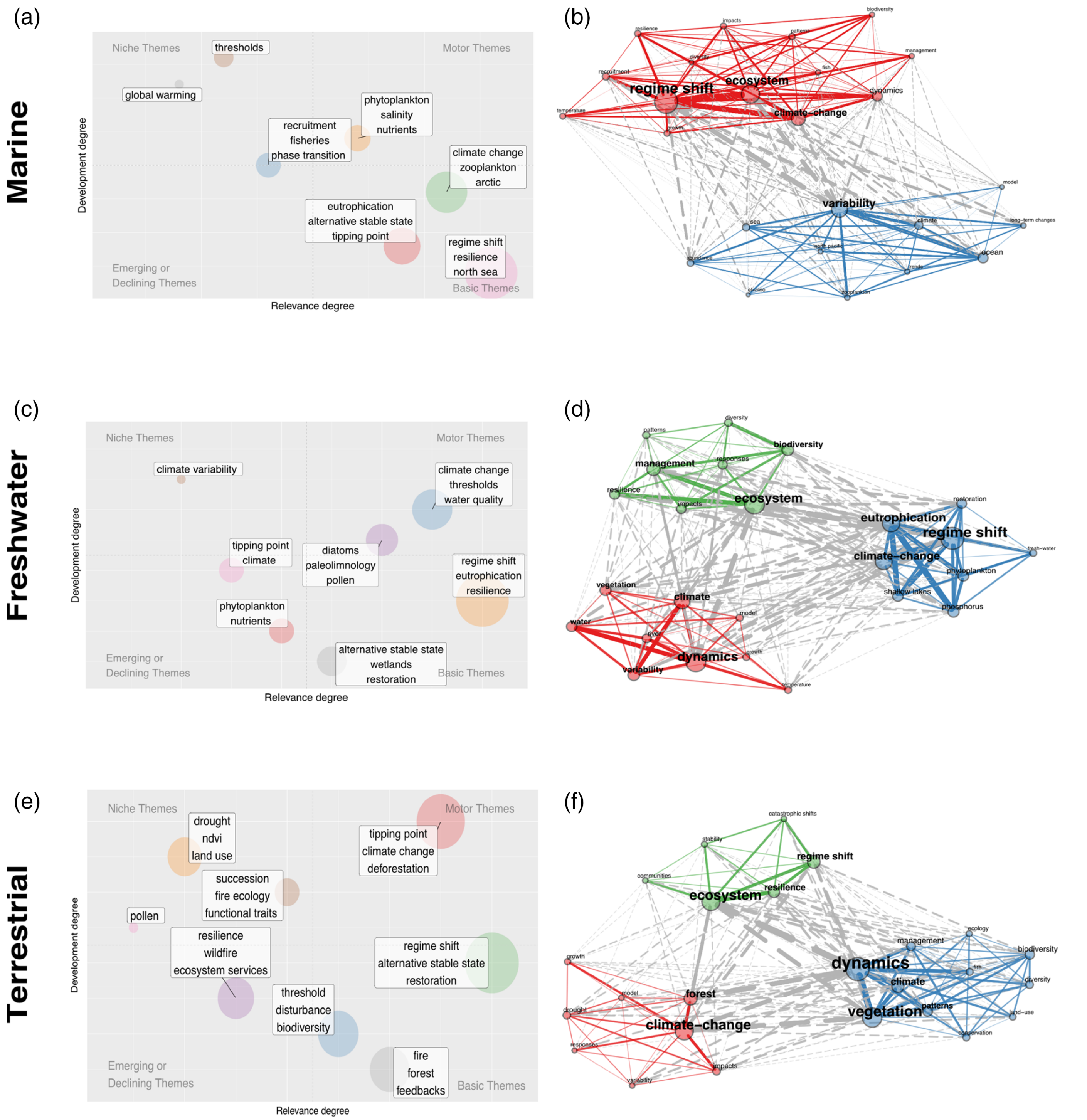

Fig. 7. Bibliographic analysis of publications on tipping point studies divided by marine (**a**, **b**), freshwater (**c**, **d**), and terrestrial habitats (**e**, **f**). (**a**, **c**, **e**) Thematic network of keywords based on co-word analysis through the authors keyword co-occurrences. The four quadrant represent the four kinds of themes for every keyword: motor themes (upper-right), niche themes (upper-left), emerging or declining themes (lower-left), and basic themes (lower-right). (**b**, **d**, **f**) Keyword co-occurrences based on the 25 most cited publications.

together in the literature. Interestingly, *regime shift*, *climate-change*, and *ecosystem* are three abundant terms but are not used in the same way for all three habitats. They are not part of the same clusters for marine, freshwater, and terrestrial studies. We also found terms related to management, such as *conservation*, *restoration*, *impact*, or *land-use* for all three habitats.

Quantitative description of experimental studies focusing on tipping points

Within the identified research articles with our first search query, we found 205 articles that focused on experimental studies between 1990 and 2020. Only 86 were relevant for the upcoming discussion: that is, focused on ecological studies in aquatic habitats and used a laboratory or field experimental approach. The others either used different types of approaches (e.g., long-term monitoring, modeling) or the use of the tipping point or any synonyms stated above referred to different concepts. Of these articles, only 28 (32.6%) specifically aimed to identify tipping points (or synonym), or tipping points were clearly stated in their hypothesis or expected results (Supplementary Table S2). The majority of studies, however, elaborated about tipping points generally in the introduction or discussion. Focusing exclusively at the works having an objective to identify a tipping point (or synonym), we found that local anthropogenic drivers (e.g., nutrient input, salinity variation) were the most commonly investigated stressor, followed by ecological processes (e.g., predation, grazing), global change drivers (e.g., CO_2 concentration), and natural events that are expected to be exacerbated by human activities or global change in the future (e.g., drought, extreme temperature events) (Fig. 8a). The preponderance of articles focused on single stressors (64.3% for the total number of studies, respectively 75% and 56.2% for freshwater and marine habitats), and fewer studies tested the effect of multiple drivers in the context of tipping points (35.7% for the total number of studies, respectively 25% and 43.8% for freshwater and marine habitats) (Fig. 8b; Table 2). However, the majority of studies (i.e., 75%) testing the effect of multiple drivers also considered ecological processes in the context of human activities or global change (Supplementary Table S2). Very few studies focused on multiple anthropogenically driven stressors (local stressors or global change), suggesting that the notions of multiple stressors and cumulative impact in the frame of tipping points are not well established.

