

Rare events, ecological dynamics, and the importance of long-term demographic studies

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Abstract

While multiple reasons make long-term demographic studies disproportionately valuable, much of their importance comes from the ability to detect and quantify rare events. We argue here that rare events can be critical for understanding important ecological and evolutionary processes. We highlight the additive or interactive nature of anthropogenic rare events with environmental rare events that may cause outsized changes in vital rates and therefore in population dynamics. Rare events may also generate complex responses in populations due to interactions between demographic processes and evolutionary responses. Complex, non-linear dynamics of populations may include threshold, extreme responses such as long transients, tipping points, regime shifts and collapse. When occurring locally, rare events may also exacerbate spatial heterogeneity with consequences for demographic processes. In sum, these effects represent substantial challenges for prediction, especially when considering the increase in the frequency of rare extreme events, and emphasise the need for long-term studies. Our perspective attempts to integrate the occurrence of rare events in variable environments and the consequences for the overall fitness, growth rates, and the spatial-temporal dynamics of populations.

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Abstract

While multiple reasons make long-term demographic studies disproportionately valuable, much of their importance comes from the ability to detect and quantify rare events. We argue here that rare events can be critical for understanding important ecological and evolutionary processes. We highlight the additive or interactive nature of anthropogenic rare events with environmental rare events that may cause outsized changes in vital rates and therefore in population dynamics. Rare events may also generate complex responses in populations due to interactions between demographic processes and evolutionary responses. Complex, non-linear dynamics of populations may include threshold, extreme responses such as long transients, tipping points, regime shifts and collapse. When occurring locally, rare events may also exacerbate spatial heterogeneity with consequences for demographic processes. In sum, these effects represent substantial challenges for prediction, especially when considering the increase in the frequency of rare extreme events, and emphasise the need for long-term studies. Our perspective attempts to integrate the occurrence of rare events in variable environments and the consequences for the overall fitness, growth rates, and the spatial-temporal dynamics of populations.

KEYWORDS: rare events, demography, vital rates, resilience, threshold, tipping point, life histories, long- and short-term impacts

INTRODUCTION

Understanding the intricacies of ecological and evolutionary processes necessitates a comprehensive grasp of the processes that shape population dynamics. While ecological

research has benefited from a diverse array of study approaches, long-term demographic studies stand out for their unparalleled ability to uncover and quantify rare events that can be pivotal in driving ecological dynamics (Gutschick & BassiriRad 2003; Neubert & Caswell 1997; Paine *et al.* 1998; van de Pol *et al.* 2017).

Rare events, ranging from hurricanes and wildfires to disease outbreaks and masting events, to droughts and floods, can result in abrupt and profound changes not only in populations, but also in entire ecosystems, including altered species compositions, disrupted food webs, and modified habitat structures (Buckley & Huey 2016; Hoffmann & Parsons 1997; Murali *et al.* 2023; Smith *et al.* 2024). Additionally, rare events may contribute to the creation of novel habitats, providing opportunities for species to colonise and establish in previously unoccupied areas (Thornton 2007). Together with physical drivers, biotic rare events such as disease outbreaks are examples of rare events not necessarily linked to environmental extremes, although sometimes triggered by density-dependent processes (Reed *et al.* 2003; Young 1994). Some anthropic activities may also be considered rare events, not only those with negative effects on ecosystem functioning (e.g. introduction of an invasive species) but also with beneficial consequences (e.g. abrupt cessation of a long-term anthropogenic impact). Rare events from anthropic activities can be deterministic or stochastic (e.g., onset of armed conflicts) but are likely to be additive or synergistic to impacts of environmental stochasticity.

Historically, one of the most discussed questions in population and community ecology is how populations fluctuate and whether they are regulated to attain an equilibrium (Murdoch 1994). Rare events, such as disease outbreaks or episodic resource availability, can profoundly impact the sizes and dynamics of populations and entire metapopulations. Additionally, they

can shape ecosystem functions like nutrient cycling and energy flow, influencing the stability and resilience of ecosystems. Notably, certain rare events possess the capacity to induce delayed and non-linear transient dynamics, or even propel populations over critical tipping points (Hastings *et al.* 2018; van Nes & Scheffer 2007). A comprehensive understanding of these effects is pivotal in unravelling the consequences of ongoing global change, thereby providing the scientific foundation needed for adaptive management strategies (Shenton *et al.* 2012). In particular, while ecologists often speak of rare events as a discrete and separate category of effects, in fact there is a gradient of frequencies and severities of effects that require long-term data to correctly estimate and thus incorporate into population predictions.

In particular, long-term demographic studies allow quantification of the effects of rare events on vital rates, and to identify the demographic mechanisms driving population dynamics and the potential occurrence of extreme responses to rare events (Clutton-Brock & Sheldon 2010; Solow 2017; Yoccoz *et al.* 2001)(Fig. 1). While long-term monitoring of population densities allows us to estimate the net effects of rare events (Butchart *et al.* 2010; Magurran *et al.* 2010), such studies don't uncover the demographic alterations that shape these population responses. For instance, extreme drops in population densities might be caused by die-offs resulting from rare events (e.g. Young 1994), but could also result from migration to other patches (Oro 2020; Youngflesh & Lynch 2017). A further interest in long-term demographic studies and the interpretation of complex ecological dynamics relies on the potential for delayed, not immediate, demographic responses after extreme events. Furthermore, the consideration of large spatial scales in long-term demographic studies is of great interest to assess the effects of rare events on dispersal and the potential extreme effects for dynamics of

metapopulations and spatially-structured populations (e.g. Alexander *et al.* 2012; Fernández-Chacón *et al.* 2013; Smith-James *et al.* 1996).

Since demographic rates may experience sharp fluctuations in the aftermath of rare events (Fig. 2), several questions of ecological and evolutionary interest may arise. Can we discern age- or sex-specific changes in survival, fertility, or dispersal rates following these events? How does the life history of a species influence its demographic responses and their temporal lags? Does the state of the population (i.e. increasing or declining) influence the magnitude of the demographic responses? Understanding these demographic responses is crucial for accurately predicting population dynamics and assessing the resilience of populations to future rare events. We aim here first to define what a rare event is in the ecological domain. Second, we summarise how to quantify an extreme, rare event. Third, we aim to unravel the demographic relevance of rare events in stochastic environments, to shed light on their overarching impact on fitness, growth rates, life-history strategies and the spatiotemporal dynamics of populations (Clutton-Brock & Sheldon 2010). Finally, we assess the importance of long-term demographic studies in unravelling ecological processes and patterns, and also understanding evolutionary life history patterns.

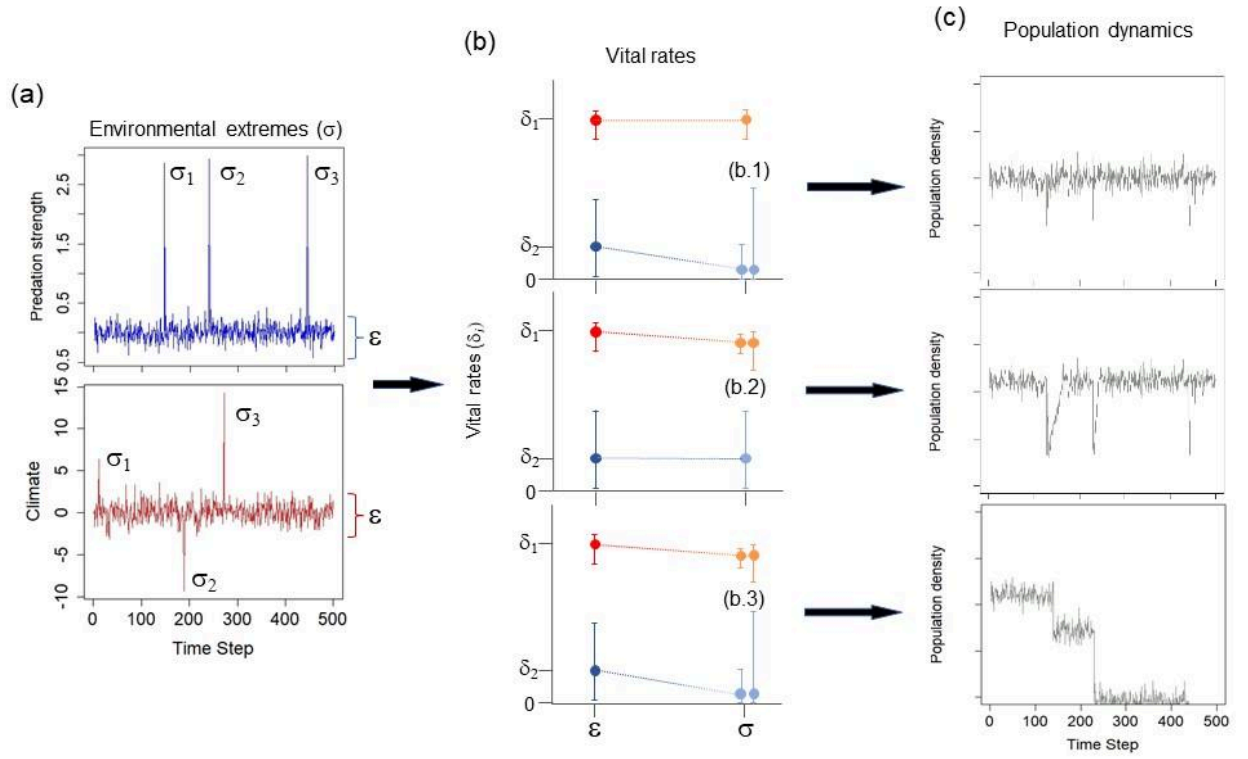


Figure 1. Conceptual representation of the value of long-term monitoring for understanding the impact of extreme events and the consequences for population dynamics. For environmental extreme events (a), we show two possible dynamics: the upper panel shows the punctuated arrival of a non-local predator (σ), whereas ϵ represents the stochastic predation rate by a local predator; the lower panel shows a climatic variable with extremes (σ) that can be above or below the normal stochastic variability ϵ . For vital rates (b), we represent two rates

