



# Identifying regime shifts, transients and late warning signals for proactive ecosystem management

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## ABSTRACT

Conservation Biology fosters the study of Earth's ecosystems and biodiversity aiming at protecting species and their habitats from menaces causing the erosion of biotic interactions and extinctions. Its ultimate goal is to preserve biodiversity and promote sustainable ecological management maintaining both ecosystem's resilience and services. Ecosystems display complex patterns in time and space due to the intrinsic nonlinear nature of their interactions and can suffer regime shifts driven by the agents of global change. During the last decades, Ecology has turned from the equilibrium metaphor to the paradigm of non-equilibrium dynamics. This involves putting into the scene multiple stable states, nonlinear regime shifts, stochasticity, and ecological transients. These aspects are also crucial for biological conservation since they play a fundamental role in species' persistence, ecosystems' resilience, and in detecting warning signals prior to either the collapse or the recovery of the ecosystem. In this contribution, we discuss ecological regime shifts caused by tipping points in real ecosystems. Then, we provide information on some known dynamical features from theoretical ecology and dynamical systems theory associated to tipping points, mainly given by transient phenomena and the characteristic statistical patterns tied to early warning signals. These features are illustrated with a single-species mathematical model including facilitation and immigration. We also introduce and provide evidence of late warning signals as a way to identify when a tipping point has been surpassed but the system still remains in a transient state and recovery may be still possible. Our main goal is to near non-equilibrium concepts in Ecology to the conservationist community and promote bridges between such concepts and the management and conservation of ecosystems.

## 1. Introduction

Ecosystems are dynamic and interconnected systems comprising abiotic and biotic components that exhibit **emergent properties**<sup>1</sup> resulting from intra- and inter-specific interactions. These interactions form a community characterized by feedback mechanisms that regulate the flow of energy and matter within the system. Furthermore, ecosystems are subject to external drivers, including natural disturbances and human-induced perturbations. Ecosystems' scales range from small ponds to entire biomes such as tropical rainforests or oceans and they are currently largely influenced by human activity, in what has been labeled as the **Anthropocene** (Lewis and Maslin, 2015). One of the major drivers of population dynamics are the intrinsic ecological interactions among

species. These mainly include symbiotic interactions such as mutualism or facilitation, or competition and victim-exploiter dynamics (Murray, 1931; May and Mclean, 2007), which can simultaneously occur. These ecological interactions, which are highly **nonlinear**, can give place to several dynamical patterns, including **deterministic** (intrinsic) fluctuations (Elton, 1924; Elton and Nicholson, 1924; Schaffer, 1984; Gamarra and Solé, 2000), **regime shifts (RSs)** (Scheffer et al., 2009; Rietkerk et al., 2004), or strong density-dependent collective responses triggered by perturbations and giving place to social **tipping points (TPs)** (Oro et al., 2023). On top of that, environmental conditions like water availability, climatic perturbations, and human-caused disturbances such as the effect of greenhouse gases, pollution, over-exploitation, fires, or introduction of invasive species, can precipitate such RSs (Folke et al.,

*Abbreviations:* TP, tipping point; RS, regime shift; Bif, bifurcation; WS, warning signal; CT, critical transition; LI, leading indicator.

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<sup>1</sup> Words in bold italics are defined in a Glossary Section at the end of the article.

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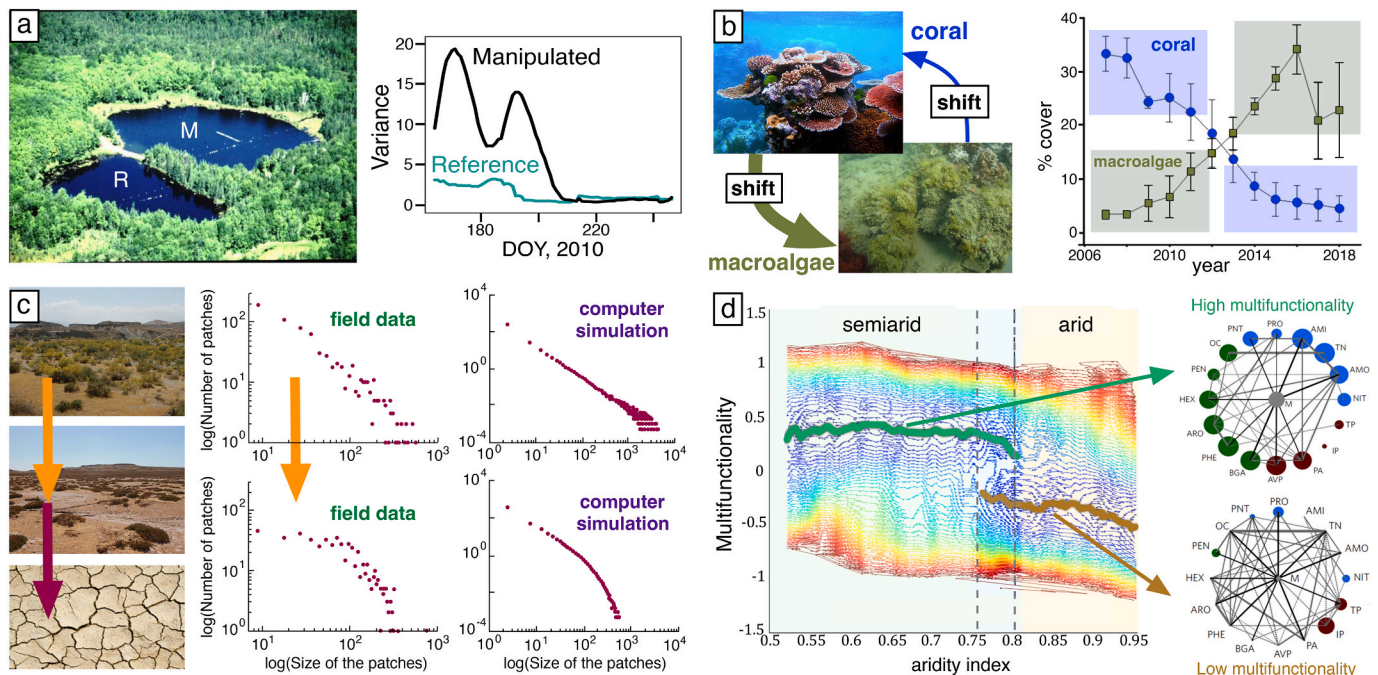
2004). These RSs when being catastrophic or abrupt are said to be driven by TPs (Scheffer et al., 2001; Conley et al., 2009; Andersen et al., 2009).

TPs involve a sudden and dramatic change to a different state after crossing a **critical transition (CT)**. The definition of TPs in scientific literature is broad (van Nes et al., 2017), but, generically, two specific interpretations, which are related, are dominant (Scheffer et al., 2001; Scheffer and Carpenter, 2003). The first one defines TPs as catastrophic **bifurcations (Bifs)** in mathematical terms (Scheffer et al., 2009), the so-called **B-tipping**. In this case, a TP represents a critical level of a given condition, such as death rates or nutrient inflow in a lake, where the system transitions to an alternative, usually **monostable**, state. Multitude of mathematical models for ecological systems show that these catastrophic transitions are usually governed by the so-called **saddle-node bifurcation** (Dakos et al., 2012; Sardanyés et al., 2020; Vidiella et al., 2018; Dakos et al., 2019; Vidiella et al., 2021; Xu et al., 2023), which is a **local bifurcation** (Strogatz, 2018). Despite this is the most common Bif abruptly separating two alternative states, other Bifs e.g., **global bifurcations**, can give place to catastrophic transitions (McCann and Yodzis, 1994; Dhamala and Lai, 1999; Sardanyés et al., 2018; Vidiella et al., 2021). The second definition describes TPs as **unstable equilibria** states (usually **equilibrium points**) that correspond to peaks in a **potential landscape** (Hodgson et al., 2015, 2016; Berdugo et al., 2017; Vidiella et al., 2021). Here, the jump from one state to the other can be driven by perturbations e.g., the so-called noise-induced transitions (**N-tipping**).

These two specifications reflect two general ways in which a system can shift to a new stable state (Beisner et al., 2003). The first scenario involves a change in external conditions (represented by parameters in models), leading to a gradual erosion of the **ecosystem resilience** until the system changes its state. At this point, one of the stable states becomes unstable or disappears. **Early warning signals**, such as resilience

indicators, **critical slowing down**, and other **leading indicators** can potentially detect when a system is approaching a TP (Dakos et al., 2012). The second perspective of a TP involves perturbing the state of the system itself, reaching and crossing an unstable equilibrium through e.g., significant stochastic mortality events in a population, such as severe winters or fires. Such stochastic jumps have been suggested to describe the Dansgaard–Oeschger events during the last ice age, with 25 occurrences of sudden climate fluctuations over a 500 year period (Ditlevsen and Johnsen, 2021). It has been suggested that, since it does not involve a change in the stability of the system, this type of TP cannot be anticipated using resilience indicators based on critical slowing down (Dakos et al., 2014). Another mechanism of tipping is the **rate-induced tipping, R-tipping** (O’Keeffe and Wieczorek, 2020), described in peatlands (Ditlevsen and Johnsen, 2021).

