Local buffer mechanisms for population persistence

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Abstract

Assessing and predicting the persistence of populations is essential for the conservation and control of species. Here we argue that local mechanisms require a better conceptual synthesis to facilitate a more holistic consideration along with regional mechanisms known from metapopulation theory. We summarise the evidence for local buffer mechanisms along with their capacities and emphasise the need to include multiple buffer mechanisms in studies of population persistence. We propose an accessible framework for local buffer mechanisms that distinguishes between damping (reducing fluctuations in population size) and repelling (reducing population declines) mechanisms. We highlight opportunities for empirical and modelling studies to investigate the interactions and capacities of buffer mechanisms to facilitate better ecological understanding in times of ecological upheaval.

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MECHANISMS FOR POPULATION PERSISTENCE

The question of how populations persist is of great importance in both conservation biology and community ecology. Many populations are at risk of decline due to anthropogenic drivers leading to habitat degradation, loss and fragmentation [1–3]. Furthermore, most species are present in low abundance in most communities and may even be locally rare [4,5]. To reliably predict and assess the local extinction risk of small or declining populations [6], intimate knowledge of the mechanisms that allow populations to persist is essential. This knowledge is needed to guide efforts in species conservation, the management of harvested species, and the control of harmful species [7].

Metapopulation and metacommunity theory focus on regional persistence mediated by two non-local mechanisms resulting from dispersal: recolonisation after local extinction [8], and the mass effect, where the inflow of individuals from source habitats keeps abundances high enough to prevent local extinction in sink habitats [9–11]. As populations become increasingly isolated and dispersal rates decrease due to habitat loss [12], these regional mechanisms can contribute less to population resilience [13]. Furthermore, regional mechanisms cannot fully unfold without sufficient local persistence [14]. Therefore, **buffer mechanisms** (see glossary) that reduce extinction risk locally are gaining importance and, as we show, play a pivotal role in understanding and managing populations and communities.

Buffer mechanisms reduce the impact of environmental fluctuations on population abundance and thus alleviate the risk of extinction, especially in small populations [15]. Therefore, buffer mechanisms can mitigate the impacts of global change on biodiversity and enable the success of conservation policies and adaptive management of natural resources. On the other hand, similar to regional mechanisms [16], they can complicate interventions on invasive species, pest control, or disease eradication. Recent research has highlighted important population-level patterns of buffering, for instance due to an adapted variation of vital rates (demographic buffering and demographic lability [17,18]). Yet, on a mechanistic level, we lack synthesis of local buffer mechanisms [17] which limits their consideration in studies of population viability [19], the coexistence of species [20] and ecosystem management [21]. Instead, knowledge about local buffer mechanisms is currently scattered across different fields of ecological research. Therefore, we summarise the knowledge of local buffer mechanisms and assign them to two basic classes to facilitate their more complete consideration in ecological studies.

TWO CLASSES OF LOCAL BUFFER MECHANISMS

In general, there are two different perspectives on buffer mechanisms. Most commonly, buffer mechanisms are described as a damping force, i.e. a force that reduces the temporal variation of a variable such as population size [15]. However, sometimes buffer mechanisms are also perceived as a force that repels an ecological system from entering a different state [22,23], including repelling a population from extinction. In both cases, the risk of reaching abundances where demographic stochasticity alone can lead to extinction is reduced. We propose that these two perspectives of either **repelling** or **damping mechanisms** relate to two basic classes of local buffer mechanisms (Fig. 1).

Damping mechanisms reduce variation of population size, e.g. caused by environmental variation and thus help to avoid low abundances. However, when populations reach low levels, damping mechanisms can no longer act as a buffer against further adverse conditions or, alternatively, can hamper recovery. Repelling mechanisms, in contrast, generally do not work against population variations but against population decline. They can also increase the persistence of small populations by reducing the impact of adverse conditions on population growth rates. Conceptually distinguishing these two classes of local buffer mechanisms improves mechanistic insight into population dynamics, facilitates reflection on their costs and other limitations, aids development of predictive models, and helps to select appropriate conservation strategies.. This conceptual examination also responds to the old but still valid call for a better distinction between small and declining populations and a more specific theory of driven population decline' [6].