with differential sensitivity ($\bar{\delta}$): $\bar{\delta}_1$ and $\bar{\delta}_2$ are vital rates with high and low demographic

sensitivity, respectively. We represent the cases in which the extreme event affects the vital rate with low sensitivity (b.1), high sensitivity (b.2) or both vital rates (b.3). Note that when the parameter decreases after an extreme event occurs, there can be either an increase or a decrease in the variability of the vital rate within the population, depending on the evolutionary forces of selection. In (c), we represent some potential outputs of population dynamics (represented here by the density of adults over time simulated with stochastic time series) depending on the vital rate affected. We assume that population dynamics, in the absence of extreme events, are stationary.

RARE EVENTS

By definition, rare events are extreme values in the distribution of environmental states that tend to be separated in time (Box 1). The identification of extreme values and their potential effects are sensitive to the temporal scale (from several hours to centuries) and the sample units (from hours to days) considered (Felton & Smith 2017). In most ecological studies the relevant timescales span years to decades, and generally rare events are considered pulsed perturbations rather than press perturbations (Bender *et al.* 1984). However, in certain ecological contexts, a rare press event may trigger an unusual long-term or permanent regime change. For instance, the arrival of a single predator to a longtime predator-free small island (that can be considered a rare event) triggers a rare perturbation regime that would last the time the predator stays on the

island (Oro *et al.* 2018, 2023a; Payo-Payo *et al.* 2018).

Rare events are commonly described by power laws, or heavy-tailed distributions, which means that the magnitude of rare events is inversely associated with their frequency following those heavy-tailed distributions (Anderson *et al.* 2017; Ghil *et al.* 2011; Malamud *et al.* 1998)(Fig. 2b).

BOX 1: Rare events: definition and terminology

Rare events are episodes occurring with extremely low probability over time frames relevant to the life history of the species. A potential temporal window to use relative to the slow-fast continuum of organisms is the mean generation time, which is the average time it takes for one generation of individuals within a population to be replaced by the next generation. For most reproductive strategies, the mean generation time can be approximated as the average age of reproductive females in a population. Thus, the temporal scale at which to explore environmental stochasticity is different for a short-lived species (scales of hours, days or weeks) than for a long-lived species (scales of years, decades or centuries). By definition, a rare event is an extreme value in a distribution of temporal stochasticity. Human activities may add some deterministic factors to that stochasticity, such as the building of a dam or the introduction of a species for biological control. At the spatial scale, a rare event may affect very different spatial scales, from very local (e.g. at the scale of a few metres) to global (e.g. planetary scale).

There is a lack of consensus regarding the definition and characteristics of extreme events across various fields, hindering our comprehensive understanding and effective management of these occurrences (McPhillips *et al.* 2018). In the ecological literature, rare events are often used rather loosely and explicitly with terms such as disturbances, perturbations and catastrophes

(Rykiel Jr 1985). Factors contributing to this loose usage include the subjective nature of event severity, ecological contextual differences, and evolving perspectives within the scientific community. We define here some terms that may be included in the definition of a rare event. Nevertheless, we acknowledge the nuanced differences, the common negative connotation of all of them (although some authors have noted the potential for a rare event to be positive and beneficial)(e.g. Harrison 1979; Higgins *et al.* 2000) and the loose employment of these terms.

Disturbances: events that cause a temporary change in environmental conditions, often leading to alterations in ecosystem structure and function (Battisti *et al.* 2016; Newman 2019). These events can vary in intensity and frequency, ranging from relatively mild, routine disturbances like seasonal fluctuations to more severe events such as wildfires, storms, or human-induced activities, which could be rather defined as perturbations. Disturbances are inherent components of ecosystems, playing a crucial role in shaping ecological dynamics (Margalef 1963). As such, disturbances may be common and should not be used when studying rare events and ecological dynamics.

Perturbations: sudden or abrupt changes in the environment that can alter ecological dynamics and processes. While similar to disturbances, perturbations are characterised by their rapid onset and potential to induce significant and lasting effects (Holling 1973). Anthropogenic impacts, invasions, and climate extremes (e.g. hurricanes, La Niña) can all be sources of perturbations. Perturbations are sometimes termed *environmental stress* (Bijlsma & Loeschcke 1997; Harrison 1979) and *threshold events* (Willis & Bhagwat 2010). The term "perturbation" is often used when emphasising the sudden nature of the event and its potential to disrupt ecological both processes and dynamics (Oro 2020). Perturbations would apply to

extreme values (often termed *anomalies*) of climate global indexes based on physical oceanographic parameters changing over time (e.g. Southern Oscillation Index SOI, North Atlantic Oscillation Index NAO).

Catastrophes: the term is used to represent the most severe and impactful events that can lead to widespread and often irreversible changes in ecosystems. These events may result from natural negative extremes, anthropogenic activities, or a combination of both. The term "catastrophe" is often reserved for events with profound, long-lasting consequences, emphasising the severity of the disruption caused. In some contexts (ecological, but also social and financial), catastrophes are labelled as black-swan events, which are stated to have profound consequences for the dynamics of the system (Anderson *et al.* 2017; Nuñez & Logares 2012). We note that the term catastrophes was used by René Thom in his Catastrophe Theory to describe sudden and often discontinuous changes in dynamical systems. The link lies in the consideration of sudden and nonlinear transitions in both Catastrophe Theory and ecological studies of rare events. However, Catastrophe Theory applied to ecological theory states that small changes in environmental conditions, i.e. not rare events, can trigger large and discontinuous changes in ecological systems.

Among the wide variety of rare events (both stochastic and deterministic, see Table S1) influencing the dynamics of ecosystems and their components, climate extremes have certainly been the most studied (Harris *et al.* 2018; Maxwell *et al.* 2019; Smith 2011; Ummenhofer & Meehl 2017). Those studies have commonly adopted the criterion used by climatologists, i.e. a threshold of $\leq 5\%$ of cases for the whole study of climate data distribution (e.g. Bailey & Van

De Pol 2016). Others have suggested using an ecological criterion based on extreme ecological consequences (e.g. a drastic drop in fertility following a sudden increase in temperature)(Gutschick & BassiriRad 2003; Smith 2011) but this criterion is less well-developed and assumes that a rare environmental event always generates a rare or extreme ecological response. Instead, we argue that these two aspects of rare events be treated separately. Rare environmental events may or may not cause extreme demographic or ecological impacts, and some rare demographic events may also occur without an extreme environmental trigger (e.g. masting events).

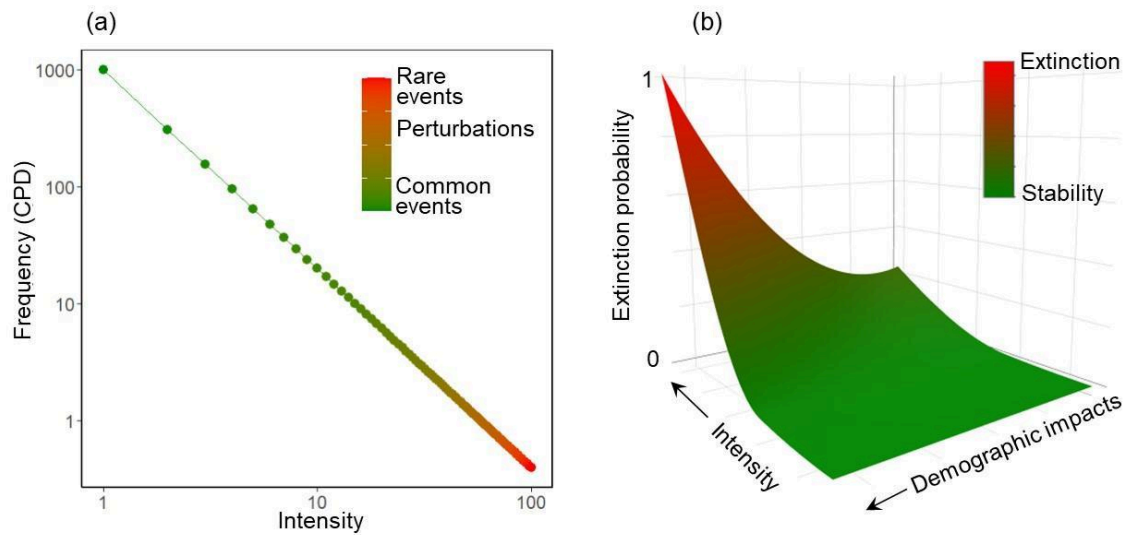


Figure 2. (a) Power law illustrating the intensity of a perturbation (e.g. a wildfire, volcano eruption) and its frequency (as cumulative probability density CPD), as it is usually represented

in the log-log scale. (b) Illustration of potential extreme effects from rare events: the plot shows how extinction probability increases non-linearly with the intensity of the perturbation and the demographic impacts (both vital rates and the number of individuals affected), which depends also on the buffering and lability of the population.