TPs are typically observed in systems where strong positive feedbacks drive the establishment of alternative stable states (van Nes et al., 2017; Dakos et al., 2019). TPs can manifest at various levels, such as populational due to e.g., Allee effects (Dai et al., 2012), and community due to priority effects and competition (Petraitis et al., 2009; Schmitt et al., 2019; Estes and Palmisano, 1974) or mutualism (Dakos et al., 2014), but they are predominantly studied at the ecosystem scale due to their potential for long-term disruption of vital ecosystem services (Barnosky et al., 2012; Carpenter et al., 2011). Illustrative examples of TPs include the overgrowth of macroalgae on coral reefs (Knowlton, 1992; Schmitt et al., 2019), the collapse of fisheries due to over-exploitation (Blöcker et al., 2023), the conversion of forests into savannah-type ecosystems due to intense fires (Staver et al., 2011; Adams, 2013), or the transformation of clear lakes into turbid ones with algal blooms (Scheffer et al., 1993; Carpenter et al., 2011), to cite some examples (Fig. 1, see also Fig. 6). In this sense, it has been suggested that shallow lakes exhibit **bistability**, meaning it can exist in either of the two



**Fig. 1.** Regime shifts (RSs) in ecosystems. (a) Warning signals detected in experiments in north Indiana lakes (photo kindly provided by S.R. Carpenter, Center for Limnology, University of Wisconsin-Madison). The time series show the variance in daily chlorophyll in the manipulated (M, black) and reference (R, green) lakes during 2008–2010 [adapted from Carpenter et al., 2011]. (b) Coral-to-macroalgae RSs reported in experiments in lagoon reefs in French Polynesia (Schmitt et al., 2019), where the shift towards dominant macroalgae took place in less than 8 years (photos: Corals on Flynn Reef, Queensland, Australia by Toby Hudson, CC BY-SA 3.0; and algae turf by Lyndon Devantie, Dpt. of Environment and Science, Queensland Government, CC BY 4.0). (c) Vegetation patch-size distributions provide information of RSs in drylands: power-law distributions (upper plot, data from Spain) change to a truncated power-law (lower plot) close to the desert transition. The same results are obtained simulating the system with the computer (adapted from Kéfi et al. (2007a), photo kindly provided by S. Kéfi, CNRS and Université de Montpellier). (d) Alternative states quantified with multifunctionalities for drylands displaying differences in nutrient composition and cycling (circular networks) at increasing aridity (adapted from (Berdugo et al., 2017)).

### Box 1 Regime shifts in simple models.

The following mathematical model describes the time change of the population numbers  $x$  considering the ecological processes of intra-specific cooperation (facilitation), competition, death, and constant immigration. The dynamics associated to this system can be studied with the following differential equation:

$$\underbrace{\frac{dx}{dt}}_{\text{population change over time}} = \underbrace{\alpha x^2}_{\text{cooperative growth}} \underbrace{\left(1 - \frac{x}{K}\right)}_{\text{logistic term}} - \underbrace{\epsilon x}_{\text{death}} + \underbrace{\beta}_{\text{constant immigration}}. \quad (1)$$

Parameter  $\alpha$  is the intrinsic growth rate of the population,  $K$  its carrying capacity, and  $\epsilon$  and  $\beta$  death and immigration rates, respectively. Notice that cooperation introduces a nonlinear growth and competition also involves another nonlinearity. Without immigration this system has a single tipping point (TP) which involves an irreversible population extinction (see left panel of Fig. 2 and Fig. 3). With immigration, the system has two TPs involving regime shifts between large and low population densities. This system can be also studied considering demographic noise by means of computer simulations (Gillespie, 1977). Demographic noise typically modifies the bifurcation parameter values predicted by differential equations (Sardanyés et al., 2020), being also able to induce stochastic jumps between coexisting regime states i.e., bistability region shown in yellow in the mid panel of Fig. 2.

alternative stable states given by clear and turbid waters. The disparity in conditions during the forward and backward shifts is known as **hysteresis**, which becomes more pronounced as the recovery of an ecosystem to its previous state becomes increasingly challenging (Dakos et al., 2019).

In this manuscript, we focus on four aspects: (i) We discuss some illustrative and recent examples of RSs in real ecosystems displaying properties identified with mathematical and simulation models. (ii) We argue how the use of theoretical and computational information can serve to investigate features of TPs such as relaxation times of **transients** towards alternative states or warning signals (WS). To do so, we use a nonlinear system which, albeit simple, reproduces the properties of a TP with two alternative stable states. (iii) Up to now, ecological research has mainly focused on the so-called early warnings signals (EWS) as a way to anticipate CTs. Here, we introduce the concept of **late warning signals (LWS)** as those indicators allowing to identify that a system has surpassed a TP but it remains in a transitory state towards the alternative state, and thus intervention is mandatory. (iv) We contextualise these topics within the framework of conservation Biology discussing possible strategies that could be followed in ecosystems' restoration to protect biodiversity and ensure long-term, sustainable ecosystem services.

## 2. Real-world instances of regime shifts

Regime shifts (RS) have been observed in Physics, Chemistry, and Biology. Their identification has often required combining empirical data with mathematical and computational models. Bifs have been identified in models in Physics (Neilsen and Schreyer, 1993; Ivanchenko et al., 2017; Kahan and Sicardi-Schifino, 1999) and in different experiments (Gil et al., 1991; Das et al., 2007; Gomes et al., 2016; Trickey and Virgin, 1998; Maselko, 1982; Strizhak and Menzinger, 1996). In this sense, a quote by the biogeographer Robert H. MacArthur well illustrates this situation: "*Scientists are perennially aware that it is best not to trust theory until it is confirmed by evidence. It is equally true ... that it is best not to put too much faith in facts until they have been confirmed by theory*" (MacArthur, 1972).

The recognition of RSs in ecosystems has been a longstanding topic in ecological research and was initially observed with theoretical models (Holling, 1973; May, 1977; Agnew, 1979). Notably, researchers early highlighted that the observation of real-life communities provided empirical evidence that could be attributed to the existence of multiple stable states (Anderson, 1979; Clark and Holling, 1978; Diamond, 1975; Janzen, 1979; Le Creen et al., 1972). The first empirical evidences of RSs were highly criticized (Wissel, 1984; Connell and Sousa, 1983). Indeed,

the existence of ecological TPs and whether they are easily identifiable from empirical data is still under debate (Boettiger and Hastings, 2013; Hillebrand et al., 2020; Dudley and Suding, 2020). Despite such a debate, the search for clear evidence of RS in real systems has been very intense in the past few decades.

To date, several investigations suggest the existence of these RSs at different scales, from groups of neurons in mice (Gu et al., 2014), experiments with yeast (Dai et al., 2012) to ecosystems (Carpenter et al., 2008, 2011; Solé and Bascompte, 2006; Foley et al., 2003; Kéfi et al., 2007a) (see Folke et al. (2004) for a review), and planetary TPs (Rockström et al., 2009a, 2009b; Steffen et al., 2018). This research is of extreme importance in order to understand the most important drivers of RSs and their nature i.e., smooth versus catastrophic transitions. Moreover, as we will discuss below, the dynamical of species or, more generically, of ecosystems close to TPs can drastically change and give place to extremely long transients. These key aspects have a deep impact on the detection of TPs, and they can, despite the difficulty of the problem, play a role in the design of management strategies and in deploying conservation actions.

In this section, we review relevant and current examples of RSs in ecosystems since the literature available on this topic is very extensive (see Dakos et al. (2019); Folke et al. (2004); Scheffer et al. (2001) and references therein). It is worth mentioning that some key properties of RSs identified in real systems have been found or explained by using mathematical and simulation models, which are often simple but powerful enough to explain real observed phenomena. That is, theoretical models have spurred empirical testing of RSs in ecosystems. Modeling should also play a crucial role in biological conservation by identifying the main factors behind CTs, and predicting the nature of RSs in a given system. The information obtained from data-calibrated mathematical models should be considered in the preservation and protection of ecosystems.

### 2.1. Fresh waters

Fresh waters, including rivers and lakes, have been widely studied in terms of TPs and RS. Their study has provided important advances in the detection of EWS in real ecosystems (Scheffer et al., 1993; Robinson and Uehlinger, 2008; Carpenter et al., 2011; Delong et al., 2021). Here, we will focus on shallow lakes.

#### 2.1.1. Shallow lakes

Lakes can undergo transitions between different stable conditions, and one extensively studied example is the rapid loss of transparency

and vegetation as a result of human-induced eutrophication (Scheffer et al., 1993; Jeppesen et al., 1993). Evidence of alternative stable states i.e., clear versus turbid, have been identified in lakes in the Great Linford sand and gravel pit complex (England) and in the Tomahawk Lagoon (New Zealand) (Scheffer et al., 1993). In these systems, the dominance of aquatic macrophytes ensures a stable and clear water environment by inhibiting the growth of algae. However, if the amount of phosphorus entering the system surpasses a critical threshold, the macrophytes become incapable of efficiently retaining phosphorus. As a consequence, the growth of algae and water turbidity escalates. This sets off a self-reinforcing positive feedback loop, ultimately causing the decline of macrophytes and the establishment of a turbid lake state (Scheffer et al., 1993).

Carpenter et al. (2011) tested WS performing a three-years experiment consisting in increasing the population of the top predator large-mouth bass (*Micropterus salmoides*), in a lake dominated by planktivorous fishes. The aim of this experiment was to disrupt the food chain and initiate a trophic cascade, ultimately resulting in the domination of the ecosystem by piscivores. An unperturbed nearby lake supporting the same ecosystem remained untouched, serving as a control reference. These authors observed changes in some indicators by comparing the results with the control lake: daily monitoring of chlorophyll concentrations showed consistency with theoretical results: one-two years after the perturbation, indicators such as the variance, coefficient of variation, or autocorrelations showed evidences of WS (Carpenter et al., 2011) (see the time evolution in the variance in the right panel of Fig. 1(a)).

## 2.2. Marine systems

Marine systems are extraordinary biodiversity reservoirs and extremely important in providing ecosystem services (see Cavanagh et al. (2016) and references therein). Several factors currently menace their integrity and the management and conservation of marine ecosystems has become mandatory, especially under the scenario of global change. Here, we focus on three important types of marine ecosystems, illustrating their fragility and the importance of non-equilibrium phenomena for their conservation. Other examples of RSs have been identified in shallow lagoons, coastal seas, and benthic food webs (see Folke et al. (2004)).