The purpose of our classification is thus to explore buffer mechanisms in a more systematic and comparative way, not to introduce a rigid scheme. Some buffer mechanisms may contain elements of both classes (Box 1), and their relative importance my change with temporal and spatial scale. The general and specific examples of buffer mechanisms provided in the following are meant as an invitation for more in-depth empirical and theoretical studies, which are needed to better support ecological management.

DAMPING BUFFER MECHANISMS

Damping mechanisms result either from **portfolio effects** or from frequency- and density-dependent interactions. Damping reduces variation in population size and primarily operates by keeping population sizes above a critical level. If population sizes continue to decrease or even become critically low, the damping mechanisms can be exhausted. For example, the capacity to dampen further may be limited as the material for portfolio effects (e.g. variation in localities or traits of individuals) is no longer available (Box 1).

Portfolio effects

While originally used in the context of (meta-)communities [24], the portfolio effect can also occur at the population scale. Here, dampened population growth rates are caused by subgroups of individuals with negatively correlated growth rates (Fig. 1A), which can be due to different locations in a spatially heterogeneous patch or **among-individual trait variation** as we show in the following subsections.

Spatial heterogeneity

In spatially heterogeneous environments, some locations may be more favourable than others. For instance, butterflies may posit their eggs at warmer and colder locations within a patch. Larvae at colder locations are more likely to develop in synchrony with their host plant when spring temperatures are above average, while larvae at warmer locations perform better in below-average spring temperatures [25]. Thus, because some (but not all) subgroups develop synchronously with their host plant, the effects of interannual environmental variability are dampened [25] via a portfolio effect. Related effects of **spatial heterogeneity** are currently intensively studied in the context of climate change, as they may facilitate persistence under otherwise lethal environmental conditions [26–28]. While increasing spatial heterogeneity increases the likelihood that some areas will provide suitable conditions in changing environment, dampening mechanism also leads to reduction in the maximum suitable area under optimal conditions.

Among-individual trait variation

Individuals differ in various traits affecting their niche and this variation can result in a portfolio effect [29]. For instance, among-individual trait variation can reduce risks from future adverse conditions at the cost of producing potentially suboptimal phenotypes at current conditions [30,31].

The ecological relevance of among-individual trait variation has recently gained increasing attention [29,32]. While corresponding empirical studies clearly demonstrating local buffer mechanisms are still rare, they may operate analogously to regional mechanisms. For instance, at the metapopulation level, among-individual variation in the proportion of time spent in freshwater and the ocean (a life-history trait) led to asynchronous population dynamics in sockeye salmon (*Oncorhynchus nerka)* [33]. This effect also holds at the population level, as recently shown for chinook salmon (*Oncorhynchus tshawytscha*) [34]. Disentangling the effects of spatial heterogeneity and among-individual trait variation is challenging [35], yet crucial for understanding their interaction with other buffer mechanisms and for predicting the fate of populations. While it is often implicitly assumed that among-individual variation increases population persistence [29,36], theoretical studies show that additional trait variation can also become detrimental as it may mean that an increasing proportion of the individuals have sub-optimal traits for given environmental conditions [37].

Frequency- and density-dependent interactions

One ubiquitous and widely recognized phenomenon in natural populations is a change in population growth rates with population size. One of the underlying mechanisms of density-dependent relationships are interactions among and within species changing with the density and frequency of a species or phenotype (Fig. 1C). In the following, we show how these interactions can act as damping mechanisms.

Density-dependent within-species interactions

Many populations show negative density-dependence, for example due to competitive interactions. In these populations, intensifying intraspecific competition reduces population growth rates when abundances increase [38] and relaxing competition improves population growth rates in phases of population decline [39]. This damping mechanism increases likelihood of maintaining a viable size so that recovery remains possible.

The buffering effect of intraspecific competition has, for example, been observed in a population of great tits that experienced a climate change-induced phenological mismatch with their prey. Under these conditions, only a portion of the population was able to successfully reproduce [40]. This resulted in a lower number of offspring, but the survival rate of the offspring increased due to strong effects of reduced competition, which led to little change in the adult population size (i.e. buffered temporal dynamics). Note that the same way relaxed competition towards low density can mitigate population decline, intensified competition towards high density hampers population growth which further dampens fluctuations.

