1	Towards a comparative framework of demographic resilience
2	A manuscript under consideration as an Opinion piece in Trends in Ecology and Evolution
3	
4	Authors: Pol Capdevila ^{1,*} , Iain Stott ^{2,3} , Maria Beger ^{4,5} & Roberto Salguero-Gómez ^{1,5,6}
5	¹ Department of Zoology, University of Oxford, 11a Mansfield Rd, Oxford, OX1, 3SZ, UK
6	² Department of Biology, Interdisciplinary Centre on Population Dynamics (CPop), University of
7	Southern Denmark, 5230 Odense M, Denmark
8	³ School of Life Sciences, University of Lincoln, Brayford Pool, Lincoln, LN6 7TS, UK
9	⁴ School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, UK
10	⁵ Centre for Biodiversity and Conservation Science, University of Queensland, St Lucia 4071 QLD,
11	Australia
12	⁶ Evolutionary Demography laboratory, Max Plank Institute for Demographic Research, Konrad Zuße
13	Straße 1, Rostock 18057, Germany
14	*Email: pcapdevila.pc@gmail.com
15	
16	Word count: Abstract (110), Main manuscript (2642), References (70), Figure legend
17	1 (137), Figure legend 2 (246), Box 1 (362), Box 2 (609), Box 3 (321), Glossary
18	(436).

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, Stage32 Structured Population Model.

34 Body

35 **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 describing natural systems' abilities 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.

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].

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 conceptualisations 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 using **transient dynamics**, extensively described in [20,21], one can quantify demographic resilience and anticipate population's and species' responses to disturbances. Thus, our framework marries two disciplines to define and quantify demographic resilience, with elements that draw from and are analogous to community resilience [11,22].

64 From classical 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 [6,20,21,22]. 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 characterised by substantially 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 [19,27], which depend on population structure, are generated by a relative over- or 86 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 simulations of disturbances impacting different life cycle stages, and enable 98 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

Demographic resistance can be estimated using population attenuation bounds, where the lower the bound the less resistant is the population or the species (Figure 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

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, while large transient envelopes indicate that the population is more sensitive to changes in its structure [21,35]. As amplification and attenuation are bound asymmetrically ([1, ∞) 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 I we do not include the transient envelope for maximal amplification and 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 structure [21]. The larger the damping ratio, the faster the population converges, and the higher the speed of recovery. Importantly, the damping ratio is a dimensionless metric [19]. Thus, damping ratio is useful to compare relative time of recovery across populations or species [36]. In contrast, though the time of convergence is similar to the damping ratio, the former is time-stamped, so it can be used both for comparative 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 autocorrelation of, or variance in, abundance [18,40]. Such momenta have been
identified in different ecosystems [17,18], potentially facilitating anticipation of critical
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 (ν) 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

Disturbances are key determinants of demographic resilience. Here, we define disturbance as a sudden event, *i.e.* a pulse of mortality caused by a temporary period of environmental stress altering the population (e.g. storm, fire) [48]. However, disturbances can vary in magnitude and duration [48,49]. 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.

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).

Disturbances can occur at different magnitude [55], frequencies [49] and also interact with other disturbances or perturbations [50,56]. The proposed framework 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 also allow the development of evolutionary questions [61,62]. Overall, the proposed 277

- 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.