We found that the effect of increasing intensities of given stressors on biological responses was mainly investigated at the community level, followed by ecosystem functioning and services (Fig. 8c). Fewer publications investigated responses at the individual and population levels. Articles primarily focused on multiple responses but concentrated their efforts on single levels of biological complexity (Fig. 8d). For instance, 75% of studies focused on single biological levels (respectively 83.3% and 68.8% in freshwater and marine habitats), while only 25% investigated responses at multiple levels of biological of complexity. No studies included all biological/ecological complexity levels, from the individual level to ecosystem functioning and services.

Conceptual and methodological shortcomings and ways forward: An integrative framework

Throughout our review, we have identified some research gaps, which may complement current research on tipping points in the context of multiple drivers. Those gaps relate to multiple drivers along environmental gradients, the continuity between terrestrial, freshwater, and marine ecosystems, the environmental and biological context of an ecosystem (legacy effect), and the biological levels of complexity investigated throughout research on tipping points. Therefore, we propose an integrative framework in order to include those aspects (Fig. 9).

Tipping points in the context of multiple drivers

A recent synthesis of 36 meta-analyses, including a total of 4600 studies, examined ecosystem responses to environmental drivers in experimental and observation settings (Hillebrand et al. 2020). This synthesis included various environmental drivers such as eutrophication, fire, nitrogen fertilization, and climate warming. While there was clear evidence for rapid changes in ecosystem responses with increasing environmental stress, Hillebrand and colleagues showed that these changes were characterized by gradual responses instead of being organized around tipping points. However, this pattern does not underestimate the importance of tipping points but suggests that they should not be expected solely along singular environmental gradients but may be caused by the interaction between pulses of drivers along environmental gradients (Benedetti-Cecchi et al. 2015; Millar and Stephenson 2015; Dudney and Suding 2020).

Few scientists have investigated tipping points in the context of multiple stressors. Benedetti-Cecchi et al. (2015) combined a pulse disturbance (e.g., a strong storm) to a press perturbation (e.g., an annual clipping of *Cystoseira amentacea* canopy) designed to generate a gradient of increasing competitive pressure on understory assemblages. The addition of a pulse disturbance was designed to magnify press perturbation effects. The authors found that superposed pulse to press disturbance amplified environmental noise and caused flickering, showing that the system was switching back and forth between alternative states (Scheffer et al. 2009; Wang et al. 2012; Benedetti-Cecchi et al. 2015).

To identify thresholds and reflect natural conditions in anthropized ecosystems, and if we want to keep the ecological concept of tipping points anew, the following points should be considered: (1) focusing on interacting drivers along environmental gradients, (2) taking into account the legacy effect of the ecosystem (i.e., impacts that previous conditions have on current processes; Monger et al. 2015), (3) considering disturbance regimes (i.e., magnitude, frequency, and spatial extent of a perturbation; Sousa 1984) along environmental gradients, and (4) considering the links among marine, freshwater, and terrestrial ecosystems. First of all, the effects of multiple drivers in aquatic ecosystems may be magnified by synergistic and antagonistic interactions (Côté et al. 2016). Investigating driver interaction along an environmental gradient may help identify (1) synergies, that may create an anticipated or intensified tipping point or (2) antagonistic

