

## Opinion

## Towards a Comparative Framework of Demographic Resilience

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**In the current global biodiversity crisis, the development of tools to define, quantify, compare, and predict resilience is essential for understanding the responses of species to global change. However, disparate interpretations of resilience have hampered the development of a common currency to quantify and compare resilience across natural systems. Most resilience frameworks focus on upper levels of biological organization, especially ecosystems or communities, which complicates measurements of resilience using empirical data. Surprisingly, there is no quantifiable definition of resilience at the demographic level. We introduce a framework of demographic resilience that draws on existing concepts from community and population ecology, as well as an accompanying set of metrics that are comparable across species.**

## Resilience as a Key Concept in Ecology and Conservation

Contemporary global change is increasingly eroding natural resources [1–3]. Thus, understanding how ecological systems withstand environmental **disturbances** (see [Glossary](#)) is a major challenge [4–6]. 'Resilience' is a key concept that describes the ability of natural systems to handle disturbances [7]. Indeed, international environmental policy objectives, including the UN Sustainable Development Goals [8] and Aichi Targets [9], specifically include preserving resilience as a key objective.

Resilience describes the ability of a system to resist and recover from a disturbance [10]. However, translating resilience into quantifiable metrics is challenging due to the complexities of ecological systems [11], and has generated multiple debates over the past decades regarding its definition, meaning, and application [10,12,13] ([Box 1](#)). Discrepancies between approaches mean that both theoretical and empirical works lack parity between the primary components of resilience studied, rendering comparisons challenging if not impossible. These limitations ultimately prevent ecologists from applying resilience-based solutions to real-world problems (e.g., [14]). Developing a unifying framework with comparable definitions and quantifications across different ecological systems is therefore an urgent task [10,15,16].

We introduce a framework to define, quantify, and compare resilience across populations and species. The framework integrates resilience concepts from community ecology [10,15,17,18] and **demographic** theory [19]. Following the conceptualizations of resilience in Hodgson *et al.* [10], we define **demographic resilience** as the ability of populations to **resist** and **recover** ([Box 1](#)) from alterations in their **demographic structure**, usually with concomitant change in population size. We show that **transient dynamics**, as extensively described in [20,21], can be used to quantify demographic resilience and to anticipate the responses of the population and of species to disturbances. Thus, our framework marries two disciplines to define and quantify demographic resilience, and includes elements that draw from and are analogous to community resilience [11,22].

## Highlights

The global biodiversity crisis demands a broad understanding of the ability of species to respond to external disturbances caused by global change.

A common framework to quantify, compare, contrast, and predict the resilience of species to global change is urgently needed.

Resilience includes the resistance of populations to change after disturbance and their recovery from it.

Measurements of short-term population growth following disturbances, and any of its longer-term consequences, allow quantification of demographic resilience.

Quantifying demographic resilience with common semantic and numeric definitions enables comparisons of resilience across species, enabling us to predict their responses to disturbances.

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## Box 1. Defining Resilience

Since its first appearance in the ecological literature in the late 1970s, the study of resilience has attracted significant attention (Figure 1). However, the rate at which resilience research has increased matches the diversity of definitions and interpretations of resilience. The term resilience was first introduced into ecology by Holling [7], who defined it as 'a measure of the persistence of systems and their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables'. Holling's definition was interpreted in different ways across subdisciplines [60]. For example, some have considered resilience to be the speed of recovery of a natural system, quantified as the time required to return to equilibrium [16]. By contrast, others have measured resilience as the probability of the system to remain in a stable state [61]. Consequently, Holling later [62] distinguished two types of resilience: engineering and ecological resilience. He defined engineering resilience as 'resistance to disturbance and speed of return to the equilibrium' following a shock. Ecological resilience was described as the 'magnitude of a disturbance that can be absorbed before the system changes its structure' [7,62].

To frame demographic resilience, we draw on ideas and terminology from community/ecosystem resilience and stability [10,11,15,22]. We define resilience following Hodgson *et al.* [10] as 'the capacity of system to persist and maintain its state and functions in the face of exogenous disturbance'. Similar to the ecological stability literature, several authors consider resilience to be a function of resistance and recovery [10,15,63–65]. Such bivariate frameworks incorporate resistance, representing the magnitude of change of the state variable, and recovery, a component of its recovery trajectory (recovery magnitude or rate) after the disturbance ends. Populations have stable demographic structures representing 'states' from which the population are displaced and then return to after disturbance. Such characteristics align demographic resilience to the general bivariate resilience [10,15,63–65] and ecological stability [11,16,22] frameworks, which both have an engineering resilience perspective.