Frequency-dependent among-species interactions

Frequency-dependent interactions have been recognized as central stabilizing mechanisms facilitating species coexistence [41–43]. If prey population sizes fluctuate and generalist predators utilize the more frequent prey (positive prey switching [44]), this frequency-dependent predation may increase the survival of prey species in times of low and reduce survival in times of high frequency [45,46], overall improving persistence via a damping mechanism [47]. For instance, when offered multiple prey species in a tank experiment, invasive lionfish (*Pterois volitans*) disproportionally consumed the most frequent prey, thus, reducing pressure on rarer prey [46]. Besides frequency-dependent interactions, in certain circumstances, antagonists may be more affected by adverse conditions and become less abundant leading to an “antagonistic release” [48].

REPELLING BUFFER MECHANISMS

Repelling mechanisms increase population growth rate, particularly in response to adverse conditions. Adverse conditions usually lead to adaptation or microevolution, while after temporary adverse conditions individuals that are not affected prevent further decline. Unlike damping mechanisms, repelling mechanisms do not generally reduce fluctuations (i.e. positive and negative) in population size.

Adaptation

Adaptive processes include **within-individual trait variation** (individual plasticity) and microevolution (Fig. 1B). Here we consider processes that enable populations to increase their performance under adverse conditions, for example through behavioural or morphological adjustments. Within-individual variation can enable rapid adaptive responses, while microevolution can extend over several or more generations.

Adaptive within-individual variation

Individuals may alter morphological, behavioural, physiological or life-history traits [49] in response to adverse conditions. For instance, bivalves (*Anadara trapezia*) buried themselves less deeply in the sediment to evade hypoxic conditions caused by an invasive seagrass *(Caulerpa taxifolia)*. Due to this adaptive response, seagrass-invaded populations that were originally thought to face extinction persisted [50]. Sessile organisms with more limited behavioural responses can adapt to recurring stressors by stress priming, described both in plants and fungi [51,52]. Still, buffer mechanisms due to within-individual variation are sometimes limited by the ability of individuals to perceive or respond appropriately to changing environmental conditions [53,54].

Microevolution

Microevolution of life-history traits in response to adverse conditions is known from fish species that have adapted adult body sizes to the fishing techniques used [55,56]. The speed at which microevolution occurs depends on trait heritability, the standing level of genetic among-individual variation in these traits and their mutation rate, selection pressure and generation time.

Hierarchical filtering

Some subgroups of individuals can perform better consistently, i.e. regardless of population size. These individuals are qualitatively better, e.g. because they live in safe locations or have otherwise acquired the ability to better withstand adverse conditions (“hierarchical trait” [57]). Under such conditions, the high-quality subgroups should form a “floor” [22] from which populations can recover (Fig. 1D). We call this repelling mechanism **hierarchical filtering** because it is based on the hierarchy of high- and low-quality subgroups [57]. Hierarchical filtering means that the buffering subgroup performs consistently well and its effect increases with the relative proportion of this subgroup, while the portfolio effect means that the individuals in the buffering subgroups change with environmental conditions.

Among-individual variation in quality due to site differences

At the regional level, site quality differences and effects on local persistence are often viewed in the context of source-sink dynamics [10,11]. At the local scale, differences in site quality are mainly discussed in terms of "safe sites" or “refuges” [58], with safe sites resulting in higher vital rates compared to less safe sites under adverse conditions [22]. The “habitat heterogeneity hypothesis” states that differences in site quality contribute to higher fecundity at lower population sizes as individuals favour high-quality sites. For instance, clutch sizes of blue tits (*Cyanistes caeruleus*) were higher in nest boxes with entrances too small to be occupied by great tits (*Parus major*) [59], providing safe sites in times of stronger interspecific competition. This is shown in further examples where bird populations at low-quality sites can express phases of strong declines whereas populations at high-quality sites remain stable and large [54,60]. Promoting this repelling mechanism (i.e. increasing site quality) is explicitly the rationale behind conservation measures to improve nesting, foraging and resting sites [61,62].

