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1   **Towards a comparative framework of demographic resilience**

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19

20   **Abstract**

21   In the current global biodiversity crisis, developing tools to define, quantify,

22   compare, and predict resilience is essential for understanding species' responses to

23   global change. Disparate interpretations of resilience have, however, hampered the

24   development of a common currency to quantify and compare resilience across natural

25   systems. Most resilience frameworks focus on upper levels of biological organisation,

26   especially ecosystems or communities, which adds complication to measuring

27   resilience with empirical data. Surprisingly, a quantifiable definition of resilience does

28   not exist at the demographic level. Here, we introduce a framework of demographic

29   resilience that draws on existing concepts from community and population ecology,

30   with an accompanying set of metrics that are comparable across species.

31   **Keywords:** Global Change, Life History Strategies, Regime Shifts, Stability, Stage-

32   Structured Population Model.

33

34 **Body**

35 **Resilience as a key concept in ecology and conservation**

36 Contemporary global change is increasingly eroding natural resources [1–3]. Thus,

37 understanding how ecological systems withstand environmental **disturbances** (see

38 Glossary) is a major challenge [4–6]. "Resilience" is a key concept describing natural

39 systems' abilities to handle disturbances [7]. Indeed, international environmental

40 policy objectives, including the UN Sustainable Development Goals [8] and Aichi

41 Targets [9], specifically include preserving resilience as a key objective.

42 Resilience describes the ability of a system to resist and recover from a

43 disturbance [10]. However, translating resilience into quantifiable metrics is

44 challenging due to the complexities of ecological systems [11], which has generated

45 multiple debates over the past decades regarding its definition, meaning and

46 application [10,12,13] (Box 1). Discrepancies among approaches mean both

47 theoretical and empirical works lack parity between the primary components of

48 resilience studied, rendering comparisons challenging if not impossible. These

49 limitations ultimately prevent ecologists from applying resilience-based solutions to

50 real-world problems (e.g. [14]). Developing a unifying framework with comparable

51 definitions and quantifications across different ecological systems is therefore an

52 urgent task [10,15,16].

53 We introduce a framework to define, quantify, and compare resilience across

54 populations and species. The framework integrates resilience concepts from

55 community ecology [10,15,17,18] and demographic theory [19]. Following the

56 conceptualisations of resilience in Hodgson et al. [10], we define **demographic**

57 **resilience** as the ability of populations to **resist** and **recover** (Box 1) from alterations

58   in their **demographic structure**, usually with concomitant change in population size.

59   We show that using **transient dynamics**, extensively described in [20,21], one can

60   quantify demographic resilience and anticipate population's and species' responses

61   to disturbances. Thus, our framework marries two disciplines to define and quantify

62   demographic resilience, with elements that draw from and are analogous to

63   community resilience [11,22].

64   **From classical resilience theory to demographic resilience**

65   Established resilience theories assume that natural systems can exist in alternative

66   stable states [7], where the forces influencing the system are in balance [6,20,21,22].

67   When a disturbance displaces the system to an unstable state, these forces usually

68   draw it back to stable state (Figure 1A). However if a disturbance forces the system

69   beyond a domain of attraction, a **tipping point**, the system may transition to an

70   alternative stable state [17,18]. This new system state is characterised by substantially

71   different structures and maintained by processes of **hysteresis** or feed-backs [17,24].

72   Populations show similar properties to those in classical views of ecological

73   resilience. Just like communities, populations are structured [19]. As distinct species

74   in a community contribute differently to community dynamics [25], individuals of

75   distinct age, size, or developmental stage in a population contribute differently to

76   population dynamics [19]. In a constant environment, a population will attain a stable

77   demographic structure with **stable population growth** [19,21]. Therefore, just like

78   classical resilience views, populations are systems with a stable state defined by their

79   demographic structure and growth.

80   Disturbances change a population's size and structure, displacing it from stable

81   structure (e.g. a fire affects younger rather than older tree individuals [26]). Such

82 alterations to structure and size are akin to changes in community composition and

83 biomass. Disturbances result in short-term dynamics that can differ from those at

84 **demographic stability**, with either faster or slower growth than at stability

85 (**amplification** and **attenuation** respectively [21]). These **transient dynamics**

86 [19,27], which depend on population structure, are generated by a relative over- or

87 under-representation of individuals with high survival and reproduction. The largest

88 population amplification and attenuation after a disturbance represent the **transient**

89 **bounds**; akin to resistance in classic resilience theory (Figure 1). As under-

90 represented individuals are repopulated, the population is drawn back towards

91 demographic stability; akin to recovery in classic resilience theory (Figure 1). Transient

92 dynamics are thus ideal to estimate the intrinsic ability of populations to respond to

93 disturbances.