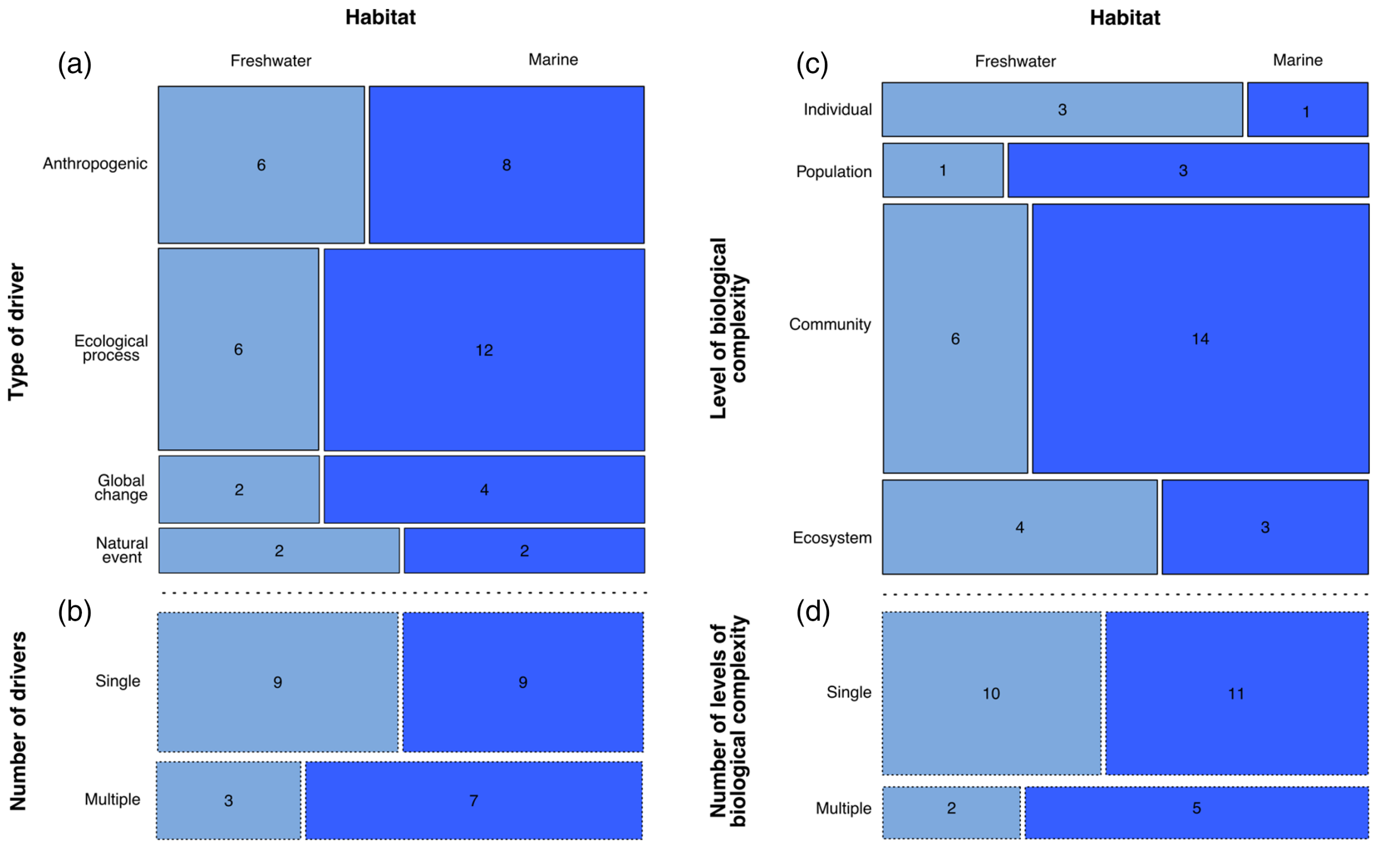

Fig. 8. Mosaic plot showing (**a**) the type of driver (anthropogenic, ecological process, global change, and natural event); (**b**) if single or multiple stressors were investigated in the study; (**c**) the level of biological complexity (individual, population, community, and ecosystem), and (**d**) if single or multiple levels of biological complexity were considered in the study. The surface of the rectangles is proportional to the frequency of studies in freshwater (light blue) or marine (dark blue) habitats. Those results are based on the 28 publications that had for objective to identify a tipping point.

relationships, which could delay the reach of a tipping point. This can be done by looking at the effect of pulses or presses of drivers along increasing environmental conditions and can be done experimentally or with observational data. Modeling or observational studies can help choose the investigated drivers or set the levels of locally relevant drivers (Côté et al. 2016). Ultimately identifying driver interactions along environmental gradients could provide useful information to managers or conservationists by informing them on which stressor to act upon, when, and where (Côté et al. 2016). Second of all, tipping points can be altered by the legacy effect of an ecosystem. For instance, the nature of past disturbances and conditions may affect the critical value at which a system might reach a threshold, suggesting that universal tipping points should not be expected equally across all systems (Monger et al. 2015; Dudney and Suding 2020). Third of all, the disturbance regimes of drivers along an environmental gradient should also be considered, especially in experimental studies, as different components of a disturbance will affect ecosystems and push them beyond their thresholds of tolerance (Miller et al. 2011; Brooks and Crowe 2019). Long-term observational study and modeling work can also help identify the magnitude, frequency, and spatial extent of a driver. Finally, terrestrial and aquatic ecosystems are interlinked and while drivers may emerge from one ecosystem, they may affect adjacent ones. Therefore, terrestrial and coastal environments (freshwater or marine) must be incorporated since coastlines are not impermeable barriers (Beauchesne et al. 2020). To do so, we can investigate the effect of land-based drivers on freshwater ecosystems and vice versa (e.g., terrestrial nutrient input to freshwater or marine coastal waters).

Tipping points and multiple levels of biological complexity

The effect of individual or combined environmental drivers often differ based on the observed level of biological organization (Crain et al. 2008); effects of isolated stressors on populations are not proportional to those on individuals as the effect can be of lesser (Galic et al. 2017, 2018; Schmolke et al. 2017) or greater magnitude (Gergs et al. 2013). In addition, combined stressors often have antagonistic effect at the individual level (Nys et al. 2017; Galic et al. 2018). However, at the population and ecosystem levels, properties tend to be synergistically impacted by stressor combinations (Crain

Table 2. Results of the literature review of in situ and laboratory experimental studies focusing on tipping points in freshwater and marine ecosystems that considered multiple drivers of change (two or more). Results are shown for the type of study, the ecological habitat, the environmental driver(s) of interest, the biological response(s), the level of biological compartment, the vocabulary used, and the main statistical analysis used to accomplish the objectives. Environmental drivers may be of physical and chemical origin, biotic factors or anthropogenically driven. Please refer to Supplementary Table S2 for the comprehensive list of studies focusing on both single and multiple drivers.

Source	Type of study	Ecological habitat	Driver 1 [levels]	Driver 2 [levels]	Driver 3 [levels]	Biological response	Biological/ ecological compartment	Vocabulary used	Statistical analysis
Pinckney et al. (2020)	Bioassays	Estuary	Dissolved inorganic nitrogen [12]*	Irradiance [2]*	Salinity [2]*	Phytoplankton diversity and presence of focal groups	Population; community	Alternative stable state; breakpoint	Segmented regression; Davies test
Menge et al. (2017)	Laboratory experiment	Rocky shore; intertidal zone; coastal	Ascophyllum clearance [2]*	Barnacle removal [2]*	—	Abundance of sessile and mobile communities; barnacle recruitment	Community	Alternative stable states	ANOVA
He et al. (2017)	In situ experiment	Salt marsh	Natural ennemis (grazers) [2]*	Drought [3]*	—	Vegetation cover	Community	Regime shift	ANOVA
Dal Bello et al. (2019)	In situ experiment and model simulations	Rocky shore; intertidal; coastal	Extreme temperature events [2]	Sediment deposition [2]	—	Biofilm biomass	Community	Regime shift	Frequency distribution; binomial generalized linear model
Han (2016)	In situ experiment and field surveys	Coral reef	Aggregation size of individuals [2]	Urchin abundance [6]	—	Urchin mortality rates	Population	Regime shift; alternate attractors; alternate stable state	ANOVA
Bajer et al. (2016)	In situ experiment	Lake	Carp biomass [continuous variable]	Carp abundance [2]	—	Species richness and submersed aquatic plant cover	Community	Threshold	Simple and multivariable linear models
Wang et al. (2016)	Laboratory experiment	Mangrove; river	Intensity of flood discharge [5]	Frequency of flood discharge [16]	—	Vegetation establishment and survival	Community	Alternative stable state; threshold	Frequency distribution
Benedetti-Cecchi et al. (2015)	In situ experiment	Intertidal	Macroalgal canopy removal [4]*	Storm [2]*	—	Fucoid canopy and algal turf biomass	Community	Regime shift; tipping point; alternative state	Autocorrelation and standard deviation based on interpolated data

