

Forum

Resilience trinity: safeguarding ecosystem functioning and services across three different time horizons and decision contexts

Hanna Weise, Harald Auge, Cornelia Baessler, Ilona Bärlund, Elene M. Bennett, Uta Berger, Friedrich Bohn, Aletta Bonn, Dietrich Borchardt, Fridolin Brand, Antonis Chatzinotas, Ron Corstanje, Frederik De Laender, Peter Dietrich, Susanne Dunker, Walter Durka, Ioan Fazey, Jürgen Groeneveld, Camille S. E. Guilbaud, Hauke Harms, Stanley Harpole, Jim Harris, Kurt Jax, Florian Jeltsch, Karin Johst, Jasmin Joshi, Stefan Klotz, Ingolf Kühn, Christian Kuhlicke, Birgit Müller, Viktoriia Radchuk, Hauke Reuter, Karsten Rinke, Mechthild Schmitt-Jansen, Ralf Seppelt, Alexander Singer, Rachel J. Standish, Hans-H. Thulke, Britta Tietjen, Markus Weitere, Christian Wirth, Christine Wolf and Volker Grimm

H. Weise, F. Bohn, J. Groeneveld, K. Johst, B. Müller, H. H. Thulke and V. Grimm (<https://orcid.org/0000-0002-3221-9512>) ✉ (volker.grimm@ufz.de), Dept. of Ecological Modelling, Helmholtz Centre for Environmental Research –UFZ, Leipzig, Germany. – HW, C. S. E. Guilbaud and B. Tietjen, Inst. of Biology, Freie Univ. Berlin, Germany. BT also at: Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany. – H. Auge, C. Baessler, W. Durka, S. Klotz and I. Kühn (<https://orcid.org/0000-0003-1691-8249>), Dept. of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Halle (Saale), Germany. – I. Bärlund and D. Borchardt, Dept. of Aquatic Ecosystems Analysis and Management, Helmholtz Centre for Environmental Research – UFZ, Magdeburg, Germany. – E. M. Bennett, Dept. of Natural Resource Sciences and McGill School of Environment, McGill Univ., Ste-Anne-de-Bellevue, QC, Canada. – JG and U. Berger, Dept. of Forest Sciences, Inst. of Forest Growth and Forest Computer Sciences, Technische Univ. Dresden, Tharandt, Germany. – A. Bonn, Dept. of Ecosystem Services, Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany, and: Inst. of Biodiversity, Univ. of Jena, Jena, Germany. – C. Wirth, AB, JG, VG, SK, IK, SD, SH, FJ, RS and CW also at: German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany. – F. Brand, ZHAW School of Management and Law, Winterthur, Switzerland. – A. Chatzinotas, Dept. of Environmental Microbiology, Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany. – R. Corstanje, Cranfield Soil and Agrifood Institute, Cranfield Univ., Cranfield, Bedfordshire, UK. – F. De Laender, Research Unit in Environmental and Evolutionary Biology, Univ. of Namur, Namur, Belgium. – P. Dietrich, Dept. of Monitoring and Exploration Technologies, Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany. – S. Dunker and S. Harpole, Dept. of Physiological Diversity, Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany. – I. Fazey, School of the Environment, Univ. of Dundee, Dundee, UK. – H. Harms, Dept. of Environmental Microbiology, Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany. – J. Harris, Cranfield Inst. for Resilient Futures, Cranfield Univ., Cranfield, Bedfordshire, UK. – K. Jax, Dept. of Conservation Biology, Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany, and: Chair of Restoration Ecology, Technische Univ. München, Freising, Germany. – VG and F. Jeltsch, Plant Ecology and Conservation Biology, Univ. of Potsdam, Potsdam, Germany. – J. Joshi, Biodiversity Research/ Systematic Botany, Univ. of Potsdam, Potsdam, Germany, and: JJ also at: Berlin-Brandenburg Inst. of Advanced Biodiversity Research (BBIB), Berlin, Germany. – C. Kuhlicke, Dept. of Urban and Environmental Sociology, Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany. – V. Radchuk, Dept. of Ecological Dynamics, Leibniz Inst. for Zoo and Wildlife Research (IZW), Berlin, Germany. – H. Reuter, Dept. of Theoretical Ecology and Modelling, Leibniz Centre for Tropical Marine Research (ZMT), Bremen, Germany. – K. Rinke, Dept. of Lake Research, Helmholtz Centre for Environmental Research – UFZ, Magdeburg, Germany. – M. Schmitt-Jansen, Dept. of Bioanalytical Ecotoxicology, Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany. – R. Seppelt, Dept. of Computational Landscape Ecology, Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany, and: Inst. of Geoscience and Geography, Martin Luther Univ. Halle-Wittenberg, Germany. – A. Singer, Swedish Species Information Centre, Swedish Univ. of Agricultural Sciences, Uppsala, Sweden. – R. J. Standish, School of Veterinary and Life Sciences, Murdoch Univ., Murdoch, WA, Australia. – M. Weitere, Dept. of River Ecology, Helmholtz Centre for Environmental Research – UFZ, Magdeburg, Germany. – C. Wolf, Dept. of Environmental Politics, Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany.

Oikos

00: 1–12, 2020

doi: 10.1111/oik.07213

Subject Editor and
Editor-in-Chief: Pedro Perez-Neto
Accepted 20 December 2019



NSO
NORDIC SOCIETY OIKOS

www.oikosjournal.org

© 2020 The Authors Oikos published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Ensuring ecosystem resilience is an intuitive approach to safeguard the functioning of ecosystems and hence the future provisioning of ecosystem services (ES). However, resilience is a multi-faceted concept that is difficult to operationalize. Focusing on resilience mechanisms, such as diversity, network architectures or adaptive capacity, has recently been suggested as means to operationalize resilience. Still, the focus on mechanisms is not specific enough. We suggest a conceptual framework, resilience trinity, to facilitate management based on resilience mechanisms in three distinctive decision contexts and time-horizons: 1) reactive, when there is an imminent threat to ES resilience and a high pressure to act, 2) adjustive, when the threat is known in general but there is still time to adapt management and 3) provident, when time horizons are very long and the nature of the threats is uncertain, leading to a low willingness to act. Resilience has different interpretations and implications at these different time horizons, which also prevail in different disciplines. Social ecology, ecology and engineering are often implicitly focussing on provident, adjustive or reactive resilience, respectively, but these different notions of resilience and their corresponding social, ecological and economic tradeoffs need to be reconciled. Otherwise, we keep risking unintended consequences of reactive actions, or shying away from provident action because of uncertainties that cannot be reduced. The suggested trinity of time horizons and their decision contexts could help ensuring that longer-term management actions are not missed while urgent threats to ES are given priority.