281 References

- Pecl, G.T. *et al.* (2017) Biodiversity redistribution under climate change: Impacts
 on ecosystems and human well-being. *Science* 355, eaai9214–eaai9214
- 284 2 Scheffers, B.R. *et al.* (2016) The broad footprint of climate change from genes to 285 biomes to people. *Science* 354, aaf7671
- 286 3 Vitousek, P.M. *et al.* (1997) Human domination of Earth's ecosystems. *Science*287 277, 494–499
- Hughes, T.P. *et al.* (2005) New paradigms for supporting the resilience of marine
 ecosystems. *Trends Ecol. Evol.* 20, 380–386
- 290 5 Parmesan, C. et al. (2011) Overstretching attribution. Nat. Clim. Change 1, 2–4
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate
 change. *Annu. Rev. Ecol. Evol. Syst.* 37, 637–669
- 7 Holling, C.S. (1973) Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23
- 8 Nations, U. (2015) Transforming our world: the 2030 Agenda for Sustainable
 Development,
- 297 9 CBD, Decision X/2, The Strategic Plan for Biodiversity 2011–2020 and the Aichi
 298 Biodiversity Targets, Nagoya, Japan, 18 to 29 October 2010,
- 10 Hodgson, D. *et al.* (2015) What do you mean, "resilient"? *Trends Ecol. Evol.* 30, 503–506
- 301 11 Donohue, I. *et al.* (2013) On the dimensionality of ecological stability. *Ecol. Lett.* 302 16, 421–429
- 303 12 Allen, C.R. et al. (2019) Resilience reconciled. Nat. Sustain. 2, 898–900
- 304 13 Pimm, S.L. *et al.* (2019) Measuring resilience is essential to understand it. *Nat.* 305 Sustain. 2, 895–897
- 306 14 Donohue, I. *et al.* (2016) Navigating the complexity of ecological stability. *Ecol.* 307 *Lett.* 19, 1172–1185
- Ingrisch, J. and Bahn, M. (2018) Towards a comparable quantification of resilience.
 Trends Ecol. Evol. 33, 251–259
- 310 16 Pimm, S.L. (1984) The complexity and stability of ecosystems. *Nature* 307, 321
- 311 17 Scheffer, M. *et al.* (2009) Early-warning signals for critical transitions. *Nature* 461,
 312 53–59
- 313 18 Dakos, V. *et al.* (2014) Resilience indicators: prospects and limitations for early
 314 warnings of regime shifts. *Philos. Trans. R. Soc. B Biol. Sci.* 370, 20130263–
 315 20130263
- 316 19 Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and* 317 *Interpretation*, (2nd edn) Sinauer Associates.
- Neubert, M.G. and Caswell, H. (1997) Alternatives to resilience for measuring the
 responses of ecological systems to perturbations. *Ecology* 78, 653–665

- Stott, I. *et al.* (2011) A framework for studying transient dynamics of population
 projection matrix models. *Ecol. Lett.* 14, 959–970
- 322 22 Hillebrand, H. *et al.* (2018) Decomposing multiple dimensions of stability in global
 323 change experiments. *Ecol. Lett.* 21, 21–30
- 324 23 Holling, C.S. (1996) Engineering resilience versus ecological resilience. *Eng. Ecol.* 325 *Constraints* 31, 32
- 326 24 Folke, C. *et al.* (2004) Regime shifts, resilience, and biodiversity in ecosystem
 327 management. *Annu. Rev. Ecol. Evol. Syst.* 35, 557–581
- Levin, S.A. and Paine, R.T. (1974) Disturbance, patch formation, and community
 structure. *Proc. Natl. Acad. Sci.* 71, 2744–2747
- 26 Enright, N.J. *et al.* (2015) Interval squeeze: altered fire regimes and demographic
 responses interact to threaten woody species persistence as climate changes.
 Front. Ecol. Environ. 13, 265–272
- 333 27 Stearns, S.C. (1992) *The Evolution of Life Histories*, OUP Oxford.
- 334 28 Nimmo, D.G. *et al.* (2015) Vive la résistance: reviving resistance for 21st century
 335 conservation. *Trends Ecol. Evol.* 30, 516–523
- 336 29 Jelbert, K. *et al.* (2019) Demographic amplification is a predictor of invasiveness
 337 among plants. *Nat. Commun.* 10, 1–6
- 338 30 Akçakaya, H.R. *et al.* (2018) Quantifying species recovery and conservation 339 success to develop an IUCN Green List of Species. *Conserv. Biol.* 32, 1128–1138
- 340 31 Solé, R.V. and Montoya, M. (2001) Complexity and fragility in ecological networks.
 341 *Proc. R. Soc. Lond. B Biol. Sci.* 268, 2039–2045
- 342 32 Donohue, I. *et al.* (2017) Loss of predator species, not intermediate consumers,
 343 triggers rapid and dramatic extinction cascades. *Glob. Change Biol.* 23, 2962–
 344 2972
- 345 33 Kordas, R.L. *et al.* (2017) Herbivory enables marine communities to resist
 346 warming. *Sci. Adv.* 3, e1701349
- 34 Yang, Q. *et al.* (2019) The predictability of ecological stability in a noisy world. *Nat.* 348 *Ecol. Evol.* 3, 251–259
- 349 35 Csergő, A.M. *et al.* (2017) Less favourable climates constrain demographic
 350 strategies in plants. *Ecol. Lett.* 20, 969–980
- 36 Salguero-Gómez, R. *et al.* (2016) Fast–slow continuum and reproductive
 strategies structure plant life-history variation worldwide. *Proc. Natl. Acad. Sci.*113, 230–235
- 354 37 Kéfi, S. *et al.* (2019) Advancing our understanding of ecological stability. *Ecol. Lett.* 355 22, 1349–1356
- 38 Hoover, D.L. *et al.* (2014) Resistance and resilience of a grassland ecosystem to
 climate extremes. *Ecology* 95, 2646–2656
- 358 39 de Vries, F.T. *et al.* (2012) Land use alters the resistance and resilience of soil
 a food webs to drought. *Nat. Clim. Change* 2, 276–280
- 360 40 Scheffer, M. *et al.* (2015) Generic indicators of ecological resilience : Inferring the
 361 chance of a critical transition. *Annu. Rev. Ecol. Evol. Syst.* 46, 145–67