Holmgren et al. (2015)	In situ experiment	Bog	Schrub abundance [2]*	Tree abundance [2]*	—	Seedling condition and survival	Community	Critical transition	ANOVA
Dieleman et al. (2015)	Laboratory experiment	Bog	Temperature [3]*	CO_2 concentration [2]*	Water table level [2]*	Plant species abundance and richness	Community	Regime shift	RM-ANOVA
Trush et al. (2014)	In situ experiment	Sandflat	Nutrient concentration [3]*	*Macoma* sp. densities [3]*	Light intensity [3]*	Ecosystem interactions; biogeochemical fluxes, productivity; macrofauna structure and abundance	Community; ecosystem functioning	Threshold; critical transition	Structured equation models; best fit models; chi-square
Martins et al. (2010)	In situ experiment	Intertidal	Grazing [3]	Size of disturbance [3]*	Timing of disturbance [3]*	Algae and macroinvertebrate abundance	Community	Alternative stable state	ANOVA; confidence interval

RM-ANOVA, repeated measures analysis of variance.

et al. 2008; Galic et al. 2017). This suggests that investigating responses solely at the individual level may result in underestimated risk evaluation. This can be explained by the fact that stressor combinations will target different processes (e.g., feeding or reproductive rates, somatic growth, etc.) and result in a different interacting scenario or that compensatory or dispensatory processes and feedbacks across levels of organization may arise from induced stress (Galic et al. 2018).

Although many papers looked at various responses, most studies focused on an individual biological or ecological level of organization. However, some examples of studies focusing on multiple levels of organization in the context of single or multiple drivers are worth highlighting. For instance, Pinckney et al. (2020) investigated the effect of multiple drivers (i.e., dissolved inorganic nitrogen [DIN], irradiance) on phytoplankton diversity (community) and the presence of focal groups (population) in two contrasting estuarine systems. The authors showed that DIN additions change algal group diversity and the abundance of different groups, suggesting that ambient DIN concentrations should not exceed breakpoint concentrations (25 and 50 μmol L^{-1}). On the other hand, Green and Fong (2015) focused on the effect of eutrophication on macrofauna and microphytobenthos diversity (community) as well as sediment iron and sulfide concentrations (ecosystem functioning). The authors identified a point beyond which macroalgal mat thickness (used to represent eutrophication) reduced macrofauna biodiversity (> 1.5 cm).

Responses to multiple stressors are rarely additive across different biological organization levels, suggesting that stressors' pathways of action differ, and so differ the resulting processes and feedback revealed at different scales (Galic et al. 2018). To move forward within this field of research, we propose experimental studies should explore and link responses at the individual (cellular, metabolism, physiology, evolution, and behavior), population (dynamics), community (structure, complexity, and dynamics), and ecosystems (functions and services) level in order to identify tipping points within the context of single and multiple stressors. This can be achieved by building simplified communities that reflect natural assemblages to capture the natural complexity of ecosystems (Carrier-Belleau et al. 2021). This will also help identify which components of an ecosystem are most likely to be impacted by single or multiple stressors (Carrier-Belleau et al. 2021). By including multiple scales of organization, we will likely be able to provide a mechanistic understanding of species or communities responses to ecological change, this being a key component in predicting ecosystem sensitivity to gradual and sudden changes (Somero 2012) and perhaps more important than identifying critical threshold values, that are quite context-dependent (Dudney and Suding 2020; Hillebrand et al. 2020).

Tipping points, experimental designs, and statistical analyses

Experimental approaches are a promising avenue to provide evidence for the occurrence of thresholds and alternative

