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The Asymmetric Response Concept explains ecological consequences of multiple stressor exposure and release

Statement of authorship

MV and DH conceived the original concept. MV, DH, FL, JB, RT, RM and BS further developed the framework. All authors contributed to discussing and refining the concept and to compiling examples. MV and DH wrote the initial draft of the manuscript, with additions notably by MOG, FL, RBS, RT and BS. All authors have approved the final version of the manuscript.

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Highlights

- Multiple stressors can affect species indirectly through either abiotic variables or impacts on non-target species
- Stress tolerance is the key determinant of responses to increasing stress intensity
- Dispersal and biotic interactions are the two key mechanisms governing responses to the release from stressors

Abstract

Our capacity to predict trajectories of ecosystem degradation and recovery is limited, especially when impairments are caused by multiple stressors. Recovery may be fast or slow and either complete or partial, sometimes result in novel ecosystem states or even fail completely. Here, we introduce the Asymmetric Response Concept (ARC) that provides a basis for exploring and predicting the pace and magnitude of ecological responses to, and release from, multiple stressors. The ARC holds that three key mechanisms govern population, community and ecosystem trajectories. Stress tolerance is the main mechanism determining responses to increasing stressor intensity, whereas dispersal and biotic interactions predominantly govern responses to the release from stressors. The shifting importance of these mechanisms creates asymmetries between the ecological trajectories that follow increasing and decreasing stressor intensities. This recognition helps to understand multiple stressor impacts and to predict which measures will restore communities that are resistant to restoration.

Introduction

As the UN Decade of Ecosystem Restoration unfolds, we witness efforts worldwide to restore degraded ecosystems in an attempt to halt and reverse losses in biodiversity and ecosystem functions (Suding 2011, Wohl et al. 2015, Fischer et al. 2021). Strategies to achieve this goal include promoting the reestablishment of natural communities, reinitiating impaired processes and, often first and foremost, alleviating anthropogenic stressors (Perring et al. 2015). Anthropogenic stressors are defined here as any disturbance factor causing environmental variables, individuals, populations, communities, or ecosystem functions to exceed the range of normal variation relative to undisturbed reference conditions (modified after Piggott et al. 2015; compare also original descriptions of the stress concept in Barrett et al. 1976 and Odum 1985). In practice, however, restoration strategies have often failed in that the recovery of populations, communities and ecosystem functions remained incomplete following the implementation of measures (Bernhardt et al. 2005, Palmer et al. 2010, Jähnig et al. 2010, 2011). This has compromised ecological restoration for decades (Duarte et al. 2009, Suding 2011, Lorenz et al. 2018). In part, this failure is due to an insufficient understanding of the intricate nature of ecological responses to both ecosystem degradation and the restoration measures taken. More advanced mechanistic insight is required to predict when different types of ecological trajectories will occur and to provide tailormade solutions in each of these cases.

A key concept for ecosystem restoration is return time, i.e. the rate at which recovery takes place following disturbance by a stressor. This is one of the ways resilience is classically defined (Pimm 1982, DeAngelis 1992). However, the concept only applies where systems actually do recover or ‘return’. Especially full recovery does not always occur; it is only one of several possible outcomes when stressors are removed (Lake et al. 2007). Additionally, resilience, as treated by Pimm (1982) and DeAngelis (1992), focused on food web responses to single stressors, from which the system was fully released.

Ecosystems are typically exposed to multiple stressors (e.g. Birk et al. 2020, Spears et al. 2021, Simmons et al. 2021), which may act simultaneously or sequentially and may be magnified or mitigated at different times and to different degrees (Jackson et al. 2020, Orr et al. 2020). When multiple stressors interact in non-additive ways, impacts on biodiversity and ecosystem functions can be magnified through synergistic effects (Schäfer & Piggott 2018). Exposure to both single stressors and their combinations may also prime ecosystems towards the effects of subsequent stressor exposure (Jackson et al. 2020), which is in case of individual species often referred to as “co-tolerance” (Vinebrooke et al. 2004). Importantly, the timing, magnitude and frequency of a release from any of multiple co-occurring stressors may vary, implying that those not specifically targeted by restoration measures persist, or their intensity increases even further. Thus, variable responses to multiple stressors and their interactions affect ecological trajectories and the resulting ecosystem states both during ecosystem degradation and after the release from stressors by restoration measures.

This complexity calls for a concept that explicitly considers both single and multiple stressors and that captures the mechanisms determining ecosystem responses and community trajectories during periods when stressor intensities increase and decrease. Such a conceptual framework would need to factor in that multiple stressors may occur as combinations of short-term pulses and ramp or press disturbances that persist for extended periods (Lake 2003). It is these stressor combinations that define the effective impact in situations both where ecosystems are expected to follow a recovery trajectory and when degradation has led to crossing a threshold, or tipping point, that caused a shift to an alternative state (Holling et al. 1973, Folke et al. 2004, Hodgson et al 2016, O'Leary et al. 2017). Finally, an improved concept needs to consider that trajectories are not only governed by the effective combined intensity of multiple stressors, but also by dispersal limitation of species and a suite of direct and indirect interactions in ecological communities (Menge & Sutherland 1987). These factors, in combination, determine the propensity of ecosystems after stressor release to be recolonised by previously lost or new species (Tielke et al. 2020).

Here we propose the Asymmetric Response Concept (ARC) to provide a testable basis for predicting alternative ecological trajectories, for application in restoration. The ARC has two components. It addresses (1) the (a)symmetry of degradation and recovery patterns under conditions of increasing vs. decreasing intensity of single or multiple stressors and (2) the mechanisms responsible for these trajectories, which differ in importance between phases of degradation and recovery. Pivotal to the understanding of these trajectories and patterns are the ways how multiple stressors affect populations and communities. Examples of these components are given in Annexes 1 to 3.