DEMOGRAPHIC IMPACTS OF RARE EVENTS

Rare events may trigger demographic alterations and shape population dynamics (Fig. 1). The potential extreme effects on the population will depend on the intensity of a perturbation (e.g. a wildfire, volcano eruption) and the demographic impact (Fig.2b). The demographic impact will be stronger or weaker depending on a) the magnitude of the change on the vital rate, i.e. the decrease or increase on the vital rate b) the vital rate affected, being more pronounced the impact when population growth is most sensitive to changes on that vital rate c) the number of vital rates affected d) the portion of the population affected (Fig. 3).

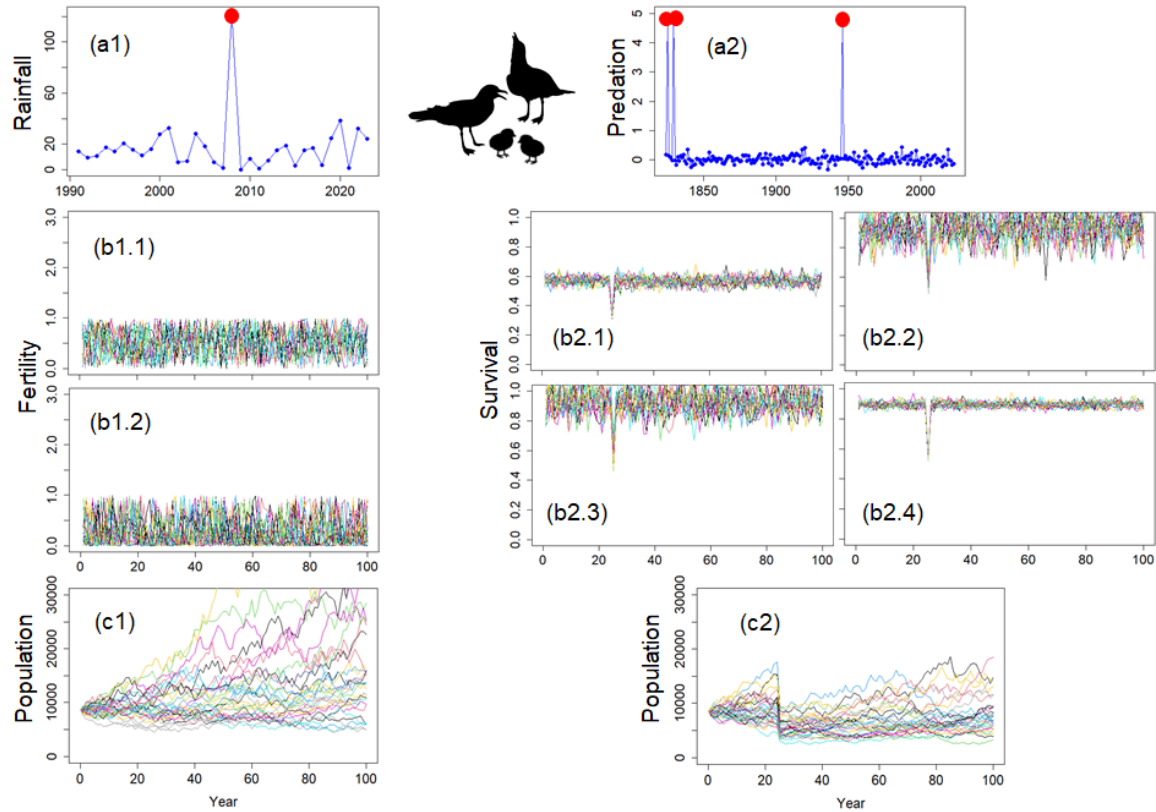


Figure 3. Simulations of population dynamics of a long-lived species under the influence of rare events that caused a drop of 40% on fertility or survival in a population at equilibrium. We observe here that, as expected in a long-lived species, population dynamics are more sensitive to changes in adult survival than in fertility. Additionally it seems that one puntual extreme rare event affecting the most sensitive parameter may not necessarily cause a population collapse (but see below the section “Nonlinear responses”). (a) We consider two environmental extreme events: rainfall and predatory events (a1 and a2 respectively, shown by red dots over time). We simulate the rare event at time step 25. (b) effects of rainfall on fertility (as number of female chicks per breeding female) in first time breeders and on consequent occasions (b1 and b2 respectively) and of predation on survival (b2). Survival is age-dependent: juvenile (b2.1),

immature (b2.2), sub-adult (b2.3) and adult (b2.4). (c) Projections of population dynamics after the rare events. We used estimates of vital rates (survival, recruitment and fertility) published in the literature for a long-lived bet hedger, the Audouin's gull (Genovart *et al.* 2017). We formulated a seven stage-class matrix population model with age-dependent survival rates. We set three years as the age at first breeding, with lower breeding success than older breeders, and also that full recruitment occurred at 6 years old. Our stochastic projections included parameter uncertainty in almost all demographic parameters except in a few cases when uncertainty was unknown (Bakker *et al.* 2009) and the covariance between juvenile and adult survivals (Morris & Doak, 2002).

The scientific literature has identified and studied the occurrence of rare events, their impacts on vital rates and their demographic and ecological consequences, with some instances in which how the populations behaved after the events were analysed (Table S1). Many other ecological studies have lacked clear quantification of either the frequency or impacts of rare events, but nonetheless have sought to estimate their impacts on extinction risk or population growth. Most valuable are detailed case studies which offer unique opportunities to explore a range of ecological dynamics caused by rare events that are well understood due to long-term monitoring.

A long-term demographic study case: the Audouin's gull

Since most Audouin's gulls breed on the edge of the western Mediterranean (ca. 90% of the total world population), a long-term monitoring of the species was initiated in Spain in the early

80s. At that time, the species was an endemic species of the Mediterranean and the most endangered gull species in the world. Over more than 5 decades and ca. in 80 patches, the monitoring has included the record of environmental rare events, anthropogenic impacts, population density, colonisation-extinction turnover and demographic vital rates. Records of this monitoring are the counts of ca. 167000 nests, ca. 55 extinction events, 49 colonisation events and 35 re-colonization events, >73000 ringed chicks and >94000 resights of marked individuals performed at the main breeding patches (Fernández-Chacón *et al.* 2013). Several rare events have occurred over the study: one deterministic, i.e. the legal and effective protection of many coastal areas in Spain in the mid-80s and several stochastic, i.e. some climate extremes and the arrival of invasive predators in the late 90s to the patch holding up to 73% of the total world population (the Ebro Delta)(Oro 2020) .

The protection of saltmarshes triggered the colonisation of the Ebro Delta, and the monitoring of vital rates (survival, fertility, recruitment and dispersal) at the metapopulation level allowed us to assess the importance of immigration to explain the dramatic growth rate experienced here (growth rate geometric mean during 1981-1997 = 1.436) before the arrival of predators (Oro & Ruxton 2001). The field monitoring allowed us to identify the importance of the phenology of extreme climate events and their consequences (Fig. 4). Different extreme values of rainfall were detected depending on the temporal scale studied: only when the extreme rainfall was considered when it coincided with the most sensitive phase of the breeding cycle, we observe the association between the extreme rainfall and breeding failure (Fig. 4d and e). That failure, together with fluctuations of fertility occurring at the Ebro Delta, which was the main demographic source and the largest world population, affected metapopulation

dynamics (Genovart *et al.* 2018).

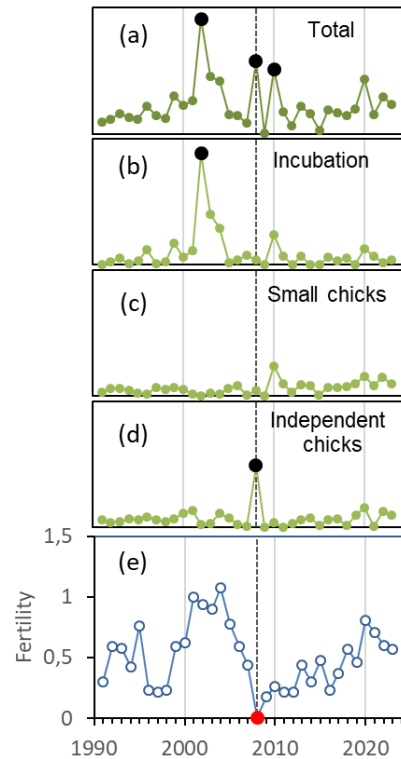


Figure 4. Long-term monitoring fertility (as mean values of fledgling produced annually per breeding female) at the Ebro Delta (lower panel e). There was only a total breeding failure over the 33 years of study (red dot, 2008), when a heavy rainfall lasting two days killed ca. 25000 chicks by hypothermia. Panel a shows the total rainfall over the breeding season of the gulls for each spring, with black dots showing statistically extreme values. While an extremely wet spring occurred in 2008, similar years (even with higher values) did not cause the same demographic response. The reason was the phenology of heavy rain extremes: when they occurred out of the phase when chicks were small and became unattended by adults (panels b and c), adults were able to protect eggs and hatching chicks from thermal stress.