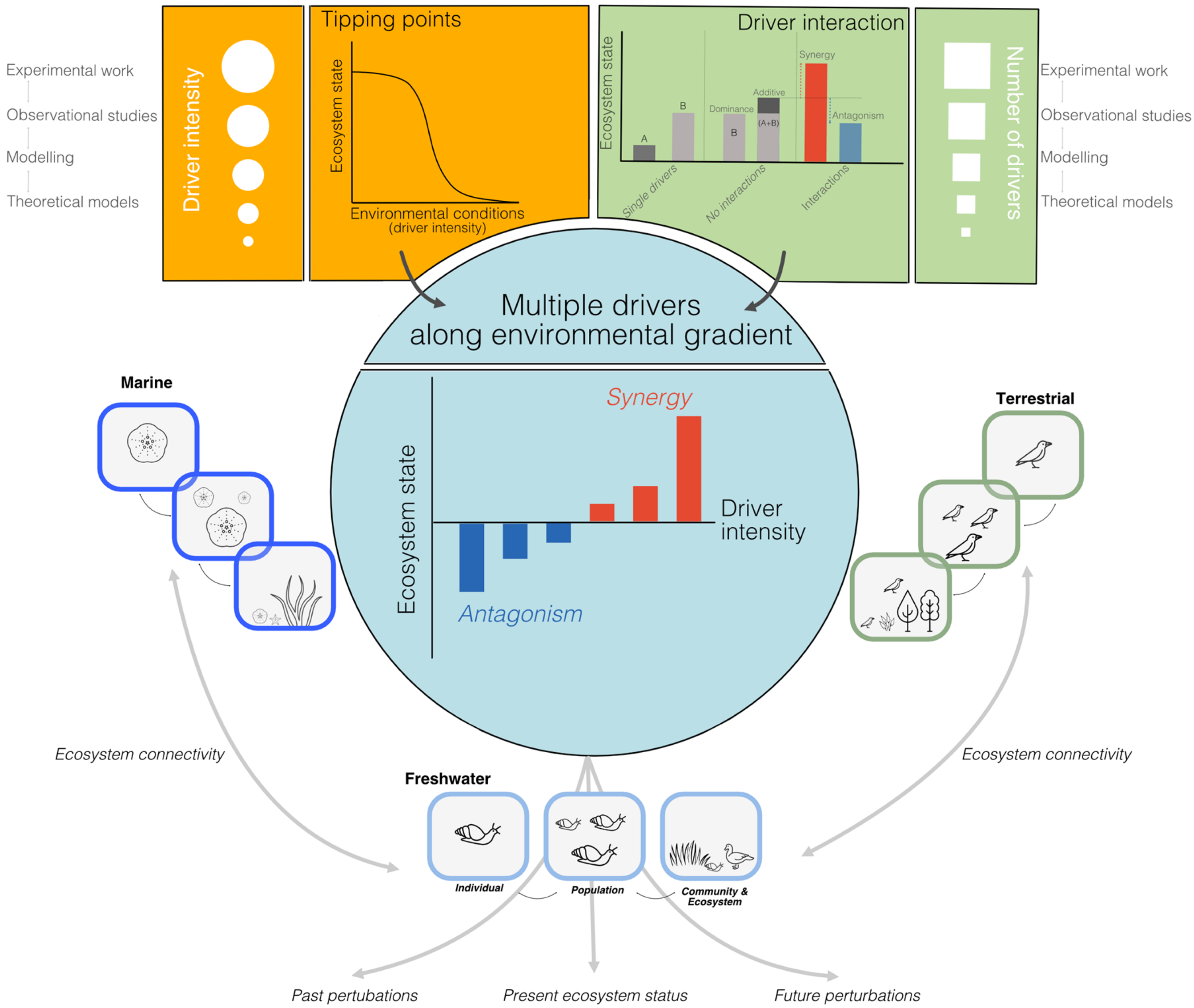

Fig. 9. Proposed framework considering both concepts of tipping points and multiple drivers in marine, freshwater, and terrestrial habitats. To combine both concepts, stressor interaction (synergistic and antagonistic interactions) should be investigated along increasing environmental gradients. This would allow to understand how stressor interactions can alter tipping points. The investigated stressors should be informed by experimental, observation, modeling studies as well as theoretical work and should consider the connectivity between marine, freshwater, and terrestrial habitats. The observed responses should include responses at the individual, population, community levels as well as ecosystem functioning and services. Finally, the legacy effect (e.g., previous impacts) of an ecosystem as well as future scenarios of change and species distribution should be taken into consideration.

stable states (Scheffer and Carpenter 2003). However, to identify tipping points, experiments need to be purposely designed and appropriate statistical analyses need to be used (Underwood 1991). Our results showed that many experimental studies aimed at identifying a tipping point but used very few levels (i.e., number of positions/intensities along an environmental gradient), and in some cases only using the presence or absence of a driver. The number of levels used to identify tipping points ranged from 2 to 21. While studies using only very few levels provide relevant results to understand the effect of environmental drivers on biological components, their approach does not help to identify a threshold or a tipping point but can point out to catastrophic shifts. As an example of good practice in identifying regime shifts, He et al. (2017) investigated regime shifts in vegetation cover in salt marshes when plant communities were exposed to two levels of natural enemies (pathogens) and three drought levels. He and colleagues used ANOVA to identify this regime shift. Another positive example, this time on the identification of breakpoints, was provided by Aspin et al. (2019)

who wished to identify a breakpoint in macroinvertebrate community composition along 21 levels of drought in streams using segmented regression analysis. These two experimental approaches had distinctive objectives (identifying a regime shift vs. a breakpoint) and used appropriate designs and statistical analyses to reach their objectives.

Multiple levels of the environmental driver need to be used to identify tipping points along environmental gradients. These levels need to reflect present natural conditions and potential future pressure magnitudes to detect changes along gradients of environmental pressures (Petraitis and Dudgeon 2004; Hillebrand et al. 2020). Using a broad range of environmental driver will also ensure that the tipping point is completely bracketed (Petraitis and Dudgeon 2004). The number of levels needs to be established depending on multiple aspects: available literature on the subject, the number and combination of investigated drivers, the natural temporal and spatial variation of the drivers, the species' or ecosystems' sensitivity to the drivers, etc. Incorporating extremes along an environmental gradient will also help identify whether a system has one or more basin of attraction (Petraitis and Dudgeon 2004).

Experiments aiming to identify tipping points need to be analyzed using regression approaches, such as broken-line linear regression models, to determine where the regression relationship varies (Muggeo 2008; Vanacker et al. 2015). Alternatively, if the objective is to identify drastic changes between two environmental states, we suggest fewer levels could be used and analyses of variance could help identify the effect of experimental treatments and identify driver interactions when relevant (Piggott et al. 2015). However, when investigating tipping points along environmental gradients in the context of multiple drivers, combining both statistical approaches (regression and ANOVA) and using purposely designed experiments (e.g., factorial design) will help understand how multiple environmental drivers can affect ecosystem resilience along a perturbation gradient. Ultimately, this could link both concepts of stressor interactions (i.e., synergistic and antagonistic relationships) and tipping points.

Concluding remarks

Tipping points and driver interactions are essential concepts to help identify the underlying causes of ecosystem resilience to environmental drivers. These concepts become even more trivial as human activities and anthropogenically induced global changes create irreversible changes in aquatic ecosystems. We have to ask ourselves the best ways to characterize tipping points in the actual context with these ongoing changes. Looking at the interaction among multiple drivers along environmental gradients, investigating responses among multiple scales of biological complexity, and using appropriate experimental design and statistical analyses will enable a mechanistic understanding of ecosystems' sensitivity to environmental drivers and contribute to identifying critical values at which functions are lost. These actions will ultimately provide helpful information to balance ecosystem utilization and the preservation of natural resources successfully.

