



## Ecological non-equilibrium and biological conservation

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### ABSTRACT

How to establish efficient conservation actions and policies for the long-term persistence of ecological systems remains a challenge. Conservation biology was born as a discipline of crisis, targeting the recovery of altered ecosystems under the paradigms of equilibrium and ecological stability. However, we argue that the concepts of ecological equilibrium and balance still hinder wildlife managers from optimizing proper decision-making and correctly prioritizing conservation actions. This is still the case, despite the prevailing paradigm has recently shifted to a more realistic view of non-equilibrium dynamics in ecosystems, even in the absence of anthropogenic impacts. The challenge for managers and policymakers is now even greater. First, because non-equilibrium is the basis for the Darwinian adaptive response of ecosystems, and hence maintaining variance, rather than decreasing it, should be the target of conservation. Secondly, ecosystems show non-linear responses (e.g. transients and critical transitions), which hamper diagnosis and prediction. Even though we are unable to suggest solutions to this conundrum, we warn here about potential biases when conserving non-equilibrium ecosystems. We suggest that insights from island ecology and medical science may be helpful when dealing with non-equilibrium in applied conservation. Incorporating the advances of the discipline of complex systems into the conceptual framework of management and policymaking may also contribute to improving the prioritization of actions, especially regarding some agents of global change. Finally, we advocate for the strengthening of the feedback between ecologists (both theoretical and empirical) and conservation practitioners to improve our knowledge on how ecosystems respond to perturbations.

While there are infinite ways to be far from equilibrium, there is only one way to be in.

Jorge Wagensberg

Ecological equilibria are as impossible as stable economies.

Ramon Margalef

### 1. Introduction

The field of conservation biology was born as a discipline of crisis to respond academically to the need of preserving endangered populations, species, communities, and ecosystems. In the late 1970s, several researchers, led by Bruce A. Wilcox and Michael E. Soulé, organized 'The First International Conference on Research in Conservation Biology'. A few years later, Soulé (1985) published a seminal paper stating the basis of the new discipline and its multidisciplinary mission. Importantly, the essay displayed the following headline: '*Although crisis oriented,*

*conservation biology is concerned with long-term viability of whole systems*'. While Soulé advocated for an urgent need to act to reverse the decline of populations and the deterioration of ecosystems, he also noted that that reversal had to be applied over long periods. The two processes (reversal and maintenance) conceptually imply an equilibrium, a stable state from which the system departed in the past and to which it should return. At this point, we may wonder what stability is. The question has troubled not only scientists from the natural sciences, but also other scientists, such as chemists, physicists, sociologists, and medical scientists (Hansson and Helgesson, 2003; McCoy and Shrader-Frechette, 1992).

The ecological concept of a stable state or equilibrium comes from a truism in population ecology: no population may grow exponentially without a limit. Population growth should stop once resources per capita and interspecific interactions limit that growth and stabilize the population around a conceptual value (the carrying capacity), that arises from the logistic model (e.g. Morris and Doak, 2002). The same applies to communities and ecosystems, since their dimensions (e.g. biomass)

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are limited by matter and biogeochemical cycles and energy fluxes, and simply because they persist over time (Margalef, 1975). In summary, stability of ecological systems has long attracted ecologists (e.g. Donohue et al., 2016), has influenced conservation science (Levin, 1999), and has even been proposed to have quantifiable economic values (Armstrong and Roughgarden, 2003).

Over time, tension has emerged between protectionism, which advocates for strict preservation and non-interference with natural ecosystems, and conservationism, which takes a more dynamic and adaptive approach by promoting sustainable resource management and human interaction with nature (Robert et al., 2017). Conservationism, with its openness to finding a balance between human needs and ecological preservation, has evolved as a more inclusive and pragmatic philosophy within the environmental movement. In turn, in recent decades, there has been a shift from a stable view of natural systems to a non-equilibrium view, in which the essential pattern is ecological change. The equilibrium view has shifted (more in academia and to a lesser extent in applied conservation and policy-making) to a more unbalanced view of how ecosystems function and how biodiversity should be managed (Clark and Luis, 2020; Mori, 2011; Robert et al., 2017; Van Meerbeek et al., 2021; Wallington et al., 2005). Let us illustrate what constant change represents in a conservation framework using real examples of butterfly dynamics. When considering the two above-mentioned processes (i.e. reversal and maintenance), population decline translates into a density decrease over time, from a real or assumed stable state, with a much larger population density, to a lower (undesirable) density value (Fig. 1). Long-term viability implies a return to equilibrium, far from the potentially negative effects of demographic or environmental stochasticity. This second goal is much more challenging, first because it requires a reference value that is not unique (Margalef, 1972). Secondly, it requires some type of metric of a state that we call equilibrium, which changes over time (Fig. 2). Finally, it requires a diagnosis to assess when the deviation from equilibrium is jeopardising the viability of the ecosystem.

What we argue here is that the concept of ecological equilibrium and

related terms (i.e. such as the balance or stability of nature) (Cuddington, 2001; Curtin and Parker, 2014), which have been instrumental for the conceptual advance of ecology as a discipline (McArthur and Wilson, 1963), are ideas that still prevent managers from optimizing decision-making and from prioritizing conservation actions. In the following sections, we first outline how ecology has addressed the topics of stability and non-linearity in ecological systems, and how the study of Earth's paleoclimate and of complex systems might shed some light on applied conservation. Secondly, we review three potential biases that commonly occur when setting a conservation diagnosis or when planning management actions: temporal and spatial scales (Ranta et al., 2005), and the creation of dogmatic and reified ideas that may mislead decision-making (Kareiva et al., 2017; Martínez-Abraín and Oro, 2013). Then, we briefly describe the eco-evolutionary dynamics occurring in islands, which may be useful for rethinking the concept of non-equilibrium in ecological systems for applied conservation management and policies. We finally make a comparison with medical science, owing that it deals with the resilience and disease of the human body, which can be considered as the capacity of an individual to buffer against perturbations, and a non-equilibrium state far from health, respectively.

## 2. The non-linearity of ecological systems

Ecosystems are a paradigmatic example of a complex system: their functioning cannot be fully explained by the sum of their parts, which show the occurrence of non-linear emergent properties that are difficult to predict (Box 1). Complexity emerges at all hierarchical levels, from individuals to populations and communities, including intra and inter-level interactions.

Furthermore, dynamics of ecosystems are influenced by physical drivers, and among them, climate is crucial by affecting energy cycles, food webs, and the interactions of individuals and species in both population and community dynamics. It is thus not a surprise that climate, which is a non-equilibrium system par excellence, drives stochastic

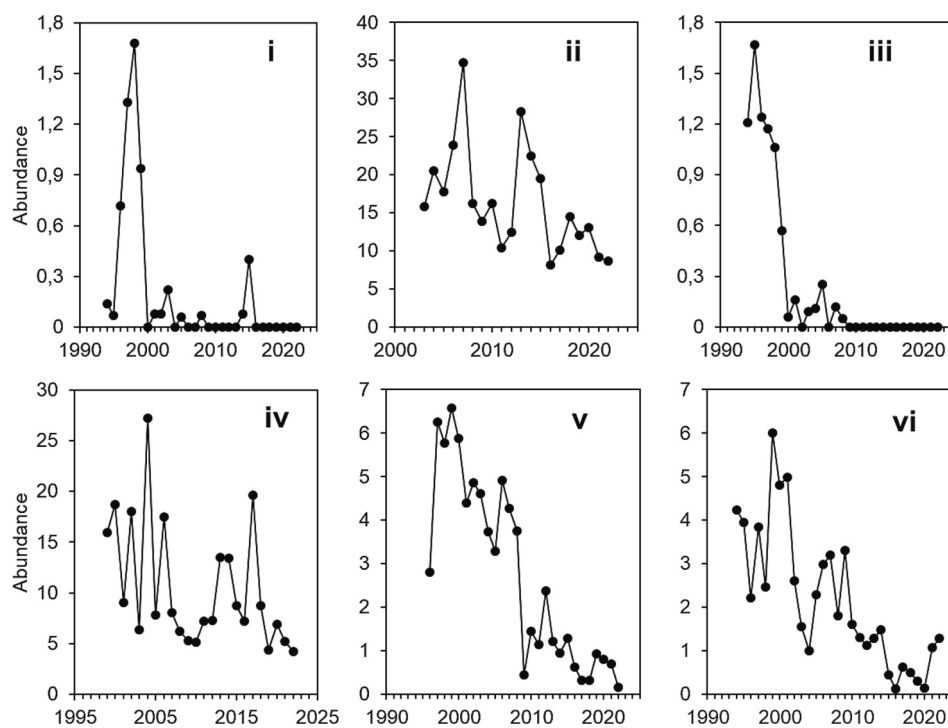


Fig. 1. Examples of butterfly long-term population dynamics that statistical modelling describes as showing declining trends (CBMS, <https://www.catalanbms.org>): (i) *Cupido alcetas*; (ii) *Pieris rapae*; (iii) *Melanargia occitanica*; (iv) *Pyronia bathseba*; (v) *Papilio machaon*; (vi) *Melanargia lachesis*. Time series depict an annual abundance index. Note that time series may have different scales in abundance, and different temporal windows.