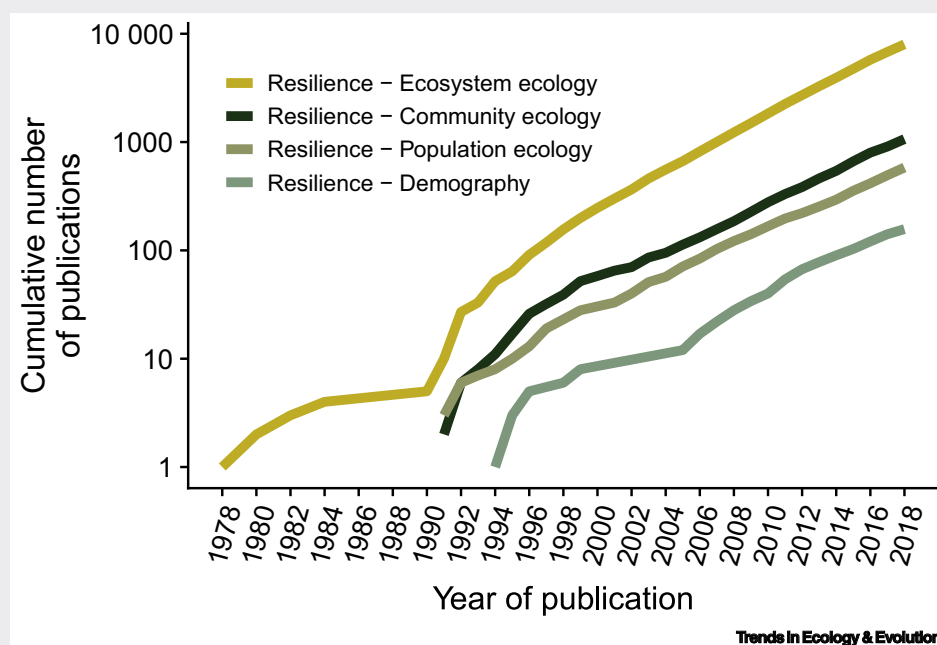


Figure 1. The Cumulative Number of Ecological Studies in Web of Science Concerning Resilience Has Increased Exponentially in Recent Decades. There are higher numbers of publications about higher-level ecological systems (ecosystems, communities) than about lower-level systems (populations, demography).

## From Resilience Theory to Demographic Resilience

Established resilience theories assume that natural systems can exist in alternative stable states [7], where the forces influencing the system are in balance [6,20–22]. When a disturbance displaces the system to an unstable state, these forces usually draw it back to stable state (Figure 1A). However, if a disturbance forces the system beyond a domain of attraction, a **tipping point**, the system may transition to an alternative stable state [17,18]. This new system state is characterized by substantially different structures and is maintained by **hysteresis** processes or feedbacks [17,23].

## Glossary

**Amplification:** a short-term increase in population density relative to the population at stable growth.

**Attenuation:** a short-term decrease in population density relative to the population at stable growth.

**Critical slowing down:** the phenomenon when a system approaches a tipping point, leading towards a slower rate of return to the previous state of the system.

**Demography:** the study of the dynamics of populations resulting from the processes of birth, death, development, and migration.

**Demographic compensation:** the inherent ability of a population to increase its size after a disturbance.

**Demographic resilience:** the inherent ability of a population to resist and recover after a disturbance.

**Demographic resistance:** the inherent ability of a population to avoid a decrease in size or density after a disturbance.

**Demographic recovery:** the time that a population requires to recover its stable demographic structure after a disturbance.

**Demographic stability:** the dynamics of a population when they are at the stable demographic structure and stable growth.

**Demographic structure:** the distribution of individuals of different ages, sizes, or stages within a population.

**Disturbance:** an exogenous, discrete event that alters the demographic structure of a population, displacing it from its stable demographic structure.

**Hysteresis:** feedback mechanisms that maintain a system in its current state.

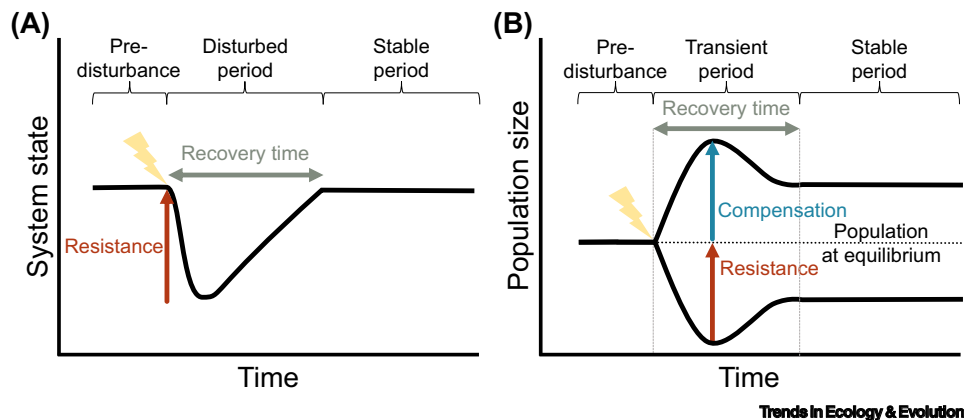
**Perturbation:** exogenous alterations that affect the vital rates of a population, thus modifying the stable demographic structure.

