# Defining ecological buffer mechanisms should consider diverse approaches


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In their response letter, Gascoigne et al. propose a relevant approach to characterizing ecological buffer mechanisms, akin to the study of buffer mechanisms in chemistry [1]. Their chemistry-inspired viewpoint enables them to pinpoint opportunities for further advances in the population buffering framework. We welcome the authors' response and concur with their belief that ecology stands to gain significantly from increased crosstalk with chemistry and other more mechanistic, first-principles-driven fields of natural sciences.

However, it is essential to emphasize that ecological systems inherently differ from chemical systems in fundamental ways. In particular, the constituent elements of ecological systems are living organisms, each possessing unique characteristics and adaptive behaviours. The systems emerging from their interactions are self-organized and have complex and dynamic stability properties. These distinctions may render Gascoigne et al.'s proposed approach limited or impractical for ecologists, as it may narrow the scope of buffer mechanisms.

The authors propose four specific criteria to be included in future studies of population


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buffer mechanisms. To maintain coherence in our response, we have opted to alter the sequence in which these criteria were originally presented. Below we address these four points.

i) Intrinsic versus extrinsic buffer mechanisms: We concur with the importance of explicitly delineating the system under consideration. However, while we agree that, as Gascoigne et al. state in their first example, legislation to reduce wolf culling does not represent an *ecological* process operating as a buffer mechanism [1], ecological and social systems are fundamentally intertwined and therefore should be studied more coherently [2]. Policies such as fishing and hunting quotas can be mechanistically linked to (anticipated) population status via harvest control rules, for instance [3]. Such legislation may dampen populations dynamics compared to a fixed quota [4]. So even when driven by legislation or consumer choices, effects on populations can be studied with similar methods to those for purely ecological processes as buffer mechanisms. Thus, while we focus on ecological processes in our original article [5], we do not see a reason to exclude socio-ecological buffer mechanisms from ecology-centred studies.

ii) Link a buffer mechanism to a specific perturbation: While this recommendation is valuable in principle, it may not always be practical, beneficial, or theoretically sound to link buffer mechanisms in ecology to a particular type of perturbation. For instance, in cases where intraspecific competition varies in response to population size and resource fluctuations [6], the damping buffer mechanism is not mechanistically working against a specific perturbation but against another factor limiting population growth rate, i.e. intraspecific competition. In other cases, buffer mechanisms emerging through stochastic accumulation of mutations may provide a damping portfolio effect buffering against a range of perturbations [7]. The exploration of the specificity of buffer mechanisms and their overall capacities in the context of multiple perturbations is a highly relevant research subject, which still requires more attention [5,8,9].

iii) A well-defined metric for population buffering: On this point, we agree. Ecologists should indeed develop methodologies to quantify population-level response variables, commencing with specifying the metric in use, as suggested by the authors (e.g., population density, mean, variance or change in demographic rates or extinction risk). To note, in some cases considering multiple metrics, such as mean time to extinction and extinction risk, may be preferential as they have different implications [10].

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iv) Quantifying the population-level metric against a reference value: We generally concur with this point, and ecologists should indeed strive to implement this approach whenever practical. Ideally, one could study systems with and without the perturbation, as well as with and without the candidate buffer mechanism in operation, such as populations with and without behavioural adaptation [11]. Ecological modelling, ideally based on first principles, allows us to define and simulate reference states and to quantify differences to buffered systems. Yet, unlike in chemistry, the study of reference states via ecological models is more limited as we lack a comparable degree of mechanistic insights. Thus, we should still describe ecological buffer mechanisms even when corresponding reference states cannot be measured or precisely assessed.

In conclusion, we find the authors' response letter to be a valuable contribution, touching not only on the topic of population persistence but also on the wider ongoing debate regarding mechanistic versus phenomenological approaches in ecology. Nevertheless, caution is required, considering that the inherent nature of open and highly complex ecological systems does not always readily permit the direct transposition of approaches from other domains of natural sciences with deeper mechanistic understanding and more controllable experimental setups. Ecologists must consider a multitude of hypothetical operating mechanisms resulting from complex interactions, population structure and environmental conditions. As such, the study of local buffer mechanisms should remain open to diverse approaches, including those that work with limited knowledge of the study system, but still can provide valuable mechanistic insights or management recommendations.

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MB and AM wrote the first draft. All authors contributed to the manuscript.

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