94 **Measuring demographic resilience**

95 Population ecology has a corollary of tools to measure demographic resilience,

96 overcoming a key criticism of many resilience frameworks in communities, which lack

97 operationalisation [10,14]. **Structured population models** facilitate explicit

98 simulations of disturbances impacting different life cycle stages, and enable

99 calculation of the consequent transient responses [19,21]. Bivariate resilience

100 frameworks [10,15,28] decompose resilience into two components, resistance and

101 recovery (Figure 1; Box 1). Here we distinguish resistance into two different processes,

102 **demographic compensation** and **demographic resistance** (Figures 2; see details

103 below). In addition, we provide a distinction between recovery to a particular

104 population size and recovery to a particular structure and growth (Figure 2).

105 *Demographic compensation*

106 Demographic compensation incorporates amplifications in population size after

107 disturbance (Box 2, Figure 2), which compensate for post-disturbance reductions in

108 population size. We advocate the use of *reactivity, maximal amplification* and

109 *amplification inertia* [21] to estimate changes in population size at various times after

110 a disturbance, relative to stable growth (Figure 2). Reactivity quantifies the immediate,

111 short-term response to a disturbance; maximal amplification is the highest density that

112 the population can reach at any time step; and inertia measures the total displacement

113 of the population in the long-term, after the transient period. Reactivity, therefore,

114 quantifies immediate compensation of a population, whereas maximal amplification

115 measures the overall ability of the population to compensate, and inertia quantifies

116 how far away from the stable state the population ends up following disturbance (Box

117 2).

118 Classical views of resilience consider compensation as lack of resistance (e.g.

119 [22]). Nevertheless, given the importance of distinguishing population amplification

120 and attenuation in management, we advocate distinguishing demographic

121 compensation from demographic resistance in resilience studies. Demographic

122 compensation is fundamental for understanding population crashes [21], and

123 compensation metrics are of particular interest for management actions targeting

124 potential invasive species [29]. For instance, for species showing high population

125 increases after disturbance, management interventions can be adapted according to

126 the potential demographic compensation [29,30].

127 *Demographic resistance*

128 Demographic resistance can be estimated using population attenuation bounds,

129 where the lower the bound the less resistant is the population or the species (Figure

130 2). Similarly to population compensation, we suggest using *first-step attenuation,*

131 *minimum attenuation*, and *attenuation inertia* [21] to estimate the potential change in

132 population size and structure after a disturbance (Box 2). The first-step attenuation

133 quantifies the immediate response to a disturbance, whereas the maximal attenuation

134 is the lowest density that the population can reach at any time, and attenuation inertia

135 measures the total displacement in the long term. Consequently, first-step attenuation

136 quantifies the magnitude of population decay or lack of resistance, maximal

137 attenuation measures the overall lack of resistance, and inertia quantifies how far

138 away from the stable state the population ends up.

139   At the community level, most works express resistance as a measure of the loss

140 or gain of species after a disturbance [31–33] or change in community functions [22].

141 Community resistance can be measured as the maximal Euclidean distance between

142 vectors representing a perturbed and an unperturbed community. The higher the

143 Euclidean distance the lower the community resistance, and *vice versa* [11,34], whilst

144 multi-dimensional variables are aspects of the quality and diversity of the community

145 before and after the disturbance [11,34]. Contrastingly, demographic resistance is

146 measured using differences in population size, *i.e.* the sum of the population's size,

147 age or stage vector.

148 *Transient envelope*

149 The combination of population amplification and attenuation can serve as a metric of

150 the overall response of the population to disturbances. Transient bounds, the most

151 extreme increases or decreases of transient population size after a disturbance,

152 together represent the **transient envelope** (Figure 2; [21]). A small transient envelope

153 means that the population is robust against disturbances, while large transient

154 envelopes indicate that the population is more sensitive to changes in its structure

155 [21,35]. As amplification and attenuation are bound asymmetrically ([1, ∞) for

156 amplification; (0, 1) for attenuation [21]), geometric rather than arithmetic comparisons

157 are more relevant. Then, the transient envelope is either the ratio between

158 amplification and attenuation or the difference between log-transformed indices. Note

159 that in Table I we do not include the transient envelope for maximal amplification and

160 attenuation, given that both can happen at different times (Box 3).