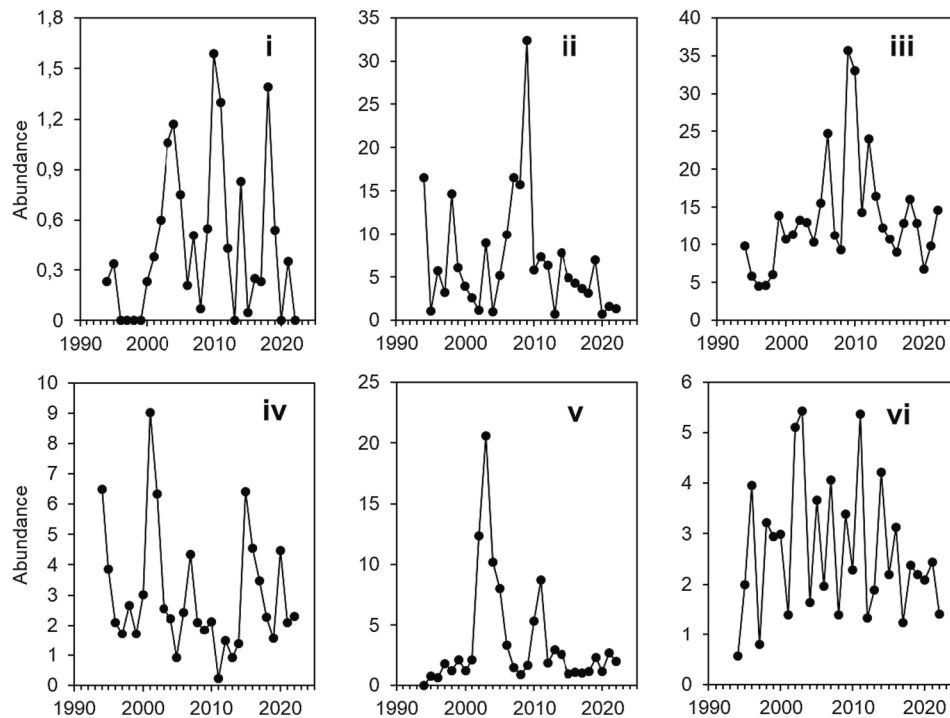


Fig. 2. Examples of butterfly local population dynamics (made on repeated transects) that statistical modelling describes as showing stable dynamics (CBMS <https://www.catalanbms.org>): (i) *Libythea celtis*; (ii) *Cupido alceatæ*; (iii) *Argynnis paphia*; (iv) *Colias crocea*; (v) *Melitæa celadussa*; (vi) *Polygonia c-album*. Time series show an annual abundance index. Note that time series may have different scales in abundance, whereas they have all the same length (29 years).

changes in ecosystems and their components (Box 2).

To explore and understand how ecosystems function, ecology has grown as a scientific discipline inspired both by the observation of nature and by the development of theoretical principles and models that have eased and stimulated the study of non-linearities within ecosystems, in which a large number of interactions are occurring in space and time. Almost five decades ago, May (1976) was one of the first to challenge the equilibrium paradigm. By using simple mathematical models, without considering any stochasticity, he showed that single-species models with discrete (non-overlapping) generations may exhibit dynamics such as bifurcations and chaos. A bunch of later works have provided solid evidence for those type of complex dynamics in biological systems, from insects and plankton to vertebrate populations (Benincà et al., 2008; Dennis et al., 2001; Gamarra and Solé, 2000).

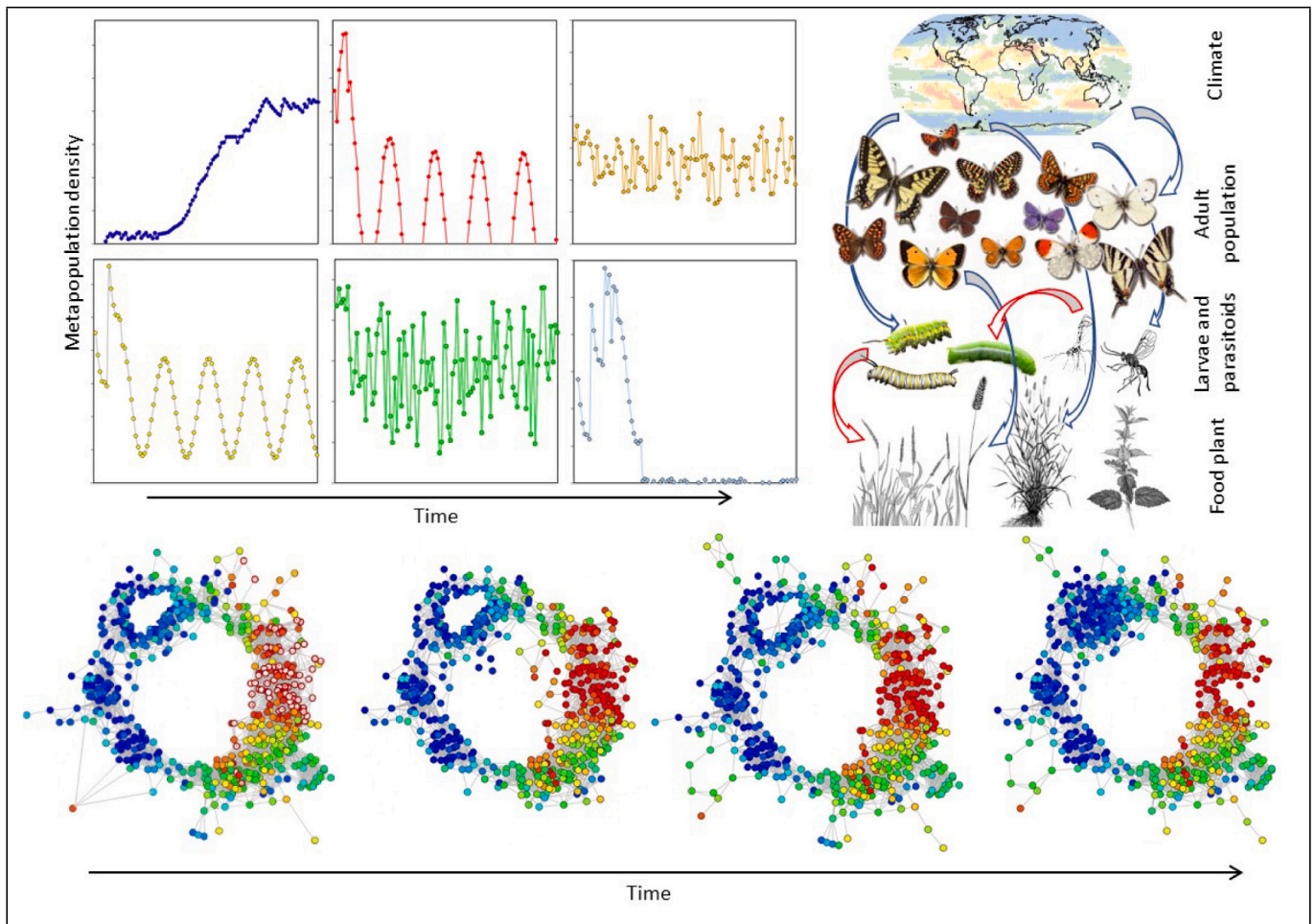
Dynamical systems (e.g. ecosystems) may exhibit complex non-linearities, such as chaos. In recent years, the development of several theories (e.g. catastrophe theory, information theory) have pervaded the ecological arena to show that non-linearity can be extreme: some small pressed changes may trigger critical transitions to different ecological states (Moniz et al., 2011; Scheffer et al., 2009). Examples are a dry savannah that rapidly becomes an arid ecosystem without a strong pulsed perturbation, or a population that collapses after a press perturbation (e.g. Kéfi et al., 2007; Oro et al., 2023). Theoretical studies have also shown that ecosystems may be in a transient phase between two different states of dynamic equilibrium (Hastings et al., 2018; Morozov et al., 2020). An example is transient dynamics in a population that would undergo large fluctuations between states of rarity and commonness, even with a population geometric rate of increase close to 1 (i.e. almost stable) (Ferriere et al., 2006). Fishing stock collapses, abrupt changes in lake ecosystems, transients lasting over tens to hundreds of generations, confirm that transients and strong non-linearities occur in ecosystems (especially when several orthogonal factors interact), and their detection is crucial to interpret the dynamics of the study system and applying proper conservation actions (Boettiger, 2021; Francis et al., 2021; Oro et al., 2022; Stott et al., 2010). Relying on the

development of those powerful theories, that are confirmed in the real world, ecologists currently agree (and perhaps slowly managers too), that management decisions are best guided by models that are grounded in ecological theory. All in all, the conceptual theory of ‘ecology of non-linearity’ challenges initial concepts of equilibrium in nature and the viability of management actions and conservation policies based on concepts of self regulation. Despite we cannot offer here a magical solution for the conundrum of managing the non-linear behavior of ecological systems, we make next an interpretive review of potential biases in ecological studies when applied to conservation, which at least may help saving time and resources, currently devoted to non-priority management actions.