The ARC emphasises that different ecological mechanisms are dominant during periods when the intensities of multiple stressors increase and decrease, without requiring that the actions of different stressors are fully in phase. As a consequence, trajectories of community structure and ecosystem functions during stressor increase and release, as well as the start and end of exposure to stressors can differ, potentially resulting in asymmetric responses to increases vs decreases in stressor intensities. Key mechanisms to consider include (i) species-specific tolerance to single and multiple stressors, (ii) dispersal capacity determined by species traits and connectivity, and (iii) biotic interactions, such as competition, facilitation, predation and parasitism, including the associated chains of indirect interactions in the community. The ARC lays out how changes over time in the dominance of these mechanisms result in fast or slow recovery of a degraded ecosystem to its previous state, to partial recovery, to persistence of the degraded state despite release from the stressors, or to the emergence of novel ecosystems comprising new communities.

According to the ARC, full recovery of community structure and ecosystem functions is one out of several possible outcomes and by no means the default expectation. When recovery fails following release from a stressor, as is often the case in reality (Bernhardt et al. 2005), the question arises which obstacles obstruct the trajectory towards full recovery and which processes need to be promoted to initiate, direct or accelerate the desired trajectory.

Effective restoration requires a detailed mechanistic understanding of how multiple stressors, and the release from those stressors, act on species and ecosystems in both additive and non-additive ways. Such a level of understanding has not yet been achieved (Spears et al. 2021, Simmons et al. 2021). Therefore, we first clarify the ways in which impacts can arise, either as direct effects on organisms, or as indirect effects mediated by environmental variables, or by other members of the community. Then we describe the shifting importance of different mechanisms during phases of increasing and decreasing intensities of multiple stressors. On basis of this, we propose a practical approach for testing both the components of the ARC and its overall performance and address the implications for ecosystem management. For the sake of consistency, we illustrate the concept based on examples drawn from freshwater ecosystems, particularly from rivers, which are well suited for that purpose because rivers provide numerous ecosystem services, are heavily affected by multiple stressors (Reid et al. 2019, Lemm et al. 2021), and are among the ecosystem types frequently restored (Bernhardt et al. 2005). Notwithstanding this focus on rivers, the principles underlying the ARC apply to a wide range of systems, from forests and grasslands to salt marshes, lakes and oceans, examples of which are provided in Annexes 1 to 3.

Scenarios of multiple-stressor effects

There are five main effect types when two stressors affect species, communities or ecosystems: (i) Stressor dominance occurs when one of the stressors has an overriding effect on the considered response variable; (ii) additive effects describe a situation where the combined effects add up without strengthening or weakening each other; (iii) synergistic or (iv) antagonistic effects relate to interactions of stressors that strengthen or weaken the individual effects such that the joint effect is stronger or weaker, respectively, than the additive effect; and (v) reversal occurs when the joint effect is in the opposite direction of the individual stressor effects (Jackson et al. 2016, Birk et al. 2020). Thus, the net effect of two (or more) stressors on species, communities and ecosystem functions strongly hinges on the effect type of multiple stressors. These effect types are frequently diagnosed assuming a linear relationship (of transformed or untransformed data) between stressor and response variables (Turschwell et al. 2022). This assumption is particularly problematic in the case of untransformed data, where in case of a sigmoid stressor-response relationship, the adding up of single stressors would yield departures from linearity, i.e. be diagnosed as synergism or antagonism. Given that our concept applies irrespective of how additivity or non-additivity is diagnosed, we employed the simplifying assumption of linearity here.

Responses to a full or partial release from one or several stressors will also differ among effect types (Figure 1). If the effect of two stressors is additive, the removal of one of them will lead to a partial, but not full, recovery (Figure 1A). If one stressor dominates effects, restoration will be successful if the dominant stressor is removed (first scenario; Figure 1B), unless the effect of the subordinate stressor increases once it is no longer masked by the dominant stressor (second scenario; Figure 1C). If, however, restoration targets the subordinate stressor, improvements will be small or undetectable (third scenario; Figure 1D). If two stressors are similarly important and act synergistically, removal of either of the two would already lead to a notable improvement (Figure 1E). Conversely, if stressors act antagonistically, removal of only one of them could have a very limited effect or even worsen the situation (Figure 1F). In cases of reversal, removal of one of the stressors could also increase the overall impact (Figure 1G). If only a single stressor is present, the prediction is straightforward in that its removal will eliminate stress completely (Figure 1H). The different effect types pertain not only to effects on individual species, but also to variables describing community structure and ecosystem functions (e.g. Birk et al. 2020).

All of these effect types can affect species within communities in different ways. Clearly distinguishing the different types is crucially required to conceptualise, model and predict how multiple stressors exert effects. For simplicity, we present two-stressor scenarios only, although the principles apply to any number of stressors acting simultaneously, examples of which are given in Annex 1. Figure 2 shows three basic scenarios:

1.) Direct effects: both stressors directly affect the focal species.

2.) Indirect effects through an abiotic environmental variable: Both stressors jointly affect an environmental variable that in turn affects a focal species.

3.) Indirect effects through other species: Both stressors affect one or several species that interact with the focal species (e.g., through predation, competition, mutualism, commensalism or parasitism). Given the multitude of biotic interactions in communities, most species will experience such a net combined effect of other species in the same community.

Combinations of these three basic cases are also possible. For example:

4.) Combination of direct and indirect effects through an abiotic environmental variable: One or both stressors directly affect a focal species in addition to indirect effects of one or both stressors mediated by an environmental variable.

5.) A combination of direct and indirect effects through one or more other species. Most species in a community will experience such a net combined effect through other species (compare case 3.).