### 2.2.1. Coral reefs degradation

Having among the most valuable ecosystem services per unit area, coral reefs are vital to biodiversity. However, they are also among the most vulnerable of all ecosystems on the planet. Ocean warming caused by the global climate change is the main cause for mass coral bleaching (which can occur by an increase of 1°C in the mean water temperature) and degradation (Goreau and Hayes, 2021; van Woesik et al., 2022a, 2022b). Although corals can survive the bleaching, they are under more stress during the bleaching event which increases mortality. Similarly, more frequent bleaching events reduce the chances of recovery and lead to global declines in coral cover and diversity. A mass bleaching event was first documented in the 1980s with other severe bleaching events reoccurring in 1998, 2002 and 2016 (Gilmour et al., 2013; van Woesik et al., 2022b). Since then, the data shows that the average time between coral bleaching events is shortening thus decreasing the likelihood of full recovery of the coral reefs (Hughes et al., 2018). The Great Barrier Reef has suffered three major bleaching events; in 1998, 2002, 2016 (van Woesik et al., 2022b). From primarily coastal and with most severe bleaching in the central and southern regions in 1998, to a more widespread bleaching which affected offshore reefs in the central region in the 2002. Finally, in 2016 the proportion of reefs experiencing extreme bleaching (> 60% of corals bleached) was over four times higher than that in 1998 or 2002, indicating the nonlinear nature of this process.

### 2.2.2. Kelp forests overgrazing

Kelp forests are one of the most productive and dynamic ecosystems on the planet (Dayton, 1985), yet they faced an increased degradation during the last few decades due to overgrazing and overexploitation of predator species in the nearshore ecosystems. This decreases the pressure on the herbivore prey and results in their population growth above the normal levels which, in turn, result in the overgrazing of kelp and other algae. For example, sea urchins at high densities are able to remove large erect algae and induce the formation of coralline barren landscapes (Sala et al., 1998; Norderhaug and Christie, 2009). Small scale grazing events have been reported all along NE Atlantic coast due to the increasing populations of sea urchins. Furthermore, a large scale overgrazing event has been reported along the Norwegian and Russian coast – kelp forests were grazed by sea urchins during the early 1970s and barren ground area has persisted since.

The combined effects of overfishing and climate change caused kelp forests to disappear in many vulnerable places such as Tasmania's east coast and the coast of Northern California. Kelp forests restorations attempts have also been reported and are currently undergoing in some places (most notably Australia) with variable success for different strategies (Layton et al., 2020). The implementation of *marine protected areas* (MPAs) is one management strategy which seems promising in addressing the kelp forests degradation issue due to human impact. Resolving the impact due to the climate change, however, seems to be much more challenging.

### 2.2.3. Overexploitation of the ocean's fish stock

Overfishing and regulating fishing quotas is a major global challenge in the 21st century in terms of food provision for humankind and ocean's ecosystems preservation. Constant increase in demand for fish results in overexploitation which is one of the main threats to marine biodiversity. Fisheries collapses provide probably the best known examples for realizing TPs with catastrophic consequences of ecological, economic and social nature. Möllmann et al. (2021) showed that Western Baltic cod is beyond such a TP which was caused by ignoring the EWS by fisheries and unsustainable exploitation levels. In addition, the climate change stabilizes (likely irreversible) low productivity state of the fish stock that is not adapted to the warming environment. To tackle the problem of fish overexploitation, establishing MPAs where fish harvesting is prohibited (or highly regulated) presents a promising tool in managing transient responses in long-generation species. One goal is to increase and stabilize the yield from fisheries which is now restricted to the part of habitat where fishing is allowed, while the protected part acts as a reserve area (Francis et al., 2021; Hopf et al., 2019).

## 2.3. Terrestrial systems

Regime shifts are also widespread in terrestrial systems. Major ecosystemic changes were reported in the Sahara and Sahel biomes. About 6000 years ago, Sahara's region was wet and formed by tropical forests and lakes. Around 5500 years ago, the wet environmental conditions suddenly came to an end. Despite the absence of abrupt, external climatic change, plant productivity declined and the topsoil was lost. Eventually, the green Sahara became the desert Sahara that we know today (Foley et al., 2003) (see Fig. 6(e)). Other examples of RSs in terrestrial ecosystems include forests (see Haug et al. (2015) for drought-induced tipping points in conifer forests), savanna and grasslands, and arctic and sub-arctic systems (see Folke et al., 2004) and references therein). Here, we focus on drylands, which are among the most sensitive ecosystems to climate change (Schröter, 2005) and occupy over 41 % of the Earth's surface also hosting 38 % of the total world's human populations (Adeel et al., 2005).

### 2.3.1. Drylands

The relentless increase in global temperatures has led to heightened aridity levels, resulting in significant changes across diverse ecosystems

(Cherlet et al., 2018; Yao et al., 2020). The pressure from excessive grazing further pushes arid ecosystems towards the brink of extinction, while the escalating aridity can trigger desertification in a nonlinear manner, with minimal chances of recovery (Noy-Meir, 1975; Scheffer et al., 2001; Rietkerk et al., 2004; Kéfi et al., 2007b). These ecological transformations, influenced by the interplay of climate change and ecosystems' dynamics, are profoundly reshaping our planet. As temperatures continue to rise, the intensification of aridity acts as a catalyst for ecosystem shifts, setting off a chain reaction of alterations across various biomes. This escalation of aridity, driven by global warming, initiates specific mechanisms that drive the observed transformations in ecosystems (Berdugo et al., 2020, 2022). Within forested regions, the combination of rising temperatures and diminishing moisture availability prompts a transition from dense forests to savannas (Nobre et al., 1991; Zemp et al., 2017; Nepstad et al., 2008).

The arid conditions impede the growth and survival of certain tree species, leading to the expansion of open grassland areas within what was once a densely forested landscape. Human activities, such as agriculture, fires, and livestock management, also contribute to these transitions. The expansion of agricultural practices, involving deforestation for the establishment of croplands or pastures, accelerates the conversion of forests into savannas. Widespread forest clearing for agriculture, exemplified by the Amazon basin (Lapola et al., 2023), disrupts the delicate ecological equilibrium and fosters the transformation of once-thriving forests into savannas (Touboul et al., 2018; Amigo, 2020; Boulton et al., 2022).

In savannas, intensified aridity results in a gradual loss of trees, favouring savannas to transition into grasslands. As droughts become more frequent and severe, trees struggle to access sufficient water, leading to a decline in their populations. Consequently, the balance between woody vegetation and grasses is altered, resulting in a shift towards a grass-dominated ecosystem. This phase has been labeled as "vegetation decline phase" (Berdugo et al., 2020, 2022). Moreover, intentional or accidental fires set for land management purposes in savannas and grasslands exacerbate tree loss and promote the dominance of grasses (Bond and Zaloumis, 2016).

Even grasslands are not safe from the impacts of increasing aridity. With rising temperatures, shrubs and woody vegetation take advantage of drier conditions and encroach upon grasslands. This encroachment alters the structure and composition of grasslands, transforming them into shrublands (Eldridge et al., 2011; Maestre et al., 2016; D'Odorico et al., 2012). The proliferation of shrubs disrupts the dominance of grasses, affecting nutrient cycling, species interactions, and overall ecosystem dynamics. Furthermore, human activities play a facilitating role in the transition from grasslands to shrublands. Grasses are particularly vulnerable to wildfires due to the continuous cover provided by their vegetation, and livestock management practices, particularly overgrazing, can contribute to shrub growth by competing with grasses (Adams, 2013).

Additionally, human-influenced fire regimes can impact the expansion of deserts (Archibald et al., 2013). Mismanagement of fires in arid regions can lead to increased fire frequency and intensity, which, coupled with the already arid conditions, further impede vegetation regeneration and promote desertification. The expansion of deserts stands as a striking consequence of aridity intensified by global warming. In the most extreme environments characterized by limited moisture availability and harsh climatic conditions, vegetation struggles to survive. As temperatures rise and rainfall decreases, deserts expand, and vegetation eradication becomes prevalent, resulting in barren landscapes dominated by sand and rocks.

These anthropogenic factors synergistically interact with the effects of global warming and aridity amplification, accelerating the ecological transitions from forests to savannas, savannas to grasslands, and grasslands to shrublands (Albert et al., 2023; Cherlet et al., 2018; Berdugo et al., 2022; Eswaran et al., 2019). When studying ecosystem dynamics and formulating management strategies to address ecological TPs and

RS, it is imperative to consider these human-induced drivers. Drylands are thus extremely sensitive to global change and prone to suffer RSs towards deserts. Hence, conservation and protection actions are mandatory in these regions.

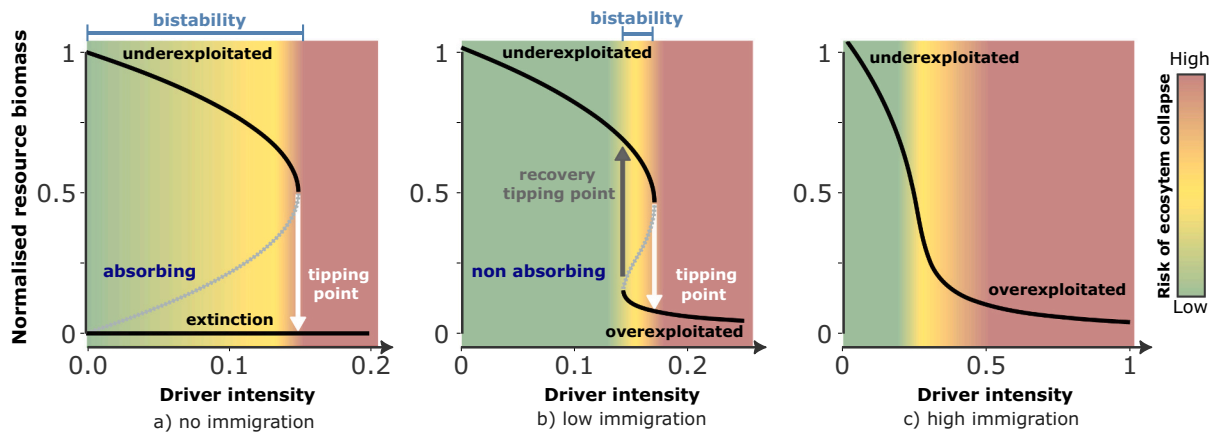
Recent studies have proposed the use of principles derived from synthetic biology (Solé, 2015; Solé et al., 2015) to mitigate e.g., the impacts of drought. These principles involve the engineering of microbial organisms. By introducing these engineered microorganisms into the ecosystem, their enhanced ecological capabilities could contribute to shifting the ecological conditions away from critical thresholds. Mathematical and computational works have provided evidence that this strategy could work in ecosystems (Solé et al., 2016; Vidiella et al., 2020). These kind of approaches deserve further experimental research but they open promising avenues in enhancing ecosystems' resilience aiding in their conservation.