The rare event of predator invasion offered us an opportunity to explore the demographic responses for vital rates and the consequences for population and metapopulation dynamics (Oro 2020; Oro *et al.* 2023a). We did not observe a bust of fertility or survival because breeders responded behaviourally by selecting more protected breeding habitats (Payo-Payo *et al.* 2018). The small decrease in those parameters was compensated by an increase in recruitment (Genovart *et al.* 2018). Nevertheless, the main change occurred for a boom in dispersal, and the Ebro Delta collapsed by runaway emigration to other patches (Oro *et al.* 2023a; Payo-Payo *et al.* 2018). Furthermore, there were changes in the age-structure of the different patches demographically connected with the Ebro Delta by dispersal processes, since dispersal was differential for age-classes. While experienced birds colonised new patches, younger breeders preferentially dispersed to occupied patches (Oro *et al.* 1999; Payo-Payo *et al.* 2017, 2018). There was a sharp increase in colonisation rates within the metapopulation and in cultural innovations for breeding patch selection, including the colonisation of Atlantic patches. Importantly, demographic responses in vital rates and metapopulation dynamics occurred non-linearly, mainly by transient phenomena and tipping points (Oro 2020; Oro *et al.* 2023a)(Fig. 5).

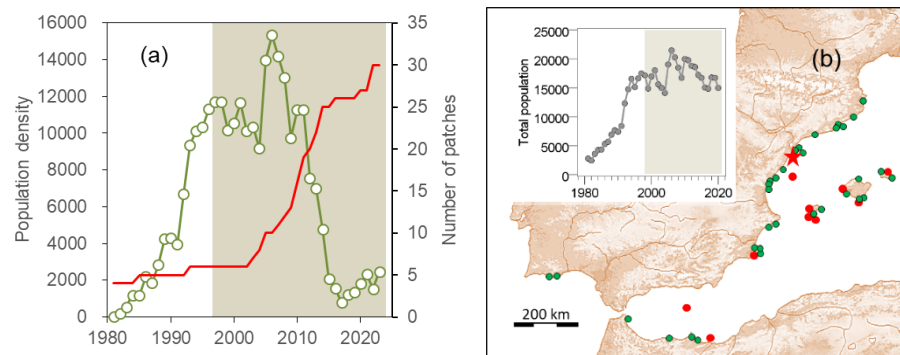


Figure 5. Panel (a) shows the fluctuations in population density at the Ebro Delta from colonisation (1981) to 2023. The coloured background shows the period that started with the rare event of predator invasion: the phase of collapse started in 2006, several years later (see details in Oro *et al.* 2023a). The red line shows the accumulated number of colonised patches in the metapopulation over time. The colonisation process also accelerated several years later coinciding with the start of the collapse phase. Panel (b) shows the location of the Ebro Delta (red star), other occupied patches when predator invasion occurred (red dots) and the colonised patches (green dots). The inner panel shows the population density for the whole metapopulation, which has not decreased since the rare event at the Ebro Delta.

Dispersal and colonisation at large spatial scales allowed the metapopulation level to be relatively stable, regulated mainly by density-dependent processes (Genovart *et al.* 2018)(Fig. 5b). Finally, demographic monitoring for the whole seabird community at the Ebro Delta showed that the rare event of predator invasion caused community reorganisations and global decays in population synchrony, which disrupted the pattern of interspecific interactions (Almaraz & Oro 2011).

Long-term monitoring of rare events and their demographic consequences

Long-term studies offer a unique opportunity for discerning the influence of rare events, whose infrequency often belies their potential to shape ecological processes and dynamics (Lindenmayer *et al.* 2012). As long as the monitoring is consistent over time, there is an increased chance to observe a rare event, dissect its dynamics (e.g. pulse perturbations or press

perturbations) and document population responses (Ariño & Pimm 1995).

Owing that ecosystems and their components have the features of complex systems, long-term field monitoring of demographic processes and environmental variability is fundamental for studying ecological dynamics, such as the interaction between physical and biological variables (Blossey 1999; Cerini *et al.* 2023; Gitzen *et al.* 2012; Lindenmayer *et al.* 2012; Willig & Walker 2016). The importance of such monitoring at large spatial-temporal scales increases when we consider rare events because it is out of equilibrium when we observe the range of organisms' responses and their limits.

In general, climate extremes have been the most often monitored variable because of their physical nature and the relative easiness of monitoring long-term climate data, as well as the ability to reconstruct climate extremes at geologic time scales (paleoclimate) (Easterling *et al.* 2000). This far greater ability to characterise the occurrence and magnitude of rare events at proper spatial-temporal scales (Felton & Smith 2017). Other physical phenomena, such as earthquakes, volcanic eruptions, tropical hurricanes, wildfires, dust storms and landslides can also, in at least some cases, be traced back in time to have a more reliable estimation of their occurrence and magnitude. Together with physical variables, which are nowadays recorded automatically, technology allows researchers to have long-term monitoring of other variables with ecological consequences (e.g. biogeochemical and hydrological dynamics and extremes in aquatic ecosystems)(Bernal *et al.* 2013). Unlike automated monitoring of physical-chemical variables, obtaining long-term ecological demographic data is inherently more challenging, despite the general agreement of the necessity to gather these data for a better understanding of crucial ecological dynamics (Morris *et al.* 2020; Turner *et al.* 2003). Besides, analysing ecological

time-series data is fraught with challenges arising from the difficulty of long-term monitoring (Gitzen *et al.* 2012; Williams *et al.* 2002). As previously stated, long-term demographic studies are pivotal if we are to identify the demographic mechanisms driving population dynamics and the potential occurrence of extreme responses to rare events (Clutton-Brock & Sheldon 2010; Solow 2017; Yoccoz *et al.* 2001)(Figs. 1 and 2). Long-term demographic studies involving individual monitoring are more common for some taxa due to e.g. ease of monitoring, the attractiveness of the organism or biological group, chances for large sample sizes, long history of monitoring, endangered species, and economic importance of harvested flagship species. Birds (and particularly seabirds), salmon, ungulates, marine mammals breeding at land, and some small rodents are over-represented (e.g. Gamelon *et al.* 2020; Genovart *et al.* 2017; Lima *et al.* 1999; Vincenzi *et al.* 2016; Volzke *et al.* 2021), whereas less is known for many plants, invertebrates and most marine organisms (e.g. Doak *et al.* 2002; Doak & Morris 2010; Linares & Doak 2010; Oro *et al.* 2023b; Pascarella & Horvitz 1998; Sielezniew & Nowicki 2017). First, the shortness of ecological time series often hinders our ability to discern long-term trends and patterns, making it challenging to draw robust conclusions about the impact of rare events on population dynamics (Magurran *et al.* 2010). Sampling errors represent another challenge in long-term ecological monitoring since they can bias the detection and magnitude of ecological processes (Staples *et al.* 2004; Sugihara *et al.* 1997). Finally, the spatial scale of data collection is often limited, leading to challenges in extrapolating findings to larger ecosystems or understanding the broader implications of rare events in demographic rates, particularly dispersal, and the consequences for local populations and metapopulations (Bowler & Benton 2005; Crawley *et al.* 1997). Representativeness of sampled populations to assess the effects of

rare events should also be considered, since responses in a particular local population may depend not only on environmental extremes but also on inherent life history of the species and the demographic features of that particular population (e.g. age-structure)(Genovart *et al.* 2003; Tavecchia *et al.* 2008). Importantly, spatial limitations of long-term monitoring of dispersal may decouple the relationship between population growth and rare events from that between those events and vital rates (Tavecchia *et al.* 2016). This can be especially true for very mobile organisms such as fish, bats, or birds and for plants with high seed dispersal rates (Tavecchia *et al.* 2016; Venable & Brown 1993).

In addition to long-term monitoring studies, paleo-ecological and archaeo-ecological studies, often provide a compelling picture of how rare events (e.g. climate extremes) may influence ecological dynamics and non-linear population phenomena (Delcourt *et al.* 1982; Gray *et al.* 2006; Laperrière *et al.* 2008; Morris 1995; Oro *et al.* 2022; Willis & Birks 2006).

Despite these challenges, technological advancements and interdisciplinary collaborations offer promising avenues for overcoming the constraints associated with long-term ecological monitoring. Integrating automated sensor networks, remote sensing technologies, and citizen science initiatives can enhance the spatial and temporal resolution of ecological data, thereby providing more comprehensive insights into the dynamics of rare events and vital rates (Dornelas *et al.* 2013; Tulloch *et al.* 2013).