Interactions among more than two stressors can easily yield complex outcomes, including changes in the direction of effects (Suleiman et al 2022). This can occur, for example, when several stressors affecting environmental variables or species simultaneously translate into indirect effects on focal species (Gessner & Tlili 2016). The basic distinction, however, between direct and indirect effects through environmental variables and different species also applies to complex multiple-stressor situations.

Overview of mechanisms governing responses to stressor exposure and removal

Multiple stressor effects following cases 1, 2, 4 and 5 (Figure 2), all relate to species-specific tolerances (i.e. resistance) to stressors. In addition, biotic interactions can be important, as depicted in cases 3 and 5 (Figure 2). Dispersal is another critical factor influencing to what extent other species in a community are available to interact with a focal species. Therefore, it is expected that the combined effects of tolerance, biotic interactions and dispersal govern the overall responses of species to multiple stressors and also determine community structure and associated ecosystem functions (Lake et al. 2007).

Crucially, however, the relative importance of these ecological mechanisms differs fundamentally between phases of increasing and decreasing stressor intensities, potentially leading to asymmetric trajectories before and after the release of populations, communities and ecosystems from stressors (Figure 3). Sarr (2002) coined terms for alternative types of recovery trajectories, i.e. the “rubber band”, “broken leg” and “no recovery” models (Figure 3). In Annex 2, we provide multiple examples for these alternative trajectories to underline that such trajectories are frequently occurring in a wide variety of systems in the real world. However, Sarr (2002) did not explain when or why these alternatives occur, while Smith et al. (2009) list some of the governing principles, but put them not in relation to recovery. We propose that variation in how exactly the three governing forces, i.e. tolerances, dispersal and biotic interactions, take dominance over time explains much of the actual variation in outcomes, i.e. in the degree of asymmetry among trajectories before and after stressor release. Below we focus on the factors driving variation among outcomes, before we further develop how the ARC can be used to advance a more predictive restoration ecology.

Factors driving alternative ecological trajectories

Tolerance

For some environmental factors, among which temperature is the most prominent example, tolerance can be described by a bell-shaped curve (Shelford’s tolerance law curve; Erofeeva 2021). In these cases, the factor acts as a stressor when its range of normal variation relative to undisturbed reference conditions is exceeded. For most others (e.g. concentrations of oxygen in water or persistent pollutants), tolerance is well described by a monotonically increasing or decreasing curve. Tolerance varies among species and also depends on environmental context, with the ranges of some species being broad, and narrow for others, or slopes of species responses to stressors being steep or shallow. An important consideration in multiple-stressor scenarios is that the stressor level for a given environmental factors may narrow the tolerance ranges, or change slopes, for others (i.e. co-tolerance; Vinebrooke et al. 2004). A single factor exceeding a critical threshold for a given species will lead to mortality, even when all other factors are within a benign range (Odum 1971, Erofeeva 2021). Furthermore, organisms must cope with multiple factors in fluctuating environments, some of which are suboptimal for the species’ requirements, even in undisturbed environments or after restoration measures have been completed. Therefore, to predict the success of restoration measures, information is critical on how intensities of stressors, both individually and in combination, relate to the tolerance ranges of the species characterising the target community after the release from stressors. The ARC proposes that in systems where dispersal is not limited and biotic interactions do not lead to alternative community states, community responses can be accurately predicted on basis of sufficient knowledge about species tolerances.

When stressor intensities increase only slightly, tolerance is the principal mechanism to maintain community structure by providing initial resistance. Tolerance levels preventing mortality are sufficient in the short run to ensure persistence when stressor intensities increase, although in the long run successful reproduction will be essential as well. Tolerance may be conferred by genotypic traits for physiological and behavioural responses, and may include the regulatory responses that shape phenotypic plasticity. Tolerances differ not only among species, but also among genotypes within species (Visser et al. 2014). Small increases in stressor intensity may thus accentuate differences in natural mortality rates. This in turn will change the relative abundance of different genotypes within populations and communities (Sturmbauer et al. 1999, Jacob et al. 2017), suggesting that eco-evolutionary dynamics need to be accounted for when assessing responses to increasing or decreasing stressor intensities.

As long as all genotypes remain present at some sufficient density, an increase in stressor intensity only alters relative densities, which may be readily reversed following release from the stressors. Sarr (2002) referred to such a rapid recovery as the “elastic” or “rubber band model,” which depicts a “symmetric response” during increasing and decreasing stressor intensities (Figure 3, case 1).

Whenever increased stressor intensities lead to greater mortality, a local loss of the more sensitive genotypes will likely occur. A stressor thus acts as a selective pressure and can result in a erosion of local genetic (and hence phenotypic) variation (Inostroza et al. 2016), especially when stressors or stressor combinations act in sequence (Vinebrooke et al. 2002, Nimmo et al. 2015). This reduces the adaptive potential of the population for future stress events. However, as long as all species persist that were present in the community before stressor exposure, recovery assessed in terms of the re-establishment of the original community structure can still be rapid following stressor removal. Consequently, recovery may be symmetric at the community level, even when populations may have experienced significant genetic loss. Nevertheless, if the erosion of genetic variation involves the loss of important trait values affecting fitness (e.g. competitiveness, see below), species may be locally lost. If increases in stressor intensity cause direct mortality in one or several populations of a community, it will result in species sorting, meaning that some species persist, whereas others become locally extinct.

Biotic interactions and dispersal

When species are lost from communities and local recruitment is precluded or limited, community recovery relies on dispersal. This tends to delay recovery, as captured by the “broken-leg model” (Figure 3, case 2) according to Sarr (2002), because the re-establishment of lost species requires prior recolonisation. A temporary absence of species may have several important ecological consequences. Firstly, prey species availability for some consumers may be reduced. Secondly, some species may no longer benefit from mechanisms supporting coexistence, such as keystone predation (Paine 1966, Menge et al. 2021), if the benefit was provided by the lost species (Tielke et al. 2020). Thirdly, some species may no longer profit from ecosystem functions, such as nutrient cycling, formerly assured by the extinct species. Changes in all of these species interactions, which relate to combined stressor effects 3 and 5 in Figure 2, may affect some species strongly enough to cause secondary local extinctions.