### 3. Theoretical knowns: the saddle-node bifurcation

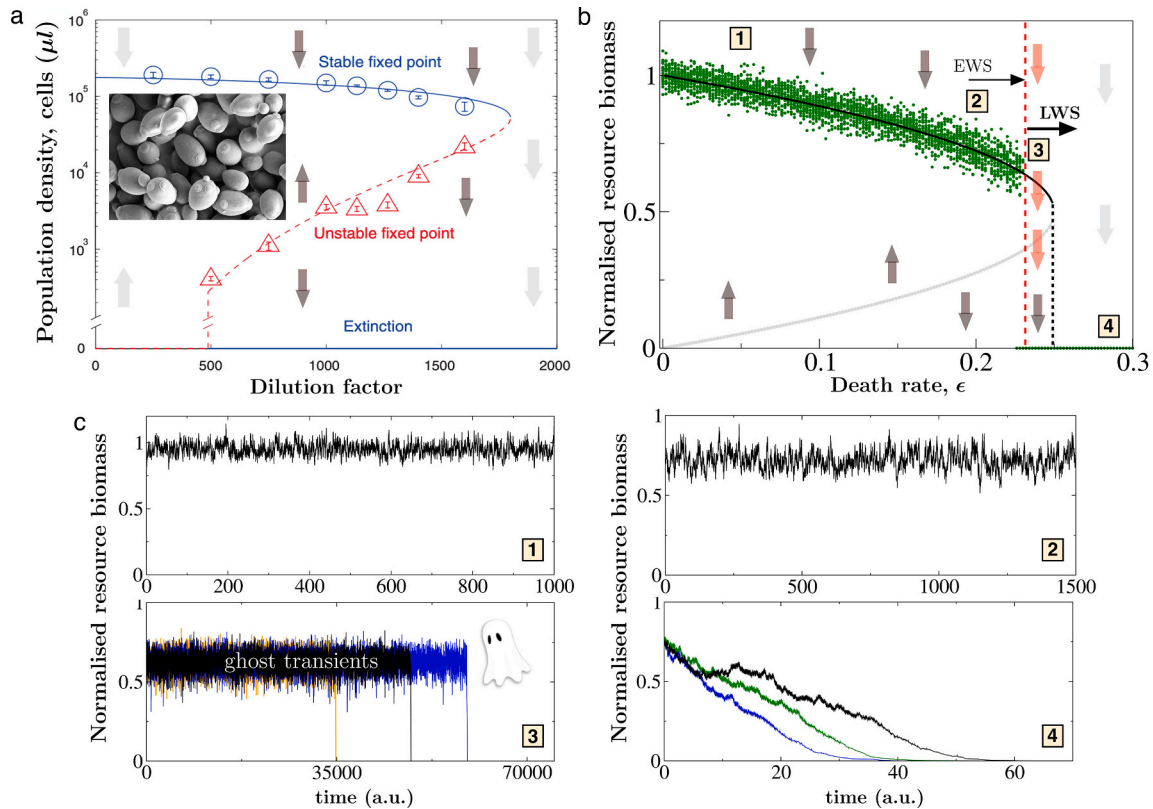
The study of species' dynamics considering different ecological interactions using theoretical approaches has a very long tradition. Since the initial works by Malthus on population growth (Malthus, 1826), to the first dynamical models by Verhulst (1838), Lotka (1910) and Volterra (1931), multitude of theoretical and computational models have been investigated to explain changes in species abundances. The same has happened for regime shifts (RS), although more recently (Holling, 1973; May, 1977; Agnew, 1979; Brauer and Soudack, 1979; Wissel, 1984). These works have inspired many scientists who have seek for these mathematically-described phenomena in real systems. For instance, this has led to the identification of strong evidence of complex nonlinear dynamics in ecological systems such as deterministic chaos (Cushing et al., 1998; Schaffer, 1984; Gamarra and Solé, 2000). Research on Bif theory and phase transitions has generated a paramount of theoretical results which have not yet been identified in real ecological data.

This manuscript provides a bunch of examples of real systems with alternative states. As we mentioned above, different types of Bifs can give place to abrupt RS. In this section, we will focus on the saddle-node (s-n) Bif, which typically involves two alternative stable states. Mathematics indicates that the s-n Bif involves the collision of a stable equilibrium with an unstable one (Strogatz, 2018). This behavior can involve the sudden extinction of the population, even when population density is large, as Dai et al. (2012) showed experimentally with yeast (Fig. 3 (a)). When the two equilibrium points approach each other, the likelihood of transitioning from one state to the other due to stochasticity increases because the stable branches get closer to the unstable ones, as we show in e.g., Figs. 2(a,b), 3(a,b), 4(left). Moreover, the chances to move from one state to the other and vice versa may not be symmetric (see Fig. 4(a) where the unstable branch is more separated from the upper stable branch than from the lower one).

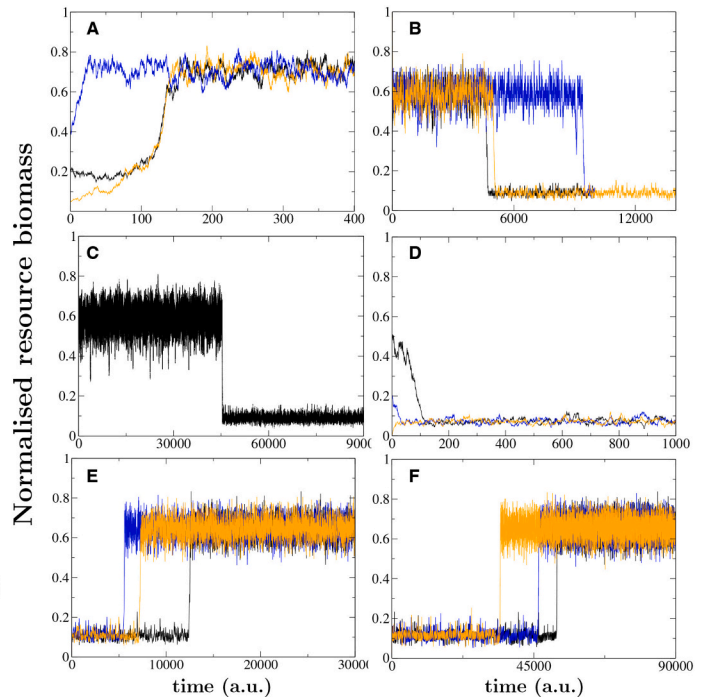
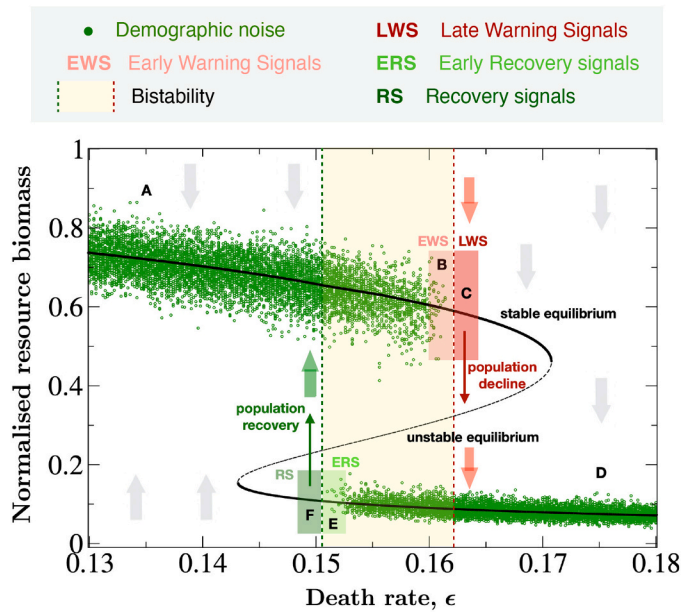
S-n Bifs have been identified in multitude of mathematical models describing cooperation (Sardanyés and Solé, 2006a, 2006b; Vidiella et al., 2018, 2021; Canela et al., 2022). It is known that a special kind of transients (also named *delayed transitions*) appear right after this Bif: a type of slowing-down caused by the so-called *ghost* (Strogatz and Westervelt, 1989; Strogatz, 2018; Sardanyés and Solé, 2006a; Calsina et al., 2023; Canela et al., 2022). Indeed, the length of these transients is known to follow well-defined scaling laws as the driver parameter increases beyond its critical value, such as power-laws (Strogatz, 2018; Vidiella et al., 2021; Sardanyés et al., 2020). These laws involve that, extremely close to the CT, transients are extremely long and their duration rapidly decreases as the driver increases beyond the critical value. Despite this is a local phenomenon, the scaling law for the s-n Bif has been found in an electronic circuit (Trickey and Virgin, 1998). To date, this phenomenon has not yet been found in a biological system. We argue that, due to the generality of this type of Bif, it may be possible to characterize this phenomenon experimentally or in e.g., vegetation time



**Fig. 2.** Different regime shifts in a simple mathematical model (see Box 1). (a) Without immigration the resource can transition from an underexploited state towards an irreversible, extinction (absorbing) state by a tipping point (TP) attained at increasing the death rate (driver). (b) For low immigration rates the resource can still transition from an underexploited to an overexploited state through a TP, having the possibility for recovery since the overexploited state is non-absorbing. (c) When immigration is large the system becomes monostable and an increase in the death rate involves a continuous transition between both regimes.