Immediate and longer term effects of rare events

While much of the ecological literature implicitly assumes that the consequences of rare demographic events are fairly straightforward to ascertain, there are in fact several nuances to

these effects. Perhaps most problematic is the confounding of immediate vs longer-term impacts of rare events. The general assumption is that rare events that have extreme impacts are important demographically. At this extreme, this is clearly true: catastrophes that lead to extinction are important. However, many species (especially plants and some invertebrates) have resting stages like seeds or cysts that are highly resistant to perturbations, limiting the extent of catastrophic effects a population will experience. For demographic effects that fall short of utter disaster, the rarity of an event can more than balance its immediate impacts on long term dynamics (Fig. 3 and Box 2). For example, demographic modelling of the short-tailed albatross, a critically endangered seabird, shows that catastrophic losses due to volcanic eruptions on the single main breeding island (an active volcano) are predicted to have very small effects on long term stochastic growth rate or extinction risk, especially when contrasted with the effects of modest but continual bycatch mortality (Finkelstein *et al.* 2010). More generally, one can estimate how important rare events are in driving long term growth rates, and see that the impacts of rare events must be large in comparison to their probabilities, in order for them to have disproportionate long term effects (Box 2). However, as we discuss below, these simple estimates do not consider rare events with longer-lasting effects that can dramatically increase their importance.

Extreme demographic impacts may also be attenuated by other population processes. While massive die-offs and extinctions can result from a dramatic drop in at least one vital rate after an extreme event (Anderson *et al.* 2017; Cerrano *et al.* 2000; Reed *et al.* 2003), a lack of those population processes does not necessarily mean an absence of an extreme event or an extreme impact of the rare event on some vital rate. For instance, immigration or recruitment at earlier

ages, can compensate for a sharp decrease in adult survival after a rare event in a local population (Sanz-Aguilar *et al.* 2016; Tavecchia *et al.* 2007, 2016). Other related processes that can dampen effects of rare events include demographic compensation, the opposite response of different demographic rates to the same perturbation, and demographic buffering, the evolution of demographically important vital rates to be resistant to environmental perturbations (Doak & Morris 2010; Vilellas *et al.* 2015). In addition, population density may decrease after an event and we would expect a relaxation of density-dependent processes (Oro & Doak 2020; Young 1994). In sum, populations may be able to compensate for rare negative events by several processes (Fig. 5). Despite the myriad population processes triggered by perturbations, simply observing no immediate changes in population density does not assure population stability. Populations possess finite resilience against environmental disturbances, which can gradually erode their capacity to adapt. This heightened vulnerability may lead to abrupt regime shifts or even population collapses.

BOX 2: Considering the long as well as short-term impacts of rare events

Rare events can lead to substantial changes in demographic rates and hence population growth. Most often, ecologists have focused on catastrophes, rare events that have strongly negative effects, often on multiple vital rates. However, other rare events, such as high rainfall at the right time in desert systems, can lead to bonanzas, boosting reproduction and recruitment, in particular to record levels.

While these sharp, transitory changes in vital rates are the hallmark of demographically

important rare events, they do not necessarily mean that rare conditions are always strongly important in shaping long term population performance or even extinction risk. This is because the potentially large impacts of rare events are weighted by their (by definition) low frequency. To illustrate this effect, we can consider a simple non-structured population model, where annual growth rate, λ_i , is dependent on the environmental state in that year, i . If p_i is the probability of a given environmental state, then the mean stochastic growth rate is $\overline{\log(\lambda)} = \sum p_i \log(\lambda_i)$. To ask how much the performance in each environmental state contributes to the mean growth rate, we can calculate $p_i(\log(\lambda_i) - \overline{\log(\lambda)})$, which sum to zero.

We show results from a Gaussian distribution of environments, and assuming that the performance, λ_i , is maximized at the mean environment and declines in proportion to the relative frequency of the environmental state. For two different power functions of how λ_i depends on event frequency (0.1 and 3), we see the same pattern, with conditions of intermediate rarity having considerably higher effect on long term growth than do the rarest events (Fig. 6). As this simple simulation emphasises, true rarity dictates against importance for long-term performance, unless there are exceptionally extreme effects of these conditions. One implication of this pattern is that events such as fires and hurricanes, which often have return intervals between decades and centuries, are more likely to be important than are much rarer events. A second point is that while long term studies are needed to estimate effects of rare events, unrealistically long studies, needed to include very rare conditions, may not be needed

for accurate forecasting.

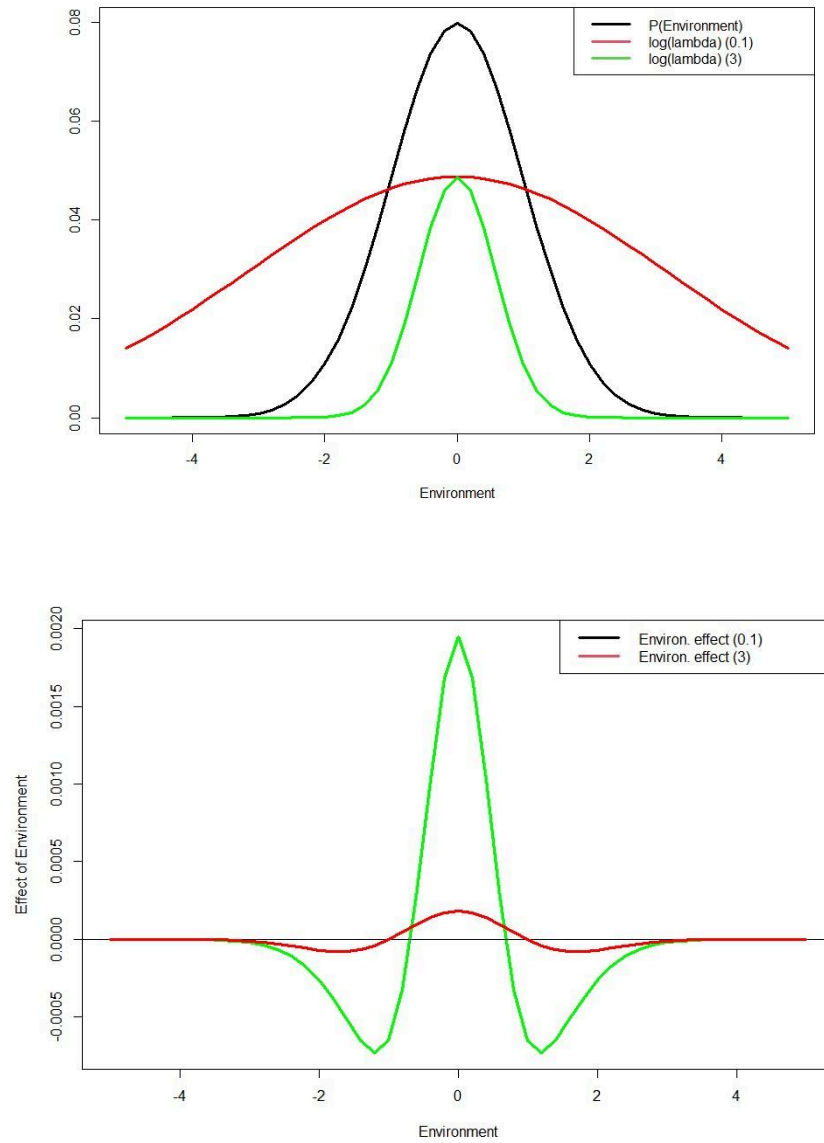


Figure 6. Gaussian distribution of environments, and assuming that the performance, λ_i , is maximized at the mean environment and declines in proportion to the relative frequency of the

environmental state. For two different power functions of how λ_i depends on event frequency (0.1 and 3), we see that conditions of intermediate rarity have considerably higher effect on long term growth than do the rarest events.

Interacting rare events

While rare events may generate abrupt and short changes in vital rates (e.g. Bertolero *et al.* 2007; Langtimm & Beck 2003; Reed *et al.* 2003; Thomson 2005; Young 1994), events of different environmental states may occur simultaneously, which may result in different demographic consequences (Silliman *et al.* 2005)(Fig. 7). A detailed long-term demographic monitoring study shows the importance of the interaction between pressed changes, such as long-term trends in environmental conditions, and rare events (Clark-Wolf *et al.* 2023). Yet, this study shows that each type of environmental change (trends and rare events) differentially influence each life stage and its vital rates and that press perturbation regimes and pulsed rare events may work both synergistically and antagonistically to affect animal population persistence. Other examples involve the synergetic effect of extreme climate events to anthropogenic press perturbations to generate extreme responses such as mass mortalities (Linares & Doak 2010), or the additive effects of both rare climate events with ongoing human impacts such as harvesting (Montero-Serra *et al.* 2018, 2019). Finally, consecutive rare events increase the chances for extreme responses, such as regime shifts for lower and long-lasting population densities and local extinction, since species demographic buffering capacity has limited effectiveness when adverse conditions occur frequently (Matthews *et al.* 2013; Payo-Payo *et al.* 2015;

Rodríguez-Caro *et al.* 2021).