161   The transient envelope has a similar interpretation as resistance in community

162 ecology [11,15,22]. Here, we distinguish the transient envelope from the demographic

163 compensation and resistance, because the latter provide different information about

164 the ability of populations to respond to disturbances. While the transient envelope

165 indicates the range of potential population sizes following a disturbance, it does not

166 allow to depict whether this happens through compensation or resistance. Still, we

167 provide the transient envelope given its usefulness in comparative studies [35], and

168 its similarities with community resistance [11,22].

169 *Demographic recovery*

170 Recovery is a critical metric of demographic resilience that explicitly considers time.

171 Similar to resistance, there exist a number of metrics to quantify the time required to

172 reach population stability [21]. For populations, the key question is *time of recovery to*

173 *what?* Stable state, or a desired population size or structure? We propose two

174 measures to describe the time of recovery to population stability after a disturbance:

175 *damping ratio* and *time of convergence* (Box 2). We distinguish between metrics which

176 estimate *time to recover previous population size* and *time to recover previous*

177 *population structure* (Box 2).

178   *Speed of recovery to stable state.* The damping ratio measures how quickly

179 transient dynamics decay following a disturbance, regardless of the population

180   structure [21]. The larger the damping ratio, the faster the population converges, and

181   the higher the speed of recovery. Importantly, the damping ratio is a dimensionless

182   metric [19]. Thus, damping ratio is useful to compare relative time of recovery across

183   populations or species [36]. In contrast, though the time of convergence is similar to

184   the damping ratio, the former is time-stamped, so it can be used both for comparative

185   analyses and to inform managers about the expected post-disturbance recovery times.

186   *Time of recovery to population size and structure.* It is also possible to estimate

187   return time required to recover previous population size and/or the original, stable

188   structure (Figure 2). Because these return times can be measured relative to original

189   structure, they are useful for informing conservation plans or restoration actions.

190   For communities, time of recovery is often defined as engineering resilience

191   [14,37]. Recovery time has been estimated using a wide variety of measurements,

192   sometimes specific to the study system, such as net primary productivity [38] or

193   biomass [39]. The common denominator is that such metrics are compared between

194   the disturbed and undisturbed communities after certain intervals of time. In the case

195   of empirical studies, such intervals are constrained to the length of the study, and so

196   a full recovery is not always observed [38,39]. In contrast, modelling studies can

197   project the community and measure its recovery at long temporal scales [34].

198   **Additions to ecological resilience indicators**

199   Classical theoretical frameworks triggered the development of a myriad of ecological

200   resilience indicators [17,18,40]. These indicators are based on the idea of critical

201   slowing down, whereby a system approaching a tipping point may exhibit decreasing

202   ability to recover its previous state [17,40]. Approach to a critical tipping point can be

203   detected with temporal and spatial statistical signatures, such as increased

204   autocorrelation of, or variance in, abundance [18,40]. Such momenta have been

205   identified in different ecosystems [17,18], potentially facilitating anticipation of critical

206   system transitions [41,42].

207   Detecting approaches to tipping points is debated [14,43], given their limitations

208   related to (*i*) assuming abrupt regime shifts [44], (*ii*) assuming regime shifts exhibit

209   critical slowing down [18,44], and (*iii*) the inability to compare systems with dissimilar

210   properties and/or environments [18,40]. This theoretical framework is further unable

211   to (*iv*) explicitly account for different responses to disturbances for the different species

212   life history strategies [45,46], and (*v*) distinguish population responses prior to collapse

213   [40,47] from responses to disturbance. Such constraints (discussed further in [40,47])

214   have hampered the use of ecological resilience theory [13,14] in applied ecology and

215   conservation.

216   Demographic resilience allows to overcome the main challenges of measuring

217   resilience. Demographic resilience relaxes the assumption of systems experiencing

218   regime shifts and tipping points (limitations *i* and *ii*), because it focuses on the

219   responses of the populations to disturbances [21]. Demographic resilience also allows

220   to compare of the same fundamental processes (survival, development, and

221   reproduction) across different populations and/or species (*iii*) [27] (Box 3). This

222   approach also accounts for the differences in the life histories (*iv*) and estimates the

223   population responses prior to a collapse (*v*) by quantifying their dynamics [36].