Keywords: concepts, ecosystems, ecosystem services provisioning, management, resilience

Introduction

Resilience has many different definitions. Holling's definition as the 'ability of ... systems to absorb changes ... and still persist' (Holling 1973) has become the most widely used one, in particular with regard to social-ecological systems. It focusses on the 'persistence of relationships' (Holling 1973) and thus the functioning and self-organization of entire systems. This holistic focus is in contrast to more reductionist interpretations, which prevail in ecology and focus on specific state variables and decompose resilience into the ability to resist, or recover from, disturbances and thereby persist (Oliver et al. 2015). Still, both interpretations imply that a loss of resilience might put the continued provision of ecosystem functioning and services (ES) at risk. Thus, understanding resilience of ecosystems is of fundamental interest because humans depend on ecosystem services (Millennium Ecosystem Assessment 2005, Díaz et al. 2015). Management for sustainable ES provisioning must safeguard, strengthen or restore ecosystems' resilience. However, the utilization of these insights in practice is still limited. While it makes intuitive sense to manage for resilience it is unclear which actions should follow from this goal (Standish et al. 2014).

If resilience is to be operationalized, its broad range of interpretations creates at least confusion, many cases of false labelling (Donohue et al. 2016), and at worst loopholes for mismanagement (Schoon et al. 2015, Newton 2016). Likewise, quantification of resilience (Allen et al. 2016, Angeler and Allen 2016) will remain a major issue unless the multiple meanings and implications of resilience are disentangled and reconciled.

As a way forward it has been suggested to focus on managing specific mechanisms that underlie the resilience of ecosystem functioning and thus support the recovery, resistance and persistence of the whole system (Biggs et al. 2012, Oliver et al. 2015, Berthet et al. 2018) instead of focusing on managing for resilience per se. Focusing on mechanisms helps us to be more specific about which outcome exactly we want to be resilient and about the concrete steps to achieve an increase in resilience. We argue, however, that a focus on resilience mechanisms is still not specific enough for two reasons: 1) recovery and resistance are reductionist concepts, while persistence is a holistic one, and 2) we need to take into account different time horizons and, hence, decision contexts.

An example from forestry illustrates the importance of time horizons: bark beetle infestations can kill off entire stands of spruce and cause great damage (Wermelinger 2004). Thus, the ES of wood provision is strongly reduced in a short-term perspective. A countermeasure could be spruce reforestation, where increasing tree vigour and stability through thinning (Spittlehouse and Stewart 2003) would aim at increasing the fitness of individual trees and thus focus on resilience mechanisms at the level of the individuals (Seidl et al. 2016). However, if we consider a longer time horizon (e.g. centuries), the effects of insect outbreaks in temperate European forests may be exacerbated by other disturbances, such as water limitation, forest fires or outbreaks of tree-killing pathogens (Lindner et al. 2010, Seidl et al. 2016). In that longer time frame, just spruce reforestation and thinning would not be the most useful way to strengthen the resilience of wood production. Instead, fostering resilience mechanisms at the community level, for example by increasing stand heterogeneity, would be a better choice because interspecific differences in reactions to disturbances can be utilized to ensure long term wood supply (Seidl et al. 2016, p. 127). There is thus a tradeoff between 1) addressing long time horizons where you can increase general resilience at the forest community level, which is likely to reduce economic revenue, in particular because wood production may be reduced and take longer, or 2) addressing shorter time horizons where you focus on fast-growing species such as spruce and increase the individual resilience through thinning, with increased economic revenue but reduced community resilience. Similar tradeoffs are common when resilience on different time horizons is addressed.

Approaches are needed that account for our limited understanding of system responses at different time horizons while advocating the use of natural mechanisms ('nature-based solutions', Cohen-Shacham et al. 2016), for example for bark

beetles natural diversity in species composition and local age and size structure (Rademacher et al. 2004). Here, we suggest a simple framework that comprises resilience mechanisms and time horizons to facilitate better decisions to safeguard future ecosystem service provisioning. We 1) discuss the reductionist and holistic aspects of resilience and why they need to be reconciled, 2) provide a brief review and a new categorization of resilience mechanisms, 3) suggest three time horizons for the management of ecosystem services, show that they imply different decision contexts, and try to relate these time horizons to resilience mechanisms and 4) give an example on the linkage of time horizons and possible resilience mechanisms.

Our main message is that resilience has three main different interpretations in different decision contexts which are determined by different time horizons ('resilience trinity'). Clarifying these interpretations according to decision context and time horizon is key to effectively managing for resilience of ecosystem services. Although it certainly has been known before that management actions to bolster resilience will depend on the time scale under consideration, we believe that the real problem lies deeper and can be traced back to different interpretations and schools of thought.

Resilience research between reductionism and holism

Current interpretations range from resilience as a way of thinking in sustainability science (Folke et al. 2010, Biggs et al. 2015) to resilience as a multidimensional metric comprising recovery, resistance and persistence in ecology and biodiversity research (Oliver et al. 2015, Donohue et al. 2016, Ingrisch and Bahn 2018), through to adopting resilience as a management paradigm in response to national policy (Isaac et al. 2018).

Recovery refers to a specific state variable of an ecosystem and is defined as the process of the variable returning, after a disturbance, to the values of the reference state or dynamics. (Note that this has often been, and still is, called 'resilience'; we follow Standish et al. (2014) to use 'recovery' for this interpretation of resilience.) Two qualifiers of recovery are 'domain of attraction' (Grimm and Wissel 1997), (i.e. how much a variable may change and still show at least some recovery) and 'return time' (i.e. the time it needs until it returns to the reference state of dynamics). The domain of attraction is the maximal 'amplitude' allowing for recovery (see resistance).

Resistance refers to a specific state variable of an ecosystem (e.g. species number) and is defined by the change of the variable following a disturbance relative to the value before the disturbance (Donohue et al. 2016). Resistance can be quantified immediately after the end of the disturbance event (Oliver et al. 2015), or after a new (or the old) reference state of dynamics has been reached (Shade et al. 2012). Both of these aspects are related to each other but not necessarily always in the same way. 'Amplitude' is a metric of resistance and quantifies how much a variable has changed.

Persistence refers to the existence of an ecosystem through time as an identifiable unit. For populations, 'existence' is easy to define, but for ecosystems we can use different sets of functional or structural criteria (Jax et al. 1998, Cumming and Collier 2005). In practice, persistence can be defined by a set of state variables remaining within certain ranges which then indicates 'persistence of relationships' (Holling 1973).

Recovery and resistance are reductionist concepts because they often reduce the representation of ecological systems to single state variables, for example abundance or total biomass of populations, or functional diversity for communities. Recovery and resistance could in principle also be explored for entire systems, but that would require that we know what set of variables fully characterizes the system, which usually is not the case.

Moreover, in addition to the requirement to define state variables, other features limit the scope of the reductionist concepts even further. According to Grimm and Wissel (1997), an 'ecological situation' for which recovery and resistance can be unambiguously defined, assessed and communicated, is defined by: level of organization, state variable, characteristics of the disturbance, definition of the reference state to which responses to disturbances can be related (Jax et al. 1998, Cumming and Collier 2005), and spatial and temporal scale. Similarly, Carpenter et al. (2001) suggest that operationalizing resilience requires specifying 'of what to what', that is what is the state variable or feature used to characterize the system, and what kinds of disturbances are considered? The choice of any of the elements of a certain 'ecological situation' is likely to affect our assessment of a stability property and our ability to detect the underlying mechanisms.