Among-individual variation in quality due to life-history differences

The "individual heterogeneity hypothesis" states that differences in survival and production result from among-individual variation in overall quality such as body condition [63,64]. In the context of buffer mechanisms, high-quality individuals should better withstand adverse conditions and, thus, increase the persistence of small populations [65]. Quality does not affect an individual's position on a niche axis, but its ability to withstand adverse conditions. In many species, young individuals show higher mortality rates [66] which leads to a disproportionate loss of young individuals under adverse conditions, while older individuals can persist and contribute to population growth. Especially in long-lived slow species, older individuals tend to perform better [18,67]. Hence, populations' age structures may greatly affect how they resist and recover from adverse conditions. After long periods of stress, populations may therefore consist mainly of old individuals [68], providing a – temporally limited – floor for recovery (Box 1).

INTERDEPENDENCIES OF REPELLING & DAMPENING BUFFER MECHANISMS

Efforts to categorize ecological phenomena need to acknowledge interdependencies to provide a meaningful framework. For instance, equalizing and stabilizing mechanisms, well-known from coexistence theory, are often dependent on common quantities [43]. Similarly, repelling and damping mechanisms will often be interdependent in natural systems. While hierarchical filtering relates to variation in quality between individuals, portfolio effects arise from niche variation. Quality and niche of individuals may often covary [57]. For instance, individuals with different levels of boldness, a frequently studied behavioural type studied in animal ecology, show niche partitioning [69] potentially contributing to portfolio effects [29], i.e. a damping mechanism. At the same time, meta-analyses show that bolder individuals tend to show higher survival rates in the wild, providing evidence that these are also individuals of higher quality [70] contributing to hierarchical filtering, i.e. a repelling mechanism. Some repelling and damping mechanisms may thus covary. Based on our framework, future research can focus on quantifying the interdependencies of these mechanisms, and whether and when they are mutually exclusive or can operate simultaneously and lead to additive buffer effects.

HOW CAN WE ACCOUNT FOR BUFFER MECHANISMS IN EMPIRICAL STUDIES AND MODELS

Several issues in studying the persistence of populations have been identified in recent years. The "fallacy" [71] of averaging is a pervasive issue in ecology as it neglects the importance of variation in traits and environmental conditions for driving population dynamics [29,72]. A further issue arises from the focus on long-term equilibria in ecological theory, which complicates the analysis of small populations [20] and may overlook the presence of transient population dynamics [73,74]. Furthermore, time series of abundance (or abundance surrogates [75]), do not necessarily capture adverse conditions and operating buffer mechanisms [21,76,77]. Carefully structured monitoring programs, with attention to changes in population structure and/or spatial distribution in addition to abundance increase the likelihood of detecting a decline in buffer capacity (Box 1) and hence signals of a pending collapse. Empirical and modelling approaches are needed that explicitly observe or represent individuals together with their traits, states, environment, and interactions.

EMPIRICAL STUDIES

The empirical study of buffer mechanisms would probably not require new methods or approaches, as the phenomena we refer to are established research topics. However, empirical studies addressing multiple local buffer mechanisms and considering their interactions are rare [78], and often the exact pathways of the mechanisms remain unclear [35]. Substantial progress could be achieved by linking already known phenomena to questions of local population persistence. Besides looking for biological and ecological shifts coinciding with changes in population size, ecologists should also look more systematically for buffer mechanisms that prevent changes in population size. Suitable indicators could be changes in the frequency of life stages and phenotypes, as well as behavioural and physiological changes (see Outstanding Questions) [79].

MODELLING STUDIES

Ecological modellers should strive to adequately represent buffer mechanisms and their capacities and interactions. Improving the representation of buffer mechanisms requires increased efforts to build ecological models from first principles [80,81]. Investigating buffer mechanisms – or lack thereof –- with such approaches will foster our understanding of drivers underlying extinction events [82]. Agent-based models allow to integrate short-term behavioural changes up to evolutionary processes in spatially explicit simulations and thus fulfil the requirements for studying buffer mechanisms. Other modelling approaches such as integral projection models have been successfully applied to study the effect of within-individual variation as a buffer mechanism under climate change [83]. Such models can provide information on capacities and interactions of buffer mechanisms (see Outstanding Questions).

