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Abstract

The increasing incidence of extreme events combined with long-term pressures due to climate change and anthropogenic activities are seriously threatening ecosystems worldwide. Promoting ecological resilience (i.e., the ability of ecosystems to absorb changes and maintain their processes and functioning) is a pivotal target for biological conservation. Many empirical approaches to assess resilience have relied on the underlying assumption that, in the absence of disturbances, ecosystems would be in a 'static' baseline state. In reality, ecological systems are highly dynamic and undergo phases of development and reorganization resulting from natural successional changes and their response to multiple interacting variables. As such, ecosystem states can be better described by 'dynamic regimes' rather than stationary states. In this context, there is an urgent need to expand the common 'equilibrium-based' approaches used in empirical ecology to evaluate resilience so that they can be applied to non-static ecosystems. Here, we present our perspective on the relevance of approaches based on dynamic regimes to assess ecological resilience empirically. More specifically, we briefly review the concept of resilience and discuss the main challenges for empirical applications. Then, we review an approach based on ecological dynamic regimes and temporal trajectories that can be used to assess the ecological resilience of non-static ecosystems from empirical data. Approaches focused on dynamic regimes help evaluate the management effort necessary to restore a disturbed ecosystem. Besides, they facilitate the identification of the factors that must receive special attention for enhancing ecosystem resilience.

Keywords

Non-equilibrium, transients, ecological trajectories, stochasticity, stability, stable states

1. Introduction

As a consequence of human activities and anthropogenic climate change, terrestrial, marine, and freshwater ecosystems around the globe are experiencing important changes affecting relevant ecological processes at multiple organizational scales (Díaz et al., 2019; Scheffers et al., 2016). Such threats raise the urgent need for undertaking management actions that promote ecosystem persistence, halt the loss of biodiversity, and prevent the extinction of threatened species. In this context, safeguarding ecosystem resilience has emerged as a paradigm for researchers, practitioners, and policy-makers and has become an essential target for international organisms (CBD, 2022).

The concept of resilience was introduced in the ecology literature as the ability of ecosystems to absorb changes in ***state variables*** (see Glossary) and processes while maintaining their functioning after disturbances (Holling, 1973). In his seminal paper, Holling (1973) supported the resilience concept with dynamical systems theory, explicitly referring to terms such as stability, equilibrium, domains of attraction, and phase space (Yi and Jackson, 2021). Subsequently, much theoretical work on resilience theory has been developed using mathematical models based on differential equations to describe the post-disturbance dynamics of ecological systems. The implementation of these approaches in real systems, however, can be limited by the lack of a model describing ecological dynamics and the difficulty of incorporating ecosystems' complexity, including randomness, spatial heterogeneity, and multiple state variables (Holling, 1973).

The need for obtaining pragmatic information from empirical data to assist decision-making and prioritize conservation actions has led to a profusion of resilience metrics and analyses that are not always directly related to the theory (Quinlan et al., 2016). One of the important drawbacks of the discrepancy between the theoretical framework of ecological resilience and its quantification from empirical data is the difficulty in incorporating ***non-equilibrium dynamics*** (Van Meerbeek et al., 2021). Although there are exceptions (e.g., López et al., 2022), empirical approaches very often adopt the "balance of nature" paradigm assuming that ecological systems remain around a stationary average state that is taken as a reference while overlooking the stochasticity and variability of the dynamics (Nikinmaa et al., 2020; Yi and Jackson, 2021). Such approaches implicitly elude studies that for a long time have stressed the importance of non-equilibrium and ***transient dynamics*** in ecological systems (Abbott et al., 2021; Hastings, 2004; Hastings et al., 2018; May, 1972). In nature, ecosystems constantly fluctuate due to a multitude of reasons. An ecosystem may be out of equilibrium because its internal dynamics oscillate in regular or irregular ways (Hastings et al., 1993), because some condition (e.g., environmental variables) has changed and the system is on its way to a new equilibrium (Van Geest et al., 2007), or because it has been perturbed and has not recovered yet (Higgins et al., 1997). Furthermore, continuous small perturbations or simply a large number of species interacting within ecosystems at different scales and spatial dynamics can lead to long transient dynamics (Hastings, 2004; Hastings and Higgins, 1994).

There is, therefore, a need for tools that bridge the gap between theoretical and empirical ecology so that resilience can be quantified in non-equilibrium ecosystems accounting for their stochasticity and dimensionality (Rogers et al., 2022). A very useful approach in resilience theory is the "vector field model" proposed by Lewontin (1969). The approach consists of an *n*-dimensional space defined by a set of variables that describe the state of the system (i.e., state variables). This dynamical state space is a ***vector field*** defined by a set of transition vectors that determine the path of a system as a function of its position within the state space. As real ecosystems include random forces that make the identification of ecosystem dynamics in the dynamical space difficult, Lewontin proposed the use of probability density functions to define the trends followed by dynamical systems and, ultimately, the geometric characteristics of what he named the system's ***"basin of attraction"***. Complementarily, ***"ecological dynamic regimes"*** is another useful concept. While used in previous studies (e.g., Ellner and Turchin, 1995; Pascual and Levin, 1999), Scheffer and Carpenter (2003) highlighted the relevance of this concept to refer to stable but not-static states. They argued that whereas the term "stable state" seems to exclude the dynamic nature of ecological systems, "dynamic regime" accounts for ecosystems' fluctuations around some trend or average.