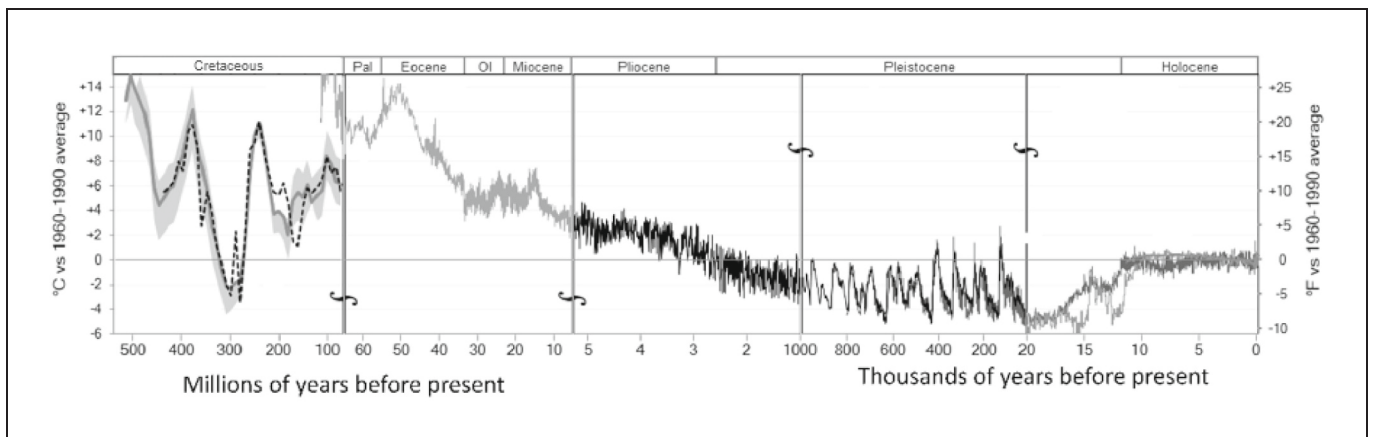
### 3. The time window: the challenges to interpreting non-equilibrium in temporal dynamics

The examples shown earlier in Figs. 1 and 2 correspond to butterfly local population dynamics, which are sensitive to climate stochasticity and to transient dynamics of socio-economic changes related to the gradual loss of open habitats, formerly generated by farming in the wealthiest regions of the world (Neff et al., 2022). Even though butterflies, like many other invertebrates, commonly show high temporal variability, other organisms with slower life histories, such as birds and mammals, may also show variability in their population dynamics over time (Fig. 5).

All the examples provided (Figs. 1-2 and 5) are representative of the nonlinear dynamics of the study populations (Carpenter et al., 1999; Clark and Luis, 2020; Pilotto et al., 2020). Yet, for most time series, an equilibrium does not become evident, and it is even difficult to detect a dynamic stable state over time. Conservation actions and policies focus mainly on populations, species, and communities that are showing negative temporal trends. However, when is a population declining toward extinction? When is a time window wide enough to detect a negative trend that is not a transient to a dynamic stable state? How sensitive are the statistical trend tests applied to the time window



**Fig. 3.** Conceptual representation of ecological complexity. Panels represent different metapopulation complex dynamics (e.g. logistic, stochastic, cyclic, boom-bust) for different species in a community over time. Network plots represent local populations of different species (represented by dots of different colours) breeding over time; local populations in the community are linked by dispersal processes and may go extinct and colonized. The upper right corner shows how climate and different ecological communities (butterflies with adults and larvae, wasp parasitoids and plants) may interact in a complex way (only some of those interactions are shown in arrows - red arrows show predation and parasitism). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 4.** Global mean Earth surface temperature reconstructions for the last 500 Mya. The horizontal solid black line crossing the y-axis value “0” represents the mean surface temperature in the early 20th century, before the modern warming (14–15 °C). Note the changing time scale in the X-axis (increased zoom) as we approach the present. Modified from [http://gergs.net/all\\_palaetemps-2/](http://gergs.net/all_palaetemps-2/). IPCC projected mean temperatures for 2050 and 2100 have been removed from the original graph due to our focus on the past Earth climate.

**Box 1**

Insights from the science of complex systems.

The interactions between climate (which is itself in non-equilibrium, see [Box 2](#)) and organisms, and among organisms (e.g. predator-prey systems, competition-facilitation, networks, parasite-hosts) occur in ecosystems in a complex way. From an ecological point of view, complexity refers to the intricacy and richness of interactions, relationships, and structures within an ecosystem. It encompasses the various components and processes that make up an ecosystem and the ways in which they are interconnected. Complexity in ecology arises from the diversity of species, the multitude of ecological interactions, and the dynamic nature of ecosystems ([Fig. 3](#)). Scientists exploring how complex systems work agree about their particularities, such as non-linearity, self-organization, robustness, and nested structure. Secondly, complex systems share several characteristics. At the level of functional features, they show adaptive behavior (i.e. selection and evolution), memory and modularity (e.g. networks of multiplicity). Finally, complex systems have properties such as non-equilibrium, diversity, the appearance of feedbacks, and openness ([Ladyman and Wiesner, 2020](#)). In his book *Fragile Dominion*, [Levin \(1999\)](#) already set several mandates linked with complexity when managing ecosystems: ‘*maintain heterogeneity*’, ‘*sustain modularity*’, ‘*preserve redundancy*’, and ‘*tighten feedback loops*’. Interestingly, complex-system scientists are continuously developing tools for quantifying the different properties of these systems although, for the time being, quantification is still far from being incorporated into the toolkit of conservation managers. However, most ecologists and managers are using (likely unconsciously) measures of numerosity, another feature of complex systems. By counting individuals and species over time and across spatial scales, or the number of interactions among individuals and organisms, we may measure numerosity and the way it varies across scales. From counting, ecologists have developed mathematical measures of diversity (e.g. the Shannon entropy of diversity), which are indicators of the amount of information contained in a certain ecosystem over time and space. The theory of information provides a powerful analytical tool: it can be used to measure diversity, disorder, memory, and self-organization. An example of information-processing systems are ecological networks.

Interestingly, it is in the regime of fluctuations, far from equilibrium, where the properties of complex systems emerge ([Nicolis and Prigogine, 1989](#)). It is far from equilibrium where population and community dynamics show non-linear responses in some unpredictable way. However, the idea that being far from equilibrium implies a conservation concern is troubling for management actions and policy roadmaps. Stochastic thermodynamics, which is an essential component of the study of complex systems, shows that ecological systems far from equilibrium are those in which order, robustness, memory, and adaptive behavior appear. This is especially true when we put all this into an evolutionary context ([Lurié and Wagensberg, 1979](#)).

A practical example would be a reintroduction or an introduction of a species (either intentional or inadvertent, e.g. biological control or invasive species, respectively), a management action that is included in many conservation guidelines. The theory of thermodynamics applied to an ecosystem would suggest that the entry of a new agent must be at the cost (loss or decrease) of some agent of the ecosystem (e.g. a competitor), since the energy flux in that ecosystem is rather stable. That also means that invasive species (natives or aliens) may generate non-linear transitions to new states, in which some species of the original system may be negatively affected, whereas others may be benefited ([Matevski et al., 2023](#); [Oro et al., 2022](#)). During the process, the host ecosystem is showing memory, robustness, and modularity (this is why most invasive species do not succeed at colonizing a new system), and it displays self-organization and feedbacks when the new species settles and forces the system to adapt. An ecosystem holds a finite amount of resources, and thus cannot harbour the same original population densities of local species when a new species arrives.

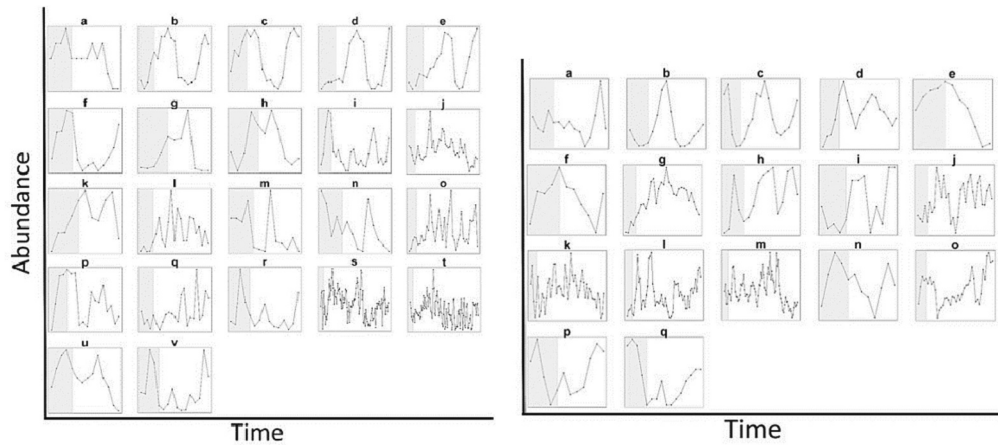
**Box 2**

Non-equilibrium of Earth’s climate.