A classic example is metapopulations: if local habitats are suitable but small, local populations are prone to extinction. Persistence of populations is thus low, but when we consider larger spatial scales and thereby the regional pool of small habitats, persistence of the metapopulation and even populations increases, and we capture recolonization as a central stability mechanism (Levins 1969). Thus, shifting the spatial scale of our perception leads us to consider the metapopulation as a more appropriate level of organisation, and to identify the relevant mechanisms of persistence: connectivity and desynchronization of local dynamics.

In contrast to recovery and resistance, persistence is a holistic concept because it refers to entire systems. Quantifying persistence requires defining the systems in the first place. This is rarely done explicitly because it is challenging and depends on the observer's purpose and conceptualization of the system. Jax et al. (1998) suggest four criteria for deciding on persistence over time: whether or not a spatial or functional definition of the system is used; the degree of expected internal relationships within the system, which is similar to Holling's 'persistence of relationships'; the selected phenomena to characterize the system, which have been named 'patterns' (Grimm et al. 2005) in ecological modelling; and the degree of aggregation in representing the system's entities or

disturbances. Overall, this approach tries to identify essentials that can be used to tell whether a system did persist or not. Similarly, Cumming and Collier (2005) define persistence as ‘system identity resides in the continued presence, in both space and time, of key components and key relationships’. For a few ecosystems such essentials and key elements can be identified (e.g. the characteristic tree–grass ratio and scattered spatial distribution of trees in savannas; Jeltsch et al. 2000). However, for most other systems they are still debated.

To conclude, depending on whether the focus is on recovery and resistance or on persistence, ecological studies either end up with reductionist assessments of stability properties of often very limited scope, or with holistic assessments, which are usually ‘metamodels’ (Cumming and Collier 2005), or conceptual models, rather than quantifications because the essential elements of defining persistence are usually not known. Ecology tends to be more reductionist, focussing in particular on recovery, while social–ecological research tends to be more holistic, referring to entire systems and their functioning.

Resilience research thus has to navigate, like Odysseus did between the two sea monsters Scylla and Charybdis, between the two extremes of reductionism and holism. Progress has been slow because results from reductionist studies are often transferred, without further evidence, to the ‘stability’ or ‘resilience’ of the entire systems, whereas holistic studies often remain conceptual by referring to ‘states’ and ‘conditions’ without carefully considering criteria for assessing change and identity. To make progress, we need to reconcile the reductionist and holistic elements of Holling’s resilience.

As a first step, we suggest addressing the resilience of ecosystem services and, hence, functioning. This forces us to ask specific questions: what specific services and potential disturbances are we talking about? That is, we have to answer the question: ‘resilience of what to what?’ (Carpenter et al. 2001). The disadvantage of this is that the concept of ES itself is subject of critical debate. Issues include tradeoffs between ES (Seppelt et al. 2011, Lautenbach et al. 2019), the delineation of ‘ES providing units’, and whether or not biodiversity is a service, a good or a mechanism (Bennett et al. 2009, Mace et al. 2012, Jax and Heink 2015). Nevertheless, a focus on ES, and hence the underlying functioning, helps us to address specific resilience mechanisms. In contrast to managing the resilience of a hard-to-define ecosystem, the relevant level of biological organization often is obvious if the goal is to manage for resilience of a specific ES. Focussing on mechanisms underlying the resilience of ES forces us to be more specific.

Resilience mechanisms

Resilience mechanisms have been explored for decades in systems as diverse as coral reefs, rangelands, rainforests or contaminated aquifers. Table 1 provides an overview of mechanisms that have been identified in review articles focusing on ‘resilience’, ‘mechanism’ and ‘ecosystem service’ (see Supplementary material Appendix 1 for the specific

definition of each mechanism). In most cases these mechanisms are based on expert knowledge or theory and are rarely validated empirically outside their holistic social–ecological contexts (Egli et al. 2018).

Grouping these mechanisms into categories helps keeping an overview but can never be perfect because mechanisms, i.e. causal relationships, cannot be separated from the context in which they operate. We grouped the mechanisms into four categories. 1) Portfolio mechanisms spread the risk of being affected by a disturbance. They are often based on diversity, redundancy or heterogeneity. Mechanisms in the category Function 2) are related to important roles that elements of a system play for functioning; they can only be observed dynamically as they unfold in the course of time. A well-known mechanism in this category is based on the presence of keystone species. Some overlap with the portfolio category exists, since for example diversity can act as portfolio mechanism but also affect function. Therefore, we here set the focus on functional aspects that are not primarily based on diversity, redundancy or heterogeneity. 3) Adaptation mechanisms share aspects of the Portfolio and Function category. They require diversity to function and are observed over the course of time. However, resilience mechanisms in this category are different because they feature adaptation via various mechanisms, including natural selection. 4) The fourth category, Structure, refers to structural features that affect recovery and resistance and that can be observed statically, in a snapshot of a system. Prominent examples are modularity and connectivity.

Table 1 demonstrates the diversity of resilience mechanisms and that any attempt to categorize them is necessarily subjective and to some degree arbitrary, as can be inferred from comparing our categories to those cited in the legend of Table 1 and the Supplementary material Appendix 1. The reason is that these mechanisms do not work in isolation but together with other mechanisms. How they do so depends on the specific system and context under consideration. Increasing connectivity, for example, can reduce extinction risk in local habitats, but increase the risk of disease spreading. Likewise, diversity in terms of species numbers is generally believed to increase resilience, but many ecosystems dominated by a few species exist, for example boreal forests.

The mechanisms listed in Table 1 represent empirical knowledge or theory. However, it is difficult to translate the knowledge they represent directly into actions. For example, intuitively it seems evident that biodiversity increases resilience, but decades of biodiversity research show how difficult it is to understand this relationship in systems that are more complex than simplified models or controlled experiments (Cardinale et al. 2012, De Laender et al. 2016). Thus, the mechanisms listed in Table 1 are only possible mechanisms. Whether they are relevant and whether some of them dominate or compromise others, depends on the specific situation and context (Biggs et al. 2012, Desjardins et al. 2015). The most important features of these situations are the time horizon considered (which also defines a spatial context) and the decision context linked to this horizon.

Table 1. Mechanisms expected to confer resilience. Here we used a literature search (Supplementary material Appendix 1 Table A2) to compile mechanisms and group them into categories (see Supplementary material Appendix 1 Table A1 for definitions of each mechanism). Those categories are not exclusive. Other possible categories are for example diversity, connectivity and adaptive capacity (Bernhardt and Leslie 2013); species, community, landscape (Oliver et al. 2015); complexity, adaptivity (Desjardins et al. 2015). For an overview of mechanisms in social–ecological systems see (Biggs et al. 2012, 2015), for attributes that confer resilience to climate change in the context of restoration see Timpane-Padgham et al. (2017), and for biodiversity-driven mechanisms in agro-ecosystems see Martin et al. (2019).

