

objectives and strategies. For example, a recent synthesis by Oliver *et al.* [7] described the resistance and recovery aspects of biodiversity to support ecosystem functions. Their main focus on ecosystem functions, summarized as ‘while species composition is typically the target of conservation, it is ecosystem functions, rather than species composition *per se*, that need to be resilient, if ecosystem services are to be maintained’ [7], is intriguing. However, the synthesis may be at odds with the specific description of resilience for an individual function such as productivity or pollination. To avoid confusion, resilience in this case should be explicitly termed as recovery or defined as the analogy of engineering resilience [1]. Despite progress in theoretical understanding of how and when the relative contributions of resistance and engineering resilience vary in a changing environment (e.g., [14]), a narrow focus on resilience may be insufficient to translate such knowledge into practice. More specifically, because the term ‘resilience’ is increasingly framed within the concept of ecological resilience for management applications [1], a whole-system perspective with a simultaneous focus on alternative stable states, system changeability, and robustness [2,3] deserves to gain further attention over the perspective based on recovery and resistance of individual functions. Resilience-based management does not typically seek to increase the rate of return to an original state, which often implicitly assumes the existence of a single equilibrium, but instead recognizes that many natural systems could have multiple attractors [2,3]. Thus, although stability is often beneficial for the reliable provision of ecosystem functioning and services, which contribute to some aspects of resilience that benefit society (e.g., crop production), it is not necessarily a sufficient condition for achieving the objectives of resilience-based management (Box 1). Interestingly, the stabilizing effects of biodiversity on ecosystem functioning are often realized through variability, asynchrony, and compensation among

different species [8]. Such mechanisms underpinning ecosystem stability illustrate the importance of instability and changeability in community dynamics. In other words, stability itself is often (but not always) supported by changes, which are inherent in ecosystems.

Although the modern science of ecology acknowledges the nonequilibrium nature of ecosystems [3], the existence of single equilibria is still often assumed in the literature, with critical implications for conservation and restoration. This has largely helped management, but at the same time has created some confusion. As discussed by Nimmo *et al.* [12], a specific focus on resistance and engineering resilience (recovery) may be widely feasible for some stakeholders. However, caution is necessary, as this framework is relevant only where change from the basin of attraction is unideal and thus of interest [12]. Here, rather than continue to make progress in parallel, I would encourage unification of the ecological and engineering resilience frameworks [6,9]. Furthermore, these efforts should also be integrated with the growing body of biodiversity–ecosystem functioning studies. Such a synthesis could inform and benefit society by supporting the vital functionality of ecosystems that contributes to the long-term maintenance of ecological resilience.

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#### Letter

## A Synthesis is Emerging between Biodiversity–Ecosystem Function and Ecological Resilience Research: Reply to Mori

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A recent paper by Mori [1] states the need for a unification of studies of ‘engineering’ and ‘ecological’ frameworks of resilience. Engineering resilience focuses on the capacity of a system to recover to equilibrium following some kind of perturbation, while ecological resilience (ER) explicitly recognizes multiple stable states and the capacity for systems to resist ‘regime shifts’ between alternative states. We find Mori’s argument somewhat surprising given the number of recent biodiversity–ecosystem functioning (B-EF) studies that incorporate aspects of both resistance and recovery (e.g., see references in [2,3]). We would argue that a synthesis is well underway and that apparent discrepancies are more due to differences in the spatial, temporal, and systems scale of focus and ambiguities in defining this study context rather than any fundamental incompatibilities in conceptual frameworks.

With regard to our recent review on the mechanisms that underpin the resilience of ecosystem functions [3], Mori states ‘To avoid confusion, resilience in this case should be explicitly termed as recovery or defined as the analogy of engineering resilience’. We clearly consider both recovery and resistance mechanisms that promote the resilience of ecosystem functions. It is unclear what would be the benefit of narrowing the focus to recovery or engineering resilience.

Mori appears to feel that although there is some consideration of resistance in recent B-EF research (red text in his Box 1) it does not adequately embrace some of the concepts in the ‘ER’ definition, such as the potential for alternative stable states. We clearly define resilience at the level of an individual function, specifically as ‘the degree to which the ecosystem