224   **Incorporating the different moments of disturbance**

225   Disturbances are key determinants of demographic resilience. Here, we define

226   disturbance as a sudden event, *i.e.* a pulse of mortality caused by a temporary period

227   of environmental stress altering the population (e.g. storm, fire) [48]. However,

228   disturbances can vary in magnitude and duration [48,49]. Our framework only provides

229   analytical solutions to explore the effects of discrete pulse disturbances. Other forms

230   of disturbance force the population towards alternative stable states, but still initiate

231   transient dynamics.

232   **Perturbations**, which are sustained (*i.e.*, long duration), 'press' disturbances

233   over time (e.g. global warming, ocean acidification), are also likely to influence

234   demographic resilience [48]. The adequacy of considering perturbations in a resilience

235   context has been debated [10,50], with some authors considering them to cause a

236   permanent system change, where a return to stability can only be achieved through

237   adaptation [10]. In a demographic resilience context, perturbations alter the **vital rates**

238   of a population, which consequentially alters the population's stable structure.

239   Although the actual population structure remains unchanged, this still creates a

240   discrepancy between the actual population structure and the stable structure.

241   Transient dynamics will also emerge in this case. If the perturbation is removed,

242   incorporating adaptation would be required to understand movement back towards the

243   previous stable state (e.g. [51,52]). However, such adaptive modelling requires

244   understanding the change in the vital rates over time, violating the density-

245   independent and time-invariant environment under which our framework operates.

246   Extinction is also a stable state common to all ecological systems: any perturbation

247   which eliminates reproduction will enforce extinction. This recruitment failure can also

248   be achieved through disturbances (e.g. if a disturbance removed all individuals which

249   reproduce and which have the capacity to grow into reproductive individuals).

250   Disturbances can occur at different magnitude [55], frequencies [49] and also

251   interact with other disturbances or perturbations [50,56]. The proposed framework

252   does not yet allow to analytically anticipate the demographic resilience to different

253   magnitudes, frequencies or their interactions. However, it does allow to quantify the

254   changes in demographic resilience after specific disturbance combination scenarios,

255   using case-specific structural population models [21]. For example, specific

256   disturbance magnitudes or frequencies can be explored by estimating case-specific

257   transient dynamics with specific population structures (simulating a specific magnitude

258   of disturbance, e.g. 20% mortality on adults) [21,57]. In addition, if the effect of a

259   perturbation is known, it will alter the stable demographic structure, and it can be

260   coupled with the impact of a given disturbance scenario. Future explorations of such

261   varied disturbance regimes with simulations or new analytical solutions will be pivotal

262   to understand complex changes of resilience [48,55].

263   **Concluding remarks and future perspectives**

264   Our proposed framework translates resilience approaches [10,15,40,58] to

265   demography, opening the door to multiple research venues (see Outstanding

266   Questions). Because the demography of a species is tightly linked to biological

267   processes taking place at lower and higher levels of organisation, our framework

268   enables exploration of the mechanisms driving resilience. Resilience is an emerging

269   property of complex systems [59], considering that ecological communities are

270   assemblages of populations of interacting species [31], demographic resilience will

271   provide important insights in community resilience. However, such scaling up from

272   populations to communities will require information on how species interact within a

273   community and how the emergent network changes when species are removed

274   [32,34]. The links between demographic resilience and physiological resilience are

275   also likely to provide mechanistic insights on how individual's resilience scales up into

276   populations and communities [60]. Such mechanistic understanding of resilience will

277   also allow the development of evolutionary questions [61,62]. Overall, the proposed

278　framework provides a coherent way of quantifying and comparing resilience across

279　populations and species, opening up new views of resilience that will likely help to

280　develop better conservation and management decisions.