Group	Mechanism	General idea	Example definitions ¹	References
Portfolio: Spreading the effects of disturbances	Redundancy (functional, species)	Losing certain species may not matter because their function can be provided by functionally equivalent species.	‘when multiple species perform similar functions (...) the resistance of an ecosystem function will be higher if those species also have differing responses to environmental perturbations’ (Oliver et al. 2015)	(Biggs et al. 2012, Bernhardt and Leslie 2013, Griffiths and Philippot 2013, Desjardins et al. 2015, Oliver et al. 2015, Sasaki et al. 2015)
	Diversity (genetic, habitat, species, trait, response)	Individuals or populations are sensitive to disturbances to different extents.	‘Species in the same functional group often show different responses to disturbances (Laliberte et al. 2010), and hence the value of redundancy’	(Palumbi et al. 2009, Chapin III et al. 2010, Traill et al. 2010, Biggs et al. 2012, Bernhardt and Leslie 2013, Griffiths and Philippot 2013, Thompson et al. 2014, Desjardins et al. 2015, Oliver et al. 2015, Sasaki et al. 2015)
	Heterogeneity (stand, landscape)	Functions lost in certain places can be compensated or restored from other, less affected places.	‘Resilience is an emergent ecosystem property conferred through biodiversity, (...), ecosystem diversity (heterogeneity and beta diversity) across a forest landscape’ (Thompson et al. 2014)	(Thompson et al. 2014, Desjardins et al. 2015)
	Area of habitat cover at the landscape scale		‘Larger areas of natural or semi-natural habitat tend to provide a greater range and amount of resources, which promote higher species richness and larger population sizes [...]. This [...] is likely to mean greater genetic diversity and functional redundancy [...]’ (Oliver et al. 2015)	(Oliver et al. 2015)
Function: Functional features that affect recovery and resistance (identifiable only in system dynamics)	Negative feedbacks	Negative feedbacks, for example density dependence, cause recovery to equilibria.	‘Negative feedback mechanisms contribute to maintain the ecosystem state’ (Conversi et al. 2015)	(Chapin III et al. 2010, Gedan et al. 2011, Biggs et al. 2012, Conversi et al. 2015, Spears et al. 2015)
	Keystone species	Keystone species (of functional types) may be the main factor maintaining a certain function or structure.	‘Loss of the keystone species can lead to cascading effects’ (Sasaki et al. 2015) ‘Loss of keystone predators can have large effects for a system through cascading effects of expansion of herbivore populations’ (Thompson et al. 2014)	(Traill et al. 2010, Thompson et al. 2014, Sasaki et al. 2015)
	Dominant species	A dominant species that is resilient will entail its resilience to the entire system.	‘If the dominant species is resilient to disturbances it will maintain ES functioning despite disturbances’ (Sasaki et al. 2015)	(Sasaki et al. 2015)
	Strength of species interaction	Weak links in an interaction network of species can dampen internal and external variations in components of the network.	‘Weakly interacting species stabilize community dynamics by dampening strong, potentially destabilizing consumer-resource interactions and facilitative interactions.’ (Bernhardt and Leslie 2013)	(Bernhardt and Leslie 2013)

(Continued)

Table 1. (Continued)

Group	Mechanism	General idea	Example definitions ¹	References
	Separation of time scales ('slow variables')	Through self-organization, slow-changing variables can emerge that constrain and control fast-changing variables and thereby reduce variation ('panarchy')	'slow variables are usually related to regulating ecosystem services, and that the strength of regulating services can attenuate the impact of shocks on ecosystems.' (Bennett et al. 2009)	(Bennett et al. 2009, Biggs et al. 2012)
Adaptation: Adaptation in order to better cope with disturbances; changes in disturbance regimes	Adaptive phenotypic plasticity	Individuals change in response to disturbance and thereby reduce the effects of subsequent disturbances.	'Capacity of individuals to respond to environmental changes through flexible behavioural or physiological strategies [...]' (Oliver et al. 2015) '(...) phenotypic plasticity may be the most important component of adaptive potential (...)' (Bernhardt and Leslie 2013)	(Bernhardt and Leslie 2013, Oliver et al. 2015)
	Adaptive capacity	Populations, communities and ecosystems have the ability to change, through change of individuals, shifts of distributions, and rapid evolution, and thereby reduce responses to subsequent disturbances.	'ability of populations, communities and ecosystems to adapt [...] through a combination of phenotypic plasticity, physiol. responses, distributional shifts, rapid evolution of traits' (Bernhardt and Leslie 2013)	(Bernhardt and Leslie 2013)
	Learning	Individuals learn and thereby recover faster or respond less to disturbances.	'The process of modifying existing or acquiring new knowledge, behaviours, skills, values or preferences at individual, group or societal levels' (Biggs et al. 2012)	(Biggs et al. 2012, 2015)
Structure: Structural features that affect recovery and resistance (identifiable in snapshots of a system)	Connectivity	Higher connectivity between habitats allows for faster recovery by moving individuals or resources.	'connections that promote stability and recovery at multiple scales of biological organization' (Bernhardt and Leslie 2013)	(Biggs et al. 2012, Bernhardt and Leslie 2013)
	Modularity	Organization in more or less disconnected compartment allows for asynchronous responses and thereby recovery.	'It refers to compartmentalization of populations in space and time. (...). For example, where populations are too closely connected, severe disturbances to one population may affect all populations.' (Bernhardt and Leslie 2013)	(Bernhardt and Leslie 2013)
	Network architecture	Depending on the type of interaction between nodes, the connectedness and other features of the interaction network determine the response to disturbances.	'A highly connected and nested architecture promotes community stability in mutualistic networks, whereas stability is increased in compartmented and weakly connected architectures in trophic networks. (...)' (Bernhardt and Leslie 2013)	(Bernhardt and Leslie 2013, Griffiths and Philippot 2013, Oliver et al. 2015)
	Spatial self-organization	Positive feedback can lead to self-organized spatial patterns that are self-similar over time and lead to recovery from disturbances.		

¹ It should be noted that no single definition can capture the heterogeneity of existing definitions, their context dependency and their overlap. See Supplementary material Appendix 1 Table A1 for the full list of definitions we extracted from the literature.

Rationale for a ‘resilience trinity’

Focussing on ES and their underlying mechanisms helps us to ask more specific questions about resilience and thereby supports operationalization. Still, context matters. Consider for example the storage of organic carbon in soils (soil organic carbon, SOC). Soils store at least three times the amount of carbon found in the atmosphere or in living plants (Parry et al. 2007). This is one key function supporting climate regulation. Soil biota mediate SOC persistence and turnover (Schmidt et al. 2011, Schimel and Schaeffer 2012). Land use is one of the main stresses on SOC levels, with persistently low and decreasing levels in more intense land uses. Stress leads to the destruction of soil structure and to a decrease in soil biodiversity on which structural reformation relies (Crawford et al. 2011, Ponge et al. 2013). Short term (-1 year) responses to conserve SOC aim at improving soil management practices, such as less intense tillage, retaining stubble in the field, or introducing cover crops when fields are temporarily not in production. Longer term (10–100 years) measures would comprise similar soil management interventions but also consider taking fields out of production permanently. Additional options are the introduction of intercropping systems or even landscape engineering, for example producing terraces or hedges, to avoid erosion. This requires the consideration of land use and its management from a long-term planning and policy perspective, for instance designating land-uses (e.g. forestry) on lands prone to SOC loss.