function can resist or recover rapidly from environmental perturbations, thereby maintaining function above a socially acceptable level’ [3]. This definition does not preclude the existence of alternative stable states of the underlying system and, indeed, we include the potential to shift to alternative states that provide lower function delivery as one of several mechanisms underpinning the provision of resilient ecosystem functions. However, there are many other factors that operate at finer scales of biological organization, such as the species level (e.g., genetic variability, sensitivity to environmental change, adaptive phenotypic plasticity, Allee effects) and the community-level (e.g., correlation between response and effect traits, functional redundancy, network interaction structure). Most importantly, we feel that a focus on system state (relative to an assumed equilibrium) is not particularly helpful. The ER literature is somewhat vague with regard to what aspects of the system should be resistant in the face of an environmental perturbation. The relevant response is varyingly defined as the system ‘state’, the ‘persistence of relationships among state variables within the system’, or the ‘ways of functioning’ [4]. In our review, we promote a definition focusing on functions that are delivered by a system because biological systems are clearly dynamic, not least because the environment is continually changing. So even a system close to equilibrium would show changes in state, not to mention that many systems of interest (e.g., agroecosystems) are far from any equilibrium or that an equilibrium may not even exist [5]. Therefore, we feel it does not make sense to focus on inconsistency of system state variables or their interrelationships, not least because changes in system state can actually ensure that ecosystem functions are maintained (the example we give is that of species turnover in bee communities under climate change, which allows resilient pollination functions). The ER literature itself highlights the importance of internal system reorganizations as a mechanism

of maintaining resilience in the face of perturbations (‘adaptive capacity’ [4]). This clearly involves changes in system state variables and their interrelationships. Similarly, in the B-EF literature, as Mori states, the stabilizing effects of biodiversity on ecosystem functioning are often realized through dynamic processes such as asynchrony and compensation among species [6]. So both camps – the B-EF and the ER research fields – seem to be in agreement here: it is not invariance in the system variables that is important but the maintenance of the ecosystem functions that the system provides.

Although Mori calls for greater synthesis, we suggest that the two research fields of B-EF and ER have already started to converge. Traditionally, B-EF research has certainly adopted a more reductionist (and empirical) approach in contrast to the holistic systems thinking of ER. As a consequence, the original B-EF studies were conducted in small-scale experiments often focusing on a single function (e.g., plant productivity) and over limited timescales. However, recent research has considered a wider range of ecosystem functions and incorporated the study of multiple functions simultaneously (e.g., [7]). Studies have moved from considering simply the species richness of assemblages to the functional diversity and interactions between species in wider food-web networks [8]. Empirical studies have also been conducted over increasingly larger spatial scales (e.g., [9]) and across scales (e.g., [7]), moving B-EF increasingly in the direction of a broader research framework. Similarly, in the ER research field, key developments have been made from the original abstract theories of systems and simple analogies with real-world examples to recent progress toward the testing and implementation of these theories (e.g., through quantification of early warning systems [10]).

To avoid further confusion, however, reducing ambiguity in the study system context is critical [11]. We propose that

Table 1. Perceived Discrepancies in B-EF versus ER Literature and Potential Reconciliation<sup>a</sup>

Perceived Discrepancy	Further Details	Clarification/Potential Reconciliation
B-EF literature has traditionally focused primarily on single ecosystem functions in isolation (e.g., plant productivity) while ER literature comprises a more holistic view of entire ecosystems (and even socioecological systems).	In recent years B-EF research has rapidly expanded beyond single ecosystem functions such as plant productivity to consider a varied range of functions in isolation as well as multifunctionality (e.g., [7]). Similarly, attempts to test and apply the abstract concepts of ER literature have led to examination of specific systems and ecosystem functions.	The two fields of research appear to be converging. To facilitate this bridging, it remains essential for studies to be specific about the characteristics of the system they are measuring, the disturbance regime, and the spatial and temporal scale of interest (see main text).
B-EF literature focuses on stability and equilibrium and ignores the existence of alternative stable states. The existence of alternative stable states is a requisite for ER.	ER definitions concern the likelihood of a system crossing thresholds between alternative stable states ('regime shifts'). A system need not have high constancy to be resilient: it may be dynamic around a semistable equilibrium (i.e., staying within a 'domain of attraction'). Therefore, ER authors have suggested that stability is not a relevant measure of resilience and it may even lead to contradictory management outcomes (also see below).	The key point here is whether the focus is on system state variables or ecosystem functions provided by the system. If the focus is the latter, studies do not rely on quantifying the return to some equilibrium state nor, indeed, do they need to posit the existence of alternative stable states as do ER studies (and some authors have questioned the extent to which these really exist [5]). With a focus on ecosystem functions, any system is suitable for study, even those that are managed far from any stable equilibrium (i.e., most managed ecosystems).
Managing for stability of ecosystem functions (as informed under a B-EF framework) can be detrimental in the longer term.	This issue is often highlighted in ER literature, a frequently cited example being the management of woodlands to prevent fires. If fires are regularly suppressed (i.e., to provide stable ecosystem functions from woodlands in the short term), this leads to the accumulation of deadwood, meaning that large fires eventually break out with detrimental effects. By contrast, an ER management perspective (adopting a wider spatial- and temporal-scale view) would allow frequent smaller fires in parts of the woodland system [4].	Rather than a fundamental disagreement, the discrepancy here is simply a result of a focus on different spatial and temporal scales. If both approaches adopt a large-scale perspective, management recommendations would not be at odds (i.e., the stability of functions across the whole woodland system in the longer term is maintained by not continually suppressing fires locally). As highlighted in the main text, clarification on the system type and spatial and temporal scales of interest is critical to avoid researchers talking at cross-purposes. Note also that under a more recent suggestion the focus of management might not be for stability of ecosystem function <i>per se</i> but just for provision consistently above some socially acceptable threshold, although the two are likely to be correlated [3].
ER literature focuses on the system state while BE-F studies are concerned with the ecosystem functions.	This statement does not hold true and in fact research fields are guilty of ambiguity in what variables are being measured (i.e., 'resilience of what to what?'). In ER literature the focus of resilience is varying defined as the system state (i.e., state variables), the relationships between variables in a system, or the ways of functioning (i.e., ecosystem functions) [4]. In BE-F literature the focus has traditionally been on measuring stability in ecosystem functions, but some more recent studies (which might arguably be included in 'BE-F literature') have focused on measuring system states (e.g., species composition) (e.g., [2]).	First, clarity is essential reduce confusion [11] and authors should be careful to avoid ambiguity. Second, a conceptual framework needs internal coherency. It is contradictory to think about system variables (such as species composition) remaining constant as the definition of a resilient system [2] while also defining resilience as the capacity to reorganize (e.g., through species turnover) to retain function [4]. Both research fields recognize the truth in this. ER literature holds that systems are dynamic and may operate away from equilibrium (i.e., they move around within a 'domain of stability', also sometimes called the 'normal operating range'), with resilience as the tendency to remain in this domain. Thus, internal reorganizations of system states may be essential in allowing a system to absorb disturbances while remaining in a stability domain that delivers better ecosystem function. Similarly, BE-F literature documents in detail both empirically and theoretically [6] how changes in the composition of communities promote the maintenance of functions provided by a system. Therefore, resilience does not mean inconstancy of system state variables, and dynamic systems are needed to provide resilient ecosystem functions.