CONCLUDING REMARKS

General mechanisms and correlates related to extinction risk are scarce, and causes of population decline appear mainly idiosyncratic [84]. We show evidence of fundamental local mechanisms that can either increase the persistence of small populations or prevent populations from becoming too small in the first place. It is a major challenge to study both local and regional buffer mechanisms and their interactions. Our concept of damping and repelling mechanisms and the overview of current evidence should encourage more ecologists to take up this challenge. In this way, we can progress towards reliable predictions about the fate of populations in times of global ecological turmoil (see Outstanding Questions). A more comprehensive understanding of buffer mechanisms will also considerably improve biodiversity conservation and, more generally, ensure the resilience of ecological systems.

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Statement of Authorship

AM wrote the first draft and developed the concept. VG provided the initial ideas. All authors contributed significantly to the manuscript by discussing concepts from early on and reviewing and editing the drafts.

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Glossary

Among-individual trait variation	Consistent differences in traits (life-history, age, stage, behaviour, morphology, physiology) between individuals
Buffer mechanism	Mechanism that increases population persistence
Damping mechanism	A buffer mechanism that operates by reducing variation in population size
Hierarchical filtering	Variation in quality of subgroups of a population mean that high-quality subgroups are more likely to persist under adverse conditions
Portfolio effect	Negatively correlated temporal dynamics of subgroups of a population reducing temporal variation of the abundance of a local population
Repelling mechanism	A buffer mechanism that operates by counteracting population decline
Spatial heterogeneity	Spatial variation in environmental conditions (here: at the scale of the space occupied by a population, e.g. a local site)
Within-individual trait variation	Change of an individual's traits in response to external or internal stimuli (also referred to as plasticity)