Thus, different time horizons require different measures, which leads us the ‘resilience trinity’ framework. Threats to ES can be acute and obvious in some contexts. In these situations, the loss of the desired functions is imminent or has already happened. Time for reaction is limited and the actions are planned for comparatively short time horizons. We call this decision context reactive. It is further characterized by a high acceptance for actions by the stakeholders involved. Examples for a reactive decision context include local pest outbreaks, an emerging wildlife disease that threatens livestock, or catastrophic floods in river flood plains. The ‘command and control’ mindset of engineering usually is dominant in this context and usually is targeting the symptoms, not the causes of a problem.

In contrast to reactive, in adjustive decision contexts ES are threatened, but not yet to a level that is critical to their provisioning. Concerns about future losses exist, but the urgency perceived by stakeholders of actions to increase resilience is lower than in a reactive context. Therefore, there are initiatives and incentives to adjust current management practices. Safeguarding ES resilience in an adjustive decision context can be slow though or even fail because of the lower perceived urgency for actions. Dealing with the decline of honey bees provides an example of the difference between reactive and adjustive decision contexts. A reactive decision was triggered by an incident in the Upper Rhine valley in 2008, where 11 500 honey bee colonies were lost due to dust from maize

seeds treated with an insecticide. Blowing out of this dust containing the active substance into the environment with pneumatic sowing machines resulted in contamination of nectar and pollen (Pistorius et al. 2010). In turn, new regulations were installed for both quality control of seed treatment and for vacuuming potential dust during sowing. In contrast, adjustive decisions regarding pollinators are for example declarations of intent of the current government of Germany (CDU/CSU SPD 2018) to stop the decline of insects by revisiting current regulation schemes, which easily could take decades to be realized. Mostly, the adjustive decision context is the one within which ecologists discuss resilience.

Third, provident decision contexts are distinguished from the two previous contexts by even longer time horizons. Here, the task is to conserve, restore or improve resilience mechanisms without a specific threat being the trigger for action. The basic motivation is that resilience of ES might erode in the future in unforeseeable ways due to (unforeseeable) changes of environmental and societal drivers. Lacking an imminent threat, the provident decision context deals with measures that generally support resilience of ES. Yet, acceptance of actions is low for provident decisions, particularly because returns from current investments are uncertain. An example is the creation of large reserve networks, which can safeguard the provisioning of ES even against unknown future threats, as they are likely to harbour the structure and functions required for resilience mechanisms. However, this benefit cannot easily be accounted for and thus not be balanced against the loss of, for example, arable land. Typically, this provident decision context is addressed in sustainability and transformation science.

Our conceptualization of provident resilience is similar to the idea of ‘general resilience’ (Folke et al. 2010), which is ‘concerned more about resilience to all kinds of shocks, including completely novel ones’ (Folke et al. 2010), while ‘specified resilience’ refers ‘to problems relating to particular aspects of a system that might arise from a particular set of sources or shocks.’ (Folke et al. 2010). Our resilience trinity framework explicitly refers to different time horizons and their decision contexts, but overlaps with the specified/general distinction by emphasizing the long-term risks of focusing solely on reactive, or specified, resilience.

Resilience mechanisms within the trinity framework

As mentioned earlier, the strength and scope of resilience mechanisms depend on the context, for example whether we focus on individuals, populations, communities, ecosystems or landscapes. The resilience trinity framework is meant to organize our thinking, debate and research on this context dependency along three different time horizons and hence decision contexts. In Table 2, the mechanisms of Table 1 are related to these time horizons. Some mechanisms are less likely to be useful on the reactive scale and need the

Table 2. Relating resilience mechanisms to the trinity of time horizons and decision contexts: reactive, adjustive, provident. The table demonstrates the possible importance of each resilience mechanism at each horizon. High importance is indicated by presence of ‘++’ and potential importance by ‘+’. Some mechanisms are not very influential at the reactive time horizon (as indicated by the absence of ‘+’) because they require longer time spans to manifest their effects on ES. Red arrows on the right of the table indicate possible tradeoffs between certain pairs of resilience mechanisms, while green arrows indicate possible synergies, where mechanisms would enhance each others’ positive effect on resilience. This table is meant as a framework for structured discussions but not as a ready-to-use solution, because virtually every ‘+’ or arrow depends on the system and context considered.

Mechanisms	Time horizon			Things to pay attention to
	Reactive	Adjustive	Provident	
Redundancy (functional, species)		+	++	
Diversity (genetic, habitat, species, trait)	+	+	+	Effects of diversity may differ in their magnitude among horizons
Heterogeneity (stand, landscape)		+	++	The effects of Heterogeneity increase with time
Area of habitat cover at the landscape scale	+	++	++	
Negative feedbacks		+	++	
Keystone species	+	+	+	
Dominant species	+	+	+	
Strength of species interactions	+	+	+	
Separation of time scales ('slow' variables)			++	
Adaptive phenotypic plasticity		+	+	
Adaptive capacity		+	++	
Learning		+	+	
Connectivity	+	+	+	
Modularity	+	+	+	
Network architecture	+	+	+	Network architecture has different effects in mutualistic and trophic networks
Spatial self-organization		+	++	



provident scale to unfold their potential, for example spatial self-organization. Other mechanisms are relevant for all three trinity aspects, e.g. diversity. Table 2 also includes possible interactions between pairs of mechanisms. Some pairs might compromise each other, for example ‘diversity’ and ‘dominant species’, while other might show synergies, for example ‘redundancy’ and ‘heterogeneity’.

Even more than Table 1, each and any element of Table 2 is open to discussion and its interpretation depends on the specific context and ES considered, and on how researchers and practitioners interpret the terms included. Table 2 thus does not provide a ready-to-use solution, but provides an invitation to explicitly and systematically discuss relevant issues of safeguarding ES in terms of increasing resilience. In the following, we demonstrate the strength of our conceptual framework by applying it to the ES of water purification (Fig. 1).

Example: water purification

Water is a fundamental resource. Societies, economies and the natural environment rely on permanent water provision in sufficient quantity and quality. A multitude of threats endanger water purification services. Some threats are acute (e.g. pulses of toxicants or the occurrence of extensive anoxia in lakes) and require immediate action. At intermediate time scales, solutions must be found to control pollution pathways, avoid structural degradation of river courses or excessive eutrophication. On longer time scales, threats are likely related to human perturbations of the global biogeochemical cycles (nitrogen, phosphorus, carbon), predominantly by farming, or structural degradations. However, direct and indirect consequences from these threats cannot be forecasted yet, which makes it more challenging to develop and justify countermeasures.

Actions related to reactive decision contexts aim to prevent the imminent danger of losing ecosystem functions. They are often based on technology and aim at preserving or restoring a certain state of a system (Fig. 1). Examples include increasing the height of dikes, or the oxygenation of deep water in lakes to prevent mass mortality of species and internal loading with pollutants (Beutel and Horne 1999). These measures profit from extensive knowledge of the ecosystem's functioning and a clear definition of the problem and its solution. Possibly high costs of these solutions are justified by strong societal pressure to act immediately, e.g. for maintaining drinking water supply from a reservoir or a lake (e.g. suppression of manganese release, Bryant et al. (2011)). In addition, they are a reaction to a specific and rather clearly described threat.