**Population ecology:** the study of the structure and dynamics of natural populations.

**Recovery:** the capacity of a system to return to undisturbed state following a disturbance.

**Resistance:** the extent of change of a system after a disturbance.

**Stable demographic structure:** the proportion of individuals in each of the stage in the life cycle of a population does not change through time. This distribution is achieved at stationary



**Figure 1.** Comparison between Disturbance Responses and the Main Components of Resilience in Communities (A) and Populations (B). When translating the population responses to disturbances from classical resilience frameworks, the system state is defined as the population size and the population structure (y axis). After a disturbance, the size of the population changes differently according to the stages affected, creating a range of possible population sizes and defining the resistance to being disturbed. The time needed to settle into one of the multiple possible stable structures is defined as the recovery time. The population decrease after a disturbance is resistance. Note that resistance is the inverse of the amount of change caused by the disturbance, and more resistance reflects less change. In demography (B) there is another possible response to disturbance, which is an increase in population size or compensation.

Populations show similar properties to those in classical views of ecological resilience. Similarly to communities, populations are structured [19]. Like distinct species in a community contribute differently to community dynamics [24], individuals of distinct ages, sizes, or developmental stages in a population contribute differently to population dynamics [19]. In a constant environment, a population will attain a **stable demographic structure** with **stable population growth** [19,21]. Therefore, as in classical resilience views, populations are systems with a stable state defined by their demographic structure and growth.

Disturbances change the size and structure of a population, displacing it from a stable structure (e.g., a fire affects younger rather than older tree individuals [25]). Such alterations to structure and size are akin to changes in community composition and biomass. Disturbances result in short-term dynamics that can differ from those at **demographic stability**, leading to either faster or slower growth than at stability (**amplification** and **attenuation** respectively [21]). These transient dynamics [19,21], which depend on population structure, are generated by a relative over- or under-representation of individuals with high survival and/or reproduction. The largest extents of population amplification and attenuation after a disturbance represent the **transient bounds**, that are akin to resistance in classic resilience theory (Figure 1). As under-represented individuals are repopulated, the population is drawn back towards demographic stability, that is akin to recovery in classic resilience theory (Figure 1). Transient dynamics are thus ideal to estimate the intrinsic ability of populations to respond to disturbances.

### Measuring Demographic Resilience

**Population ecology** has a panel of tools to measure demographic resilience, thus overcoming a key criticism of many resilience frameworks in communities, which lack operationalization [10,14].

**Structured population models** facilitate explicit simulations of disturbances that impact on different life-cycle stages [26], and enable calculation of the consequent transient responses [19,21]. Bivariate resilience frameworks [10,15,27] decompose resilience into two components, resistance and recovery (Figure 1 and Box 1). We distinguish resistance into two different processes, **demographic compensation** and **demographic resistance** (Figure 2; details below).

equilibrium, regardless of whether the population is growing, stays demographically stable, or declines.

**Stable population growth:** population growth that the population attains in the lack of disturbance, perturbation or density-dependence.

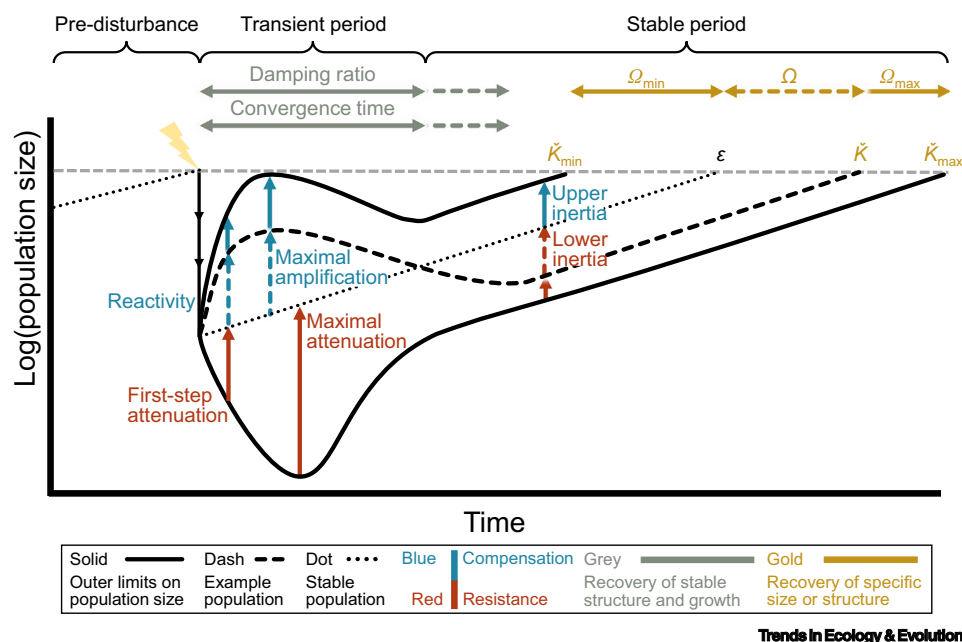
**Structured population models:** mathematical representations of the life cycle of the population of a species that account for the differential survival, development, and reproduction of individuals belonging to different ages, sizes, or ontogenetic stages of the population.