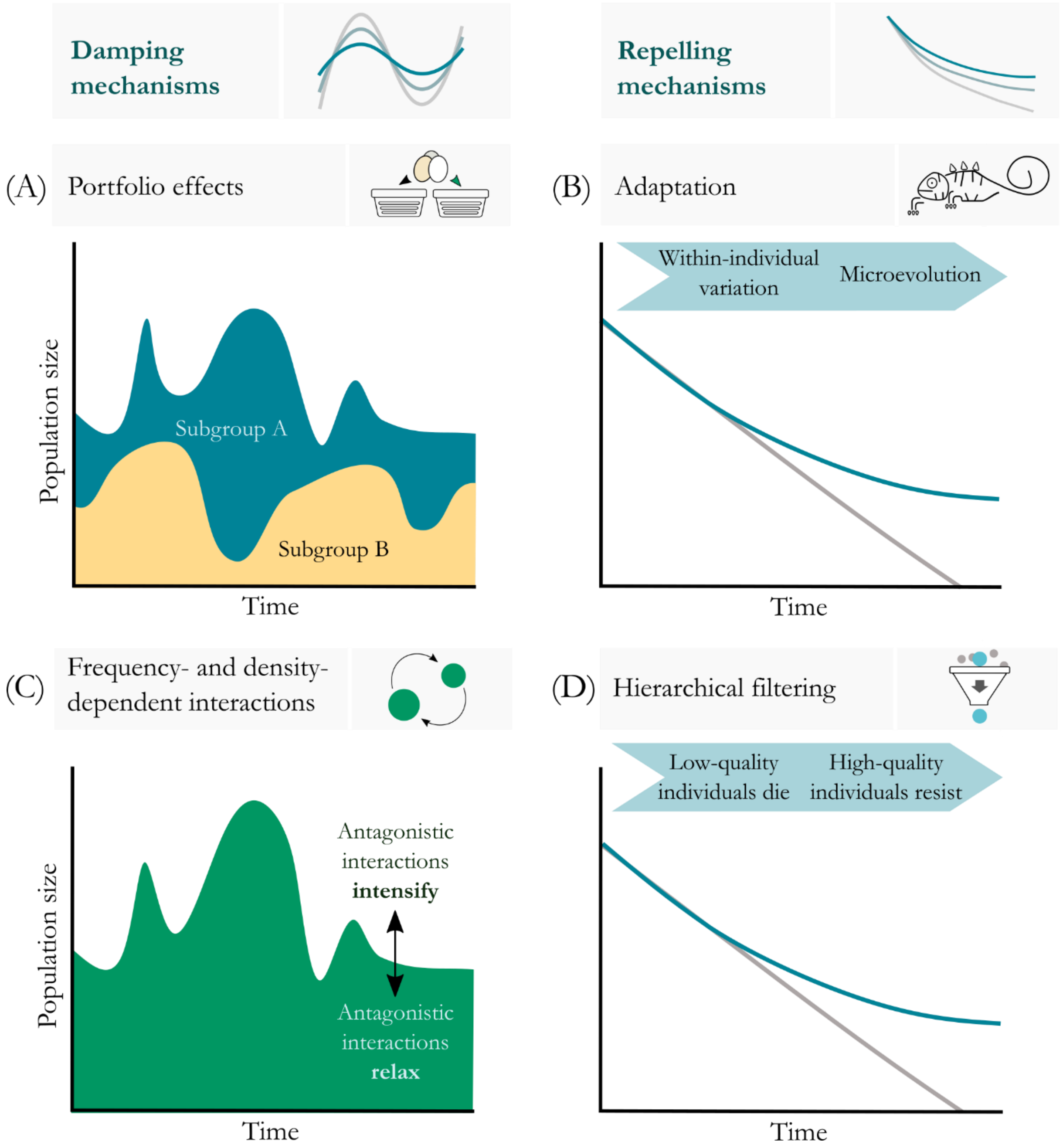

Figure 1. The two basic classes of local buffer mechanisms and their underlying processes. Damping mechanisms (panels A and C) reduce variation in population size via portfolio effects and frequency- and density-dependent interactions. (A) Portfolio effects arise from non-correlated dynamics of subgroups within a population with subgroup A and B each showing phases of low size whereas the total population size remains above a certain level. (C) Buffering frequency- and density-dependent interactions are foremost changes in antagonistic interactions such as competition that occur when population size varies. Repelling mechanisms (panels B and D) operate under adverse conditions and facilitate population persistence at low abundances (buffered line: blue, non-buffered line: grey). Repelling mechanisms include (B) adaptive processes (adaptive within-individual variation and microevolution) and (D) hierarchical filtering of high-quality individuals.

Box 1: Lurking extinction? Capacity of buffer mechanisms

Global change causes gradual shifts in mean environmental conditions as well as an increase in environmental variability, leading to more frequent, intense and often abrupt adverse extreme events [85]. The contribution of different local buffer mechanisms to population persistence depends on the abruptness, intensity and pre-occurrence of other adverse conditions [86]. Some buffer mechanisms, such as (micro)evolution and plasticity in certain traits, cannot operate if extreme events occur too abruptly or are too novel in character [87]. In other cases, within-individual variation may be triggered by a series of similar adverse events, as experience and morphological changes prime the population [50]. Conversely, buffer mechanisms may also degrade and become exhausted over subsequent instances of adverse conditions [67]. As population size decreases following adverse events, damping mechanisms lose their capacity to buffer further adverse conditions as the portfolio becomes “narrower” and the effects of competition have already relaxed.

Every buffer mechanism has a limited capacity, but when are buffer capacities exhausted or exceeded, and when can they be sufficient? Recent studies on phenological asynchrony show that buffers mediated by portfolio effects [25,35] and adaptation [83,88] prevent extinction only up to a certain threshold. For instance, once there is no combination of microhabitat characteristics and weather [25,27] that still matches at least some individual niches, portfolio effects cease to act. As soon as environmental change overtakes microevolution and novel conditions lead to a complete mismatch, populations at higher trophic levels can quickly become extinct [83]. Populations may thus be buffered until their capacities are exceeded and sudden declines occur. Such sudden events, also known as regime shifts, remain difficult to predict [74]. So far, mainly single buffer mechanisms in response to individual (i.e. non-interacting) global change drivers were studied. However, populations have to cope with multiple drivers of global change with specific temporal patterns [89] and non-additive effects [90]. In addition, as we show, different types of individual-level variation can allow for both damping and repelling mechanisms to occur, and these mechanisms interact. For instance, heritable among-individual variation leading to portfolio effects can also affect evolutionary processes or the degree of intraspecific competition [29]. Therefore, complementary to the study of multiple drivers of global change, future research should also embrace multiple buffer mechanisms to reliably estimate buffer capacities and explore how they can be used to respond to combinations of multiple drivers of global change.