<sup>a</sup>To aid researchers a more extensively referenced version of this table is available online (Table S1 in the supplemental information online).

many of the apparent discrepancies between the B-EF and ER research fields are simply a result of researchers focusing at different temporal or spatial scales and talking at cross-purposes. We highlight some of these apparent discrepancies and their potential reconciliation in Table 1.

To conclude, both B-EF and ER approaches had initial weaknesses, such as the limited focus of empirical B-EF studies and the limited approach to quantification in more abstract, holistic ER theories. However, researchers in both fields have recognized this and, by increasing the

scope of B-EF studies and adopting a more empirical perspective on ER theories, the two fields are now beginning to merge. It is hoped that this emerging synthesis will help in understanding, predicting, and delivering solutions for the management of resilient ecosystem functions [12].

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## Supplemental Information

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## Letter

# Consumptive Tourism Causes Timidity, Rather Than Boldness, Syndromes: A Response to Geffroy et al.

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Geffroy et al. [1] proposed that nature-based tourism reduces the fearfulness and antipredator behavior of animals, leading towards a boldness syndrome that elevates natural predation rates and could trigger cascading effects on populations and communities. We agree with the framework, hypotheses, and future research needs proposed in [1], but they apply strictly to nonthreatening human–wildlife interactions. However, nature-based tourism is often consumptive, where wild-living animals are chased, stressed, and eventually harvested in activities such as recreational fishing and hunting. No threatening forms of human use of animals

were elaborated in [1]. As a complementary perspective, we here propose that consumptive nature-based tourism might lead to opposite behavioral outcomes to those proposed in [1] by inducing a timidity, rather than a boldness, syndrome (Figure 1).

Human exploitation of wild-living animals creates a 'landscape of fear' [2,3]. A commonly reported plastic behavioral response of animals to human-induced predation risk involves increased antipredator behavior and heightened timidity, characterized by a greater use of refuges and reduced activity [2–8]. For such effects to happen, the experience of non-lethal, yet threatening stimuli caused by humans are often sufficient. For example, catch-and-release angling is increasingly common in tourism-based fishing operations. Being hooked, physiologically stressed, and eventually released promotes refuge-seeking behaviors that reduce vulnerability to fishing, which may also affect nonhooked conspecifics through social learning [8,9]. In addition to plastic effects within the behavioral reaction norm, lethal consumptive tourism may also cause evolutionary responses in a range of life-history and behavioural traits that collectively increase the average timidity levels of surviving individuals [3,6,7,10–12]. For example, bold, explorative, aggressive, and active behavioral types (aka 'personalities') within exploited wildlife populations are often selectively harvested [3,7,10–12]. The positive heritability characterizing most personality traits in turn could facilitate an evolutionary (i.e., genetic) response of timidity-related behaviors [6,7,12]. Increased timidity due to learning and/or evolutionary adaptation can occur in both predator and prey populations when they are exposed to threatening stimuli by recreational fishers or hunters. The net result for a prey species should generally involve a reduction, rather than an increase [1], in natural mortality risk because either the prey becomes shyer when they are exploited or it benefits from an increased timidity of the exploited predator, thereby being