Climatic reconstructions in geological (and evolutionary) time scales show that climate has always changed ([Fig. 4](#)). The Cambrian explosion of multi-cellular life occurred with temperatures 2–7 °C higher than present. With the exception of an ice age (Late Paleozoic icehouse), temperatures changed but remained high until the Eocene Optimum (50Mya). From that point in time on, temperatures started dropping, leading first to the glaciation in Antarctica (ca. 35 Mya) and later on to the Plio-Pleistocene glaciations (2.6Mya) that have lasted until present. We currently live in an interglacial period (the so-called Holocene, i.e. the last 12,000 years) within the periodic oscillations (stadials and interstadials) since the onset of the Pleistocene glaciations. Hence, overall the Earth’s climate is not in equilibrium and varies between two extreme points, i.e. the icehouse and the hothouse Earth, although during the last 750 My, the Earth has been free of ice in the poles 42 % of the time.

In the border between the last glacial period of the Pleistocene and the current interglacial period, the planet experienced a rapid and intense cooling that lasted ca. 1200 years (the Younger Dryas; 12,900–11,700 years ago), that was followed by a rapid and intense warming. Temperature changes in both directions ranged 7–10 °C in just a few decades. During the cooling stage temperatures returned for some time to the levels of the previous glacial stadial, inverting the strong previous warming. The Younger Dryas brings to light the non-linearity of the Earth’s climate that can be subjected to rapid and profound changes in temperature in a matter of decades ([Alley et al., 2003](#)). Changes of this duration and magnitude cannot be compared with any of the changes detected during the Holocene plateau. The current warming has increased Earth’s temperature by 1.1–1.2 °C in 150 years, despite the intense supply of CO<sub>2</sub> by human activities to the atmosphere with current CO<sub>2</sub> levels getting closer and closer to Miocene times, when mean temperatures were 5–6 °C higher than present.

Within interglacial periods, temperatures oscillate around an equilibrium (that reminds a carrying capacity in population ecology), but only if looked at a large time scale. When a zoom is made, the Holocene becomes a dwarfed fractal version of the larger-scale situation, with a sequence of smaller warming and cooling events. Hence, it does not have a well-defined mean equilibrium temperature (such as the famous 15 °C usually taken to be the basal reference), although variance is certainly smaller than at larger time scales ([Ruddiman, 2008](#)).



**Fig. 5.** Variability in population dynamics for several populations of birds (Galliformes) (A) and mammals (B) (Global Population Dynamics Database, reproduced with permission from (Clayson, 2015)). Species are indicated by letters as follows in panel (A): a) Willow grouse (*Lagopus lagopus*), b) to g) Rock ptarmigan (*Lagopus mutus*), h) Ruffed grouse (*Bonasa umbellus*), i) Hazel grouse (*Bonasa bonasia*), j) Bobwhite (*Colinus virginianus*), k) Grey partridge, l) California quail (*Callipepla californica*), m) Willow grouse, n) Red-legged partridge, o) Black grouse, p) Northern bobwhite, q) Rock ptarmigan, r) Wood grouse, s) and t) Red grouse (*Lagopus lagopus*), u) Hazel grouse, v) Wood grouse. In panel (B) species are indicated by letters as follows: a) San Joaquin kit fox (*Vulpes macrotis*), b) and c) Canadian lynx (*Lynx canadensis*), d) Chamois (*Rupicapra rupicapra*), e) and f) Greater kudu (*Tragelaphus strepsiceros*), g) Lion, h) Grey wolf, i) African wild dog (*Lycan pictus*), j) American marten (*Martes americana*), k) Fox (*Vulpes* spp.), l) and m) Wolverine (*Gulo gulo*), n) Dall Sheep (*Ovis dalli*), o) Chamois (*Rupicapra rupicapra*), p) Brown bear (*Ursus arctos*), q) Black rhinoceros (*Diceros bicornis*). Some species are represented by more than one single local population.

observed? Most of the tools commonly employed are testing a statistical hypotheses consisting of a negative trend of a time series against a null model assuming no trend at all (i.e. an uninformed null model of no effects, that is, of equilibrium) unless informed prior information is provided in the form of Bayesian priors or a priori frequentist power tests. Importantly, the reliability of the statistical tests are sensitive to the time window considered (Nichols and Williams, 2006). All time series in Fig. 2 show ‘stable trends’ over a long time window, a diagnosis made using a standard statistical tool to detect trends (e.g. Stefanescu et al., 2011). However, when we select random 10-y windows for the three commonest species in Fig. 2, we see qualitatively that trends may be quite different among windows, and different from the stability described for the whole time series (Fig. 6).

Another case in which the time window considered may bias the conservation diagnosis and the triggering of management actions, is that of invasive species. These species offer a good opportunity to study population dynamics since colonization, which should show, following the logistic model of population growth, an initial exponential growth followed by a stabilization around a carrying capacity. However, when the invasive species successfully settles in the new environment or community, it may show boom-bust dynamics, i.e. the growth of a population to outbreak levels, followed by a strong decline or a stabilization around a dynamic equilibrium (Strayer et al., 2017). This equals to transient dynamics occurring after a perturbation, in which there is amplification and attenuation before attaining long-term dynamic stable states (Stott et al., 2010). This is the opposite that happens, for example, in the more gradual and predictable changes that take place in ecological succession. This non-linear boom-bust phenomenon has been described for several taxa, e.g. irruptive dynamics in ungulates and population collapses in human societies (Downey et al., 2016; Forsyth and Caley, 2006; Oro, 2020). Fig. 7 shows some examples of boom-bust dynamics for waterbirds colonizing some wetlands patches of the western Mediterranean after legal protection: maximum population densities were attained during the first years after colonization, and later on there was a strong decline by overcompensation to much lower values (Martínez-Abraín et al., 2016). Therefore, observing a time window encompassing less than a few generation times may bias the

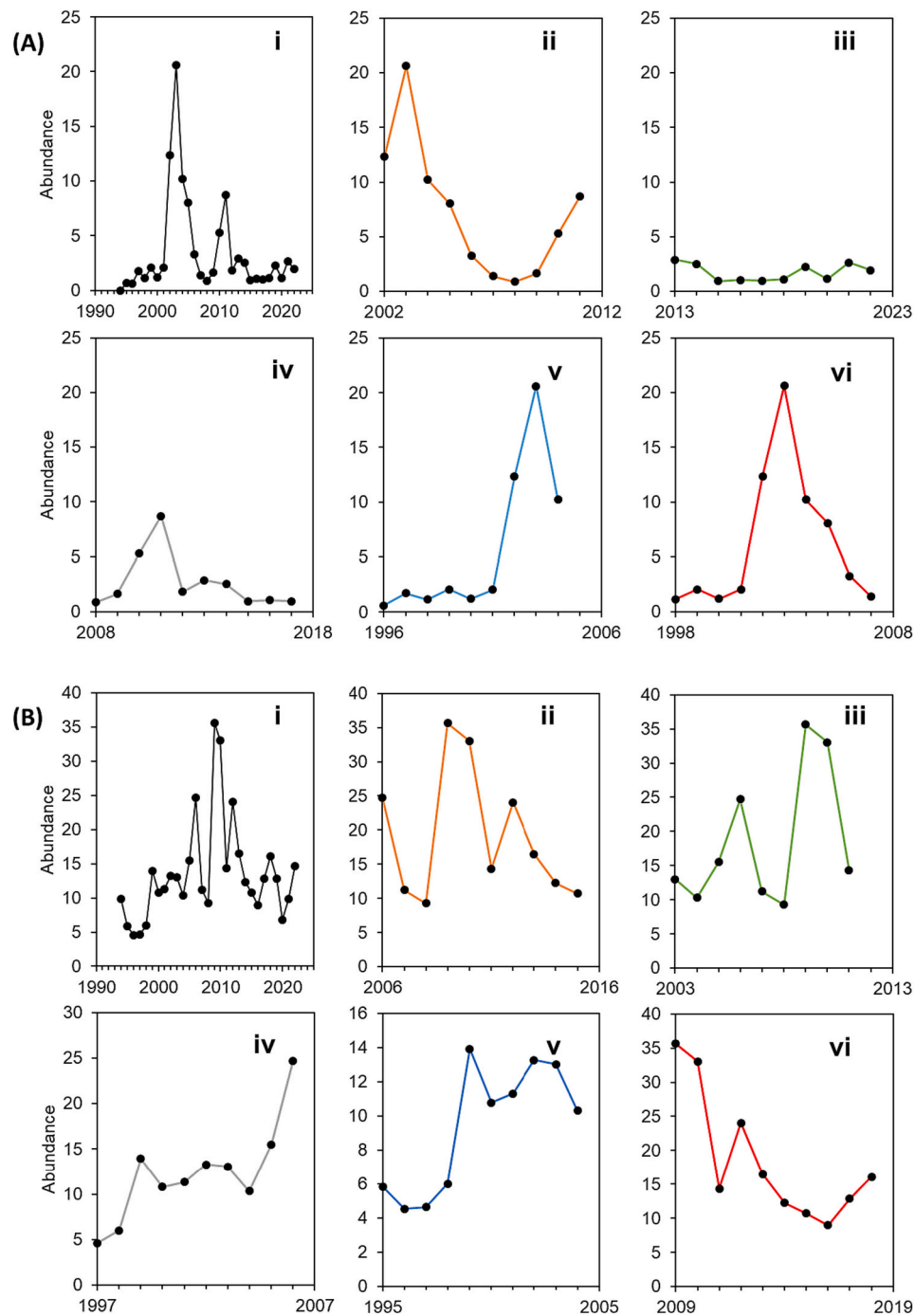
conservation diagnosis and the expected impact of certain species when colonizing a habitat.