**Tipping point:** the threshold beyond which a system becomes too unstable and transitions into another stable state.

**Transient bounds:** the upper and lower extreme values of the transient dynamics resulting from alterations in the demographic structure.

**Transient dynamics:** the short-term dynamics of a population that result from demographic structures that differ from the stable demographic structure.

**Vital rates:** the variation of survival, development, and reproduction with age, size, or stage of the individuals of a population.



**Figure 2. Resilience Framework Measurements for Population Responses to Disturbances.** Example of a population whose size structure has been disturbed and the consequent changes in population size. Before the disturbance, the population is increasing with a stable growth rate (but could also be decreasing or remain stable). The disturbance creates a discrepancy between the actual population size/structure and the structure that would exist given stable growth, resulting in transient dynamics. Demographic compensation: increases in population size immediately after disturbance are measured as reactivity, the highest increase during the transient period is measured as maximal amplification. Once at demographic stability, the population size/structure increase compared with the initial stable structure is a measure of amplification inertia. Demographic resistance: the lack of resistance can be measured using decreases in population size as a result of a disturbance. At the first-time step, measured as first-step attenuation, the lowest value is the maximal attenuation, and the decrease in population size is a measure of attenuation inertia. Demographic recovery: the time required to recover the initial stable population structure has its minimum at  $\tilde{K}_{\min}$  and maximum at  $\tilde{K}_{\max}$ . To measure how much more or less time the system will require to reach the stable structure, we can estimate the difference between  $\tilde{K}_{\min}$  and  $\tilde{K}_{\max}$  to the structure at the stable population growth,  $\varepsilon$ , to calculate  $\Omega$  and  $\Omega_{\max}$ , respectively. It is similar for population size, where  $\tilde{K}$  is the time to reach stability and  $\Omega$  is the difference from stable growth.

In addition, we provide a distinction between recovery to a particular population size and recovery to a particular structure and growth (Figure 2).

## Demographic Compensation

Demographic compensation incorporates amplifications in population size after disturbance (Box 2 and Figure 2), which compensate for post-disturbance reductions in population size. We advocate the use of reactivity, maximal amplification, and amplification inertia [21] to estimate changes in population size at various times after a disturbance, relative to stable growth (Figure 2). Reactivity quantifies the immediate, short-term response to a disturbance; maximal amplification is the highest density that the population can reach at any time-step, and inertia measures the total displacement of the population in the long-term, after the transient period. Reactivity, therefore, quantifies immediate compensation of a population, whereas maximal amplification measures the overall ability of the population to compensate, and inertia quantifies how far away from the stable state the population ends up following disturbance (Box 2).

Classical views of resilience consider that compensation equates to lack of resistance (e.g., [22]). Nevertheless, given the importance of distinguishing between population amplification and attenuation in management, we advocate distinguishing demographic compensation from

## Box 2. Transient Calculations

In Table I we present a compendium of equations to estimate the aforementioned transient metrics using the most common structural population models used in demography – matrix population models [19]. However, the estimation of transient dynamics can be done using different structured population models (e.g., integral projection models [66]) and other approaches [21]. Transient dynamics can be measured by estimating the absolute changes in the population size, which combine the transient rates and the asymptotic rate. Asymptotic effects can be discounted by using a standardized matrix population model  $\hat{A}$ , by dividing matrix  $A$  by  $\lambda_{\max}$ . In addition, the population vector  $n$  can also be standardized,  $\|\hat{n}\|$ , to sum to 1. Such standardizations allow fair comparisons between models [21].

Table I. Calculation of Transient Dynamics Using Matrix Population Models<sup>a</sup>