Priority effects (De Meester et al. 2016) and chains of indirect interactions (Lundberg et al. 2000) could take effect in these new remnant communities and cause reintroduction resistance to the species originally present (Tielke et al. 2020). Resistance of established communities to invasive species is often referred to as biotic resistance (Elton 1958, Frame et al. 2016), but this term can be misleading in that it is used in relation to both exotic invaders and former community members. The term reintroduction resistance more clearly refers to the latter (Tielke et al. 2020). As the remaining resident species may have changed their relative densities and tolerant immigrants may have invaded during the stressor exposure period, net pressures of competition and predation may be too high for successful recolonisation by former community members. This phenomenon is referred to as community closure (Lundberg et al. 2000). Depending on the degree of such community changes, the new dynamics may lead to partial recovery (Figure 3, case 3) or to no recovery (Figure 3, case 4). Which of the above scenarios applies to a particular restoration effort, is often unclear in practice (e.g. Louhi et al. 2011, Friberg et al. 2014, Leps et al. 2016, Lorenz et al. 2018). It can for instance be difficult to distinguish between recovery that is slow and recovery that is simply not happening. However, it is crucially important to know whether a community is slowly recovering or in a closed state, as each of these cases requires profoundly different management measures.

An important consideration is that different components of communities, or ecosystem functions, may recover at different times after stressor removal. Linked to this, recovery completeness can be assessed as the difference between the achieved post-recovery state and the original state before stressor exposure (Lake 2000, Nimmo et al. 2015).

Outcomes of the interplay between species' tolerances and biotic interactions can further be affected by dispersal (Smith et al. 2009). Population declines of sensitive species can be delayed or halted, if the loss of individuals is (partly) compensated by the movement of others from nearby source populations. In rivers, this frequently occurs through drift from upstream reaches, including tributaries (Dedecker et al. 2006, Downes et al. 2017). This recolonisation can be sufficiently important, especially in severely degraded ecosystems, to determine the structure of communities after stressor removal (Winking et al. 2016). Dispersal is governed by species traits that facilitate movement, the presence of potential source populations, and dispersal pathways, which requires consideration of any barriers impeding movement (Parkyn & Smith 2011). Mass effects, which refer to a constant or recurring influx of individuals from source populations, increase the likelihood of species re-establishment (Stoll et al. 2016), either before invaders have firmly established or by driving out species established in the meantime. Conversely, absence or limited colonisation potential of source populations of the lost species reduce the probability that the original communities re-establish (Tonkin et al. 2014).

Shifting importance of mechanisms after stressor exposure and removal

In case of a single stressor, it is straightforward from a theoretical perspective to predict the effects of reducing stress acting on a community. However, predictions can be complex when multiple stressors interact (see Figure 1) or when the specific ways matter in which stressors affect species and communities (see Figure 2). Therefore, to allow mechanisms driving recovery to take effect, it is critically important to reduce the overall stressor intensity affecting species and communities.

After release from stressor exposure, degraded communities may resist the reintroduction of former species, due to effective community closure, irrespective of how effectively stressor intensity has been reduced. The subsequent ecological trajectory is, in this case, no longer dominated by tolerances or dispersal, but by biotic interactions such as competition and predation. Note, however, that tolerance in the form of resting stages can still play a role after stressor removal. Importantly, the recolonising former community members will not encounter the original conditions that define such interactions, since the previous extinctions and population declines of species changed relative population densities in the remnant community (Young et al. 2021). This double shift affects the outcomes of competitive, predator-prey and other biotic interactions and may generate reintroduction resistance. This in turn affects the order and success of species re-establishing during community re-assembly from the regional species pool. If such reintroduction resistance constrains the sequence of species re-assembly, the resulting community structure will hinge on the interplay between biotic interactions and the order of species arrival, which is influenced by dispersal. Alternative re-assembly trajectories and end-points may be the consequence. Therefore, the prime mechanism governing ecological responses to multiple stressor exposure is tolerance with dispersal and later biotic interactions assuming greater importance during recovery trajectories after stressors have been removed (Figure 4). The exact trajectories may vary. Tolerance will clearly dominate the phase before stressor release, but the importance of biotic interactions may already increase somewhat during this phase, as secondary extinctions and population declines set in that follow the primary loss of less-tolerant species (Figure 4).

Tolerance, dispersal and biotic interactions differ in the degree of stochasticity in their effects. Specific tolerances of species to different stressors will produce rather deterministic outcomes. For instance, in the case of two stressors affecting a species indirectly through a single environmental variable (Figure 2B), the joint stressor effect may simply be derived from physical laws. An example is the effect on species by reduced dissolved oxygen concentrations in river water, which is determined by temperature and flow rate.

Dispersal effects, in contrast, are much more stochastic, as they are contingent on many factors, including the species' dispersal traits, location and size of the source populations, barriers obstructing movement, and also weather conditions. Short distances may be crossed by a large number of specimens, whereas "long jumps" tend to be rare (Fer & Hroudova 2008, Knighton et al. 2014). The number of specimens eventually arriving at a destination depends on the interplay of all these factors in determining colonisation and reproductive success, i.e. whether dispersal is effective.

In principle, the outcome of many biotic interactions is also deterministic, but which species will interact with each other at any stage of community re-assembly is stochastic, depending on the dispersal process and the sequence of arrival. Interestingly, the combination of highly stochastic dispersal and much more predictable reintroduction resistance can lead to counterintuitive "ecological surprises". These "emergent outcomes" include asymmetric responses such as the persistence of depauperate communities or shifts during recovery towards a new, alternative community structure.