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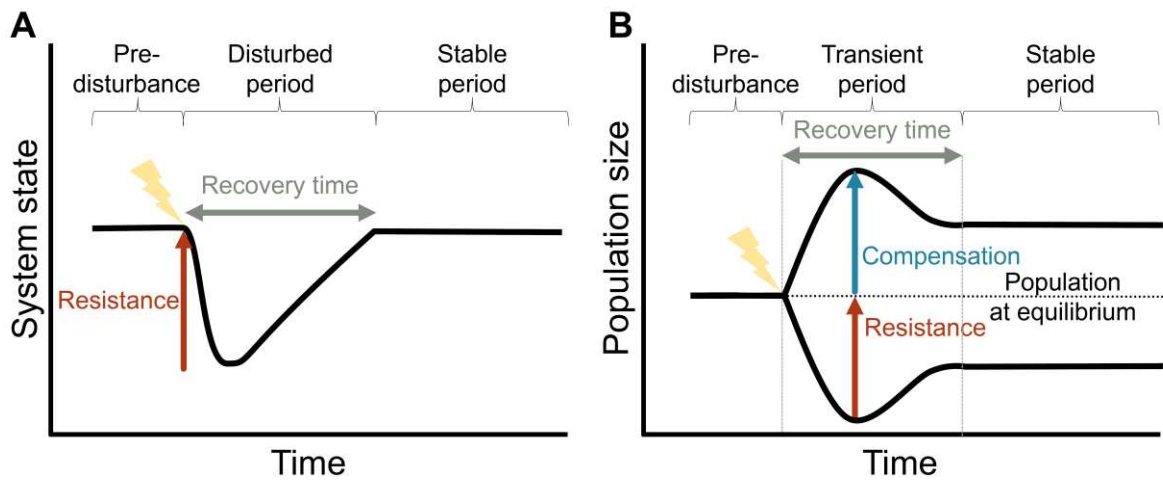401   *disturbance and maintain function*, Island Press.

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437 **Figure 1**

438

439   **Figure 2**

Pre-disturbance   Transient period   Stable period

Damping ratio

Convergence time

Ω_{min} Ω Ω_{max}

$\check{K}_{min}$ ε $\check{K}$ $\check{K}_{max}$

Log(population size)

Upper inertia

Lower inertia

Maximal amplification

Reactivity

Maximal attenuation

First-step attenuation

Time

| SOLID ⎯⎯ | DASH ⎯ ⎯ | DOT ••••• | BLUE ▌Compensation | GREY ⎯⎯ | GOLD ⎯⎯ |
| Outer limits on population size | Example population | Stable population | RED ▌Resistance | Recovery of stable structure and growth | Recovery of specific size or structure |

440

Figure legends

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 impacted, creating a range of possible population sizes, and

defining the resistance of being disturbed. The time needed to settle to one of the

multiple possible stable structures is defined as the recovery time. The population

attenuation after a disturbance is resistance. Note that resistances is the inverse of

the amount of change caused by the disturbance, the more resistance the less

change. In demography (B), there is another possible response to disturbance, which

are increases in population size or compensation.

Figure 2. Resilience framework measurements for populations' responses to

disturbances. Example of a population whose size structure has been disturbed and

its 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 one 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 to the initial stable one is measured as

amplification inertia. *Demographic resistance:* the lack of resistance can be measured

using decreases in population size due to a disturbance. At the first-time step,

466   measured as *first-step attenuation*, the lowest value is the *maximal attenuation*, and

467   the decrease in population size compared to the initial stable one is measured as

468   *attenuation inertia*. *Demographic recovery*: The time required to recover the initial

469   stable population structure has its minimum at $\check{K}_{min}$ and maximum at $\check{K}_{max}$. To measure

470   how much more or less time the system will require to reach the stable structure, we

471   can estimate the difference between $\check{K}_{min}$ and $\check{K}_{max}$ to the structure at the stable

472   population growth ε, to calculate Ω_{min} and Ω_{max}, respectively. It is similar for population

473   size, with $\check{K}$ being the time to reach stability and Ω being the difference with stable

474   growth.

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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 I). However, the rate at which resilience research has increased matches the diversity of definitions and interpretations of resilience. The term resilience was first introduced to 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 sub-disciplines [63]. For example, some authors considered resilience as the speed of recovery of a natural system, quantified as the time required to return to equilibrium [16]. In contrast, other authors have measured resilience as the probability of the system to remain in a stable state [64]. Consequently, later on, Holling [23] 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" [7,23].