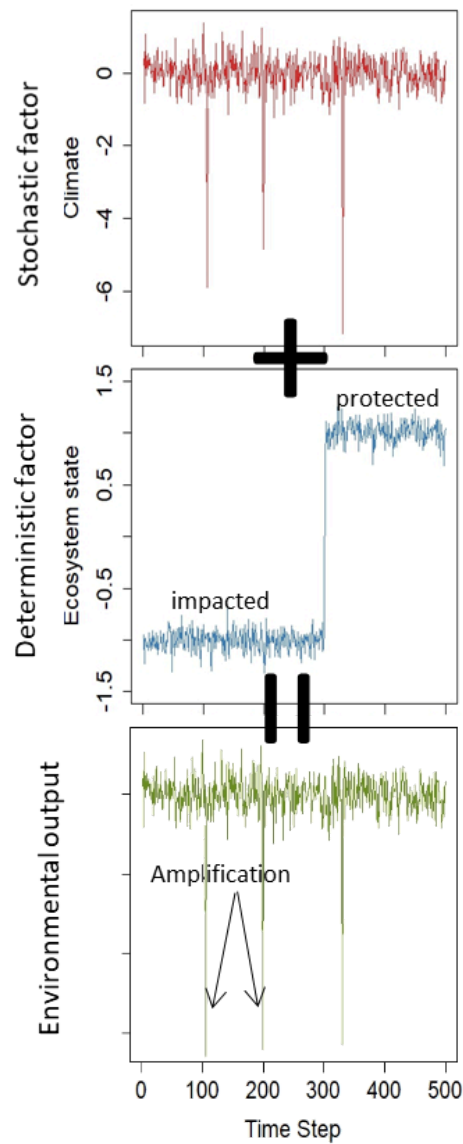


Figure 7. Conceptual representation of the interaction between environmental stochasticity with rare events (panel (a), climatic variable) and a deterministic anthropogenic rare event (panel (b), here representing the effective protection of a patch). As a result, environmental output would show an amplification of rare climatic events when the patch was affected by

anthropogenic impacts, which ceased abruptly once the patch was effectively protected.

RARE EVENTS AND ECOLOGICAL DYNAMICS

Responses of populations

Ecosystems are exposed to inherently stochastic environments. Since the physical forces (e.g. climate variables) are stochastic, ecological responses at any hierarchical level (e.g. ecosystem, community, population) are expected to be also stochastic. If we focus on a population of a certain species, it should respond to stochasticity in physical drivers, which act directly or through the changes they generate on interacting species (e.g. competitors, predators, parasites). From a demographic point of view, environmental stochasticity is going to influence vital rates such as survival, reproduction, recruitment and dispersal (Koons *et al.* 2017; McDonald *et al.* 2017). Under a stationary theoretical scenario with density-dependence, vital rates in a population fluctuate stochastically over time and keep this population under the attractor of dynamic equilibrium (this has been termed *reactivity*). Perturbations are part of environmental stochasticity that push populations away from that equilibrium, and how vital rates are affected and respond to compensate would influence transient dynamics (Hastings *et al.* 2018). The ecological dynamics of perturbations and the responses of populations have been extensively studied in theoretical, experimental and field studies (e.g. Bender *et al.* 1984; Ozgul *et al.* 2012; Sutherland 1990). However, rare environmental events, due to their uncommonness and potentially uniqueness, are less studied from all points of view, although a recent interest has

been raised by climate extremes (van de Pol *et al.* 2017 and references therein). This biased knowledge results from the fact mentioned earlier that climate variables are monitored automatically and extremes are easier to detect. Furthermore, climate can be the main physical driver affecting the primary producers in ecological food webs and cascading up to the tertiary consumers (but see Morris *et al.* 2020). Finally, there is a focus on scrutiny of climate extremes as their frequency would increase from anthropogenically forced climate change.

The relatively little knowledge gathered so far on the mechanisms that may generate changes (extreme or not) in population dynamics following rare events contrasts with the historical interest about the importance of extreme, rare events in ecology and evolution. For instance, Margalef (1997) summarised the crucial role played by rare events as a fundamental force for successional dynamics, resetting of ecological processes and evolutionary changes (see also Hoffmann & Parsons 1997). Some ecological and evolutionary dynamics such as punctuated equilibria, the universality of power laws, entropy and information, Dollo's law, the inherent occurrence of evolution with succession, and criticality have been discussed in the frame of rare events. Power laws governing rare events underscore the non-linear relationship between event magnitude and occurrence frequency. This non-linear nature often results in a few events exerting disproportionately significant impacts on ecological systems (Box 2, Fig. 2). However, until one reaches the most extreme of events, it is not clear that the intensity of a rare event will outweigh its rarity in influencing long term population dynamics.

Non-linear responses

Beyond this heuristic prediction, some emergent properties in the spatial-temporal dynamics of

populations and metapopulations may arise from the complexity of ecological and demographic processes when at least one vital rate suffers a larger, extreme change following a rare event. That extreme change may exacerbate or significantly alter some processes, such as Allee effects, founder effects, demographic stochasticity, age structure, and the change in the carrying capacity of the system. As a result, those emergent properties would favour the occurrence of non-linear responses of populations, such as regime shifts, extinction and collapses, tipping points and the occurrence of long transients (Hastings *et al.* 2018; Scheffer & Carpenter 2003) (Fig. 8). Several long-term empirical studies show those types of complex, non-linear consequences for populations after the occurrence of rare events, from insects, birds and reptiles to vegetation communities (Keevil *et al.* 2018; Ludwig *et al.* 1978; Lynch *et al.* 2014; Oro 2020; Payo-Payo *et al.* 2015).

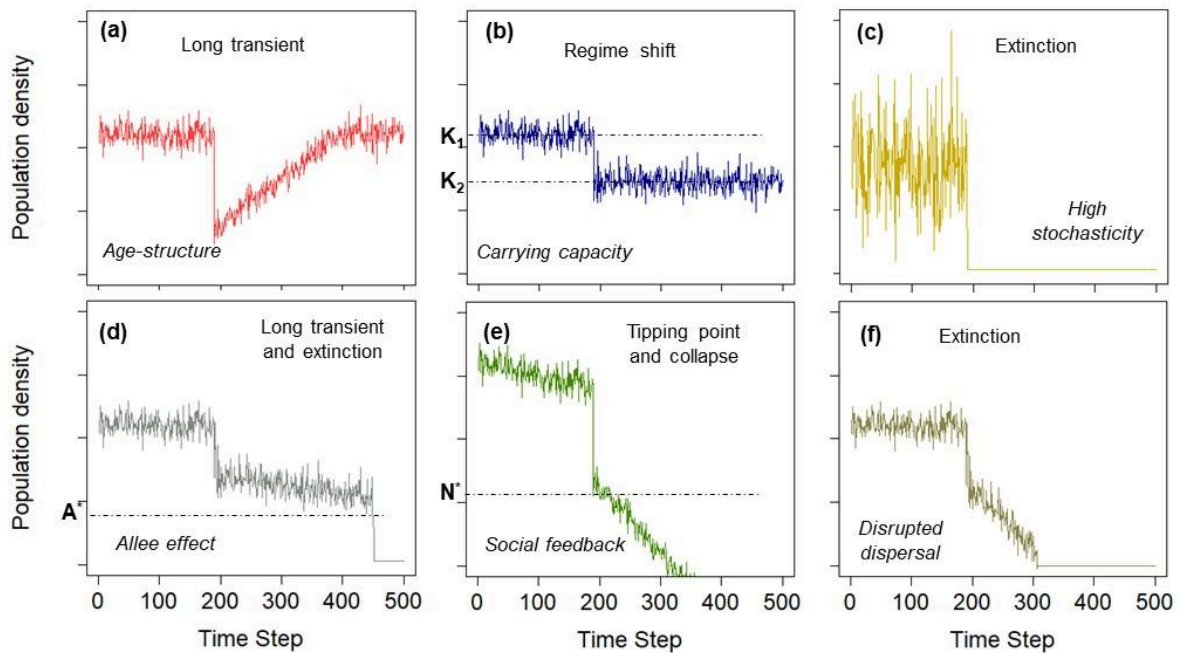


Figure 8. Illustration of the complex, non-linear behaviour of population dynamics after a single pulse extreme negative stochastic event (from a to f; dynamics are shown as title panels and the mechanisms are shown in italics). Scenarios simulate single ecological and demographic dynamics occurring after an extreme event around time 190 mimicking stochastic population dynamics in a patch. (a) Long transient after population drop due to a detrimental change in age (or stage) structure. (b) Regime shift to a lower state of population density due to a decrease in carrying capacity from K_1 to K_2 . (c) Extinction due to high stochastic population dynamics (e.g. an organism with a fast life history). (d) Long transient after the extreme event due to the appearance of Allee effects (e.g. a social organism) and a non-linear extinction once the population attains the critical Allee threshold A^* . (e) Tipping point for population collapse in a population in which, after the extreme event, there is a dispersal runaway, an acceleration of dispersal to other patches due to social feedback once the population attains a threshold value N^* . (f) the scenario represents a sink population with stationary dynamics due to the rescue effect of immigration from a source; if the extreme event affects both the source and the sink, the dispersal process is disrupted and the sink may go extinct.