References

Aria, M., and C., Cuccurullo. 2017. Bibliometrix: An R-tool for comprehensive science mapping analysis. J. Informetrics **11**: 959–975. doi:10.1016/j.joi.2017.08.007

Aspin, T. W. H., and others. 2019. Drought intensification alters the composition, body size, and trophic structure of invertebrate assemblages in a stream mesocosm experiment. Freshw. Biol. **64**: 750–760. doi:10.1111/fwb.13259

Bajer, P. G., M. W. Beck, T. K. Cross, J. D. Koch, W. M. Bartodziej, and P. W. Sorensen. 2016. Biological invasion by a benthivorous fish reduced the cover and species richness of aquatic plants in most lakes of a large North American ecoregion. Glob. Change Biol. **22**: 3937–3947. doi:10.1111/gcb.13377

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Front. Ecol. Environ. **1**: 376–382.

Benedetti-Cecchi, L., L. Tamburello, E. Maggi, and F. Bulleri. 2015. Experimental perturbations modify the performance of early warning indicators of regime shift. Curr. Biol. **25**: 1867–1872. doi:10.1016/j.cub.2015.05.035

Beauchesne, D., and others. 2020. Characterizing Exposure to and Sharing Knowledge of Drivers of Environmental Change in the St. Lawrence System in Canada. Frontiers in Marine Science **7**: 383. doi:10.3389/fmars.2020.00383

Boyd, P. B., and D. A. Hutchins. 2012. Understanding the responses of ocean biota to a complex matrix of cumulative anthropogenic change. Mar. Ecol. Prog. Ser. **470**: 125–135. doi:10.3354/meps10121

Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. Synergies among extinction drivers under global change. Trends Ecol. Evol. **23**: 453–460. doi:10.1016/j.tree.2008.03.011

Brooks, P. R., and T. P. Crowe. 2019. Combined effects of multiple stressors: New insights into the influence of timing and sequence. Front. Ecol. Evol. **7**: 387. doi:10.3389/fevo.2019.00387

Brown, C. J., M. I. Saunders, H. P. Possingham, and A. J. Richardson. 2013. Managing for interactions between local and global stressors of ecosystems. PLoS One **8**: e65765. doi:10.1371/journal.pone.0065765

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. Bioscience **35**: 634–639. doi:10.2307/1309989

Carrier-Belleau, C., D. Drolet, C. W. McKindsey, and P. Archambault. 2021. Environmental stressors, complex interactions and marine benthic communities' responses. Sci. Rep. **11**: 4194. doi:10.1038/s41598-021-83533-1

Chisholm, R. A., and E. Filotas. 2009. Critical slowing down as an indicator of transitions in two-species models. J. Theor. Biol. **257**: 142–149. doi:10.1016/j.jtbi.2008.11.008

Cobo, M. J., A. G. López-Herrera, E. Herrera-Viedma, and F. Herrera. 2011. An approach for detecting, quantifying, and visualizing the evolution of a research field: a practical application to the fuzzy sets theory field. J. Informetrics **5**: 146–166. doi:10.1016/j.joi.2010.10.002

Côté, I. M., E. S. Darling, and C. J. Brown. 2016. Interactions among ecosystem stressors and their importance in conservation. Proc. R. Soc. B Biol. Sci. **283**: 1–9. doi:10.1098/rspb.2015.2592

Crain, C. M., K. Kroeker, and B. S. Halpern. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecol. Lett. **11**: 1304–1315. doi:10.1111/j.1461-0248.2008.01253.x

Dakos, V., and others. 2019. Ecosystem tipping points in an evolving world. Nat. Ecol. Evol. **3**: 355–362. doi:10.1038/s41559-019-0797-2

Dal Bello, M., L. Rindi, and L. Benedetti-Cecchi. 2019. Temporal clustering of extreme climate events drives a regime shift in rocky intertidal biofilms. Ecology **100**: 1–10. doi:10.1002/ecy.2578

Dieleman, C. M., B. A. Branfireun, J. W. Mclaughlin, and Z. Lindo. 2015. Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. Glob. Change Biol. **21**: 388–395. doi:10.1111/gcb.12643

Dreujou, E., and others. 2020. Holistic environmental approaches and Aichi Biodiversity Targets: Accomplishments and perspectives for marine ecosystems. PeerJ **8**: e8171. doi:10.7717/peerj.8171

Dudney, J., and K. N. Suding. 2020. The elusive search for tipping points. Nat. Ecol. Evol. **4**: 1449–1450. doi:10.1038/s41559-020-1273-8

Estes, J. A., and others. 2011. Trophic downgrading of planet earth. Science **333**: 301–306. doi:10.1126/science.1205106

Faassen, E. J., A. J. Veraart, E. H. Van Nes, V. Dakos, M. Lürling, and M. Scheffer. 2015. Hysteresis in an experimental phytoplankton population. Oikos **124**: 1617–1623. doi:10.1111/oi.02006

Filbee-Dexter, K., and R. E. Scheibling. 2014. Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Mar. Ecol. Prog. Ser. **495**: 1–25. doi:10.3354/meps10573

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annu. Rev. Ecol. Evol. Syst. **35**: 557–581. doi:10.2307/annurev.ecolsys.35.021103.30000021

Folt, C.L., C.Y. Chen, M.V. Moore and J. Burnaford. 1999. Synergism and antagonism among multiple stressors. Limnol. Oceanogr. **44**: 864–977. doi: 10.4319/lo.1999.44.3_part_2.0864, 3part2

Forbes, S. 1887. The lake as a microcosm. Illinois Nat. Hist. Surv. Bull. **15**: 537–550. doi:10.21900/j.inhs.v15.303

Forbes, V. E., and others. 2017. A framework for predicting impacts on ecosystem services from (sub)organismal responses to chemicals. Environ. Toxicol. Chem. **36**: 845–859. doi:10.1002/etc.3720

Galic, N., V. Grimm, and V. E. Forbes. 2017. Impaired ecosystem process despite little effects on populations: Modeling combined effects of warming and toxicants. Glob. Chang. Biol. **23**: 2973–2989. doi:10.1111/gcb.13581