An example for an action in an adjustive decision context is the nutrient reduction by flocculation, which is used to remove nutrients from lakes or reservoirs (Mehner et al. 2008) and add substances such as aluminium to remove phosphate from the water column. Lowering phosphate concentrations reduces eutrophication in general and shifts

algal communities from a dominance of potentially toxic cyanobacteria towards a community consisting of eukaryotic algae and therefore comes along with a major improvement of water quality. Such measures require more careful planning than reactive decisions, for example adapted dosing and application of flocculants, as well as detailed pre-studies. Another example of a decision in an adjustive context is the activation of major reactive zones, for example wetlands or hyporheic zones in riverbeds (Rode et al. 2015) for water quality regulation.

Decisions in provident contexts often follow a systems approach. In the water sector they often include the landscape context. Implementation of buffer strips along rivers, for example, can reduce nutrient exports from land into the water cycle and therefore weaken environmental pressures from agriculture (Mayer et al. 2007). Another example is key species, which are often important for self-purification within aquatic environment such as bivalves filtering the water or other organisms with similar functions (McCay et al. 2003, Kathol et al. 2011). The protection of key species is one example for safeguarding ES resilience at long time horizons.

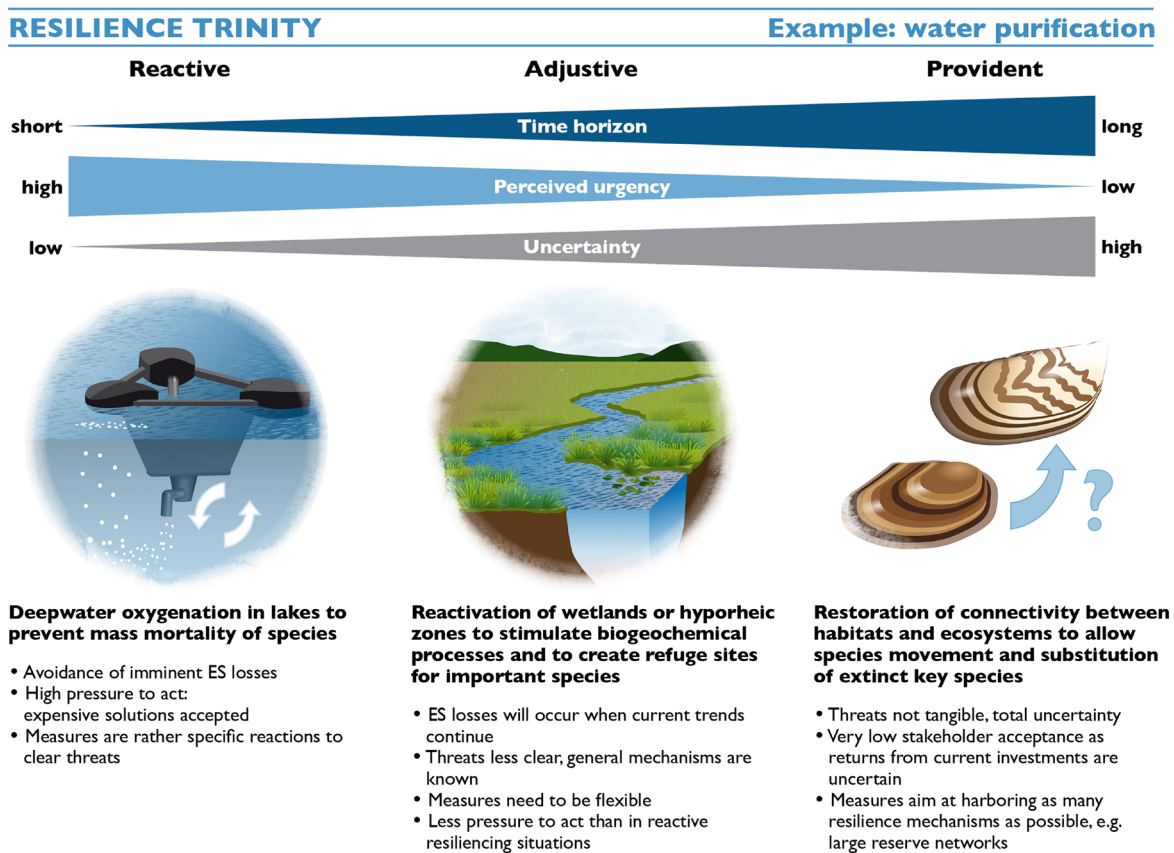


Figure 1. Measures to safeguard the ecosystem service (ES) of water purification across different time horizons. The time horizon of interest determines the decision context (upper arrow). If an ES needs to be safeguarded now (very short time horizon) the pressure to act is high and uncertainty is comparatively low. In contrast, uncertainty is very high and the pressure to act very low for long time horizons. The resulting decision contexts will warrant different measures; thus we propose to distinguish reactive, adjustive and provident contexts. It is important to be aware of the different decision contexts because they will lead to different decisions and tradeoffs. Our resilience trinity framework tries to create and establish this awareness.

This includes the restoration of habitats and refuges for key species. Even so, current key species may not prevail under future conditions. Thus, actions that allow other species with the same functions but a better fitness to thrive under new conditions could be an important measure in provident decision contexts. Managing connectivity between ecosystems and habitats to allow for spread of better adapted species while monitoring the effects of species' movements on the functionality of food webs could thus be a core element to safeguard the resilience of water purification at long time horizons. In that sense, invading species may even substitute the loss of natural key species. In the future, invading mussels and clams could substitute for native unionids in rivers of the Northern Hemisphere, a pattern which is already present in several systems (Strayer and Smith 1996, Caraco et al. 2006). This may, however, be at odds with various other goals such as biodiversity conservation, maintaining existing ecosystem functions, functionality of human infrastructures or human recreation (Minchin et al. 2002). Policy makers and decision makers must explicitly recognize the tradeoffs in this situation and recognize that ecosystems are multi-scaled and nonlinear with inherent uncertainty and managing for one spatial or temporal context ignores reality and tends to reduce resilience at other spatial and temporal scales (see also Schlüter et al. 2019).

Table 1 and 2 can be used as a tool in this context: which resilience mechanisms are employed by the potential actions for increasing reactive, adjustive or provident resilience, that were discussed so far for this example? Increasing the height of dikes, or the oxygenation of deep water, are engineering solutions that clearly represent a reactive context. They address the symptom, i.e. flood risk and pollution, respectively, but not the causes of these risks. As a result, in the long term they might even severely increase the risk of losing ES of interest, as the reasons for the erosion of resilience might accumulate. Increasing the height of dikes and oxygenation do not mimic any natural resilience mechanism. In contrast, the measures discussed for the provident context, i.e. buffer strips, keystone species and improving connectivity, represent mechanisms that actually do exist in nature and can affect water quality in a positive way. However, a focus on a specific species that directly affect water quality, such as bivalves, may compromise efforts to restore biodiversity, in particular if non-native bivalves are considered.