- 362 41 Clements, C.F. *et al.* (2019) Early warning signals of recovery in complex systems.
 363 *Nat. Commun.* 10, 1681
- 42 Kéfi, S. *et al.* (2007) Spatial vegetation patterns and imminent desertification in
 Mediterranean arid ecosystems. *Nature* 449, 213–217
- 43 Montoya, J.M. *et al.* (2018) Planetary boundaries for biodiversity: Implausible
 science, pernicious policies. *Trends Ecol. Evol.* 33, 71–73
- 44 Hughes, T.P. *et al.* (2013) Living dangerously on borrowed time during slow,
 unrecognized regime shifts. *Trends Ecol. Evol.* 28, 149–155
- 45 Morris, W.F. *et al.* (2008) Longevity can buffer plant and animal populations
 against changing climatic variability. *Ecology* 89, 19–25
- 46 McDonald, J.L. *et al.* (2017) Divergent demographic strategies of plants in variable
 environments. *Nat. Ecol. Amp Evol.* 1, 0029
- 47 Clements, C.F. and Ozgul, A. (2018) Indicators of transitions in biological systems.
 Ecol. Lett. 21, 905–919
- 48 Jentsch, A. and White, P. (2019) A theory of pulse dynamics and disturbance in
 ecology. *Ecology* 100, e02734
- 49 Ratajczak, Z. *et al.* (2017) The interactive effects of press/pulse intensity and
 duration on regime shifts at multiple scales. *Ecol. Monogr.* 87, 198–218
- 380 50 Ratajczak, Z. *et al.* (2018) Abrupt change in ecological systems: inference and
 381 diagnosis. *Trends Ecol. Evol.* 33, 513–526
- 51 Coulson, T. *et al.* (2011) Modeling effects of environmental change on wolf
 population dynamics, trait evolution, and life history. *Science* 334, 1275–1278
- 52 Ozgul, A. *et al.* (2010) Coupled dynamics of body mass and population growth in
 response to environmental change. *Nature* 466, 482–485
- Sourchamp, F. *et al.* (1999) Inverse density dependence and the Allee effect.
 Trends Ecol. Evol. 14, 405–410
- 54 Field, C.R. *et al.* (2019) Framework for quantifying population responses to
 disturbance reveals that coastal birds are highly resilient to hurricanes. *Ecol. Lett.* 22, 2039–2048
- 391 55 Gladstone-Gallagher, R.V. *et al.* (2019) Linking traits across ecological scales
 392 determines functional resilience. *Trends Ecol. Evol.* 34, 1080–1091
- 393 56 Darling, E.S. and Côté, I.M. (2008) Quantifying the evidence for ecological
 394 synergies. *Ecol. Lett.* 11, 1278–1286
- 395 57 Townley, S. and Hodgson, D.J. (2008) Erratum et addendum: transient
 396 amplification and attenuation in stage-structured population dynamics. *J. Appl.* 397 *Ecol.* 45, 1836–1839
- 398 58 Dakos, V. *et al.* (2012) Methods for detecting early warnings of critical transitions
 399 in time series illustrated using simulated ecological data. *PloS One* 7, e41010
- 400 59 Walker, B. and Salt, D. (2012) *Resilience practice: building capacity to absorb* 401 *disturbance and maintain function*, Island Press.