The spatial scale

There is a general agreement that long-term demographic monitoring allows researchers to study demographic and life history parameters that cannot be explored from cross-sectional studies (Mills *et al.* 2015). Over the years, the focus of long-term demographic monitoring has moved to testing hypotheses about how changes in the environmental conditions, such as climate, may affect demographic processes. Due to the inherent challenges of monitoring

individual demographic rates over extended periods of time, a lower number of studies have simultaneously monitored several patches at spatial scales (e.g. Fernández-Chacón *et al.* 2011, 2013; Frederiksen *et al.* 2021; Hernández-Matías *et al.* 2013; Smith-James *et al.* 1996).

Nevertheless, these studies can be important for the study of metapopulation dynamics and for informing effective conservation strategies in fragmented and changing landscapes (Oro 2013).

Dispersal processes

One of the significant ecological processes that has been shown by these studies to mediate effects of rare events is dispersal. Dispersal is influenced by environmental variation, and it largely increases after detrimental rare events (both stochastic and deterministic)(Cam *et al.* 2004; Payo-Payo *et al.* 2017) and by the different density in each local population (Fernández-Chacón *et al.* 2013; Péron *et al.* 2010). Population density is not independent of local environmental conditions and owing that habitat suitability shows spatial heterogeneity, dispersal between two patches is seldom symmetrical (Cam *et al.* 2004; Oro *et al.* 2023b). Dispersal can also be state-dependent, e.g. different for each age class, and this state-dependent dispersal is exacerbated following rare events (Oro *et al.* 1999; Payo-Payo *et al.* 2018). Since vital rates, especially in long-lived species, are strongly age-dependent, local population dynamics and resilience are very sensitive to age-structure.

We still know little about how rare events may influence extreme responses in dispersal and the dynamics of local populations and metapopulations. While it seems evident that dispersal increases after rare events, the spatial scale at which those events occur (see Table S1) would likely influence the role of dispersal to generate extreme responses in populations. We expect

that even under spatial large-scale rare events, dispersal would still be a demographic response for the persistence of populations, since spatial heterogeneity for habitat suitability would not necessarily change. Nevertheless, some anthropogenic rare events, such the setup of intensive agricultural policies, may increase habitat homogeneity with extreme demographic consequences such as non-linear extinctions.

Habitat-specific demography

Spatial heterogeneity in habitat suitability and the potential effects that rare events may have to affect this heterogeneity is important not only for dispersal but also for local population dynamics. It is known that different local populations of a species may show differential density trends at each patch, but most studies do not address the demographic processes influencing those differences. Long-term demographic monitoring shows that demographic processes change in each local population, either because the habitat-specific environmental conditions (Doak & Morris 2010; Fernández-Chacón *et al.* 2015; Frederiksen *et al.* 2021; Linares & Doak 2010; Murphy 2001; Smith-James *et al.* 1996; Vincenzi *et al.* 2016) or because the age-stage-structure of the population (e.g. ages, states) may change between local populations (Lynch *et al.* 2014; Reichert *et al.* 2016). Strikingly, variability in age structure may occur between neighbouring populations sharing the same environment (Genovart *et al.* 2003; Tavecchia *et al.* 2008). Rare events of invasive predation occurring at local scales trigger changes in age-structure in each local population with potential extreme consequences (Oro *et al.* 1999; Payo-Payo *et al.* 2018). Other local rare events (e.g. local flash floods and debris flows) have extreme consequences for local extinctions and die-offs in riparian ecosystems (Vincenzi *et al.*

2016). These ecosystems are also a good example of how spatial heterogeneity at the scale of a stream may generate differential effects from a rare, catastrophic event (Hawkins & Sedell 1990). Habitat-specific responses to the same rare event are important for the responses of ecosystems: these differential responses may buffer for the effects of rare events since patches less affected by die-offs act as refugia for future colonisation (Hawkins & Sedell 1990).

Spatial ecological dynamics and patterns

Landscape configuration and spatial heterogeneity influence several ecological dynamics for local populations and metapopulations. For instance, anthropogenic deterministic favourable rare events, such as habitat protection, significantly increase dispersal to restored patches, colonisation rates and non-linear boom-bust population dynamics (Dugger *et al.* 2016; Pagel *et al.* 2014). Empirical studies show the relevant role of dispersal in source-sinks dynamics, transient dynamics, colonisation processes and metapopulation dynamics (Gundersen *et al.* 2001; Hanski & Ovaskainen 2000; Hernández-Matías *et al.* 2013; Iles *et al.* 2018; Murphy 2001; Oro & Ruxton 2001). A rare event of invasive predation occurred during a detailed long-term demographic study of a colonial bird at large spatial-temporal scale (see above). The study recorded most of those ecological dynamics: it altered source-sink dynamics since it caused dispersal and a tipping point for non-linear population collapse (Oro *et al.* 2023a). Non-linear increases of colonisation rates occurred, as well as punctuated jumps in cultural innovations with demographic consequences for local population dynamics (Payo-Payo *et al.* 2017, 2018). In fact, the most important driver of colonisation and recolonization likely are detrimental rare events, such as natural catastrophes (e.g. oceanographic extremes and volcanic eruptions)(Dale

et al. 2005; Loya 1976). Contrarily, unfavourable rare events of deterministic nature, such as the construction of infrastructures, may impede dispersal, which would drive extreme consequences for metapopulation dynamics (e.g. gene flow, extinction-colonisation turnover, see also Fig. 8).

Heterogeneity in habitat suitability also drives distributional ranges and the existence of core and marginal populations, the later commonly showing lower demographic rates, smaller populations, and higher extinction probabilities (Lynch *et al.* 2014). During invasion dynamics, the contrary may be true: expanding populations at the edge show demographic processes operating at their maximum capacity and populations show high growth rates (Oro 2020; Sanz-Aguilar *et al.* 2014)(see above).

However, spatial configuration of habitat suitability is dynamic and influenced by the environmental spatial-temporal variability. Rare events, when local, may alter these dynamics, but we know very little about their influence and the occurrence of extreme effects on populations. The same occurs for other spatial ecological dynamics, such as population synchrony for metapopulation stability and transient phenomena involving spatial structure in populations.

Succession and biotic interactions in communities

Natural extreme events, such as volcanic eruptions and climate extremes, are exceptional opportunities to assess their consequences at ecosystem level, focusing on changes in species compositions in communities over succession, and in some cases, resetting of the system (Carrillo & Díaz-Villanueva 2021; Dale *et al.* 2005; Hawkins & Sedell 1990; Ubach *et al.* 2022). For instance, a disease outbreak wiping out most individuals in a predator population may

increase a demographic parameter of a competitor and of the prey community. Several decades ago, Bender (1984) reviewed the opportunities and caveats that perturbation experiments had to understand species interaction in a community at spatial-temporal scales. Gradual and directional change in communities may be altered by rare events through regime shifts, and the capacity to return to the original state is influenced by the life histories of the species and the spatial-temporal dynamics of rare events (Matthews *et al.* 2013). Since a rare event may have differential demographic consequences for different species in a community, we expect changes across multiple levels of ecological organisation on the processes occurring at the patch (Felton & Smith 2017; Frederiksen *et al.* 2008; Sanders *et al.* 2003). A review on how climate extremes affect plant species and communities shows that processes such as species niche partitioning and compensatory responses commonly provide stability to those communities (Felton & Smith 2017). When the spatial scale is taken into account, disruption of dispersal in metacommunities after rare events would increase spatial heterogeneity in local community dynamics (e.g. species diversity) and demography (Alexander *et al.* 2012).

Some insightful empirical studies show interesting results about the consequences of rare events on succession and community dynamics. Lutz & Halpern (2006) studied tree community succession after an experimental extreme event of clear-cut lodging. Mortality greatly increased for the whole community, but mechanical damage generated a loss of biomass and increased structural heterogeneity. Elderd & Doak (2006) showed that even though the direct effects of physical rare events (e.g. flooding) played a critical role in shaping population dynamics of riparian plants, the biotic interactions with herbivores also had important and lasting impacts on population growth. Similarly, Gross *et al.* 2008 showed how the balance of negative and

positive effects of fire events alter population performance of a rare but well-studied plant (Gross *et al.* 1998). Dayton (1999) studied how a kelp forest community was structured following rare oceanographic events. While species competition after rare events increased and had pervasive long-term effects, the study opened unsolved questions such as the interaction between rare events and density-dependence, changes in the trade-off between inter- and intra-specific competition and whether rare events generated nonequilibrium states overriding a dynamic equilibrium of the community dynamics. Mittelbach (1995) carried out a long-term monitoring of the effects of two consecutive rare events on the food web (the removal of the top fish predator in a lake ecosystem and its reintroduction several years later). Removal generated a transient to a new ecological state, characterised by cascading effects on ecological dynamics: herbivore fishes increased in density, and large zooplankton disappeared and were substituted by smaller species. There was a new transient until the system went back to the original state once the top predator was reinstated. Almaraz & Oro (2011) found that the rare event of a predator invading a patch triggered community reorganisations and global decays in population synchrony, which disrupted the pattern of interspecific interactions for species of the same ecological guild.