Conclusion

Resilience is an important concept that refers to the ability of ecosystems to self-organize in a way that they can 'absorb changes ... and still persist' (Holling 1973). Quantitative features of this ability are resistance, recovery and persistence. While persistence is a holistic concept focusing on the whole system and the persistence of all relationship within, recovery and resistance are reductionist concepts looking at single state variables. Although resilience has become a concept that is popular among scientists, actors and stakeholders alike

(Newton 2016), the dichotomy of holistic and reductionist interpretations of this concept have so far hampered its use for planning, management and environmental decision making (Standish et al. 2014). Focussing more on the mechanisms underlying resilience and grouping them into categories, like the ones we used in Table 1, is a first step towards operationalizing resilience. Still, at least one more step, distinguishing different time horizons and decision contexts, is required.

Our framework, dubbed resilience trinity, tries to keep the attractiveness of the concept of resilience while demanding more specification. Our main purpose is to create awareness for different time horizons (short, intermediate and long-term). These imply different decision contexts and management attitudes (reactive, adjustive and provident). None of the three contexts is more important than the others – they all need to be considered and finally to be reconciled. Otherwise, exclusively focusing on reactive management could compromise long-term resilience of certain services. Solely provident actions could lead to short-term losses of services, or unacceptable risks. There is no simple, generic solution to reconcile the tradeoffs of the different time horizons and decision contexts. Rather, our framework is designed to add structure to decision making and policy development. Further examples and, preferably, case studies will be needed to learn about, and possibly improve, its usefulness.

A main criterion for the design of the resilience trinity framework was simplicity: focusing on three time horizons and clarifying the decision context can facilitate operationalizing resilience and ecosystem services, both complex and multidimensional concepts. Our vision is to ultimately foster a proactive approach that does not ignore the consequences of reactive and adjustive decisions for the time scale of provident decisions. To be clear, decisions for all three time scales need to be made now, but they address different time scales.

Acknowledgments – We would like to thank P. Peres-Neto for his insightful comments. We would like to thank Sebastian Fiedler, Hans-Jörg Vogel, Steve Railsback and Graeme Cumming for helpful comments on an earlier version of this manuscript. We thank Lisa Vogel and Daphne Braun for professional revision of the illustrations.

Funding – HW acknowledges funding support through the German Research Foundation DFG project TI 824/2-1 'Ecosystem resilience towards climate change – the role of interacting buffer mechanisms in Mediterranean-type ecosystems and through the project Emerging Ecosystems'. We also thank UFZ's Integrated Project 'Emerging Ecosystems' within the research program 'Terrestrial Environment' of the Helmholtz Association for funding workshops to develop ideas that are presented in this manuscript.

References

- Angeler, D. G. and Allen, C. R. 2016. Quantifying resilience. – J. Appl. Ecol. 53: 617–624.
- Allen, C. R. et al. 2016. Quantifying spatial resilience. – J. Appl. Ecol. 53: 625–635.

- Bennett, E. M. et al. 2009. Understanding relationships among multiple ecosystem services. – *Ecol. Lett.* 12: 1394–1404.
- Bernhardt, J. R. and Leslie, H. M. 2013. Resilience to climate change in coastal marine ecosystems. – *Annu. Rev. Mar. Syst.* 5: 371–92.
- Berthet, E. T. et al. 2018. Applying ecological knowledge to the innovative design of sustainable agroecosystems. – *J. Appl. Ecol.* 56: 44–51.
- Beutel, M. W. and Horne, A. J. 1999. A review of the effects of hypolimnetic oxygenation on lake and reservoir water quality. – *Lake Reservoir Manage.* 15: 285–297.
- Biggs, R. et al. 2012. Toward principles for enhancing the resilience of ecosystem services. – *Annu. Rev. Environ. Resour.* 37: 421–448.
- Biggs, R. et al. 2015. Principles for building resilience: sustaining ecosystem services in social–ecological systems. – Cambridge Univ. Press.
- Bryant, L. D. et al. 2011. Solving the problem at the source: controlling Mn release at the sediment–water interface via hypolimnetic oxygenation. – *Water Res.* 45: 6381–6392.
- Caraco, N. F. et al. 2006. Top–down control from the bottom: regulation of eutrophication in a large river by benthic grazing. – *Limnol. Oceanogr.* 51: 664–670.
- Cardinale, B. J. et al. 2012. Biodiversity loss and its impact on humanity. – *Nature* 486: 59.
- Carpenter, S. et al. 2001. From metaphor to measurement: resilience of what to what? – *Ecosystems* 4: 765–781.
- CDU/CSU SPD. 2018. Ein neuer Aufbruch für Europa Eine neue Dynamik für Deutschland Ein neuer Zusammenhalt für unser Land. Koalitionsvertrag zwischen CDU, CSU und SPD, 18. – Legislaturperiode. <<https://www.bundesregierung.de/resource/blob/975226/847984/5b8bc23590d4cb2892b31c987ad672b7/2018-03-14-koalitionsvertrag-data.pdf?download=1>>
- Chapin III, F. S. et al. 2010. Ecosystem stewardship: sustainability strategies for a rapidly changing planet. – *Trends Ecol. Evol.* 25: 241–249.
- Cohen-Shacham, E. et al. 2016. Nature-based solutions to address global societal challenges. – IUCN, Gland, Switzerland, pp. 97.
- Conversi, A. et al. 2015. A holistic view of marine regime shifts. – *Phil. Trans. R. Soc. B* 370: 20130279.
- Crawford, J. W. et al. 2011. Microbial diversity affects self-organization of the soil–microbe system with consequences for function. – *J. R. Soc. Interface* rsif20110679.
- Cumming, G. and Collier, J. 2005. Change and identity in complex systems. – *Ecol. Soc.* 10(1):29.
- De Laender, F. et al. 2016. Reintroducing environmental change drivers in biodiversity–ecosystem functioning research. – *Trends Ecol. Evol.* 31: 905–915.
- Desjardins, E. et al. 2015. Promoting resilience. – *Q. Rev. Biol.* 90: 147–165.
- Díaz, S. et al. 2015. The IPBES conceptual framework – connecting nature and people. – *Curr. Opin. Environ. Sustain.* 14: 1–16.
- Donohue, I. et al. 2016. Navigating the complexity of ecological stability. – *Ecol. Lett.* 19: 1172–1185.
- Egli, L. et al. 2018. Exploring resilience with agent-based models: state of the art, knowledge gaps and recommendations for coping with multidimensionality. – *Ecol. Complex.* 40: 100718.
- Folke, C. et al. 2010. Resilience thinking: integrating resilience, adaptability and transformability. – *Ecol. Soc.* 15(4): 23.
- Gedan, K. B. et al. 2011. Uncertain future of New England salt marshes. – *Mar. Ecol. Progr. Ser.* 434: 229–238.
- Griffiths, B. S. and Philippot, L. 2013. Insights into the resistance and resilience of the soil microbial community. – *FEMS Microbiol. Rev.* 37: 112–129.
- Grimm, V. and Wissel, C. 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. – *Oecologia* 109: 323–334.
- Grimm, V. et al. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. – *Science* 310: 987–991.
- Holling, C. S. 1973. Resilience and stability of ecological systems. – *Annu. Rev. Ecol. Syst.* 4: 1–23.
- Ingrisch, J. and Bahn, M. 2018. Towards a comparable quantification of resilience. – *Trends Ecol. Evol.* 33: 251–259.
- Isaac, N. J. B. et al. 2018. Defining and delivering resilient ecological networks: nature conservation in England. – *J. Appl. Ecol.* 55: 2537–2543.
- Jax, K. et al. 1998. The self-identity of ecological units. – *Oikos* 253–264.
- Jax, K. and Heink, U. 2015. Searching for the place of biodiversity in the ecosystem services discourse. – *Biol. Conserv.* 191: 198–205.
- Jeltsch, F. et al. 2000. Ecological buffering mechanisms in savannas: a unifying theory of long-term tree–grass coexistence. – *Plant Ecol.* 150: 161–171.
- Kathol, M. et al. 2011. Contribution of biofilm-dwelling consumers to pelagic–benthic coupling in a large river. – *Freshwater Biol.* 56: 1160–1172.
- Laliberte, E. et al. 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. – *Ecol. Lett.* 13: 76–86.
- Lautenbach, S. et al. 2019. Blind spots in ecosystem services research and challenges for implementation. – *Regional Environ. Change.* 19: 2151–2172.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. – *Am. Entomol.* 15: 237–240.
- Lindner, M. et al. 2010. Climate change impacts, adaptive capacity and vulnerability of European forest ecosystems. – *For. Ecol. Manage.* 259: 698–709.
- Mace, G. M. et al. 2012. Biodiversity and ecosystem services: a multilayered relationship. – *Trends Ecol. Evol.* 27: 19–26.
- Martin, E. A. et al. 2019. Assessing the resilience of biodiversity-driven functions in agroecosystems under environmental change. – *Adv. Ecol. Res.* 60: 59–123.
- Mayer, P. M. et al. 2007. Meta-analysis of nitrogen removal in riparian buffers. – *J. Environ. Qual.* 36: 1172–1180.
- McCay, D. P. F. et al. 2003. Restoration that targets function as opposed to structure: replacing lost bivalve production and filtration. – *Mar. Ecol. Progr. Ser.* 264: 197–212.
- Mehner, T. et al. 2008. Rapid recovery from eutrophication of a stratified lake by disruption of internal nutrient load. – *Ecosystems* 11: 1142–1156.
- Millennium Ecosystem Assessment (MEA). 2005. Ecosystems and human well-being. – Island Press.
- Minchin, D. et al. 2002. Zebra mussel: impacts and spread. – In: *Invasive aquatic species of Europe. Distribution, impacts and management.* Springer.
- Newton, A. C. 2016. Biodiversity risks of adopting resilience as a policy goal. – *Conserv. Lett.* 9: 369–376.
- Oliver, T. H. et al. 2015. Biodiversity and resilience of ecosystem functions. – *Trends Ecol. Evol.* 30: 673–684.