Time window may also bias the prognosis made when a conservation or management action is set to assess its goodness (e.g. using an adaptive management strategy). Examples are fishing policies for sustainable fisheries, eradication of invasive species, habitat restoration, and reintroduction of endangered species. Hastings (2016) emphasized the need for an explicit consideration of time in ecological models, since ecosystems commonly delay their responses to management actions (Kuussaari et al., 2009). Moreover, those responses are non-linear and correspond to transient dynamics that may last long periods of time (Francis et al., 2021).

A rule of thumb to avoid or to reduce the potential biases of using too-short time windows could be to encompass at least 2–3 generation times of a species, considering that generation time varies with the species’ life history and increases with its body size. For medium and long-lived species, this means that time windows should consider multi-decadal time scales for proper diagnosis. Life histories may also help interpreting temporal dynamics and the potential bias of short time windows for assessing population decline with reliability. For example, some insects show outbreaks and cyclic dynamics (Hastings et al., 2018), while others use ephemeral resources and show highly stochastic dynamics (Hanski and Cambefort, 2014). Finally, there is a deep-time dimension (from million years to centuries) provided by palaeontology and archaeology, to interpret properly the temporal dynamics and the occurrence of transients in ecological systems, with consequences for managers and policymakers, e.g. in restoration (Gillson, 2015; Jackson and Erwin, 2006; Martínez-Abraín et al., 2022; Oro et al., 2022; Rick and Lockwood, 2013; Vidiella et al., 2021). After all, the composition of ecosystems is mainly a matter of contingent events that have happened over long historical windows (Margalef, 1975, p. 197).

#### 4. The spatial window: the challenges to interpreting non-equilibrium in spatial dynamics

Many empirical ecological studies have historically ignored the spatial scale of population dynamics because monitoring at large spatial



**Fig. 6.** (i) Time series over 29 years of butterflies showing stable dynamics for the period 1990–2020: (A) *Melitea celadussa*, (B) *Argynnis paphia*, (C) *Cupido alcetas* on repeated transects (CBMS <https://www.catalanbms.org>). Panels (ii) to (vi) show five random 10-y temporal windows for each 29-y time series in (i).

scales is commonly challenging (May, 1999; Oro, 2013). Spatial heterogeneity is inherent to all ecological systems, and it generates local populations inhabiting either suitable patches or patches at the edge of the distribution range, where habitat suitability tends to be lower. Yet, spatial heterogeneity is dynamic over time and it influences contractions and expansions of spatial distributions of any species. All those spatio-temporal dynamics determine that for most species, some local populations are necessarily small and decreasing, even showing local extinctions by demographic stochasticity. Fig. 8 shows the local population dynamics in several patches where a colonial waterbird breeds in the western Mediterranean. At the local level, some patches show

ephemeral colonizations, and most of them go extinct after some breeding seasons. Nevertheless, at a large spatial scale the metapopulation shows some dynamics that resemble a logistic growth reaching a dynamic equilibrium, in which fluctuations are bounded within a stochastic range of density. In highly nomadic species the metapopulation is the right spatial scale to consider. This example shows that looking at any of the local populations individually may only inform about local dynamics, which responds to the connectivity between local populations, especially in highly vagile organisms (e.g. insects, fish, and birds). The processes of dispersal (i.e. immigration and emigration) influence local population dynamics, whereas the global dynamics are

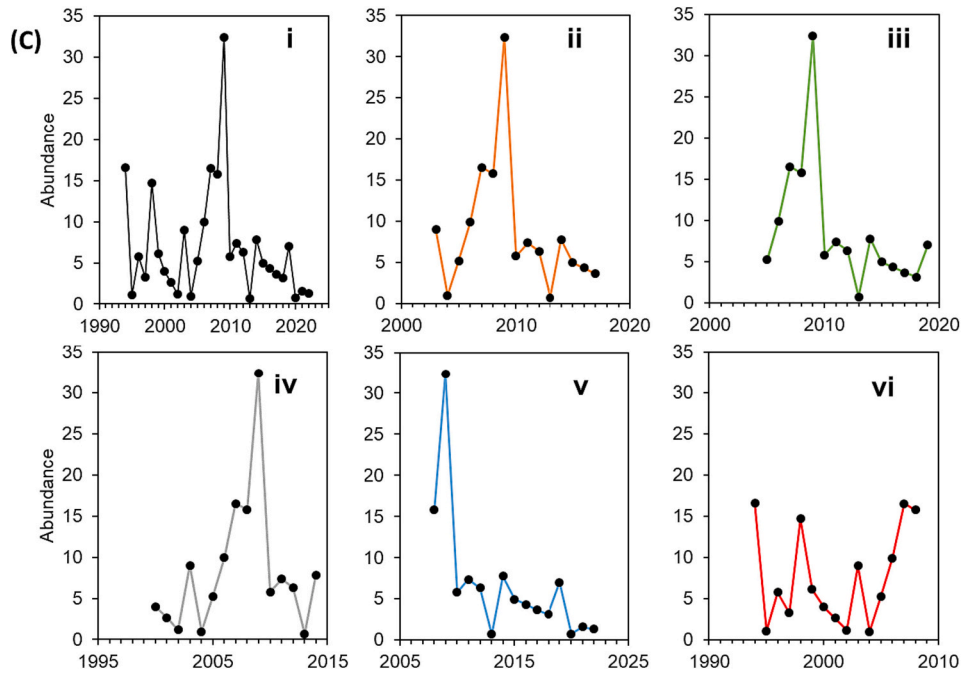


Fig. 6. (continued).

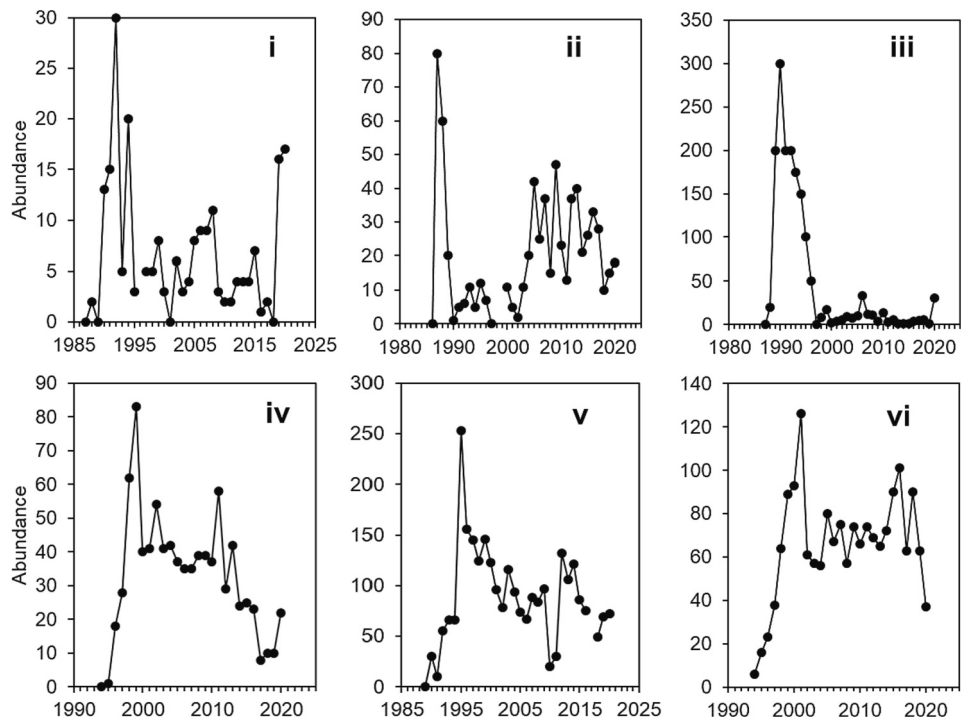


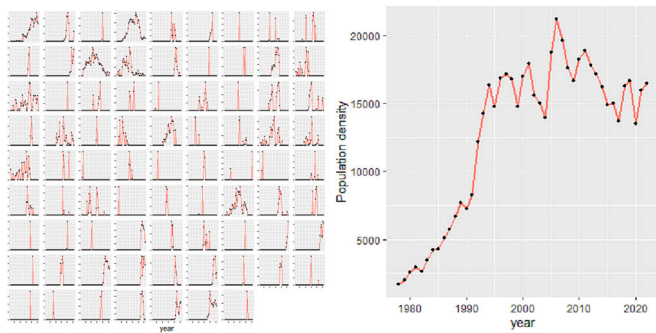
Fig. 7. Examples of boom-bust dynamics for different local populations of breeding waterbirds recolonizing a set of wetlands in the western Mediterranean after effective protection (updated from Martínez-Abraín et al., 2016): (i) Red-crested pochard (*Neta ruffina*); (ii) Common pochard (*Aythya ferina*); (iii) Eurasian coot (*Fulica atra*); (iv) Purple swamphen (*Porphyrio porphyrio*); (v) Stilt (*Himantopus himantopus*); (vi) Pied avocet (*Recurvirostra avosetta*).

more influenced by environmental stochasticity together with deterministic factors, such as the establishment of protected areas.