| Resilience component | Index                                   | Calculation   | Interpretation  |
|----------------------|---|---|---|
| Compensation         | Reactivity                              | $\bar{\rho}_1 = \ \hat{A}\ _1$                                    | The largest population density that can be reached in the first-time step after disturbance.  |
|                      | Maximal population amplification        | $\bar{\rho}_{\max} = \max_{t>0} (\ \hat{A}^t\ _1)$                | The largest population density that can be reached at any time after disturbance.   |
|                      | Inertia amplification                   | $\bar{\rho}_{\infty} = \frac{v_{\max} \ w\ _1}{v^T w}$            | The largest possible long-term population density.  |
| Resistance           | First-step population attenuation       | $\underline{\rho}_1 = \min CS(\hat{A})$                           | The lowest population density that can be reached in the first time step after disturbance.   |
|                      | Maximal population attenuation          | $\underline{\rho}_{\min} = \min_{t>0} (\min CS(\hat{A}^t))$       | The lowest population density that can be reached at any time after disturbance.  |
|                      | Long-term population attenuation        | $\underline{\rho}_{\infty} = \frac{v_{\min} \ w\ _1}{v^T w}$      | The lowest possible long-term population density.   |
| Transient envelope   | Reactivity envelope                     | $\ \hat{A}\ _1 / \min CS(\hat{A})$                                | The lower the value, the more the population resists changes in size.   |
|                      | Inertia envelope                        | $\frac{v_{\max} \ w\ _1}{v^T w} / \frac{v_{\min} \ w\ _1}{v^T w}$ | The higher the value, the greater the displacement of the population from its stability in the long term after disturbance.   |
| Time of recovery     | Damping ratio                           | $\rho = \lambda_1 / \ \lambda_2\ $                                | Dimensionless measure of convergence to stable growth. Smaller numbers represent slower convergence.  |
|                      | Convergence time                        | $t_x = \log(\rho) / \log(x)$                                      | The time $t_x$ required for the contribution of the dominant eigenvalue ( $\lambda_1$ ) to become $x$ times as great as that of the largest subdominant eigenvalue ( $\lambda_2$ ). Absolute measure of time of convergence to stable structure. Smaller numbers represent quicker convergence. |
|                      | Minimum time to recover initial size    | $\Omega_{\min} = \varepsilon - \tilde{\kappa}_{\min}$             | The lower the value the less time required to recover the initial population structure.   |
|                      | Maximal time to recover initial size    | $\Omega_{\max} = \varepsilon - \tilde{\kappa}_{\max}$             | The lower the value the less time required to recover the initial population structure.   |
|                      | Time to recover initial population size | $\Omega = \varepsilon - \tilde{\kappa}$                           | The lower the value the less time required to recover the initial population size.  |

<sup>a</sup> $A$  is the matrix population model.  $\hat{A}$  is the standardized matrix population model, which is calculated as  $A/\lambda_{\max}$ , where  $\lambda_{\max}$  is the dominant eigenvalue of  $A$ .  $w$  is the dominant right eigenvector and the stable demographic structure of  $A$ .  $v$  represents the dominant left eigenvector, the reproductive value vector of  $A$ . The vector  $\hat{n}_0$  represents the initial demographic distribution, standardized to sum to 1.  $\min CS$  denotes the minimum column sum of a matrix, and  $\|\mathbf{m}\|_1$  is the one-norm of a vector  $\mathbf{m}$  (equal to the sum of its entries). The values  $m_{\min}$  and  $m_{\max}$  are the smallest and largest entries of a vector  $\mathbf{m}$  respectively. Transient bounds are represented using  $\rho$ , as well as the damping ratio following the notation of [19,54]. Transient bounds are distinguished with an overbar ( $\bar{\phantom{x}}$ ) or underbar ( $\underline{\phantom{x}}$ ) to indicate amplification and attenuation, respectively. Transient metric subscripts provide information regarding the timeframe of a study, where 1 indicates first time-step indices; max and min are maximal amplification or attenuation, respectively, and  $\infty$  is inertia.  $\lambda_1$  is the dominant eigenvalue,  $\lambda_2$  is the largest subdominant eigenvalue,  $\tilde{\kappa}$  is the time to reach stability,  $\tilde{\kappa}_{\min}$  and  $\tilde{\kappa}_{\max}$  are the minimum and maximum time required to recover the initial stable population structure, respectively, and  $\varepsilon$  is size at stable population growth.

demographic resistance in demographic resilience studies. Demographic compensation is fundamental for understanding population crashes [21], and compensation metrics are of particular interest for management actions targeting potential invasive species [28]. For instance, for species showing high population increases after disturbance, management interventions can be adapted according to the potential demographic compensation [28,29].

## Demographic Resistance

Demographic resistance can be estimated using population attenuation bounds, where lower bounds indicate that the population or the species is less resistant (Figure 2). Similarly to

population compensation, we suggest using first-step attenuation, minimum attenuation, and attenuation inertia [21] to estimate the potential change in population size and structure after a disturbance (Box 2). First-step attenuation quantifies the immediate response to a disturbance, whereas the maximal attenuation is the lowest density that the population can reach at any time, and attenuation inertia measures the total displacement in the long term. Consequently, first-step attenuation quantifies the magnitude of population decay or lack of resistance, maximal attenuation measures the overall lack of resistance, and inertia quantifies how far away from the stable state the population ends up.

At the community level, most studies express resistance as a measure of the loss or gain of species after a disturbance [30–32] or the change in community functions [22]. Community resistance can be measured as the maximal Euclidean distance between vectors representing a disturbed and an undisturbed community. A higher Euclidean distance indicates lower community resistance, and vice versa [11,33], whereas multidimensional variables are aspects of the quality and diversity of the community before and after the disturbance [11,33]. By contrast, demographic resistance is measured using differences in population size, in other words the sum of the size, age, or stage vector of the population.