**Fig. 3.** Irreversible tipping points (TPs) due to the saddle-node bifurcation. (a) TP at increasing dilution in yeast experiments (inset: microscopic image of *Saccharomyces cerevisiae* by M.D. Murtey and P. Ramasamy CC BY-SA 3.0). Blue circles and red triangles are experimental data while blue solid and red dashed lines are, respectively, the stable and unstable states predicted by a mathematical model. The arrows indicate towards which equilibrium the system will evolve for different initial populations (dark gray and light gray arrows denote, respectively, the deterministic bistable and monostable regimes). Beyond the critical dilution factor ( $\sim 1800$ ) the population cannot persist even with extremely large initial populations [adapted from (Dai et al., 2012)]. (b) Same critical transition shown in (a) using the model from Box 1 setting  $\beta = 0$  (black and gray lines show stable and unstable equilibria, respectively). The same system is simulated including intrinsic noise (green dots, with a system's size  $N = 10^3$ ). With noise, the regime shift occurs at lower death rates (dashed red line) as Sardanyés et al. (2020) shown. Here, thick red arrows show the monostability behavior with noise which is enlarged compared to the deterministic case. Early warning signals (EWS) arise while approaching a TP while late WS (LWS) may allow to identify that the system has already crossed the TP and is going to collapse (see Section 6 and Fig. 5). (c) Time series (in arbitrary units a.u.) for the labels indicated with capital letters in (b): single realisation in (1) with  $\epsilon = 0.05$  and in (2) with  $\epsilon = 0.2$ ; (3) three runs using a death rate right after the stochastic bifurcation,  $\epsilon \gtrsim \bar{\epsilon}_c^{(st)}$ ; and (4) far away the stochastic bifurcation with  $\epsilon = 0.285$ . Note that despite example in (3) has surpassed the stochastic threshold, the population is able to remain in an apparently stable state (ghost transient) for very long times before collapsing. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 4.** Complexity of systems with two reversible stable states. (Left) Bifurcation diagram with two non-absorbing alternative stable states (upper and lower branches shown with solid black lines) is obtained from the mathematical model in [Box 1](#) with immigration ( $\beta = 0.01$  and  $\alpha = 0.6$ ). Overlapped we display with green dots several stochastic realisations at time  $t = 10^5$  (system's size  $N = 10^3$ ) for the same parameter values used in the mathematical model. The thick arrows indicate the stability of the branches in the bistable (dark gray, green, and red) and monostable (light gray) states for the deterministic model. The yellow area denotes the stochastic bistability regime. The capital letters denote different dynamics, shown in the time series for three different realisations, except for panel (C) with a single one. Here, (A) fast achievement of large populations ( $\epsilon = 0.135$ ); (B) stochastic jump in the stochastic bistability region ( $\epsilon = 0.161$ ); (C) transient beyond the stochastic bistable region ( $\epsilon = 0.1615$ ); (D) fast transients to low population values for large  $\epsilon = 0.175$ ; (E) noise-induced jump to large populations within the stochastic bistable region ( $\epsilon = 0.152$ ); and (F) transients in the stochastic monostable region delaying the recovery of the system ( $\epsilon = 0.1507$ ). Panels B, C, E, and F show examples of N-tipping involving a regime shift. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

series in drylands. More recent research has explored the impact of demographic noise on such transients and scaling laws ([Sardanyés et al., 2020](#); [Lázaro et al., 2023](#)), finding substantial changes even though the delays given by the ghost remained after the *stochastic s-n bifurcation*. The effects of intrinsic noise in the s-n Bifs are illustrated in [Fig. 3\(b,c\)](#) and [Fig. 4](#).

[Fig. 3](#) shows an example where one of the two alternative regimes is an *absorbing state*: if the population transitions to this state it becomes extinct with no possibility of recovery (Eq. (1) without immigration). The addition of demographic noise indicates that the CT occurs at a lower value of the driver given by the death rate (see [Fig. 3\(b\)](#)). That is, large noise values attained at small systems' sizes make the system to collapse at lower decay rates (see [Sardanyés et al. \(2020\)](#) for details on the analysis of the stochastic bifurcation). Here, the Bif value for the deterministic model is  $\epsilon_c = 0.25$ , while with the noise considered here is  $\bar{\epsilon}_c^{(s)} \approx 0.23357 \pm 5.650 \times 10^{-6}$  (system's size  $N = 10^3$ ). Despite the value is rather similar, lower systems' sizes further decrease this critical threshold ([Sardanyés et al., 2020](#)). [Fig. 3\(c\)](#) displays several time series for different values of the driver parameter far away and close to the stochastic threshold. For instance, for  $\epsilon = 0.05$  the population fluctuates around an equilibrium (panel 1). If the driver parameter is increased, the population diminishes and the size of the fluctuations increase (panel 2). For these cases, despite the probability of extinction is not zero, the dynamics will likely remain in the attractor for very long times. Right after the stochastic bifurcation (panel 3), studied in [Sardanyés et al. \(2020\)](#), the dynamics stays in an apparently stable state (the ghost) for a very long time but it suddenly collapses. Finally, when the parameter has greatly exceeded its threshold, transients to extinction are very fast (panel 4).

Transients are also found when the two stable states are non-absorbing, as occurs for the system modeled with Eq. (1) considering constant immigration ([Fig. 4](#)). Here, we have also overlapped the deterministic dynamics (solid black lines) with the stochastic one (green dots) in the left panel of [Fig. 4](#). Notice that the transition from the upper branch to the lower one also occurs before the deterministic prediction when noise is included. The mean values for the decay rates (obtained following the methodology in [Sardanyés et al. \(2020\)](#)) involving the switch from bistability to monostability are:  $\bar{\epsilon}_{u \rightarrow l} = 0.16210 \pm 4.145 \times 10^{-5}$  (transition from upper to lower branches); and  $\bar{\epsilon}_{l \rightarrow u} = 0.15068 \pm 3.871 \times 10^{-5}$  (transition from lower to upper branches). Expected time series for this diagram are shown at the right of [Fig. 4](#). These include very fast transients towards the upper (panel A) and lower (panel D) stable states and stochastic jumps between these states (panels B, C, E and F). These RSs display *hysteresis*. From a conservational perspective, the possibility to recover the system once has jumped to the lower branch would be to decrease the driver until the transition point to the upper branch is achieved. However, such a decrease may be sometimes difficult to achieve. Another option may be to decrease the driver and introduce more individuals to the population to achieve a population size able to cross the unstable branch and the dynamics itself would allow to recover the system towards the upper branch. This effect, driven by this dual action, could be tested in experimental set-ups to investigate its feasibility and robustness.

#### 4. Nature's dance: the importance of ecological transients

The traditional view of ecosystems as stable and balanced systems has been widely utilized in modeling, management, and conservation

practices. However, recent research has shed light on the significance of ecological transients, which refer to out-of-equilibrium dynamic phenomena. This section explores the various dimensions of transients and their implications for understanding and managing ecosystems. Various authors have addressed the topic of transients from different angles, including classifying long transients or super-transients (Hastings, 2004; Hastings et al., 2018; Morozov et al., 2020; Sardanyés et al., 2020; Vidiella et al., 2021; Liu and Magpantay, 2022). Dynamical systems theory, with its rich history in ecological studies, serves as the foundation for our understanding of transients. Furthermore, early identification of transients in biological populations has contributed to our growing awareness of their importance (Cushing et al., 1998), see also Oro et al. (2023).

Theoretical and computational research on Ecology has proposed different mechanisms causing transients. For instance, the ghosts (Sardanyés and Fontich, 2010) previously discussed, which are typically found in models with strong feedbacks such as cooperation or facilitation (Sardanyés and Solé, 2006b; Sardanyés et al., 2018; Vidiella et al., 2018). Other mechanisms responsible for transients are chaotic saddles responsible for transient chaos (McCann and Yodzis, 1994; Dhamala and Lai, 1999), spatial systems (Hastings and Higgins, 1994), linear systems with varying time scales, coupled oscillators, stochasticity and recurrent transients (Hastings, 2004), see also Morozov et al. (2020); Hastings (2001); Hastings et al. (2018); Francis et al. (2021) and Table 3 in Hastings et al. (2018). Recent research has shown that the impact of space in enlarging transients may not be the norm close to bifurcations (Calsina et al., 2023).

Transients have been underestimated because of the difficulty to identify them in ecological time series, specially under scenarios of global change giving place to non-stationary time series. However, concepts such as critical slowing down, trophic downgrading, ecological meltdown or extinction debt have implicit transient dynamics. The intricate nature of ecosystems gives rise to two additional phenomena, namely top-down and bottom-up regulations, which sustain the diverse wildlife. When top-down regulation is disrupted, it can lead to trophic downgrading (Estes et al., 2011; Guimarães, 2020), resulting in previously coexisting species becoming antagonistic and ultimately going extinct in a cascading fashion. On the other hand, when bottom-up regulation is disturbed, we observe ecological meltdown and extinction debts, where habitat degradation and loss have delayed consequences on the trophic structure (Terborgh et al., 2001), eventually leading to a sequential collapse (Tilman et al., 1994). Conservation biology has placed significant emphasis on comprehending and mitigating extinction debt (Kuussaari et al., 2009; Chase et al., 2020) due to its association with phenomena such as the empty forest (Redford, 1992), where a region may be protected but still experiences a collapse that cannot be prevented solely by area protection measures.

Transients in semiarid ecosystems are of great importance due to their impact on the carbon cycle, biodiversity, and human livelihoods. Global warming can lead to rapid shifts in these ecosystems, altering vegetation cover and diversity (Berdugo et al., 2020, 2022). In marine ecosystems, comprehending the role of transients is key to understanding how they affect sustainability and resilience (Frank et al., 2011). Fisheries and marine biodiversity have already experienced unpredictable rapid collapses (Ratajczak et al., 2018; Pinsky et al., 2011; Rocha et al., 2015). Environmental variability, overexploitation, climate change, and other factors can disrupt marine ecosystems, leading to transient dynamics towards their collapse (Thurstan and Roberts, 2010). This pattern would be expected if we bear in mind that delayed transitions can occur close to TPs (see Fig. 3c and Fig. 4c).

Similar behaviors can be observed in various ecosystems that rely on the same ecological interactions. The occurrence of tipping points, which lead to regime shifts in these ecosystems, can be attributed to either species cooperation, as seen in plant facilitation under arid conditions (Kéfi et al., 2007b; Vidiella et al., 2018), or competitive exclusion, exemplified by the interaction between urchins and kelps (Estes

et al., 1998, 2011; Wilmers et al., 2012). This suggests that under anthropogenic pressures, many ecosystems may undergo delayed transitions or exhibit transient behaviors.