Galic, N., L. L. Sullivan, V. Grimm, and V. E. Forbes. 2018. When things don't add up: Quantifying impacts of multiple stressors from individual metabolism to ecosystem processing. Ecol. Lett. **21**: 568–577. doi:10.1111/ele.12923

Gergs, A., A. Zenker, V. Grimm, and T. G. Preuss. 2013. Chemical and natural stressors combined: From cryptic effects to population extinction. Sci. Rep. **3**: 1–8. doi:10.1038/srep02036

Green, L., and P. Fong. 2015. The good, the bad and the *Ulva*: The density dependent role of macroalgal subsidies in influencing diversity and trophic structure of an estuarine community. Oikos **125**: 988–1000. doi:10.1111/oik.02860

Halpern, B. S., M. Frazier, J. Afflerbach, J. S. Lowndes, F. Micheli, C. O'Hara, C. Scarborough, and K. A. Selkoe. 2019. Recent pace of change in human impact on the world's ocean. Sci. Rep. **9**: 1–8. doi:10.1038/s41598-019-47201-9

Han, X. 2016. Persistent alternate abundance states in the coral reef sea urchin *Diadema savignyi*: Evidence of alternate attractors. Mar. Ecol. **37**: 1179–1189. doi:10.1111/maec.12285

He, Q., B. R. Silliman, Z. Liu, and B. Cui. 2017. Natural enemies govern ecosystem resilience in the face of extreme droughts. Ecol. Lett. **20**: 194–201. doi:10.1111/ele.12721

Hillebrand, H., and others. 2020. Thresholds for ecological responses to global change do not emerge from empirical data. Nat. Ecol. Evol. **4**: 1502–1509. doi:10.1038/s41559-020-1256-9

Hoegh-Guldberg, O., and others. 2007. Coral reefs under rapid climate change and ocean acidification. Science **318**: 1737–1742. doi:10.1126/science.1152509

Holling, C. S. 1973. Resilience and stability of ecological systems. Source Annu. Rev. Ecol. Syst. **4**: 1–23.

Holmgren, M., and others. 2015. Positive shrub-tree interactions facilitate woody encroachment in boreal peatlands. J. Ecol. **103**: 58–66. doi:10.1111/1365-2745.12331

Jackson, B. C., and others. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science **293**: 629–637. doi:10.1126/science.1059199

Jorda, G., N. Marba, and C. M. Duarte. 2012. Mediterranean seagrass vulnerable to regional climate warming. Nat. Clim. Change **2**: 821–824. doi:10.1038/nclimate1533

Lauerburg, R. A. M., and others. 2020. Socio-ecological vulnerability to tipping points: A review of empirical approaches and their use for marine management. Sci. Total Environ. **705**: 135838. doi:10.1016/j.scitotenv.2019.135838

Lenihan, H. S., and C. H. Peterson. 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. Ecol. Appl. **8**: 128–140. doi:10.2307/2641316

Martins, G. M., R. C. Thompson, A. I. Neto, S. J. Hawkins, and S. R. Jenkins. 2010. Exploitation of intertidal grazers as a driver of community change. J. Appl. Ecol. **47**: 1282–1289. doi:10.1111/j.1365-2664.2010.01876.x

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature **269**: 471–477. doi:10.1038/269471a0

Menge, B. A., M. E. S. Bracken, J. Lubchenco, and H. M. Leslie. 2017. Alternative state? Experimentally induced Fucus canopy persists 38 yr in an Ascophyllum-dominated community. Ecosphere **8**: e01725. doi:10.1002/ecs2.1725

Milkoreit, M., and others. 2018. Defining tipping points for social-ecological systems scholarship - an interdisciplinary literature review. Environ. Res. Lett. **13**: 033005. doi:10.1088/1748-9326/aaaa75

Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. Science **349**: 823–826. doi:10.1126/science.aaa9933

Miller, A. D., S. H. Roxburgh, and K. Shea. 2011. How frequency and intensity shape diversity-disturbance relationships. Proc. Natl. Acad. Sci. USA **108**: 5643–5648. doi:10.1073/pnas.1018594108

Monger, C., O. E. Sala, M. C. Duniway, H. Goldfus, I. A. Meir, R. M. Poch, H. L. Throop, and E. R. Vivoni. 2015. Legacy effects in linked ecological-soil-geomorphic systems of drylands. Front. Ecol. Environ. **13**: 13–19. doi:10.1890/140269

Muggeo, V. 2008. Segmented: An R package to fit regression models with broken-line relationships. R News **8**: 20–25.

van Nes, E. H., B. M. S. Arani, A. Staal, B. van der Bolt, B. M. Flores, S. Bathiany, and M. Scheffer. 2016. What do you mean, 'Tipping Point'? Trends Ecol. Evol. **31**: 902–904. doi:10.1016/j.tree.2016.09.011

Nys, C., T. Van Regenmortel, C. R. Janssen, R. Blust, E. Smolders, and K. A. C. De Schamphelaere. 2017. Comparison of chronic mixture toxicity of nickel-zinc-copper and nickel-zinc-copper-cadmium mixtures between Ceriodaphnia dubia and Pseudokirchneriella subcapitata. Environ. Toxicol. Chem. **36**: 1056–1066. doi:10.1002/etc.3628

Orr, J. A., and others. 2020. Towards a unified study of multiple stressors: Divisions and common goals across research disciplines. Proc. R. Soc. B Biol. Sci. **287**: 20200421. doi:10.1098/rspb.2020.0421

Petraitis, P. S., and S. R. Dudgeon. 2004. Detection of alternative stable states in marine communities. J. Exp. Mar. Biol. Ecol. **300**: 343–371. doi:10.1016/j.jembe.2003.12.026

Piggott, J. J., C. R. Townsend, and C. D. Matthaei. 2015. Reconceptualizing synergism and antagonism among multiple stressors. Ecol. Evol. **5**: 1538–1547. doi:10.1002/ece3.1465