### Transient Envelope

The combination of population amplification and attenuation can serve as a metric of the overall response of the population to disturbances. Transient bounds, the most extreme increases or decreases of transient population size after a disturbance, together represent the transient envelope (Figure 2) [21]. A small transient envelope means that the population is robust against disturbances, whereas large transient envelopes indicate that the population is more sensitive to changes in its structure [21,34]. Because amplification and attenuation are bound asymmetrically  $\{(1, \infty)$  for amplification;  $(0, 1)$  for attenuation [21], geometric rather than arithmetic comparisons are more relevant. Then, the transient envelope is either the ratio between amplification and attenuation or the difference between log-transformed indices. Note that in Table 1 in Box 2 we do not include the transient envelope for maximal amplification and attenuation, given that both can happen at different times (Box 3).

The transient envelope has a similar interpretation to resistance in community ecology [11,15,22]. We distinguish here the transient envelope from demographic compensation and resistance because the latter provide different information about the ability of populations to respond to disturbances. Although the transient envelope indicates the range of potential population sizes following a disturbance, it does not allow us to depict whether this happens through compensation or resistance. Nevertheless, we provide the transient envelope given its usefulness in comparative studies [34] and its similarities with community resistance [11,22].

### Box 3. Estimating and Comparing Demographic Resilience

To understand demographic resilience, we showcase two species with contrasting demographic resistance and recovery patterns (Figure 1). The Asian elephant (*Elephas maximus*, Figure 1A) experiences weak attenuation compared with the red squirrel (*Tamiasciurus hudsonicus*, Figure 1B). Note that the larger the magnitude of attenuation the less resistant the species is. Both the reactivity and inertia envelope are higher for the red squirrel than for the Asian elephant, showing that the former is more responsive to disturbances than the latter. Conversely, the red squirrel requires less time (4 years) to recover than does the Asian elephant (30 years). Taken together, these results indicate that the Asian elephant displays higher resistance to disturbances but requires a longer time to recover than the red squirrel.

The two species show different ways of achieving resilience, illustrating the usefulness of comparing demographic compensation, resistance, and recovery. For example, even with their high demographic resistance, the slow recovery rate of the Asian elephant makes them vulnerable to continuous habitat loss and frequent hunting [67]. For the red squirrel, even if this species shows low resistance, their populations recover quickly. Therefore, if this species is not subject to heavy exploitation or habitat loss, their viability seems unlikely to be jeopardized.