Measuring and predicting transients present significant challenges due to their rapid progress and complexity. Scientists have made notable progress in this area, particularly in identifying EWS that indicate the approach of critical thresholds (Carpenter et al., 2008; Hastings and Wysham, 2010; Kéfi et al., 2014). However, studies on WS and LIs for systems that have already surpassed a TP and are in a transient state are much needed. Without such tools, we currently lack the means to prevent eventual collapses, even if all the drivers are halted. In the next two sections we discuss research on WS.

## 5. Early warning signals (EWS) of critical transitions

Multitude of theoretical works and some empirical observations have shown that systems approaching a TP show characteristic changes in their spatial and temporal patterns. Such LIs e.g., variance or return times, have been suggested as a way to identifying the so-called EWS (Carpenter et al., 2008, 2011; Dakos et al., 2012; Kéfi et al., 2007a; Scheffer et al., 2012; Cline et al., 2014; Kéfi et al., 2014; Berdugo et al., 2017; Butitta et al., 2017; van Belzen et al., 2017). However, most of the time, detection of these LIs in ecosystems is very difficult due to the lack of high-frequency sampling data (Carpenter et al., 2011). It is worth noting that some studies propose the possibility that ecosystems experience state transitions without showing increased variance or long return times (Schreiber and Rudolf, 2008; Hastings and Wysham, 2010). Moreover, deterministic ecological systems typically display bifurcation-induced collapses (B-tipping) (McCann and Yodzis, 1994; Duarte et al., 2012; Dhamala and Lai, 1999; Sardanyés et al., 2018). In this sense, further research is much needed on EWS for other bifurcations beyond the saddle-node. For instance, the LIs could behave differently for populations going to collapse by means of oscillating or chaotic transients. The statistics for such time series including noise deserves intensive research, both theoretical and, despite the difficulties, experimental.

As mentioned, many works have proposed different methods to detect critical transitions (CTs). Broadly speaking, these LIs are related to memory, variability, and flickering phenomena. For example, autocorrelation (Carpenter et al., 2008) or spectral density (Kleinen et al., 2003) in ecological time series tend to increase as the system approaches a CT. Several indicators of variability in fluctuations, such as standard deviation, coefficient of variation (Carpenter and Brock, 2006; Carpenter et al., 2008), or kurtosis, among others (Dakos et al., 2012; Scheffer et al., 2012), may also serve as EWS as they typically change while approaching a TP. Finally, it is also possible to use models to detect EWS (time-varying AR(p) models, non-parametric drift-diffusion-jump models). Dakos et al. (2012) gathers a compendium of all these methods testing them on simulated ecological data. Evidences of these statistical changes in dynamics have been reported for shallow lakes (Carpenter et al., 2011) and other natural systems (Wissel, 1984; Lade and Gross, 2012; Carpenter and Brock, 2006).

As we mentioned in Section 3, different types of Bifs may produce different RS, and, possibly, each particular transition may have its most suitable LIs. This is why we claim here that the study of mathematical and computational models, either mechanistic or phenomenological, can be very useful to gain insights into the type of TP governing a particular system, and thus give clues about the LIs that may be monitored. Of course this is not a trivial thing to do, but multitude of models have been successfully used to characterize real RSs (Wissel, 1984; Claussen and Gayer, 1997; Claussen et al., 1997; Doherty et al., 2000; Eastman et al., 2001; Rial et al., 2004; Carpenter et al., 2008; Dakos et al., 2008; Dai et al., 2012).

To the extent of our knowledge, the investigation of EWS in real systems dates back to the 1980's with the work by Wissel (1984) about return times in experiments with rotifers. Since then, a lot of research is



being done to study EWS (Xu et al., 2023; Carpenter and Brock, 2006; Scheffer et al., 2012; Litzow and Hunsicker, 2016). For example, studies on EWS have been conducted in many different disciplines such as geological engineering (Ramos, 2010), physiology (Matsumoto and Kunisawa, 1978), epilepsy (McSharry et al., 2003), sociology (Neuman et al., 2011), or finance (Gorban et al., 2010). As we explained in Section 2, compelling evidence of these EWS has been provided for shallow lakes (Carpenter et al., 2011) (Fig. 1(a)).

The use of EWS in spatial systems (SEWS) has raised also some concerns. SEWS in real-world landscapes may result in misleading conclusions since spatial heterogeneity in real-world landscapes may enhance reversibility of RSs and boost landscape-level resilience to environmental change (Nijp et al., 2019). Moreover, ecosystem states are often difficult to define and spatial environmental variability and socio-economic factors may affect spatial patterns and thus SEWS predictions (see Nijp et al. (2019) for further details). Despite these issues, the importance of using LIs methodology lies in the fact that they can be directly applied to observable time series (Dakos et al., 2012; Scheffer et al., 2012) or spatial patterns (Kéfi et al., 2007a; Cline et al., 2014; Berdugo et al., 2017; Butitta et al., 2017; van Belzen et al., 2017) without the need for detailed knowledge on the ecosystems' structure or dynamics.

For terrestrial ecosystems, it has been hypothesized that vegetation patchiness could be used as a signature of imminent transitions. Changes in the statistical distributions of the number of patches ranked by size have been observed, transitioning from power-laws to truncated power laws as the ecosystem approaches a TP (Kéfi et al., 2007a), see also Rietkerk et al. (2004) and Solé (2007). These traits seem to be universal since they have been characterized in drylands in Morocco, Spain, and Greece. Moreover, computer simulation models taking into account plant colonization, competition, and local facilitation reproduced these statistical patterns and their changes identified in the field (Kéfi et al., 2007a), see panel (c) in Fig. 1 and Kéfi et al. (2007b). Power laws distributions of tree canopy cluster size were also identified in Kalahari's vegetation by Scanlon et al. (2007). These authors identified, with *cellular automata* models, that these distributions can arise from the interaction between global-scale resource constraints i.e., water availability, and local-scale facilitation. More recent research has explored aridity thresholds in drylands, identifying bistability in multifunctional traits responding to states with high and low multifunctionality. Interestingly, this study suggested that cover percentage may not provide enough information in identifying this bistable states (Berdugo et al., 2017).

### 6. Late warning signals (LWS)

The concept and study of WS has been so far developed to anticipate critical transitions (CTs), i.e. EWS. Few research has been devoted to study the restoration of systems above TPs (Sardanyés et al., 2012; Vidiella et al., 2018), especially in terms of socio-ecological processes and management. In this direction, Martin et al. (2018) explored transient social dynamics in the restoration of ecosystems beyond ecological TPs by means of simulations. Here, we claim the importance of focusing on the statistical properties of observables (time series or spatial patterns) of systems that have already surpassed a CT i.e., late warning signals (LWS). As discussed above, transient times after Bifs can experience huge delays, and this fact opens the possibility of e.g., looking for WS during these transients prior to collapse. The detection of these LWS would indicate the extreme urgency of taking actions because the system is about to collapse. Inspection of time series in this transient state could give the false impression that the system is at equilibrium (ghost state), but, having passed the transition, sooner or later the collapse would occur. Under this situation, ghost transients may provide a time window within which actions could be taken to avoid an undesired regime shift.

As mentioned above, in previous research we identified a stochastic s-n bifurcation for the system studied in this manuscript (Eq. (1) with

$\beta = 0$ ) analytically and numerically by means of Gillespie simulations (Sardanyés et al., 2020). An exhaustive and accurate numerical study determined this transition value at  $\epsilon_c^{(s)} \approx 0.23357 \pm 5.650 \times 10^{-6}$  for a system's size  $N = 10^3$ . Taking advantage of this study, we here analyze indicators for time series above this stochastic threshold. Specifically, we have studied the variance and the coefficient of variation, and both indicators seem to qualitatively change after the CT (vertical dashed lines in Fig. 5). Specifically, we have identified three qualitatively different regions at increasing the driver parameter. For low values of the driver, the variance slightly increases and, as expected, it starts rising when the transition is approached. Here we have performed a linear regression analysis for the three regions (Fig. 5(a)). The first one (far from the transition, cyan line) gives a slope  $s = 0.0277$ , with correlation coefficient  $r = 0.84$ , and standard error of the slope  $s.e. = 2.88 \times 10^{-4}$ . The second region (closer to the stochastic bifurcation, orange line) gives:  $s = 0.2728$ ,  $r = 0.87$ ,  $s.e. = 5.54 \times 10^{-3}$ . Interestingly, the variance right after the stochastic bifurcation value suffers a significant change in the rate of growth with respect to the driver (yellow line):  $s = 2.32$ ,  $r = 0.93$ ,  $s.e. = 0.051$ .