- 402 60 Felton, A.J. and Smith, M.D. (2017) Integrating plant ecological responses to
 403 climate extremes from individual to ecosystem levels. *Philos. Trans. R. Soc. B Biol.*404 Sci. 372, 20160142
- 405 61 Metcalf, C.J.E. and Pavard, S. (2007) Why evolutionary biologists should be 406 demographers. *Trends Ecol. Evol.* 22, 205–212
- 407 62 Dakos, V. *et al.* (2019) Ecosystem tipping points in an evolving world. *Nat. Ecol.*408 *Evol.* 3, 355–362
- 409 63 Quinlan, A.E. *et al.* (2016) Measuring and assessing resilience: broadening
 410 understanding through multiple disciplinary perspectives. *J. Appl. Ecol.* 53, 677–
 411 687
- 412 64 Mumby, P.J. *et al.* (2007) Thresholds and the resilience of Caribbean coral reefs.
 413 *Nature* 450, 98
- 414 65 Oliver, T.H. *et al.* (2015) Biodiversity and resilience of ecosystem functions. *Trends*415 *Ecol. Evol.* 30, 673–684
- 416 66 Darling, E.S. and Côté, I.M. (2018) Seeking resilience in marine ecosystems.
 417 Science 359, 986–987
- 418 67 Willis, K.J. *et al.* (2018) What makes a terrestrial ecosystem resilient? *Science* 359, 988–989
- 420 68 Ellner, S.P. and Rees, M. (2006) Integral projection models for species with 421 complex Demography. *Am. Nat.* 167, 410–428
- 422 69 Choudhury, A. *et al.* (2008) *Elephas maximus. The IUCN Red List of Threatened*423 *Species*, Report on the Global Conservation Status of the Asian Elephant
- 424 70 Salguero-Gómez, R. *et al.* (2016) COMADRE: a global data base of animal
 425 demography. *J. Anim. Ecol.* 85, 371–384
- 426

428 Acknowledgements

We thank the four anonymous reviewers and Mark Roper, for their valuable comments on the early version of the manuscript. P.C. was supported by a Ramón Areces Foundation Postdoctoral Scholarship. I.S. received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie Award (MSCA) grant agreement WHYAGE No 746235. M.B. was supported by a University Academic Fellowship by the University of Leeds, and EU MSCA DLV-747102. R.S-G was supported by a NERC R/142195-11-1.

Figure 1 437



439 Figure 2



441 Figure legends

Figure 1. Comparison between disturbance responses and the main 442 443 components of resilience in communities (A) and populations (B). When 444 translating the population responses to disturbances from classical resilience 445 frameworks, the system state is defined as the population size and the population 446 structure (y axis). After a disturbance, the size of the population changes differently 447 according to the stages impacted, creating a range of possible population sizes, and 448 defining the resistance of being disturbed. The time needed to settle to one of the 449 multiple possible stable structures is defined as the recovery time. The population 450 attenuation after a disturbance is resistance. Note that resistances is the inverse of 451 the amount of change caused by the disturbance, the more resistance the less 452 change. In demography (B), there is another possible response to disturbance, which 453 are increases in population size or compensation.