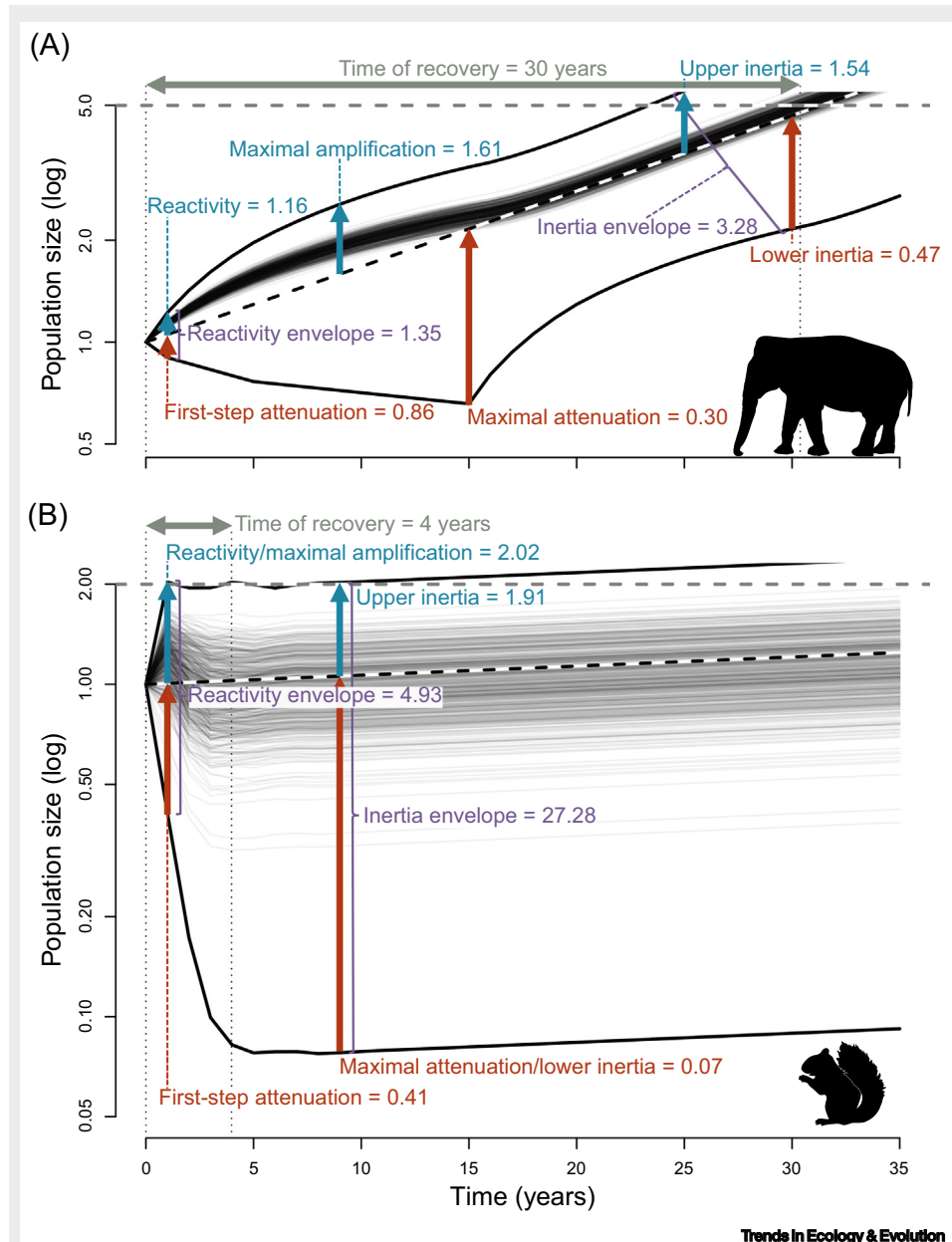


Figure 1. Population Change Projections for an Asian Elephant (*Elephas maximus*) Population (A) and a Red Squirrel (*Tamiasciurus hudsonicus*) Population (B), with Their Respective Demographic Resilience Metrics. The data were obtained from the open-access database COMADRE [68]. Blue arrows indicate compensation measurements, red arrows resistance metrics, purple brackets transient envelopes, and grey arrows recovery time. Bold black lines indicate transient bounds, the shaded area indicates the range of values in which all case specific projections lie. Broken black lines indicate population dynamics assuming stable demographic structure and growth. Dotted black lines delimit the transient period. Note that, for the red squirrel, the reactivity and the maximal amplification, and the maximal attenuation and lower inertia, have the same values.

### Demographic Recovery

**Demographic recovery** is a crucial metric of demographic resilience that explicitly considers time. Similarly to resistance, there are several metrics to quantify the time required to reach population stability [21]. For populations, the key question is – time of recovery to what? Stable

state, or a desired population size or structure? We propose two measures to describe the time of recovery to population stability after a disturbance: damping ratio and time of convergence (Box 2). We distinguish between metrics that estimate time to recover previous population size and those that estimate time to recover previous population structure (Box 2).

#### *Time of Recovery to Stable State*

The damping ratio measures how quickly transient dynamics decay following a disturbance, regardless of the population structure [21]. The larger the damping ratio, the faster the population converges, and the lower the time of recovery. Importantly, the damping ratio is a dimensionless metric [19]. Thus, damping ratio is useful for comparing relative times of recovery across populations or species [35]. We also suggest the use of the time of convergence, which is similar to the damping ratio but the former is time-stamped, and can therefore be used both for comparative analyses and to inform managers about the expected post-disturbance recovery times.

#### *Time of Recovery to Population Size and Structure*

It is also possible to estimate the return time necessary to recover previous population size and/or the original, stable structure (Figure 2). Because these return times can be measured relative to the original structure, they are useful for informing conservation plans or restoration actions.

For communities, time of recovery is often defined as engineering resilience [14,36]. Recovery time has been estimated using a wide variety of measurements, sometimes specific to the study system, such as net primary productivity [37] or biomass [38]. The common denominator is that such metrics are compared between the disturbed and undisturbed communities after particular intervals of time. In the case of empirical studies, such intervals are constrained to the length of the study, and therefore full recovery is not always observed [37,38]. By contrast, modeling studies can project the community and measure its recovery at long temporal scales [33].

### **Additions to Ecological Resilience Indicators**

Classical theoretical frameworks have triggered the development of a myriad of ecological resilience indicators [17,18,39]. These indicators are based on the idea of **critical slowing down**, whereby a system approaching a tipping point may exhibit decreasing ability to recover its previous state [17,39]. Approach to a critical tipping point can be detected with temporal and spatial statistical signatures, such as increased autocorrelation of, or variance in, abundance [18,39]. Such momenta have been identified in different ecosystems [17,18], potentially facilitating anticipation of critical system transitions [40,41].

The detection of approaches to tipping points has been debated [14,42] given their limitations related to (i) assuming abrupt regime shifts [43], (ii) assuming that regime shifts exhibit critical slowing down [18,43], and (iii) inability to compare systems with dissimilar properties and/or environments [18,39]. This theoretical framework is further unable to (iv) explicitly account for different responses to disturbances for different species life-history strategies [44,45], or (v) distinguish population responses before collapse [39,46] from responses to disturbance. Such constraints (discussed further in [39,46]) have hampered the use of ecological resilience theory [13,14] in applied ecology and conservation.