Some theoretical models, such as the ones describing source-sink dynamics, show that population sinks are only maintained if there is rescue from the source in the form of immigrant individuals. The original model assumed first a dynamic equilibrium in population density within the ensemble of patches, and secondly that a patch is a source only when there is net stability in population density (Pulliam, 1988).

When relaxing these assumptions, the occurrence of sources and sinks is expected in actual metapopulations occupying patches of heterogeneous suitability (Furrer and Pasinelli, 2016; Runge et al., 2006). The consideration of the spatial scale allows theoretical ecologists to develop predictive models based on equilibrium relationships between local populations. For example, Carpenter (2002) showed a model in which the resilience at the core distribution of a certain species should be larger than at the edge of the distribution, where mortality may be larger

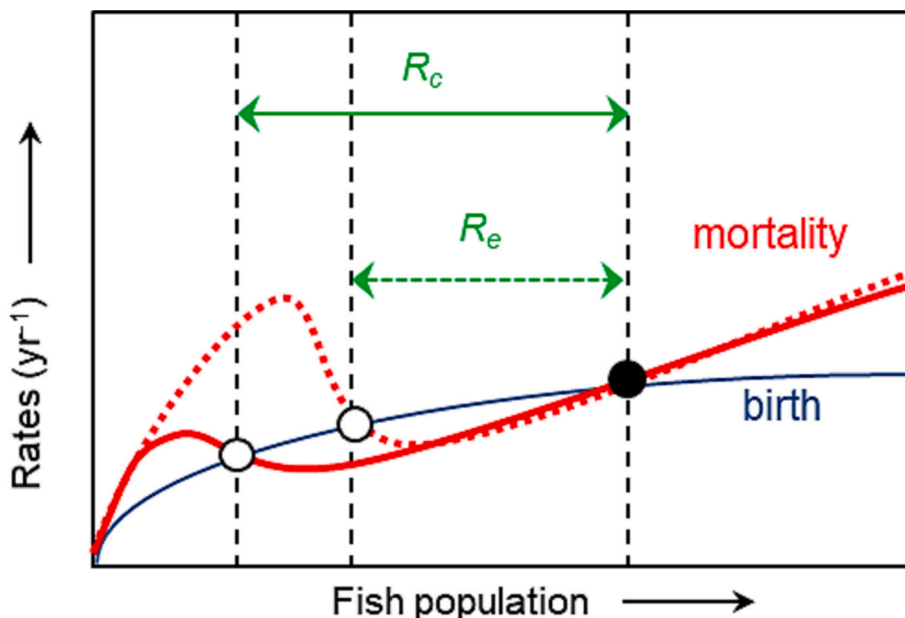




**Fig. 8.** (A) Population dynamics (in number of breeding females during 1978–2022) in 79 breeding patches of Audouin's gulls (*Ichthyaeus audouinii*) from the western Mediterranean metapopulation, which comprises >90 % of the total world population. Since some patches only have held a few breeding females, all panels are scale-free for the number of females. (B) Number of breeding females for the whole metapopulation. Note that annual fluctuations in the metapopulation density over the state of dynamic equilibrium are large.

(Fig. 9). Some empirical studies show that resilience of edge versus core populations may also be lower due to poor immigration and hence lack of rescue effect after mortality or massive emigration (Martínez-Abraín et al., 2019a, 2019b, 2023b).

Spatial heterogeneity in habitat quality in the distribution range of most organisms represents a challenge for applied conservation, especially when restoration, and actions to promote recolonizations, do not consider the relative quality of the targeted patches within the metapopulation, to which individuals may disperse looking for increasing fitness prospects (Seward et al., 2019). Furthermore, anthropogenic activities change the spatial dynamics and the distribution ranges of entire communities (Martínez-Abraín et al., 2019a, 2019b). The challenge increases because many environmental laws and management actions are set at a regional level (administrative units) rather than considering the conservation status of the targeted population or community at global level or, at least, at the level of “natural” geographic units. A change in this direction would certainly much improve the efficiency of conservation practice and would promote a reduction in legislation and paperwork.



**Fig. 9.** Theoretical model in which fish birth and mortality rates fluctuate with population density in two habitat types (core and edge): while the model considers that birth rates (blue solid line) are common between the core habitat and the edge habitat, mortality has a different shape in the two habitats (red lines). This determines a common stable attractor (solid dot) and two different unstable attractors (open dots) for each habitat (dotted vertical lines show equilibria). At the end, the two unstable attractors limit a differential resilience for the core and the edge habitats ( $R_c$  and  $R_e$  respectively) (adapted from Carpenter (2002)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

## 5. The good, the bad, and the reified: a tribute to Lawrence Slobodkin

Francis Bacon's *Novum Organum* (1620) already addressed the problem of preconceived ideas and their potential for hindering scientific progress. Applied conservation involves ecological knowledge, which is more open to mass-media opinions and slogans than many other scientific disciplines, and thus it is particularly sensitive to concepts that sometimes are embraced as general rules and truisms (e.g. equilibrium and single stable states). In an essay dealing with how some concepts in ecology and conservation have become reified, Slobodkin (2001) warned that “the designation of certain kinds of species as good or bad – specifically, alien species are bad and ‘native’ species are good – is empty and misleading. While invasive species, in some cases, actually do damage native species, the generalization that invaders will reduce species diversity is not well founded.” What is certain is that the arrival of a new species (either alien or native by colonization or re-colonization) may generate some consequences, and will introduce some kind of change in the dynamics of the host ecosystem and its populations and communities. While ecosystems are open systems and thus the arrival of species is a process commonly occurring at both evolutionary and ecological timescales, determining the fitting capacity of communities to the accelerated arrival of colonizers due to anthropogenic causes, is challenging. In extreme cases, such as islands, the arrival of humans and their associated species have caused ecosystems to shift from a non-equilibrium state formed by native species to another non-equilibrium state, commonly composed of a large number of alien species, with the extinction of several native species, if not all (e.g. Oro et al., 2022; Vellend, 2017). Empirical and theoretical studies have been controversial about the relationship between diversity, stability, and resistance to invasion, whereas studies analyzing the variability in stability after the arrival of invasive organisms are scarce (Hooper et al., 2005; Levine and D’Antonio, 1999). Soulé (1985) already stated in his seminal paper that ‘even if it could be shown that a decrease in species diversity led to desertification, eutrophication, or the piling up of organic material, it is still not a logical conclusion that such consequences are bad.’

Another reified concept in ecological studies highlighted by Slobodkin (2001) is the carrying capacity, which is strongly linked with the concept of ecological stability in populations (e.g. the logistic model). While a good fit by a logistic growth model (with an asymptotic final state of a population subjected to per-capita competition for resources)

is found in some empirical and in many experimental studies, there are many empirical examples where the carrying capacity is sensitive to environmental stochasticity. In these cases, populations show fluctuations that do not have a deterministic skeleton, corresponding to a single stable state. The example we present regarding Audouin's gulls (Fig. 8) is also valid here to show how local populations are seldom at equilibrium, whereas the whole metapopulation (the true ecological unit or the right spatial scale to work with) may follow approximately a logistic behavior, likely due to the limitation of suitable breeding habitat. Despite its limitations, there are some heuristic applications of the carrying capacity concept to conservation. For instance, populations and communities living in small patches (such as tiny islands or alpine mountaintops) are necessarily small, and thus more sensitive to the

negative effects of demographic stochasticity. Another applied example is the fact that restoring or protecting habitat that had been lost or altered, would increase the carrying capacity for a given animal community, although the population dynamics may change differently for each of the species in the community after the conservation action (see Martínez-Abraín et al., 2016 for an example with waterbirds). In general, reified ideas stimulate the waste of resources to favor particular species (e.g. many reintroductions) (Terui et al., 2023) and at the same time they preclude the application of proper conservation actions; for example, the recognition of the ecological and evolutionary roles of fire in renewing limiting resources in Mediterranean regions. The idea of stability also supports the increasingly popular idea that managers should promote the *balancing* of biodiversity losses and gains which,

### Box 3

#### Equilibrium in ecology and the architectural metaphors.

The Roman Coliseum or the Agrippa Pantheon, like all other major Roman-time constructions, were made of a special type of concrete (*opus caementicium*), with physical properties for speed of execution and extreme endurance over time. Proof of that is that we still admire them >2000 years later, despite all the major efforts done by people to disassemble these buildings to reuse materials after the fall of the Roman Empire. Hence, architecture provides a good reference for permanence, stability, constancy, and balance. Accordingly, ecologists have been tempted repeatedly to use metaphors taken from the domain of architecture to define ecological concepts based on the idea of equilibrium. We will immediately show that for three cases, but likely, there are many others.