The previous results have been obtained for a single run for each

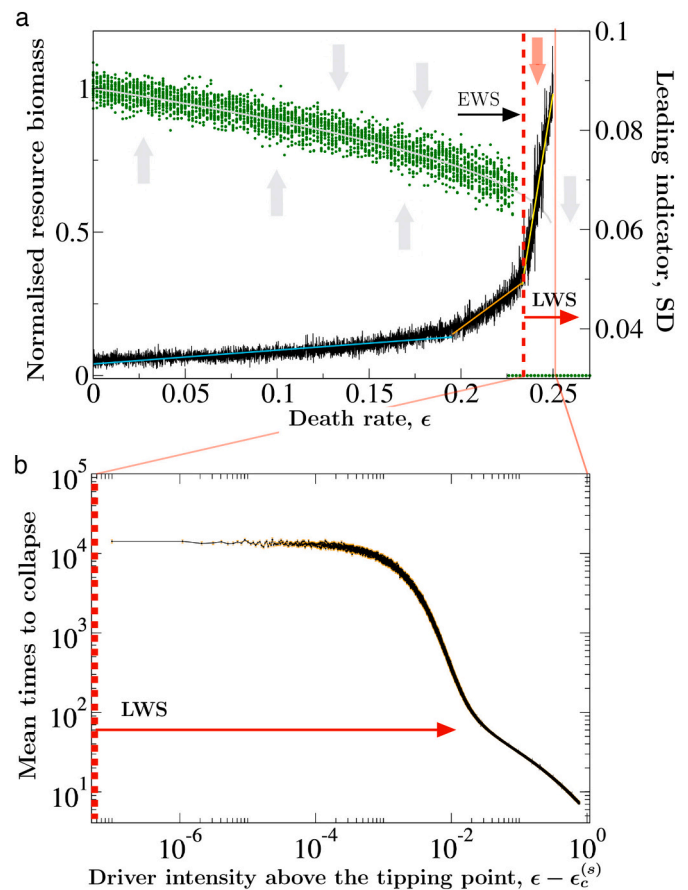
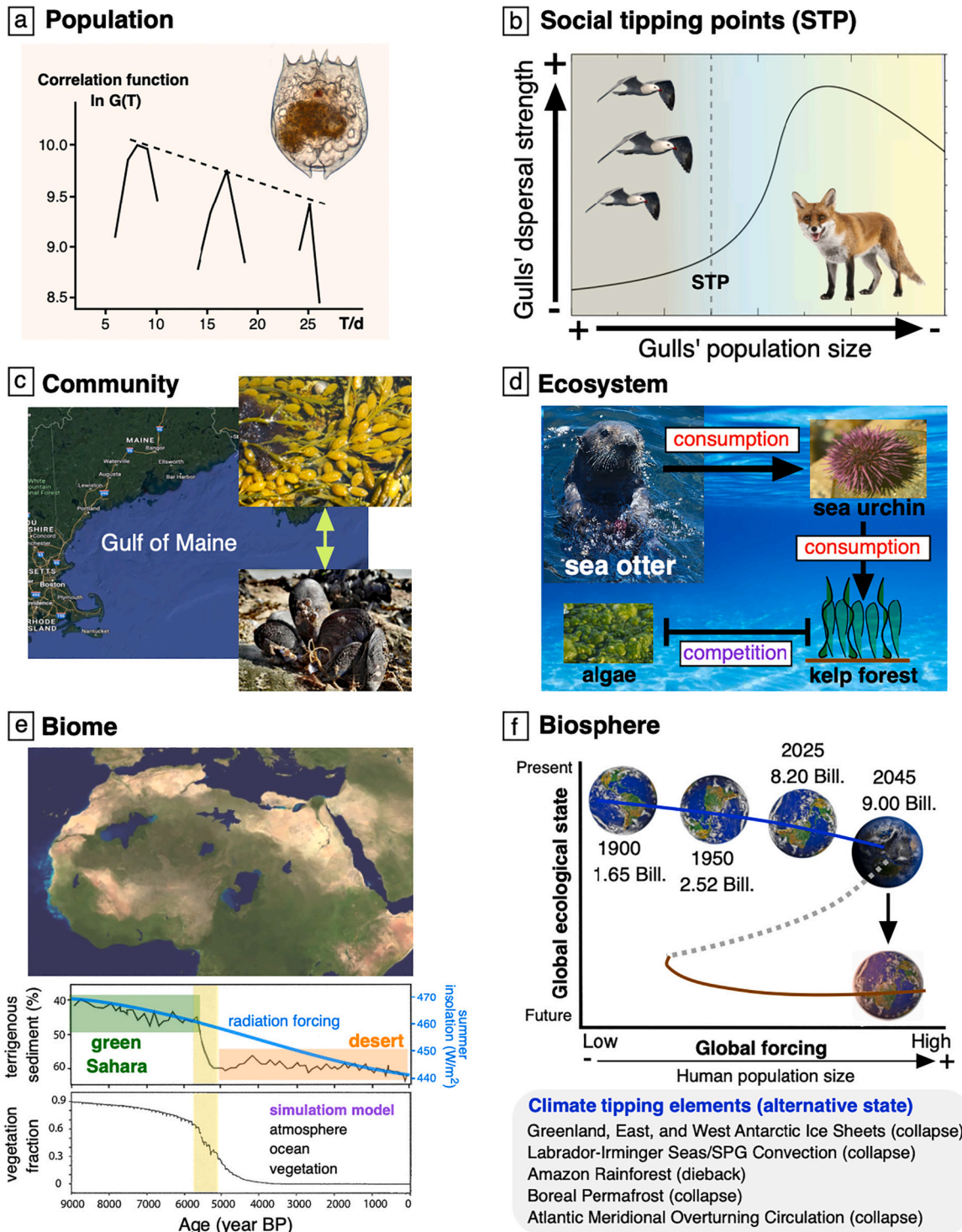


Fig. 5. Late warning signals (LWS) may indicate urgent action to avoid collapses. (a) Changes in the standard deviation (SD) at increasing the driver intensity shown in black data overlapped to the diagram of Fig. 3(b) (the unstable branch of the diagram is not shown to ease visualisation; the vertical dashed red line shows the stochastic bifurcation value). The cyan, orange, and yellow lines correspond to linear regressions performed over three different ranges of the driver parameter. (b) Mean transient times after the stochastic tipping point computed for the same system's size and parameter values as in panel (a) (see Sardanyés et al. (2020) and Lázaro et al. (2023) for further details). LWS may be detected during these transitory times previous to collapse. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 6.** The multi-scale nature of regime shifts (RSs), tipping points (TPs), and their associated characteristics. Identifying TPs across various biological scales could aid in discerning if there are shared characteristics in their dynamics that connect different levels of biological organization. (a) Increase in return times in experiments with *Brachionus rubens* (photo by M.R. Much, Pennsylvania, USA), see [Wissel \(1984\)](#) for details (see also [Dai et al. \(2012\)](#) for a population TP in yeast). (b) Social TP involving seagulls dispersal in a metapopulation patch after a biotic perturbation promoting dispersal by social copying ([Oro et al., 2023](#)). (c) Mussel beds and rockweed stands formed by e.g., *Ascophyllum nodosum* (photo obtained from the University of Maine website) are multiple stable states on intertidal shores in the Gulf of Maine, USA ([Petraitis et al., 2009](#)). (d) Community shift due to keystone specie removal such as sea otter ([Estes et al., 1998, 2011](#); [Wilmers et al., 2012](#)) (photo by Matt Knoth CC BY 2.0). (e) Abrupt shift from a tropical region to a desert at the Sahara. (Upper plot) Paleoecological data of the % of terrigenous sediment over the last 9000 years. Overlapped (blue line) we display the continuous change of the major driver parameter given by summer insolation. (Lower plot) Simulation of the green-desert Sahara using a computational model coupling atmosphere-ocean-vegetation ([Foley et al., 2003](#)). (f) Suggested biosphere TPs driven by global (adapted from [Barnosky et al. \(2012\)](#)) and climate change (adapted from [Lenton et al. \(2008\)](#); [Rocha et al. \(2018\)](#)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

value of the driver. The same pattern is obtained for other realisations, and the mean slopes ( $\pm$  SEM) for each one of these three regions averaged over 25 replicates give:  $\bar{s} = 0.0276 \pm 5.27 \times 10^{-5}$  (first region);  $\bar{s} = 0.2700 \pm 0.00154$  (second region); and  $\bar{s} = 2.2789 \pm 0.01033$  (third region). Following these results we see that the slope of the region after the stochastic bifurcation value is 82.64-fold the slope of the first region and 8.24-fold the slope of the second one. Similar results have been found for the coefficient of variation (results not shown). This simple statistical measures provide preliminary evidence of changes in these LIs pre- and post-bifurcation under intrinsic noise. More rigorous and statistically powerful research should be done on these LWS.

Recent research has suggested different approaches to indefinitely sustain ghost transients for both deterministic and noisy dynamics taking advantage of the enormous duration of these transients (Sardanyés et al., 2012; Vidiella et al., 2018, 2021). Specifically, the continuous maintenance of dynamics doomed to collapse has been successfully applied to models for single-species with non-overlapping generations under Allee effects (Sardanyés et al., 2012) and in dryland models (Vidiella et al., 2018). These works provide theoretical evidence that punctual, recurrent introductions of individuals can sustain this transient state. However, these interventions may not be trivial to apply to real ecosystems. Evidence for ghost dynamics in real biological systems has not yet been provided. Also, the difficulties of empirically finding an approximate value of a stochastic CT and the narrow parameter range at which ghosts may be observed poses big problems to deploy such interventions in cases of potential collapse after a TP. These issues deserve further experimental research or searching for ghost fingerprints in available ecological time series. Our feeling is that this may be possible, despite these difficulties.

## 7. Non-equilibrium ecology and conservation

Ecosystems face significant threats from human activities, needing effective management to ensure their long-term viability (see Francis et al. (2021) for implications of transients in management). A promising strategy for restoring ecosystems is the reintroduction of previously eradicated species, a practice known as trophic rewilding (Wolf and Ripple, 2018; Carver et al., 2021). Trophic rewilding is a conservation strategy that aims to reestablish a previously existing ecological state characterized by higher biodiversity (Seddon et al., 2014; Dirzo et al., 2014). A notable example of this approach is the reintroduction of wolves in Yellowstone National Park (Ripple et al., 2014; Schweiger et al., 2019; Soulé and Noss, 1998). Reintroduction of keystone species such as wolves can help restoring natural processes and interactions that were disrupted by human activities. This approach not only benefits individual species but also promotes the overall resilience of the ecosystem (Wilmers et al., 2012; Bartley et al., 2019).

Wolves play a vital role in ecosystems through their top-down regulation of herbivore populations. By keeping herbivore numbers in check, wolves prevent excessive browsing, enabling vegetation to grow and compete more efficiently. This, in turn, leads to the development of more diverse and heterogeneous habitats capable of supporting a greater variety of species (Svenning et al., 2016). For instance, the return of wolves has facilitated the survival of beavers, bears, and even salmon, each of which contributes to the establishment of new ecological feedback loops that sustain a higher flow of energy and matter within the ecosystem.