By contrast, 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" (*sensu* [10]). Similar to the ecological stability literature, several authors consider resilience a function of resistance and recovery [10,15,65–67]. 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" which the population are displaced from and return to, after disturbance. Such characteristics align demographic resilience to the general bivariate resilience [10,15,65–67] and ecological stability [11,16,22] frameworks, which both have an engineering resilience perspective.
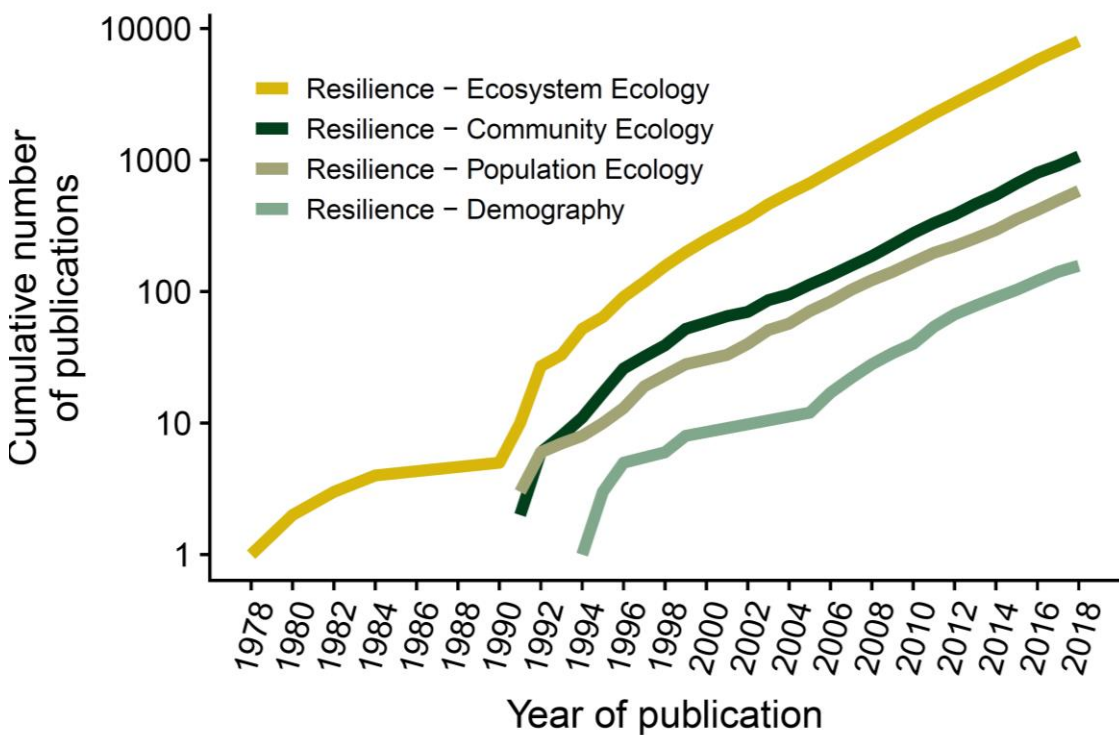

Figure I. The cumulative number of ecological studies in Web of Science concerning resilience has increased exponentially in the last decades, with higher numbers of publications about higher-level ecological systems (ecosystems, communities) than lower-level ones (populations).

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Box 2: Transient calculations

In Table I we present compendium of equations to estimate the abovementioned transient metrics using the most common structural population models utilised 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 [68]) and other approaches [21]. Transient dynamics can be measured estimating the absolute changes in the population size, which combine the transient rates and the asymptotic rate. The asymptotic effects can be discounted by using a standardised matrix population model $\hat{\mathbf{A}}$, by dividing matrix $\mathbf{A}$ by λ_{max}. Also, the population vector $\mathbf{n}$ can also be standardised $\|\hat{\mathbf{n}}\|$ to sum to 1. Such standardisations allow fair comparisons among models [21].

Resilience component	Index	Calculation	Interpretation
Compensation	Reactivity	$\bar{\rho}_1 = \|\hat{\mathbf{A}}\|_1$	The largest population density that can be reached in the first-time step after disturbance.
	Maximal population amplification	$\bar{\rho}_{max} = \max_{t>0}\left(\|\hat{\mathbf{A}}^t\|_1\right)$	The largest population density that can be reached at any time after disturbance.
	Inertia amplification	$\bar{\rho}_\infty = \dfrac{\mathrm{v}_{max}\|\mathrm{w}\|_1}{\mathrm{v}^{\mathrm{T}}\mathrm{w}}$	The largest possible long-term population density.
Resistance	First-step population attenuation	$\underline{\rho}_1 = minCS(\hat{\mathbf{A}})$	The lowest population density that can be reached in the first time step after disturbance.