#### Keystone species

A keystone is the middle stone on the top of an arch that holds all other stones in the arch in position. keystones, therefore, are key sine qua non pieces of an arch. If the keystone was to be removed the arch would fall down immediately, and no arch whatsoever would therefore exist anymore. That idea has pervaded ecology as it is very appealing to suggest that despite all species having equal weights in ecosystems, some species are "more equal than others". A keystone species is usually defined as a species with a disproportionately large effect on ecological communities in its abundance. This idea was first suggested by Robert Paine (1969), and refined later on by himself (Paine, 1995). Typical examples of the so-called keystone species are sea otters (*Enhydra lutra*) or sea stars (*Pisaster ochraceus*) which carry out top-down regulation in littoral ecosystems. However, contrary to what happens in the case of an arch, if sea stars or sea otters are removed, communities do not fall down and become something chaotic, useless, or formless. A rocky coastal community without sea stars simply becomes less diverse and more dominated by mussels (but see a critical view regarding diversity reduction in Lafferty and Suchanek (2016)). A littoral kelp "forest" deprived of sea otters moves to a bottom community dominated by sea urchins, as consumers of kelp holdfasts, leading to an intense reduction in kelp and in turn in other marine life, as kelp assemblages act as nurseries for fish. In any of these two examples, communities disappear. They are only transformed into something different, maybe more simplified (Piraino et al., 2002). However, by any means, this is equivalent to a fallen arch with no supportive function.

#### Ecological niche

A niche is a semi-circular recess in a wall typically used to place statues inside. The first ecologist tempted with borrowing this architectural concept for zoology was the American field biologist Joseph Grinnell, who defined the concept of ecological niche (Grinnell, 1917). By that, he meant the sum of the habitat requirements that allow a species to persist and reproduce. Later ecologists incorporated the term and redefined ecological niche as the role of a species in its biotic environment (Elton, 1927), or as a detailed description (n-dimensional) of the ecospace occupied by a species (Hutchinson, 1965). The problem with using the architectural concept of niche is that it forces an idea of stability of the niche (unchanging over time) and the fact that between two niches one should not find anything but a blank wall (CM Herrera, pers. com.). This definition of niche based on constancy over time and stability collides with the modern and dynamic concepts of niche construction and habitat shaping by which organisms are continuously modifying their environments and adapting to the change that they generate (Piraino et al., 2002; Shea and Chesson, 2002). Additionally, niches are not pre-defined in the background (as they are in a building), but are created depending on the species present in a community (see the section on islands below). For example, a niche for parasitism cannot exist unless a proper host or parasite is present (Martínez-Abraín et al., 2004).

#### Network architecture

Ecology moved in the 20th century from the use of models for competition, parasitism, or mutualism between two species, to the development of ecological networks in which many species are considered simultaneously, as in the study of plant-animal mutualisms (Bascompte and Jordano, 2013). Networks aim to analyze the architecture of communities, including the study of connectivity, nestedness, modularity, centrality, robustness, specialization, or dependence. Again, as in the case of keystone species, the concept of networks builds upon the idea that the removal of particular species (with a special set of connections this time) will have larger implications for the whole community, compared to the removal of other less-connected species. This idea spins around the theoretical assumption of collapse as a possible outcome of species removal. However, communities never collapse in the sense of a bridge collapse, becoming something useless for its originally planned function. There are no a priori planned stages in ecosystems (plant progressive and recessive succession in relation to forest fires is proof of that), and no stages are better than others, except from an anthropocentric viewpoint in which the maximization of the biomass or diversity functions is always seen as the most desirable stage. Communities and metacommunities never vanish after the removal of one species. They simply get transformed, as matter and energy do in the universe, as species do in evolution. The fixed idea of network architecture holds on an equilibrium-based view of communities, with some stages more desirable than others. Examples are the long-standing discussion about the interplay between diversity and stability or the highly anthropocentric concept of ecological services. Ecosystems are above all the result of a long historical process in which stochasticity and contingency play an important role, in addition to deterministic factors (Margalef, 1980).

once again, lacks a biodiversity reference value to be targeted (Kareiva et al., 2017). The term ‘conservation biology’ itself implies a static view of ecosystems. Some have argued that the term “conservation” can be misleading because it implies that the goal is to preserve ecosystems or species in a static state, rather than recognizing that ecosystems are constantly changing, and hence that it is ecological and evolutionary change potential that needs conservation (Callicott, 1997; Soulé, 1985) (Box 3).

## 6. Insights from islands’ ecosystem dynamics

Islands have traditionally been considered a paradigmatic ecosystem to study ecological and evolutionary processes (Losos and Ricklefs, 2009; Whittaker and Fernandez-Palacios, 2007). A reliable interpretation of the ecosystem dynamics in islands is dependent, to a large extent, on a good knowledge of the fossil and subfossil species that may have been present in the past (Steadman, 2006), and also on the levels of genetic differentiation reached by incoming species over time (Ricklefs and Bermingham, 2001). Among inherently open ecological systems, islands (and more especially oceanic islands) are relatively simplified and closed systems. Yet, their compositional diversity is lower than in similar-sized plots of the nearest mainland, because not all organisms have the capacity to cross large marine barriers around islands (e.g. Martínez-Abraín et al., 2023a).

The number of species in a given moment in time (snapshot) results from the predictions of the theory of island biogeography (McArthur and Wilson, 1963), that is, from the equilibrium between colonizations and extinctions, but this equilibrium is seldom stable. It moves to the right and the left as new species arrive (or evolve) and new species become locally extinct. These changes do not need to be always small, as the processes of colonization and extinction tend to be non-linear. Birds in islands are good study models to explore how their population and community dynamics are unstable. For instance, the number of successful colonization attempts on the island of Mallorca (western Mediterranean) over the last 40 years was much higher than the number of failures and the number of colonizations was not linear over the years (Martínez-Abraín et al., 2023a). That unbalance would increase connectedness among their elements, it would change the ecological reorganization, and would potentially flip into alternative domains of community dynamics. As said before (Box 1), the successful settlement of a new species could be at the cost (loss or decrease) of some component of the ecosystem (e.g. a competitor), since the energy flux in that ecosystem is rather stable, unless ways of temporal or spatial segregation are possible (Martínez-Abraín et al., 2005). The conclusion, considering several studies on community dynamics in islands, is necessarily that community dynamics of large land-bridge islands are permanently out of equilibrium, at least regarding zoological groups with great vagility.

Despite their lower and ever changing community dynamics, island ecosystems are functionally active (Naeem and Wright, 2003). One of us has studied the dispersal of fruits (acorns) of the holm oak (*Quercus ilex*) on Mallorca Island, and the only seed disperser identified so far was the wood mouse, *Apodemus sylvaticus*, a species which was introduced by colonizing humans some 4000 years ago. At least since the extinction of an endemic dormouse by colonizing humans, introduced wood mice may have been the only responsible (other than humans) for the recruitment of young holm oaks, whose forests cover a large surface of the island ranges. Obviously, this condition brings more vulnerability to the island oak forests, as the local extinction of wood mice would leave them without dispersers, with severe ecological implications. It is the redundancy in ecological tasks that makes mainland ecosystems less vulnerable to abrupt regime shifts following the extirpation of one species, compared to islands, and hence more likely to remain in time and space (Biggs et al., 2020). This is a derivative of the old diversity-stability debate, stating that constancy in community structure is more likely to be maintained over time in species-rich systems (McCann,

2000), although it can always proceed the other way around (i.e. higher diversity evolving in physically more stable systems)(Margalef, 1980).

## 7. Insights from the medical science: the challenges to optimize conservation actions

Is it possible to quantify ‘stable’ populations and communities? If so, we might tackle the challenge to identify when populations, communities, and ecosystems are far from equilibrium in a way that is altering their functioning. Managers act when they consider that their unit of management (e.g. a local population, a specific habitat) is showing signs of deterioration and decline. The parallels with the medical discipline are obvious (Soulé, 1985), although the scales of goals are different: while medicine targets the individual, conservation mostly targets more inclusive hierarchical levels, such as populations and ecosystems, which are composed of nested complex systems, from DNA repair and disordered proteins to metapopulations or entire ecosystems.