PREDICTIONS IN NATURAL POPULATIONS

Our capacity to predict the behaviour of ecosystems and their components have interested ecologists for a long time. While there is a general agreement that the complex nature of ecological systems make predictions very challenging, the search for predictive power continues. The low occurrence of rare events and spatial and taxonomic idiosyncrasies of their likely add

difficulty for predicting the consequences of these events (Buckley & Huey 2016). Complexity also arises from e.g. the potential spatial-temporal delays that may increase the occurrence of very long transients (Hastings *et al.* 2018), and from time lagged responses and the relative importance of recent and past events for trait expression (van de Pol & Cockburn 2011).

As a rule of thumb, we may hypothesise that if environmental stochasticity generates substantial changes in vital rates directly or through changes on traits such as morphology, physiology and behaviour, extreme events will generate larger changes with larger consequences for population dynamics, which eventually would drive evolutionary dynamics (Cerini *et al.* 2023; Hoffmann & Parsons 1997). Paleontological reconstructions from the Pleistocene glacial-interglacial cycles suggest that organisms responded to climate trends in a quite predictable manner by adapting their distributional ranges (Parmesan *et al.* 2000). Contrary to trends, paleontological records are less informative about responses to extreme events, except for global, planetary catastrophes (see Table S1). For the predictive discipline, one of the challenges is to assess the limits of demographic buffering and lability for dampening fluctuations in population growth rate. Incorporating life histories theory may overcome, at least partially, such a challenge (Boyce *et al.* 2006)(see also next section on ‘Eco-evolutionary dynamics’).

Ecological theory has also devoted efforts for predicting the consequences of extreme rare events, commonly termed catastrophes. Some models show that random catastrophes should not trigger extinction when the long-run population growth rate is positive, although catastrophe both rate and magnitude may change that prediction (Lande 1993). Demographic models of plants influenced by rare, catastrophic events, show that increased variability in some

vital rate after the event can, strikingly, increase the population stochastic growth rate (see Fig. 1c in Boyce *et al.* 2006). Other theoretical studies advocate for focusing on the understanding of ecological and evolutionary processes that have occurred in the study system for making more accurate predictions (Cuddington *et al.* 2013). This includes the incorporation of rare events, suitable spatial-temporal scales, threshold dynamics, and long-lasting legacy effects. Long-term demographic empirical studies have found that other ecological dynamics and processes should also be considered when modelling the effects of rare events. For instance, the state of the study population, showing either stationary or trend dynamics, can have a strong influence. Increasing populations affected by rare events, even though they show extreme responses (e.g. strong decrease of a vital rate with high sensitivity, distributional shift by habitat loss), they have high resilience to go rapidly back to the previous state (Martínez-Abraín *et al.* 2012; Oro *et al.* 2012). Thus, we may predict that populations showing positive trends may be more effective for buffering demographic impacts than declining populations. This is probably related to the importance of density-dependent processes for the responses of populations to rare events (Dayton *et al.* 1999; Haran *et al.* 2019; Lima *et al.* 1999; Reed *et al.* 2003; Rogowski *et al.* 2020; Ubach *et al.* 2022). Other processes affecting the magnitude of the responses to rare events can be resource competition between species, which can alter differentially the dynamics of each interacting species (Almaraz & Oro 2011; Thomson 2005).

Despite the complex nature of populations and their dynamics, some long-term empirical studies have recorded demographic data before and after the rare event to build predictive models to assess how rare events affect the probabilities of extinction (Buckley & Kingsolver 2012; Linares & Doak 2010; Lynch *et al.* 2014).

ECOLOGICAL DYNAMICS IN A LIFE HISTORY CONTEXT

We lack an understanding of limits to plasticity and evolutionary potential across traits, populations, and species and feedback between adaptive and demographic responses (Van Asch *et al.* 2007). Demographic long-term monitoring is crucial to improve our knowledge on how organisms with different life histories respond to rare events (Metcalf & Pavard 2007). In some cases, long-term demographic monitoring at large spatial-temporal scales have shown plasticity in a species for a fast to slow continuum of life histories between different populations subjected to heterogenous environmental conditions and occurrence of local rare events (Fernández-Chacón *et al.* 2015; Matthews *et al.* 2013; Vincenzi *et al.* 2016). That demographic monitoring is crucial to identify extreme responses to rare events, such as those shown by the red coral *Corallium rubrum*, for which some colonies show extreme shrinkage due to environmental stress (Montero-Serra *et al.* 2018). It has been suggested that phenotypic plasticity and evolution increases with environmental variability and under extreme environments (Svanbäck *et al.* 2009). Furthermore, the consequences of rare events and the eco-evolutionary strategies to cope with it may endure across multiple generations through mechanisms such as maternal, ecological, and cultural inheritance (Badyaev 2005).

Within the framework of life history theory, rare events significantly shape the adaptive strategies of organisms. Organisms exhibit diverse life history traits, balancing trade-offs between survival, growth, and reproduction, which are finely tuned to their respective environments. Rare events, such as extreme weather events, habitat transformation, or disease outbreaks, challenge these strategies by imposing unpredictable environmental stressors. Life

history theory posits that organisms have evolved to allocate resources optimally under normal conditions, yet rare events disrupt this equilibrium, prompting shifts in reproductive investment, dispersal behaviour, and population growth rates. These shifts may manifest as demographic buffering mechanisms, where populations exhibit resilience to short-term perturbations through adjustments in vital rates, or as demographic lability, where populations demonstrate high variability in response to environmental fluctuations (Le Coeur *et al.* 2022; van de Pol & Cockburn 2011). Furthermore, rare events may have not only a direct impact on vital rates, but also an indirect impact through induced variation in demographic structure and phenotypic trait distributions (see Maldonado-Chaparro *et al.* 2018).

The population consequences of rare events, as elucidated by life history theory, extend beyond immediate demographic impacts to encompass evolutionary responses and population persistence. Rare events can impose selection pressures that favour particular life history strategies, driving evolutionary shifts within populations. Additionally, rare events may alter the individual heterogeneity of vital rates within populations, which is a buffering mechanism to cope with local resilience (Maxwell *et al.* 2019; Milles *et al.* 2023). Melbourne & Hastings (2008) highlight the importance of adding demographic heterogeneity to the canonical environmental stochasticity and demographic stochasticity. Thus, long-term demographic studies should also focus on how rare events influence individual heterogeneity within and among populations. We have mentioned earlier the importance of considering that rare events may affect specific ages or stages within populations (see also Fig. 8), but many other sources of heterogeneity may be playing a role. By integrating long-term demographic monitoring with theoretical frameworks like life history theory, ecologists can unravel the complexities of population responses to rare

events, informing conservation strategies and enhancing our understanding of ecological resilience in the face of environmental uncertainty (Boyce *et al.* 2006; Morris & Doak 2002; Stearns 1992).

PERSPECTIVES

Our study highlights two main challenges: (1) understanding the range of demographic responses and ecological dynamics arising from rare events in complex ecosystems requires a special focus and integration from long-term ecological research, experimental approaches and modelling progresses, which (2) leads to the need of incorporating rare events into predictive research considering the potential for non-linearities and the limits of organismal buffering (e.g. Beckage *et al.* 2011). Long-term demographic monitoring stands as a crucial approach to address the effects of rare events on populations and communities and we recommend the continuation of already setup studies, nowadays often threatened by funding cuts (Birkhead 2014), as well as the encouragement to initiate others focusing on gaps for covering a wider range of life histories. This is particularly relevant when we deal with endangered species and communities. Another promising area of work is to focus on the synergies of simultaneous rare events, especially when they involve deterministic factors from anthropogenic activities.

Whether these deterministic events represent new challenges for organisms with a life history shaped by evolution and an environment that has been stochastic is still little known.

It is worth highlighting that rare events do not necessarily generate extreme responses nor negative responses. Rare events are a powerful driver of selection, epigenetic processes and evolutionary change. Long-lived plants are good examples of how rare events may have

beneficial effects on population growth rate (Higgins *et al.* 2000). For instance, rare events of long-distance seed dispersal are very positive for some plants that may expand their distributions (García & Borda-de-Água 2017; Nathan 2006).

It has been suggested that extreme climate events are causing gradual changes we are observing in ecosystems (Easterling *et al.* 2000). Theoretical developments in dynamical systems from physics highlight that small and pressed changes in conditions can trigger large and discontinuous changes in the system. This theory has nurtured the development of critical transitions in ecological systems, where focus has been posed on the potential effects of small changes on non-linear ecological dynamics and tipping points (van Nes & Scheffer 2007; Scheffer 2009; Trisos *et al.* 2020). Nevertheless, the original theory mostly considers that rare events do not have a relevant role in shaping physical dynamics. At this point, we would like to call for a broader integration of ecology, physics and mathematics to provide new insights about the role of rare events for populations and community dynamics.

Finally, it is important to keep in mind that rare events are an exceptional opportunity to explore what has been termed the *adjacent possible*, expressed as the potential of demographic responses beyond what we consider possible within the expected range of recorded vital rates and life histories of the affected population (Badyaev 2005; Kauffman 2000; Longo 2018; Maxwell *et al.* 2019). This little knowledge about the potential of organisms to respond beyond the demographic limits recorded during long-term monitoring and its logistic limits to study extreme events troubles our capacity to predict the responses of ecosystems to these events.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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