Reasons for incomplete recovery

The ARC provides a conceptual foundation to identify major reasons for incomplete or stalled recovery. In an idealistic scenario, community structure and ecosystem functions fully recover once stressors have been removed. This, however, would require all indicators of recovery from all stressors and their interactions to be reset to levels experienced before stressor exposure – a condition that is rarely realistic. Instead, recovery is typically obstructed by three, non-mutually exclusive factors:

1.) The intensity of one or more stressors has not been sufficiently reduced.
2.) Recolonisation is constrained by dispersal limitation because a lack of source populations or migration barriers limits the arrival of individuals to establish populations of the species lost from the community when the stressors were imposed.
3.) Biotic interactions lead to effective community closure or reintroduction resistance, that prevent the re-establishment of former community members, possibly reinforced by feedbacks involving environmental factors.

Implications for ecosystem management

The three mechanisms outlined above suggest that ecosystem restoration is successful when, first, benign conditions are restored that allow all former community members to re-establish. This includes sensitive species that show little tolerance to the (removed) stressors. When limited resources prohibit the removal of all stressors simultaneously, priorities need to be set according to the type of multiple stressor effects that have been identified (Figure 1). If the effect type is dominance, prospects for recovery are evidently best when the stressor with the largest effect size is removed first. Normally this strategy is also successful when stressors act synergistically. However, if synergistic effects prevail over the effects caused by the stressors individually, the initial removal of a subordinate stressor, if more cost-effective to remove, can sometimes be a partial solution. Risks of stressor removal arise particularly when reversal is the effect type, because the removal of one stressor can exacerbate rather than alleviate the overall stressor effects in this case. Consider, for example, that meanders recreated in an organically polluted and channelised river decrease the flow, thus reducing reaeration by atmospheric oxygen and exacerbating the impacts of the pollution-induced oxygen deficit in the river.

Once the important stressors have been removed, measures are needed, secondly, to resolve any impediments preventing effective dispersal of the original community members. This may require removal or reductions of dispersal barriers, species re-introductions or both. Re-introducing all locally lost species simultaneously, rather than sequentially, may help to overcome potential community closure effects associated with the order of species appearance during community re-assembly (Jourdan et al. 2018, Dumeier et al. 2020).

Effective dispersal does not guarantee full community recovery, however. Reintroduction resistance remains as a possible cause of incomplete success, resulting in an asymmetric community response even after extensive restoration measures. The extent of reintroduction resistance depends on the species traits of both the remaining and former members of the community. Consequently, predicting under which circumstances and at what target densities species re-introductions are successful requires detailed information about the considered community, including knowledge on a range of biotic interactions (Wolf et al 2019; Tielke et al. 2020). Chances of successful re-introductions tend to be greatest early after stressor exposure, before primary extinctions of sensitive species entail secondary extinctions that result from altered species interactions (Tielke et al. 2020). This last point is important, because secondary extinctions are one of the main causes of reintroduction resistance. It must be realised that overcoming reintroduction resistance with management measures is generally difficult and expensive. Therefore, preventing primary and secondary extinctions is likely to be much more effective than curing impoverished communities by species re-introductions.

Three important implications follow from the above. First, it is necessary to identify all environmental variables and stressors whose values exceed the tolerance levels of even the most sensitive species expected to re-establish. In practice, well-known sensitive indicator species may be used as representatives of sensitive community members. Second, all dispersal constraints need to be recognised and overcome. This can be achieved either by creating migratory corridors, or by removing migration obstacles, or by implementing reintroduction measures (Godefroid et al. 2011). Thirdly, reintroduction resistance needs to be drastically reduced or overcome, e.g. by promoting a regime of mild population fluctuations, which re-opens a closed community to successful reintroduction of former community members (Tielke et al. 2020). In addition, information is needed on whether any unwanted species established during stressor exposure persist after release from the stressors, to preclude that the originally occurring species are prevented from getting re-established. Possible countermeasures include the reduction of stressor intensities well beyond the tolerance limits of the lost species and targeted extinction measures of the persistent unwanted species.

Approaches to testing the ARC

The Asymmetric Response Concept provides a tool to plan and conduct successful restoration projects. To increase its predictive power for specific systems, it is important to test and refine it with laboratory and field experiments and observational studies, the results of which may be used for ecological model scenarios based on species traits relating to stress tolerance, dispersal and biotic interactions.

The default prediction inferred from the ARC is that tolerance best explains the degree of community and ecosystem change following exposure to stressors, whereas dispersal and biotic interactions successively assume prime importance following release from the stressors (Figure 4).

Using data from experiments and field observations, a step-wise multi-model approach can be applied to test the consequences of these values in each particular system. In a first step, magnitude and direction of change can be related to proxies for the change in stressor intensity and to species-specific tolerances towards these stressors. The testable hypothesis is that these variables better explain community changes in phases of stressor increase than in phases of stressor release. In an additional modelling step, proxies for dispersal capabilities of key species and the proximity to colonisation sources can be added to the set of explanatory variables, to test the hypothesis that these variables add more strongly to explaining recovery trajectories as compared to degradation trajectories. Finally, measured values or proxies defining predation, competition and other biotic interactions need to be added, to test the hypothesis that these are particularly relevant for explaining recovery cases, i.e. when partial or full recovery will occur, or when assembly will lead to alternative community states. This stepwise approach also allows for testing the prediction that biotic interactions are the sole determinant of whether ‘broken leg’ or ‘no recovery’ trajectories will occur, in the absence of dispersal limitation. Alternative scenarios to evaluate these predictions can be evaluated with a variety of modelling approaches ranging from Structural Equation Models to Dynamic Food Web Models. The model scenarios need to include variation in species-specific tolerances, involve periods of increase and decrease of multiple stressors, allow species reintroductions through dispersal or active management and establish the dominant species interactions, including chains of associated indirect effects, in the ecological community. Implementation of such scenarios allows to quantitatively predict the rates and endpoints that define alternative ecological trajectories (as depicted in Figure 3). These predictions can be tested in (semi-) field experiments that implement for instance alternative species reintroduction sequences as treatments.