454 Figure 2. Resilience framework measurements for populations' responses to 455 disturbances. Example of a population whose size structure has been disturbed and 456 its consequent changes in population size. Before the disturbance, the population is 457 increasing with a stable growth rate (but could also be decreasing or remain stable). 458 The disturbance creates a discrepancy between the actual population size/structure 459 and the one that would exist given stable growth, resulting in transient dynamics. 460 Demographic compensation: increases in population size immediately after 461 disturbance are measured as *reactivity*, the highest increase during the transient 462 period is measured as maximal amplification. Once at demographic stability, the 463 population size/structure increase compared to the initial stable one is measured as 464 amplification inertia. Demographic resistance: the lack of resistance can be measured 465 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 attenuation inertia. Demographic recovery: The time required to recover the initial 468 stable population structure has its minimum at \check{K}_{min} and maximum at \check{K}_{max} . To measure 469 470 how much more or less time the system will require to reach the stable structure, we can estimate the difference between \check{K}_{min} and \check{K}_{max} to the structure at the stable 471 472 population growth $\boldsymbol{\varepsilon}$, to calculate Ω_{min} and Ω_{max} , respectively. It is similar for population size, with \check{K} being the time to reach stability and Ω being the difference with stable 473 474 growth.

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.



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
	Reactivity	$\bar{\rho}_1 = \left\ \widehat{\mathbf{A}} \right\ _1$	The largest population density that can be reached in the first-time step after disturbance.
Compensation	Maximal population amplification	$\bar{\rho}_{max} = \max_{t>0} \left(\left\ \widehat{\mathbf{A}}^t \right\ _1 \right)$	The largest population density that can be reached at any time after disturbance.
	Inertia amplification	$\bar{\rho}_{\infty} = \frac{\mathbf{v}_{max} \ \mathbf{w}\ _1}{\mathbf{v}^{\mathrm{T}} \mathbf{w}}$	The largest possible long-term population density.
Resistance	First-step population attenuation	$\underline{\rho}_1 = minCS(\widehat{\mathbf{A}})$	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	$\underline{\rho}_{\infty} = \frac{\mathbf{v}_{min} \ \mathbf{w}\ _1}{\mathbf{v}^{\mathrm{T}} \mathbf{w}}$	The lowest possible long-term population density.
	Reactivity envelope	$\left\ \widehat{\mathbf{A}}\right\ _{1}/\min CS(\widehat{\mathbf{A}})$	The lower the value, the more the population resists changes in size.
Transient envelope	Inertia envelope	$\frac{\mathbf{v}_{max} \ \mathbf{w}\ _1}{\mathbf{v}^{\mathrm{T}} \mathbf{w}} / \frac{\mathbf{v}_{min} \ \mathbf{w}\ _1}{\mathbf{v}^{\mathrm{T}} \mathbf{w}}$	The higher the value, the greater the displacement of the population from its stability in the long term after disturbance.
	Damping ratio	$\rho = \lambda_1 / \ \lambda_2\ $	Dimensionless measure of convergence to stable growth. Smaller numbers represent slower convergence.
Time of recovery	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	Ω _{min} =ε-Ř _{min}	The lower the value the less time required to recover the initial population structure.
	Maximal time to recover initial size	Ω _{max} = ε - Κ _{max}	The lower the value the less time required to recover the initial population structure.

	Time to recover initial population size	Ω= ε - Κ̈́	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 \mathbf{A}/λ_{max} , where λ_{max} is the dominant eigenvalue of \mathbf{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 m _{min} and m _{max} are the smallest and largest entries of a vector m respectively. Transient bounds					
were represented using $m ho$, as well as the damping ratio following the notation of [19,57]. Transient bounds are distinguished with an overbar					
() 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. λ_1					
is the dominant eigenvalue, λ_2 is the largest subdominant eigenvalue. \check{K} is the time to reach stability, \check{K}_{min} and \check{K}_{max} are the minimum and					
maximum time required to recover the initial stable population structure, respectively. $m{\epsilon}$ is size at the stable population growth.					

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.

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.

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.