- Palumbi, S. R. et al. 2009. Managing for ocean biodiversity to sustain marine ecosystem services. – *Front. Ecol. Environ.* 7: 204–211.
- Parry, M. et al. 2007. *Climate change 2007: impacts, adaptation and vulnerability*. – Cambridge Univ. Press.
- Pistorius, J. et al. 2010. Bee poisoning incidents in Germany in spring 2008 caused by abrasion of active substance from treated seeds during sowing of maize. – *Julius-Kühn-Archiv* 423: 118.
- Ponge, J.-F. et al. 2013. The impact of agricultural practices on soil biota: a regional study. – *Soil Biol. Biochem.* 67: 271–284.
- Rademacher, C. et al. 2004. Reconstructing spatiotemporal dynamics of central European natural beech forests: the rule-based model BEFORE. – *For. Ecol. Manage.* 194: 349–368.
- Rode, M. et al. 2015. The importance of hyporheic zone processes on ecological functioning and solute transport of streams and rivers. – In: *Ecosystem services and river basin ecohydrology*. Springer.
- Sasaki, T. et al. 2015. Perspectives for ecosystem management based on ecosystem resilience and ecological thresholds against multiple and stochastic disturbances. – *Ecol. Indic.* 57: 395–408.
- Schimel, J. and Schaeffer, S. M. 2012. Microbial control over carbon cycling in soil. – *Front. Microbiol.* 3: 348.
- Schlüter, M. et al. 2019. The potential of models and modeling for social–ecological systems research: the reference frame ModSES. – *Ecol. Soc.* 24: 31.
- Schmidt, M. W. et al. 2011. Persistence of soil organic matter as an ecosystem property. – *Nature* 478: 49.
- Schoon, M. L. et al. 2015. Politics and the resilience of ecosystem services. – In: Biggs, R. et al. (eds), *Principles for building resilience: sustaining ecosystem services in social–ecological systems*. Cambridge Univ. Press, pp. 32–49.
- Seidl, R. et al. 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. – *J. Appl. Ecol.* 53: 120–129.
- Seppelt, R. et al. 2011. A quantitative review of ecosystem service studies: approaches, shortcomings and the road ahead. – *J. Appl. Ecol.* 48: 630–636.
- Shade, A. et al. 2012. Fundamentals of microbial community resistance and resilience. – *Front. Microbiol.* 3: 417.
- Spears, B. M. et al. 2015. Effective management of ecological resilience – are we there yet? – *J. Appl. Ecol.* 52: 1311–1315.
- Spittlehouse, D. L. and Stewart, R. B. 2003. Adaptation to climate change in forest management. – *BC J. Ecosyst. Manage.* 4: 1–11.
- Standish, R. J. et al. 2014. Resilience in ecology: abstraction, distraction or where the action is? – *Biol. Conserv.* 177: 43–51.
- Strayer, D. L. and Smith, L. C. 1996. Relationships between zebra mussels (*Dreissena polymorpha*) and unionid clams during the early stages of the zebra mussel invasion of the Hudson River. – *Freshwater Biol.* 36: 771–780.
- Thompson, I. D. et al. 2014. Biodiversity and ecosystem services: lessons from nature to improve management of planted forests for REDD-plus. – *Biodivers. Conserv.* 23: 2613–2635.
- Timpane-Padgham, B. L. et al. 2017. A systematic review of ecological attributes that confer resilience to climate change in environmental restoration. – *PLoS One* 12: e0173812.
- Truill, L. W. et al. 2010. Mechanisms driving change: altered species interactions and ecosystem function through global warming. – *J. Anim. Ecol.* 79: 937–947.
- Wermelinger, B. 2004. Ecology and management of the spruce bark beetle *Ips typographus* – a review of recent research. – *For. Ecol. Manage.* 202: 67–82.

Supplementary material (available online as Appendix oik-07213 at <www.oikosjournal.org/appendix/oik-07213>). Appendix 1.