	Maximal population attenuation	$\underline{\rho}_{min} = \min_{t>0}\left(minCS(\widehat{\mathbf{A}}^t)\right)$	The lowest population density that can be reached at any time after disturbance.
	Long-term population attenuation	$\underline{\rho}_{\infty} = \dfrac{v_{min}\|w\|_1}{v^T w}$	The lowest possible long-term population density.
Transient envelope	Reactivity envelope	$\|\widehat{\mathbf{A}}\|_1 / minCS(\widehat{\mathbf{A}})$	The lower the value, the more the population resists changes in size.
	Inertia envelope	$\dfrac{v_{max}\|w\|_1}{v^T w} / \dfrac{v_{min}\|w\|_1}{v^T w}$	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 (λ_1) to become x times as great as that of the largest subdominant eigenvalue (λ_2). Absolute measure of time of convergence to stable structure. Smaller numbers represent quicker convergence.
	Minimum time to recover initial size	$\Omega_{min} = \varepsilon - \check{K}_{min}$	The lower the value the less time required to recover the initial population structure.
	Maximal time to recover initial size	$\Omega_{max} = \varepsilon - \check{K}_{max}$	The lower the value the less time required to recover the initial population structure.

| | Time to recover initial population size | $\Omega= \varepsilon - \check{K}$ | The lower the value the less time required to recover the initial population size. |

Table I. Calculation of transient dynamics using matrix population models. A is the matrix population model. **Â** is the standardised matrix population model, which is calculated as **A**/λ_{max}**,** where λ_{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 $\hat{\mathbf{n}}_0$ represents the initial demographic distribution, standardised to sum to 1. **minCS** denotes the minimum column sum of a matrix and $\|\mathbf{m}\|_1$ is the one-norm of a vector **m** (equal to the sum of its entries). The values $\mathbf{m_{min}}$ and $\mathbf{m_{max}}$ are the smallest and largest entries of a vector **m** respectively. Transient bounds were represented using $\boldsymbol{\rho}$, as well as the damping ratio following the notation of [19,57]. Transient bounds are distinguished with an overbar (ˉ) or underbar (_) to indicate amplification and attenuation, respectively. Transient metrics' subscripts provide information regarding the timeframe of study, where *1* indicates first-time step indices; *max* or *min,* maximal amplification or attenuation, respectively; and ∞, inertia. $\boldsymbol{\lambda_1}$ is the dominant eigenvalue, $\boldsymbol{\lambda_2}$ is the largest subdominant eigenvalue. $\check{\boldsymbol{K}}$ is the time to reach stability, $\check{\boldsymbol{K}}_{min}$ *and* $\check{\boldsymbol{K}}_{max}$ are the minimum and maximum time required to recover the initial stable population structure, respectively. $\boldsymbol{\varepsilon}$ is size at the stable population growth.

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Box 3: Estimating and comparing demographic resilience