Let us explore here how medicine operates to manage human health at the individual level. When should a physician take part? When should a person be considered sick? Are disease and illness equal? Physicians manage illness and cure disease. Some philosophers interested in medical science state that defining the two terms is not straightforward (Boorse, 1977, 1975). In medical science, the utility of the terms ‘normality’, (in both its statistical and evaluative meaning, and ‘functionality’ (which are strongly linked with each other) have been widely debated in the literature (Boorse, 1977; Wachbroit, 1994). This is interesting when we move the debate to the arena of ecological conservation and management. Can conservation managers use statistical normality to conclude that a certain population, community, or ecosystem is out of equilibrium in a way that is threatened by extinction? There is a certain agreement in medical science that normality measures (e.g. range of values in parameters obtained in blood analysis) are helpful to detect a ‘non-equilibrium state’, but doctors know that this is not a truism, and that the opposite (i.e. a sick person having values within statistical ranges) can also occur. Similarly, it is commonly accepted that all humans have some disease or another and that some of them (such as minor lung irritation) are quite universal and often the product of a trade-off to avoid a major disease. Biological systems across scales, from DNA replication in cells to ecosystem functioning, have deficiencies and errors that have been tinkered by evolutionary forces due to the high costs of achieving 100 % accuracy (Tawfik, 2010). Natural selection works far from perfection, operating with trade-offs in which minor chronic disease remains as a consequence of selection against diseases that jeopardize the survival of the individual. Sometimes biological systems take extreme values as a defensive mechanism, such as physiological anemia linked to pregnant women as a likely mechanism of iron reduction in blood to prevent bacterial infection, but that is commonly perceived as an undesirable medical situation (Sánchez et al., 2018). Another example is basal body temperature that has been selected toward the upper end of possible values, so that when we increase our temperature by a few degrees or less, we already are under a condition of disequilibrium (i.e. fever), likely for prevention of further microbial infection (Kluger et al., 1975). Determining when a population, not to mention a community, has lost its capacity to buffer against functional deficiencies caused by stochastic environments and perturbations is extremely challenging. This is especially true when perturbations accumulate over time (e.g. spill pollutants, overharvesting, strong habitat loss) and population may respond non-linearly beyond threshold values. In an attempt to delineate limits for ecosystem functioning, Rockström et al. (2009) defined the *safe operating space*, as a range within which humanity should restrain anthropogenic pressures. At the same time, management strategies should increase variability within that range to decrease ecosystem fragility (Carpenter et al., 2015). As stated above, the non-trivial difference between medicine and ecosystem conservation is that the former focuses on the individual, and its functional capacity to cope with perturbations

that may generate disease and ultimately death, whereas the latter focuses on populations and communities composed of individuals, and the death of all individuals is a much unlikely event.

Another crucial disadvantage of biological conservation compared to medicine is the potential for experimental research to assess departures from dynamic equilibrium. Experiments allow for testing hypotheses in a formal way, and they reduce the noise (e.g. interactions, stochasticity) of open complex systems. An important body of medical research involves experimentation with biological models, and advances in medicine would be hampered in the absence of experimental research. In contrast, experiments in ecosystems to test their robustness (e.g. their resilience to recover from a perturbation and remain relatively stable), are much more challenging (Kimmel et al., 2021). Nevertheless, there are several successful examples of experiments in the field, such as the paradigmatic study of aquatic food webs in lakes (Carpenter et al., 2011). Other studies take advantage of drastic environmental changes and perturbations to study the before and the after (Elton, 2001; Hilborn and Ludwig, 1993; Hooper et al., 2005). Examples are the implementation of environmental policies (e.g. fishing and waste policies, effective protection of habitats, eradication of alien species in islands), fires, and earthquakes, which allow studying the transient dynamics outside the asymptotic phases of the systems (Lindenmayer et al., 2010; Oro et al., 2013, 2022; Tenhumberg et al., 2009). Nevertheless, there is a small room for replicability in those examples, and extrapolations to similar systems need to make critical assumptions (Elmqvist et al., 2003; Turchin, 2003). Some reductionist approaches, such as experiments in micro- and mesocosmos, yet informative in many cases, are hardly transposable to real ecosystem functioning, because they necessarily simplify the study systems to overcome the challenge of interpreting multiple interactions and responses (Carpenter, 1996).

Despite the limitations just mentioned, conservation scientists have long devoted efforts to designing programs of long-term monitoring and evaluation of environmental impacts, including anthropogenic action. An example is the BACI (Before-After-Control-Impact) approach, which involves comparing changes in ecological variables in a study area (i.e., the impact area) to changes in a control area before and after a modifying factor operates. The basis of these tools, which were born four decades ago, is to apply conservation actions and policies based on scientific evidence (Pullin et al., 2009). The limitations of BACI and other approaches have been discussed, and methodological improvements have been proposed (Conner et al., 2016; Underwood, 1991). Again, conservation, compared to medicine, is commonly limited by the literature published on specific impacts, and the tools are still under evaluation to identify its weaknesses and promote further developments (Gurevitch et al., 2018; Haddaway et al., 2015; McConnachie et al., 2016).

## 8. Concluding remarks

Complex ecological systems are not in equilibrium. Thus, we may wonder whether there is room for applied management and policy-making to harmonize the lack of ecosystem equilibrium we see in the real world with the conceptual framework of stability and equilibrium. Quantitative indicators of non-equilibrium are common in other sciences such as chemistry, physics, and physiology, but they are much more challenging in an ecological context. In populations, the extremes offer no doubt: populations formed by millions of individuals are abundant, and those formed by tens of individuals are rare and more prone to extinction. However, the passenger pigeon was an extremely abundant species that went extinct in a short period (Halliday, 1980). What happens between those two extremes? Is a population formed by 500 individuals of a given species necessarily more threatened than one composed of 50,000 individuals? How sensitive is a metapopulation and its viability to the extinction of several local populations? The responses to those apparently simple questions may be strongly context-dependent, and this highlights the limitations that ecological research

may have to be applied both in specific conservation actions and the development of comprehensive policies (Hilborn and Ludwig, 1993; Scoones, 1999; Slobodkin, 1988). Yet, managers make decisions that are constrained by laws, and they have to deal with different sets of stakeholders that may have opposing interests.

We ignore how often and how deeply managers and policymakers use the academic literature for making decisions (Pullin et al., 2004). While empirical ecological research may generate more interest to be applied by managers, theoretical ecological studies may seem to them a difficult tool to be used. In fact, the abstraction that theoretical models need to be constructed is very stimulating for the advance of conservation management. Some examples are metapopulation theory, network theory, and the theory of critical transitions. They have offered not only a conceptual framework to be considered in conservation, but they have also inspired rules of thumb and have generated empirical feedback for stimulating the development and refinement of further theoretical studies (Cuddington et al., 2013; Doak and Mills, 1994). Theoretical advances in the ecological domain should consider what the main concerns of managers and policymakers are if theoreticians want their research to be applied. Within an adaptive framework, applications should test and inform theoretical advances (Carpenter et al., 1999). It is relevant both for theoretical ecologists and managers to improve their communication to bridge the gap between generalizations and particularities (Belovsky et al., 2004; Wallington et al., 2005). Importantly, there is room for benefit from both sides. The manager gets a better knowledge of prior information (theory), and the scientists update their priors continuously with new fresh incoming information from the managers who may be closer to the occurrence of changes. This is especially interesting now, as rates of change of former theoretical principles can be fast under the current scenario of global change.

We hope that our review provides some useful take-home messages both for conservation practitioners and policymakers. First, the need to incorporate most of the features of complex ecosystems in their mind settings and professional thinking while *evaluating* all the information available to make decisions about the what, the where and the when (see Box 2). Adaptation, modularity, and nestedness increase resilience against perturbations, no matter the idiosyncrasy and environmental conditions of the managed ecosystem. Managers should promote the persistence of non-equilibrium, since this is the basis of the adaptive mechanism of stochastic ecosystems (Carpenter et al., 2015). Secondly, developing a deeper knowledge of the evolutionary life histories of the managed species and other slow processes such as the process of soil formation would help to set heuristic conservation actions and to reduce the biases we have reviewed here (Carpenter et al., 1999; Hastings, 2016; Martínez-Abraín and Oro, 2010; Norris, 2004). For instance, rarity may be a life history strategy, and the fossil record suggests that specialists (which in many cases are rarer than generalists) have not been more vulnerable to extinction than abundant species (Colles et al., 2009). Lastly, managers and policymakers should avoid the perils of developing reified and dogmatic ideas, and focus on the specific features of the systems they are acting upon, without assigning any preconceived value judgment to any component (e.g. keystone, good, bad, superior, untouched, pristine, magnificent or superabundant) (Kareiva et al., 2017; Martínez-Abraín and Oro, 2013; Slobodkin, 2001), no matter how difficult this is.

## CRedit authorship contribution statement

**Daniel Oro:** Conceptualization, Writing – original draft. **Alejandro Martínez-Abraín:** Conceptualization, Writing – review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

No data was used for the research described in the article.

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