In conclusion, the Asymmetric Response Concept provides a testable basis for exploring and predicting ecological responses to restoration measures. The ARC holds that a temporal change in the relative importance of key ecological factors is key to the outcome of ecological trajectories before and after release of multiple stressors. We suggest that such changes over time in the predominance of different governing factors may be the rule rather than the exception in defining community level patterns.

Acknowledgements

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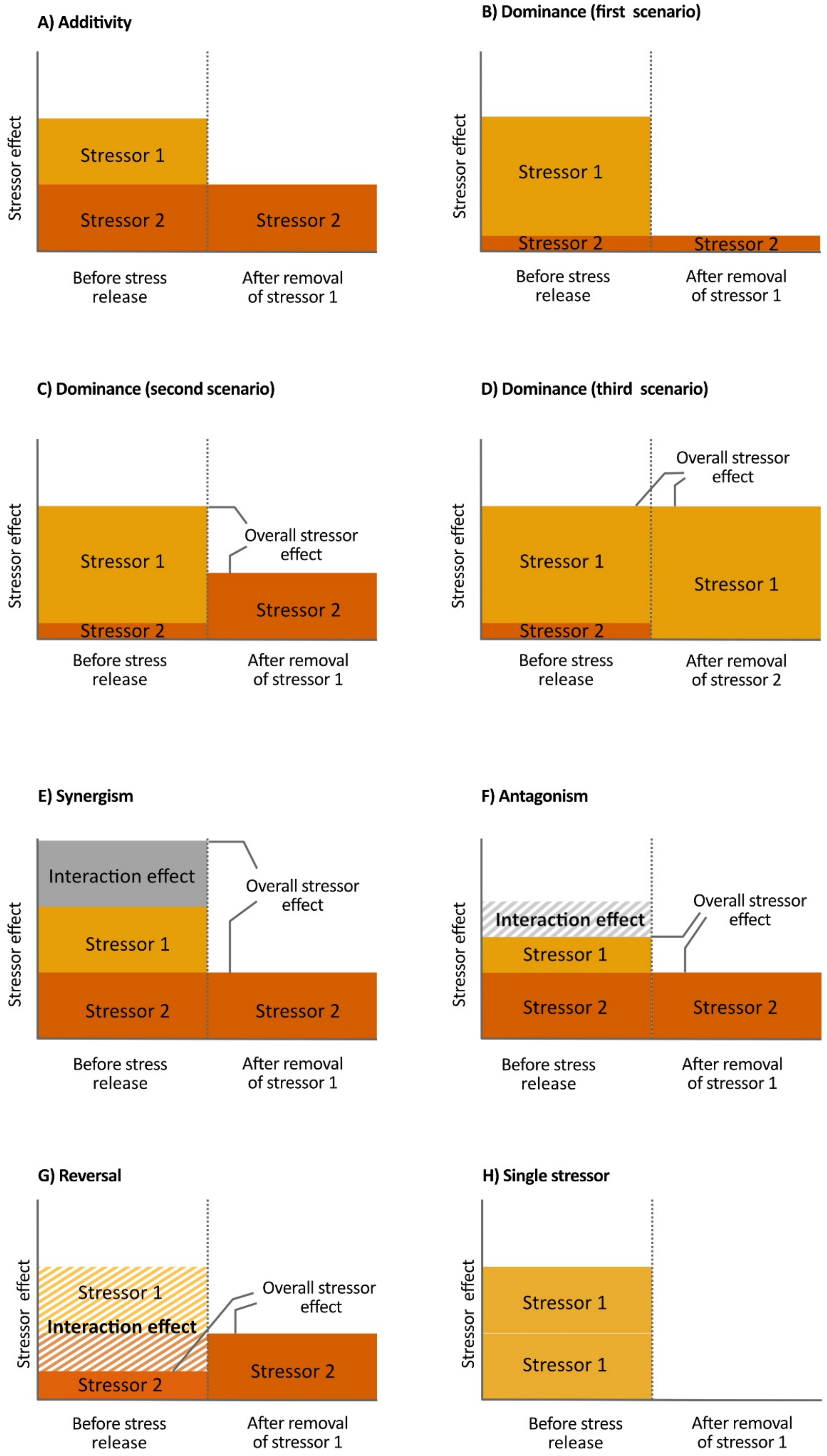
A) Additivity
Stressor effect
Stressor 1
Stressor 2
Stressor 2
Before stress release
After removal of stressor 1
B) Dominance (first scenario)
Stressor effect
Stressor 1
Stressor 2
Stressor 2
Before stress release
After removal of stressor 1
C) Dominance (second scenario)
Stressor effect
Stressor 1
Stressor 2
Overall stressor effect
Stressor 2
Before stress release
After removal of stressor 1
D) Dominance (third scenario)
Stressor effect
Overall stressor effect
Stressor 1
Stressor 2
Stressor 1
Before stress release
After removal of stressor 2
E) Synergism
Stressor effect
Interaction effect
Stressor 1
Stressor 2
Overall stressor effect
Stressor 2
Before stress release
After removal of stressor 1
F) Antagonism
Stressor effect
Interaction effect
Stressor 1
Stressor 2
Overall stressor effect
Stressor 2
Before stress release
After removal of stressor 1
G) Reversal
Stressor effect
Stressor 1
Interaction effect
Stressor 2
Overall stressor effect
Stressor 2
Before stress release
After removal of stressor 1
H) Single stressor
Stressor effect
Stressor 1
Stressor 1
Before stress release
After removal of stressor 1

Figure 1: Expected net effects when releasing species, communities or ecosystems from single stressors under different multiple-stressor effect types. Stressor 1 is being removed in all cases except for the third scenario of stressor dominance (Figure 1D). Hatched areas denote a reduction of stressor intensities. The net effects shown require a near-normal distribution of both stressor and response variables, which can generally achieved by an appropriate data transformation.