Pinckney, J. L., E. R. Knotts, K. J. Kibler, and E. M. Smith. 2020. Nutrient breakpoints for estuarine phytoplankton communities. Limnol. Oceanogr. **65**: 2999–3016. doi:10.1002/lno.11570

Ratajczak, Z., P. D'Odorico, S. L. Collins, B. T. Bestelmeyer, F. I. Isbell, and J. B. Nippert. 2017. The interactive effects of press/pulse intensity and duration on regime shifts at multiple scales. Ecol. Monogr. **87**: 198–218. doi:10.1002/ecm.1249

Rilling, M. C., and others. 2019. The role of multiple global change factors in driving soil functions and microbial biodiversity. Science **366**: 886–890. doi:10.1126/science.aay2832

Robert, P., C. W. Mckindsey, G. Chaillou, and P. Archambault. 2013. Dose-dependent response of a benthic system to biodeposition from suspended blue mussel (*Mytilus edulis*) culture. Mar. Pollut. Bull. **66**: 92–104. doi:10.1016/j.marpolbul.2012.11.003

Scheffer, M. 1998. Ecology of shallow lakes. Kluwer Academic Publisher.

Scheffer, M. 2009. Critical transitions in nature and society. Princeton Univ. Press.

Scheffer, M., S. Carpenter, J. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature **413**: 591–596. doi:10.1038/35098000

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. Trends Ecol. Evol. **18**: 648–656. doi:10.1016/j.tree.2003.09.002

Scheffer, M., and E. H. Van Nes. 2007. Shallow lakes theory revisited: Various alternative regimes driven by climate, nutrients, depth and lake size. Hydrobiologia **584**: 455–466. doi:10.1007/s10750-007-0616-7

Scheffer, M., and others. 2009. Early-warning signals for critical transitions. Nature **461**: 53–59. doi:10.1038/nature08227

Schmolke, A., R. Brain, P. Thorbek, D. Perkins, and V. Forbes. 2017. Population modeling for pesticide risk assessment of threatened species—a case study of a terrestrial plant, Boltonia decurrens. Environ. Toxicol. Chem. **36**: 480–491. doi:10.1002/etc.3576

Selkoe, K. A., and others. 2015. Principles for managing marine ecosystems prone to tipping points. Ecosyst. Health Sustain. **1**: 17–18. doi:10.1890/EHS14-0024.1

Solé, R. V., S. C. Manrubia, B. Luque, J. Delgado, and J. Bascompte. 1996. Phase transitions and complex systems: Simple, nonlinear models capture complex systems at the edge of chaos. Complexity **1**: 13–26. doi:10.1002/cplx.6130010405

Somero, G. N. 2012. The physiology of global change: Linking patterns to mechanisms. Annu. Rev. Marine. Sci. **4**: 39–61. doi:10.1146/annurev-marine-120710-100935

Sousa, W. P. 1984. The role of disturbance in natural communities. Ann. Rev. Ecol. Syst. **15**: 353–391. doi:10.1146/annurev.ecolsys.15.1.353

Steffen, W., and others. 2011. The anthropocene: From global change to planetary stewardship. Ambio **40**: 739–761. doi:10.1007/s13280-011-0185-x

Strogatz, S. H. 1994. Nonlinear dynamics and chaos - with applications to physics, biology, chemistry and engineering, 1st ed. Addison-Wesley.

Tilman, D., and others. 2001. Forecasting agriculturally driven global environmental change. Science **292**: 281–284. doi:10.1126/science.1057544

Trush, S. F., and others. 2014. Experimenting with ecosystem interaction networks in search of threshold potentials in real-world marine ecosystems. Ecology **95**: 1451–1457. doi:10.1890/13-1879.1

Underwood, A. J. 1991. Beyond BACI: Experimental designs for detecting human environmental impacts on temporal variations in natural populations. Mar. Freshw. Res. **42**: 569–587. doi:10.1071/MF9910569

Vanacker, M., A. Wezel, V. Payet, and J. Robin. 2015. Determining tipping points in aquatic ecosystems: The case of biodiversity and chlorophyll α relations in fish pond systems. Ecol. Indic. **52**: 184–193. doi:10.1016/j.ecolind.2014.12.011

Vinebrooke, R. D., K. L. Cottingham, J. Norberg, M. Scheffer, S. I. Dodson, S. C. Maberly, and U. Sommer. 2004. Impacts of multiple stressors on biodiversity and ecosystem functioning: The role of species co-tolerance. Oikos **104**: 451–457. doi:10.1111/j.0030-1299.2004.13255.x

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science **277**: 494–499. doi:10.1126/science.277.5325.494

Wang, C., and others. 2016. Biogeomorphic feedback between plant growth and flooding causes alternative stable states in an experimental floodplain. Adv. Water Resour. **93**: 223–235. doi:10.1016/j.advwatres.2015.07.003

Wang, R., J. A. Dearing, P. G. Langdon, E. Zhang, X. Yang, V. Dakos, and M. Scheffer. 2012. Flickering gives early warning signals of a critical transition to a eutrophic lake state. Nature **492**: 419–422. doi:10.1038/nature11655

Waycott, M., and others. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. USA **106**: 12377–12381. doi:10.1073/pnas

Woodward, G., D. M. Perkins, and L. E. Brown. 2010. Climate change and freshwater ecosystems impacts across multiple levels of organization. Phil. Trans. R. Soc. B. **365**: 2093–2106. doi:10.1098/rstb.2010.0055

Yue, K., D. A. Fornara, W. Yang, Y. Peng, Z. Li, F. Wu, and C. Peng. 2017. C:N:P stoichiometry: A global synthesis. Glob. Chang. Biol. **23**: 2450–2463. doi:10.1111/gcb.13569

Zeng, N., J. D. Neelin, K.-M. Lau, and C. Tucker. 1999. Enhancement of interdecadal climate variability in the Sahel by vegetation interaction. Science **286**: 1537–1540. doi:10.1126/science.286.5444.1537

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Conflict of Interest

None declared.

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