In marine ecosystems, there is a growing proposal to enhance the quality of life for whales in order to maintain their crucial contribution to the global biosphere (Doughty et al., 2016; Pearson et al., 2023). Without whales, a significant portion of the nutrients that sustain oxygen production in the ocean, essential for supporting life on our planet, would be at risk. Whales play a vital role as transporters of nutrients, releasing fecal plumes rich in nutrients after consuming prey from deep ocean waters (Johnson et al., 2022). These nutrients stimulate the

growth of phytoplankton, which are responsible for a substantial portion of global oxygen production. By facilitating the transfer of nutrients across different oceanic regions, whales contribute to the overall health and productivity of marine ecosystems.

It is important to recognize that trophic rewilding is just one facet of effective ecosystem management. The preservation of natural habitats is another critical strategy in this regard, particularly in marine environments where the establishment of Marine Protected Areas (MPAs) has proven to be highly effective (Lotze et al., 2011). In particular, MPAs have shown a really important effect in protecting kelp forest by diminishing the urchins degradation by enabling longer trophic chains controlling the urchins abundances (Peleg et al., 2023).

Another strategy to improve the effect of protected areas in the interconnection between them, the so-called green (terrestrial) (Soulé and Noss, 1998; Perino et al., 2019; Carver et al., 2021) and blue (ocean) (Johnson et al., 2022) corridors. The implications and success of these corridors have been questioned since their formulation (Beier and Noss, 1998). But mainly, they help to recover the diversity previously lost and to reduce the wildlife-human conflicts.

As expected, these strategies are used to mitigate the negative consequences of defaunation and its cascading effects (McCauley et al., 2015; Finn et al., 2023; Dirzo et al., 2014), which have been occurring since the early stages of human impact on ecosystems (Ellis et al., 2021). It is our responsibility to now take action and protect these ecosystems from further deterioration (Seddon et al., 2014; Mayer and Rietkerk, 2004; Duarte et al., 2020). Given our power to shape ecosystems, we can also explore alternative solutions such as geoengineering (Lenton, 2018; Caldeira et al., 2013) and bioremediation (de Lorenzo, 2008, 2017; Dvořák et al., 2017). In fact, synthetic biology offers a form of bioremediation that considers its effects on ecological tipping points, known as Terraformation (Vidiella et al., 2020; Conde-Pueyo et al., 2020; Sardanyés et al., 2018), which involves the application of synthetic biology techniques (Vidiella and Solé, 2022; Tran et al., 2021).

## 8. Concluding remarks

Complex systems, such as ecosystems, can suffer sudden transitions between alternative stable states due to continuous parameter changes (bifurcation-induced, B-tipping), to noise-induced jumps (N-tipping), or to rate-induced changes (R-tipping) (Dakos et al., 2008; Scheffer and Carpenter, 2003; Scheffer et al., 2001, 2012; Folke et al., 2004). Nonlinear dynamics and non-equilibrium phenomena must be taken into account to understand ecosystems' dynamics and should be seriously considered in management and conservation strategies. It becomes a great challenge to anticipate these critical transitions (CTs) and find warning signals (WS) able to clearly indicate that a system is approaching a tipping point (TP). While the literature on regime shifts is wide and many examples have been identified in natural systems (Folke et al., 2004), intensive research on how deploying conservation strategies close to TPs is much needed, specially how to detect transients and identify their properties. Here, we also emphasize in the need to identify and investigate indicators providing warning signals in systems having surpassed a TP.

Some take-home messages of our contribution are:

1. Population density e.g., vegetation cover (Berdugo et al., 2017), is not a good indicator of an ecosystems' health state: an abundant species could rapidly collapse if a TP is overcome (Dai et al., 2012; Sardanyés and Solé, 2006a; Vidiella et al., 2018). However, low population sizes could drive the population faster to a regime shift due to stochastic jumps.
2. Mathematical and computational models can be very useful to identify the nature of CTs for a particular ecosystem (or part of it) and aid in management and conservation strategies.
3. Different Bifs can give place to different TPs and each of them may have more suitable leading indicators (LIs). The most common is the

s-n Bif, for which many LIs have been proposed (Dakos et al., 2019). Further research is needed in this direction.

- To overcome the effect of hysteresis after a regime shift, it may be necessary to act simultaneously on the driver parameter and on the population size e.g., by reducing the driver intensity while re-introducing individuals forcing the system to cross the unstable branch, achieving recovery.
- Transient phenomena may be the norm and not the exception in ecosystems, which are constantly perturbed systems. Transients can also arise due to small changes in the strength in biotic interactions, as mathematical models indicate.
- Last but not least, dynamics close to TPs governed by s-n Bif experience ghost transients and they could difficult ecosystems' recovery or provide time to deploy actions once the TP has been surpassed but the system has not yet collapsed. For this later case, we provide computational evidence of late WS indicating that a CT has been overcome.

#### Declaration of competing interest

The authors declare no competing interests.

#### Data availability

Data will be made available on request.

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- Nonlinear:** system or phenomenon where the relationship between cause and effect is not proportional or directly predictable. In nonlinear systems, small changes in inputs can lead to disproportionate or unexpected outcomes. The principle: “the whole is equal to the sum of the parts” breaks down for nonlinear systems.
- Deterministic:** process resulting from a system where there is total absence of noise (intrinsic and/or extrinsic). Determinism is assumed in differential equations where the dynamics only depends on the interactions between the variables and given initial conditions.
- Regime shift(RS):** notable and long-lasting alteration in an ecosystem’s structure, function, and dynamics. It entails a shift from one stable state to another, leading to noticeable variations in ecological patterns, species composition, and ecosystem processes.
- Tipping point (TP):** critical threshold in an ecosystem where a small change or disturbance can lead to a sudden and discontinuous shift in the system’s state or behavior. It can represent a point of no return resulting in the loss of biodiversity, disruption of ecological processes, and degradation of ecosystem services.
- Critical transition (CT):** threshold value, usually determined by parameters, after which a system changes its state. This change of state can be continuous (smooth) or catastrophic (TP).
- Bifurcation (Bif):** qualitative change of the dynamics of a dynamical system due to changes in one or more parameters.
- B-tipping:** catastrophic regime shift caused by a bifurcation making the system to reach an alternative stable state.
- Monostable:** state or condition in which a system or process has a single stable equilibrium. It implies that the system tends to return to this stable state even after experiencing perturbations or disturbances.
- Saddle-node bifurcation:** bif. involving the collision and annihilation of a stable and an unstable fixed point. This Bif has been described in experiments with yeast (Dai et al., 2012) and electronic circuits (Trickey and Virgin, 1998).
- Local bifurcation:** bif that involves equilibrium or fixed points. Most typical ones are saddle-node, transcritical, pitchfork, and Hopf Bifs (Strogatz, 2018).
- Global bifurcation:** bif not involving equilibrium points (dimension 0) but objects of higher dimension such as periodic orbits or strange chaotic attractors.
- Unstable equilibria:** equilibrium states of a system that are not stable and will not be achieved by the system in the long term.
- Equilibrium point:** state of a system that involves a single constant population value achieved in sufficiently long times. These points can be calculated e.g., by setting the differential equations to zero (no change of the variable with respect to time).
- Potential landscape:** conceptual representation of the system’s behavior and stability based on energies or potentials where valleys and peaks denote stable and unstable equilibria, respectively.
- N-tipping:** achievement of an alternative stable state due to noise (stochastic fluctuations, demographic and/or environmental) allowing the system to cross and unstable state.
- Ecosystem resilience:** capacity of an ecosystem to absorb disturbances, adapt to changes, and maintain its essential functions, structure, and feedbacks (see Dakos et al. (2014)).
- Early warning signals (EWS):** signals or indicators that offer advance notice or predictions of an impending ecological RSs or CT.
- Critical slowing down:** phenomenon where system’s recovery times slow down as it nears a critical threshold and the return to a stable state becomes increasingly delayed. It has been observed in nonlinear optic experiments (Kramer and Ross, 1985) and biological systems (Wissel, 1984; Dakos and Bascompte, 2014; Lade and Gross, 2012).
- Leading indicators:** measurable temporal or spatial properties e.g., variance of fluctuations, return times, plants distribution, that offer advance information regarding the approaching to a RSs (see Dakos et al. (2012) and references therein).
- R-tipping:** tipping occurring when the change in the driver (environment) is faster than the force that restores the system to its stable state.
- Bistability:** situation in which a system or process has two distinct stable equilibria states at fixed external conditions.
- Hysteresis:** phenomenon in which the present state or behavior of a system is influenced by both its current inputs and its past history or trajectory. It is characterized by a delay or lag in the system’s response when there are changes in inputs or conditions.
- Transient:** time a given initial condition spends to achieve an equilibrium state.
- Late warning signals (LWS):** signals or indicators arising once a system has surpassed a CT and is experiencing a long transient towards the alternative state. As a difference from EWS, urgent actions may be needed to recover the system.
- Absorbing state:** state at which a system once enters cannot escape e.g., extinction of a species on Earth.
- Delayed transitions:** extremely long delays found right after a s-n Bif.
- Ghost:** remnant equilibrium causing extremely long transients right after a s-n Bif. This phenomenon has been experimentally proved with an electronic circuit (Trickey and Virgin, 1998).
- Stochastic s-n bifurcation:** in the stochastic regime, the bifurcation (or phase transition) consists of the transition from the probability density function (PDF) being unimodal (i.e., a single maximum) to bimodal (i.e., two maxima). In the mean field limit the PDF is peaked around its modes and this transition is equivalent to the bifurcation in the corresponding dynamical system.
- Cellular automata (CA):** mathematical or computational models consisting of cells grid, each having a specific state. Cells change states based on predefined rules and the states of neighboring cells. CA are used to simulate complex systems and often exhibits emergent spatio-temporal properties.

## Glossary

In this section we provide definitions for key concepts listed by order of appearance within this manuscript. For further information on the topics discussed see also Scheffer and Carpenter (2003); Selkoe et al. (2023); Dakos et al. (2019); Vidiella et al. (2021); Francis et al. (2021); Zhao et al. (2021); Hu et al. (2022).

**Emergent properties:** novel characteristics or behaviors that emerge from the nonlinear interactions of parts in a complex system. They cannot be predicted solely from the individual components but arise from their collective organization.

**Anthropocene:** present geological era marked by substantial human influence and its effects on Earth’s ecosystems, climate, and geology.