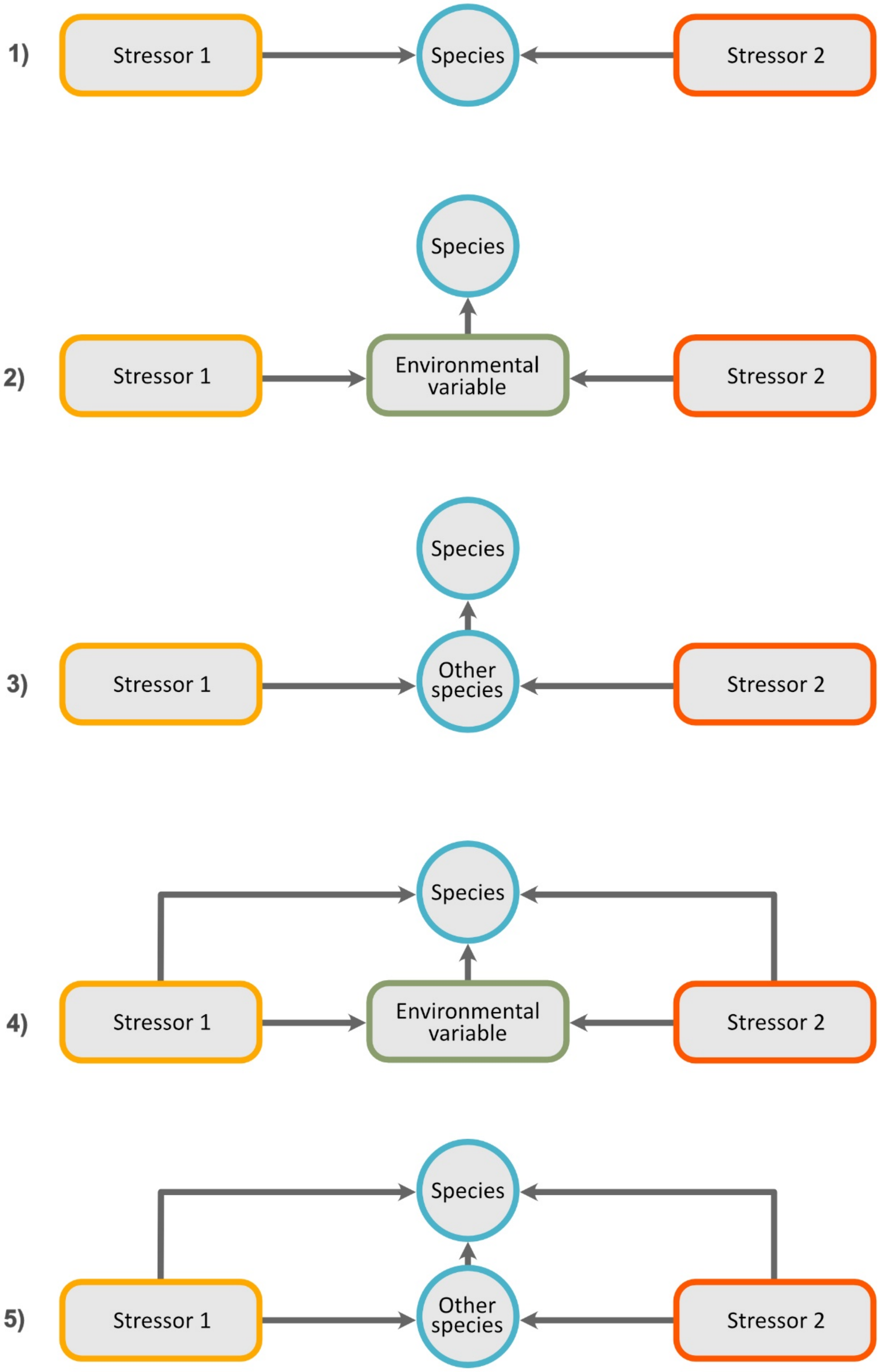

Figure 2: Five ways in which multiple stressors can affect a focal species in a community.