To understand demographic resilience, we showcase two species with contrasting demographic resistance and recovery patterns (Figure II). The Asian elephant (*Elephas maximus*, Figure IIA) experiences a weak attenuation compared to the red squirrel (*Tamiasciurus hudsonicus*, Figure IIB). 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 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 the continuous habitat loss and frequent hunting [69]. 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.
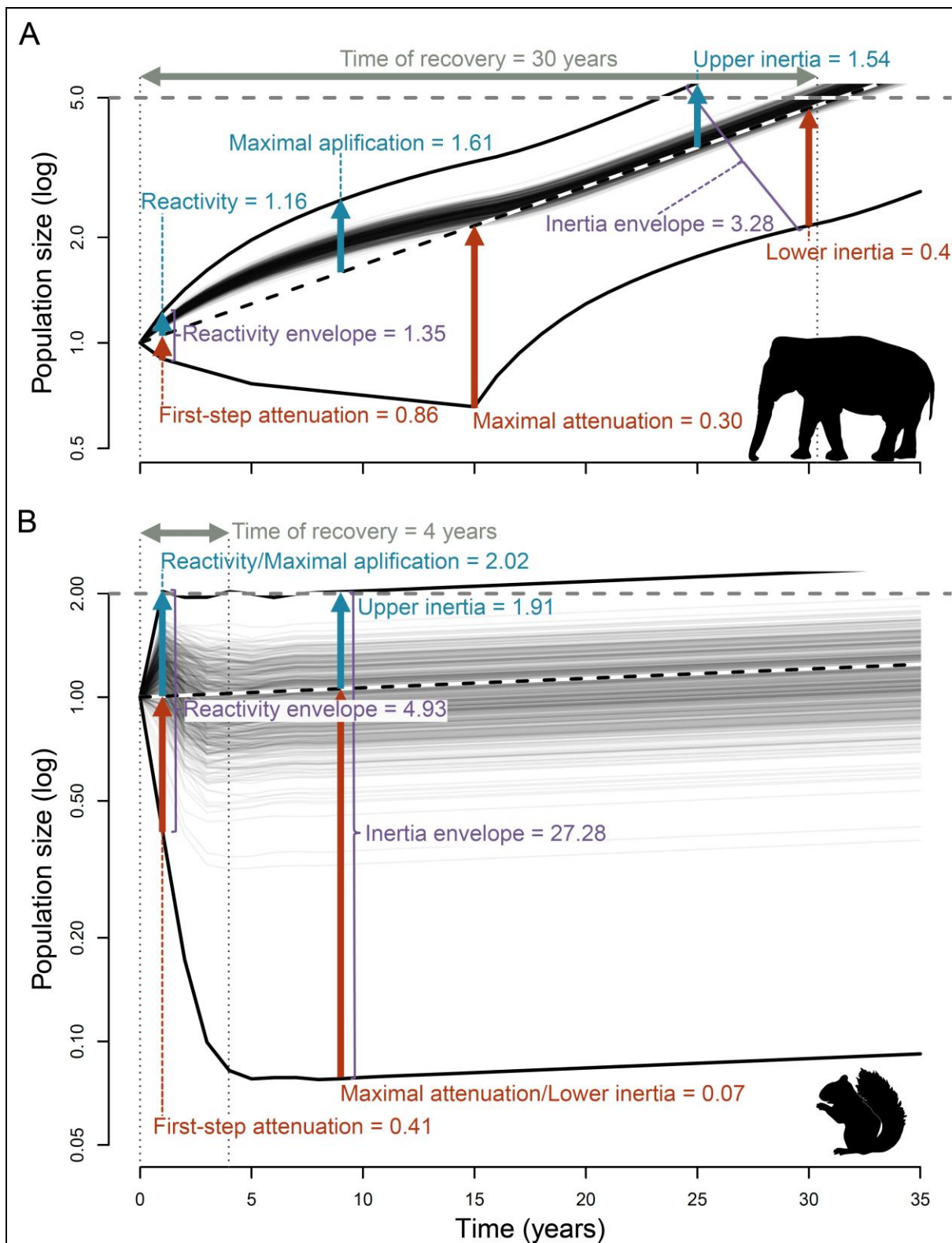
Figure II. Population projections of an Asian elephant (*Elephas maximus*) population (A) and a red squirrel (*Tamiasciurus hudsonicus*) population (B), with their respective demographic resilience metrics. The data was obtained

from the open access database COMADRE [70]. Blue arrows indicate compensation measurements, red arrows resistance metrics, purple brackets transient envelopes and grey arrows recovery time. Bold black lines indicate transient bounds, shaded area indicates the range of values in which all case specific projections lie. Dashed 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.

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Glossary

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

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

Critical slowing down: The phenomenon happening when a system approaches to a tipping point, leading towards slower rates of return to system's previous state.

Demography: Scientific discipline that studies 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 within the different ages, size or stages of a population.

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

Hysteresis: The feedbacks that maintain a system in its current state.

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

Population ecology: Ecological discipline that studies the structure and dynamics of natural populations.

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

Resistance: Extent of change of a system after a disturbance.

Stable demographic structure: The status where 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 equilibrium, regardless of whether the population is growing, stays demographically stable, or declines.

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

Structured population models: The mathematical representations of the life cycle of a species' population, accounting for the different survival, development, and reproduction of the individuals that belong to different ages, sizes, or ontogenetic stages in a population.

Tipping point: The threshold beyond which a system is too unstable that it will be dragged 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.

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