Demographic resilience allows the main challenges of measuring resilience to be overcome. Demographic resilience relaxes the assumption of systems experiencing regime shifts and tipping points [limitations (i) and (ii)] because it focuses on the responses of the populations to disturbances [21]. Demographic resilience also allows comparison of the same fundamental processes (survival, development, and reproduction) across different populations and/or species (iii) [26]



(Box 3). This approach also accounts for the differences in the life histories (iv), and estimates the population responses before a collapse (v) by quantifying their dynamics [35].

### Incorporating the Different Moments of Disturbance

Disturbances are key determinants of demographic resilience. We define here disturbance as a sudden event, that is, a pulse of mortality caused by a temporary period of environmental stress altering the population (e.g., storm, fire) [47]. However, disturbances can vary in magnitude and duration [47,48]. Our framework only provides analytical solutions to explore the effects of discrete pulse disturbances. Other forms of disturbance force the population towards alternative stable states, but still initiate transient dynamics.

**Perturbations** that are sustained (i.e., long-duration) ‘press’ disturbances over time (e.g., global warming, ocean acidification) are also likely to influence demographic resilience [47]. The adequacy of considering perturbations in a resilience context has been debated [10,49], and some consider them to cause a permanent system change, where a return to stability can only be achieved through adaptation [10]. In a demographic resilience context, perturbations alter the **vital rates** of a population, and this consequentially alters the stable structure of the population. Although the actual population structure remains unchanged, this still creates a discrepancy between the actual population structure and the stable structure. Transient dynamics will also emerge in this case. If the perturbation is removed, the incorporation of adaptation would be needed to understand movement back towards the previous stable state (e.g., [50,51]). However, such adaptive modeling requires understanding the change in the vital rates over time, violating the density-independent and time-invariant environment under which our framework operates. In such cases, simulation approaches would be more appropriate [69]. Extinction is also a stable state that is common to all ecological systems: any perturbation which eliminates reproduction will enforce extinction. This recruitment failure can also be achieved through disturbances (e.g., if a disturbance removes all individuals which reproduce and which have the capacity to grow into reproductive individuals).

Disturbances can occur at different magnitude [52] and frequencies [48], and also interact with other disturbances or perturbations [49,53]. The proposed framework does not yet allow analytical anticipation of the demographic resilience to different magnitudes, frequencies, or their interactions. However, it does allow quantification of the changes in demographic resilience after specific disturbance combination scenarios, using case-specific structural population models [21]. For example, specific disturbance magnitudes or frequencies can be explored by estimating case-specific transient dynamics with specific population structures (simulating a specific magnitude of disturbance, e.g., 20% mortality in adults) [21,54]. In addition, if the effect of a perturbation is known, it will alter the stable demographic structure, and it can be coupled to the impact of a given disturbance scenario. Future explorations of such varied disturbance regimes with simulations or new analytical solutions will be pivotal to understand complex changes of resilience [47,52].

### Concluding Remarks

Our proposed framework translates resilience approaches [10,15,39,55] to demography, opening the door to multiple research venues (see Outstanding Questions). Because the demography of a species is tightly linked to biological processes taking place at lower and higher levels of organization, our framework enables exploration of the mechanisms that drive resilience. Resilience is an emerging property of complex systems [56], given that ecological communities are assemblages of populations of interacting species [30], and demographic resilience will provide important insights into community resilience. However, such scaling up from populations to communities will require information on how species interact within a community and how the emergent network changes when species are removed [31,33]. The links between demographic resilience and

### Outstanding Questions

- Which a/biotic factors affect the different components of demographic resilience?
- What traits confer the highest resilience/resistance/recovery after a disturbance?
- Is there a link between resilience and the evolutionary history of the species? Are there tradeoffs between resistance and speed of recovery?
- How many demographic resilience metrics are necessary to fully characterize the resilience of a population?
- How can density-dependence and stochasticity be incorporated into the demographic resilience framework?
- Do resilience responses group according to life-history strategies? Do short-lived species recover faster than long-lived species? Are long-lived species more resistant than short-lived species?
- How does resource availability influence demographic resistance and recovery of species and the correlation between the two?
- Are species in fluctuating environments more resilient to constant disturbance? How do disturbance regimes affect the resilience of species?
- How do chronic stressors (e.g., global warming, ocean acidification) affect demographic resilience? Are the links between demographic resilience and community resilience affected by such changes in environmental conditions?
- How does the demographic resilience of species translate into community resilience? Are resilient communities composed of more demographically resilient species? What is the minimum number of resilient species that a community needs to sustain acceptable levels of community-level resilience?

physiological resilience are also likely to provide mechanistic insights on how the resilience of individuals scales up into populations and communities [57]. Such mechanistic understanding of resilience will also allow the development of evolutionary questions [58,59]. Future research should also focus on developing tools to analytically derive transient dynamics using density-dependent and stochastic demographic models. Overall, the proposed framework provides a coherent way of quantifying and comparing resilience across populations and species, and opens up new views of resilience that will likely help to develop better conservation and management decisions.

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