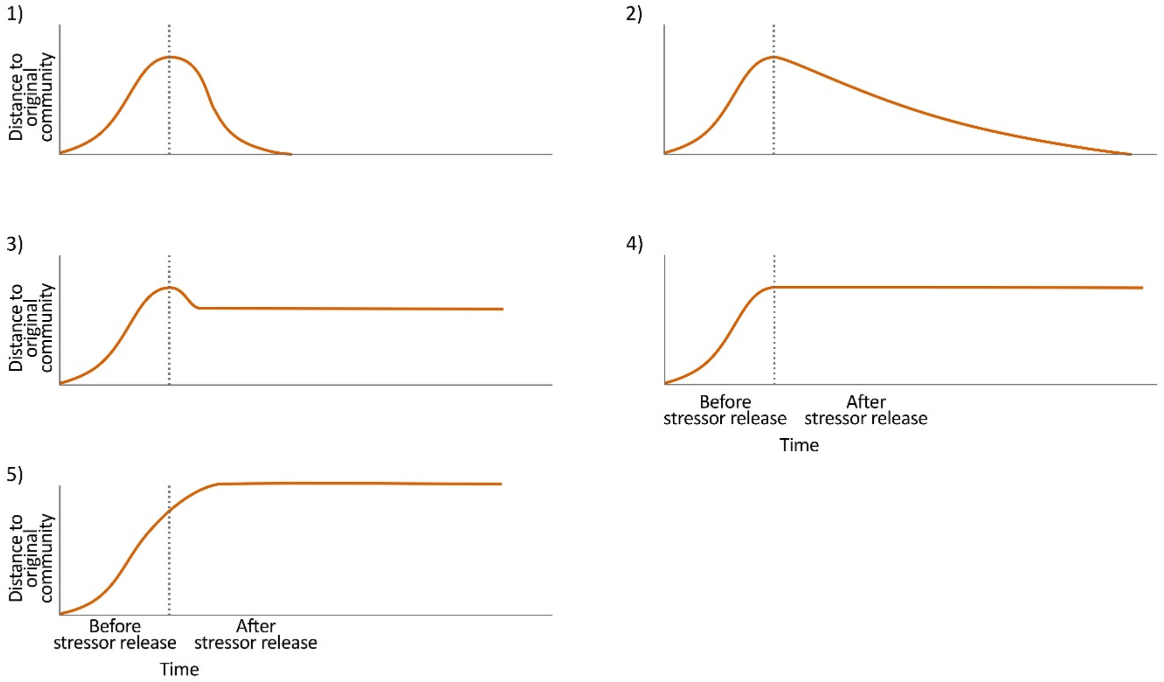

Figure 3: Ecological responses to increasing stressor levels and the subsequent release from stressors. The "rubber band" model (1) shows a practically symmetric response before and after release from a stressor or stressor combination, both in terms of the initial and final state after recovery and in terms of the trajectories. The "broken leg" model (2) is asymmetric in that the trajectories differ, although the initial and final states are the same (i.e. hysteresis effect). The "partial recovery" (3) and "no recovery" (4) models are asymmetric in terms of both the initial and final state, and the trajectories before and after release from the stressors. Similar asymmetries characterise the "new state" model (5), where release from stressors results in the community moving even further away from the original state. Note that different final states are possible for cases 3 and 5. For sake of simplicity, it is assumed that the stressor intensity is reduced at a certain point of time and not continuously over a longer time period.

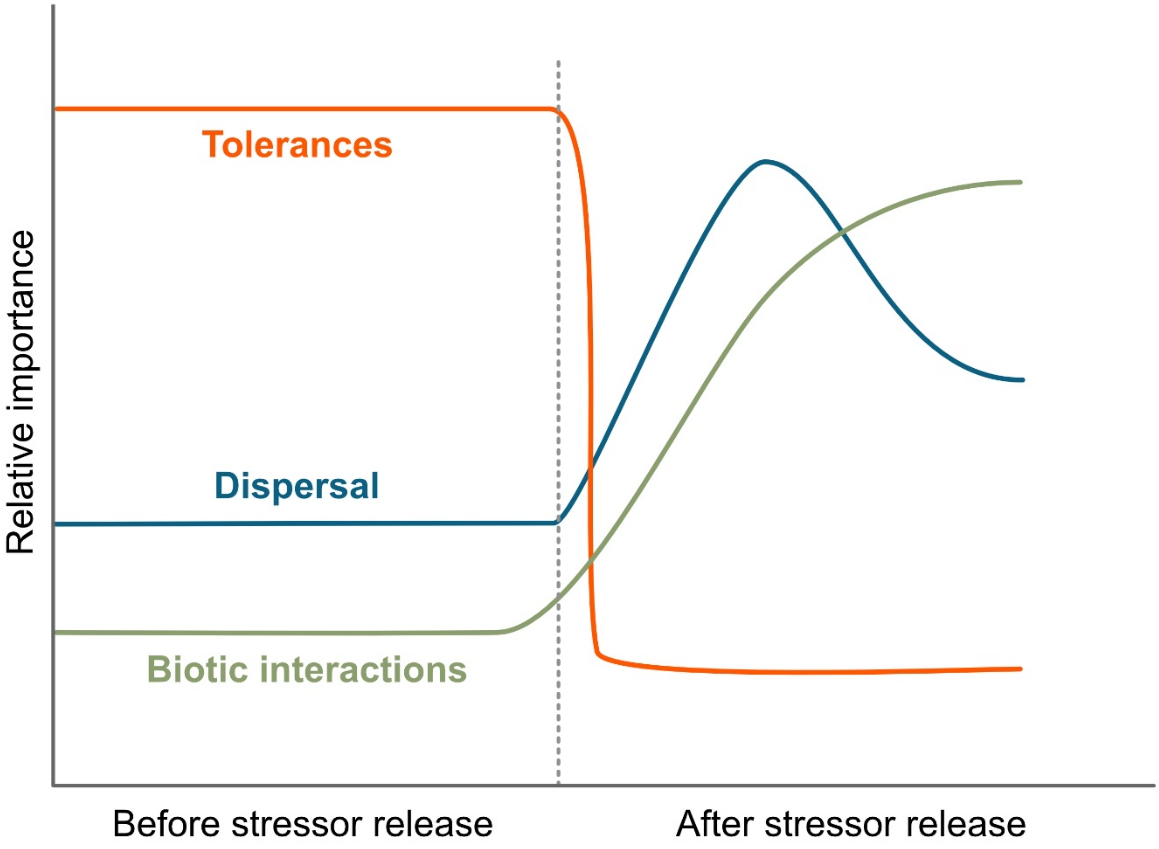

Figure 4: Variation in the relative importance of tolerance, dispersal and biotic interactions during stressor exposure and recovery trajectories after the release from stressors. The effective importance of the three mechanisms after release from stressors depends on the type and intensity of remaining stressors in multi-stressor scenarios, proximity to colonisation sources and possible community closure. Annex 3 lists real world examples of how tolerance, dispersal and biotic interactions act in phases of stressor impact and stressor release. For sake of simplicity, it is assumed that the stressor intensity is reduced at a certain point of time and not continuously over a longer time period.