Here, we present our perspective on the relevance of approaches based on the concept of dynamic regimes and vector fields to assess ecological resilience empirically. For that, we (1) briefly review the concepts of engineering resilience and ecological resilience**,** and some widely-used approaches to quantify resilience from empirical data, (2) discuss the challenges to assessing ecological resilience on empirical data, (3) review a recent approach based on ecological dynamic regimes described through temporal trajectories on multidimensional ***state spaces*** (Sánchez-Pinillos et al., 2023), and (4) propose different ways to assess ecological resilience to ***pulse*** and ***press disturbances*** using dynamic regimes. Finally, (5) we discuss the implications of our perspective for the conservation of ecosystems within the current context of global change.

2. Overview of the resilience theory and quantification from empirical data

Since its introduction in ecology by Holling (1973), the term resilience has been suggested to be decomposed into two concepts (Holling, 1996): ***"engineering resilience"*** and ***"ecological resilience"*** (see Glossary). Although both concepts are usually very correlated, the differences in their definitions have led to two different perspectives with different scopes of application and metrics (Dakos and Kéfi, 2022).

The definition of "engineering resilience" implicitly assumes that the system remains close to one possible ***attractor*** to which the system recovers after being disturbed. Within this perspective, ecosystems with shorter recovery periods after disturbances are assumed to be more resilient than those with longer or incomplete recovery periods. Hence, engineering resilience is typically quantified as the return rate of the system to its original state or the extent to which recovery is fulfilled at a specific temporal point (Hodgson et al., 2015). The quantification of engineering resilience usually requires the identification of three states of the studied system (Ingrisch and Bahn, 2018): (1) a reference state or baseline characterizing the pre-disturbance conditions, (2) a disturbed state capturing the maximum impact of the disturbance on the system, and (3) a post-disturbance state following the relaxation of the disturbance (i.e., the state to which the ecosystem recovered; Figure 1).

The comparison between the reference and the post-disturbance states informs on whether or not the system has recovered the pre-disturbance conditions. If both states are similar enough, engineering resilience is quantified as the speed of recovery or the time required by the system to recover to its reference state. In practice, this approximation is difficult to apply because it requires continuous or quasi-continuous monitoring of the system to detect the moment at which the system reaches the pre-disturbance conditions. Instead, many empirical approaches just use the similarity between the pre-disturbance and post-disturbance states as an approximation of engineering resilience or normalize this value by either the impact of the disturbance (quantified through the disturbed state) or the value of the reference state (Ingrisch and Bahn, 2018; Yi and Jackson, 2021). In that case, normalized indicators quantify the ability of the system to recover in relation to how much it is displaced by the disturbance or how difficult it is to reach the reference state. For example, a widely used approach with these characteristics is the one proposed by Lloret et al. (2011) to assess tree resilience to drought by comparing basal area increments before, during, and after drought.

Unlike engineering resilience, "ecological resilience" takes into account that disturbances or changes in the state variables can flip the system into alternative domains of attraction with possible consequences on the system's structure and function. The definition of ecological resilience is implicitly associated with a ***stability landscape*** containing a set of alternative basins of attraction. Within this perspective, the loss of ecological resilience may occur due to two different, but not excluding phenomena: severe disturbing events affecting the system state (Figure 2a-b) and changing conditions modifying the geometry of the basin of attraction (Figure 2c-d) (Beisner et al., 2003). Thus, ecological resilience may be quantified based on the characteristics of the basin of attraction (e.g., its size or width) and the magnitude of the disturbance that can be absorbed by the system before changing to an alternative basin of attraction (Dakos and Kéfi, 2022).

Probably, one of the simplest assessments of ecological resilience would consist in identifying how much change in a given environmental variable it would take for a given ecological system to shift to a different state. This requires historical data of the system documenting shifts that have happened in the past (e.g., nutrient loading thresholds identified in lakes; Scheffer et al. (1993)), but also a previous characterization of alternative stable states and their variability. Some approaches have reconstructed the stability landscape using long time series covering large spatial scales (Hirota et al., 2011). The alternative basins of attraction and the discontinuities between them can be identified through historical ranges of variability (Keane et al., 2009), probabilistic density functions or histograms (Hirota et al., 2011; Livina et al., 2010), kernel density estimations and clustering analyses in multidimensional state spaces (Barros et al., 2016; Sánchez-Pinillos et al., 2019), or statistical tests assessing multimodality and significant changes in the magnitude and variance of ecosystems' responses to environmental gradients (Hillebrand et al., 2020; Hirota et al., 2011). Once alternative basins of attraction are defined, potential shifts between them can be assessed through temporal trajectories describing post-disturbance dynamics (Sánchez-Pinillos et al., 2019; Seidl et al., 2016) (Figure 2b) and resilience can be estimated based on the size of the basins of attraction. Hirota et al. (2011), for example, identified three alternative states of tropical forest systems by assessing the frequency distribution of tree cover depending on precipitation. Assuming that such frequency relates to the size of the basin of attraction, they found that the system's resilience to external perturbations, such as drought or logging, depended on the precipitation regime.

3. Challenges when quantifying resilience from empirical data

Many approaches mentioned in Section 2 to quantify engineering and ecological resilience from empirical data rely on indicators that implicitly assume that, in the absence of disturbances, ecosystems remain in a 'static' reference state with more or less variability depending on the approach. This perspective is, paradoxically, opposed to the seminal paper by Holling (1973), who stated that "an equilibrium-centered view is essentially static and provides little insight into the transient behavior of systems that are not near the equilibrium". In reality, ecosystems are likely to be in transient states and typically undergo sequential phases of development and reorganization resulting from natural successional changes, self-organization processes, and adaptation to the experienced conditions (Gunderson and Holling, 2002; Hastings, 2004). Despite the increasing interest in the last decades, the study of ecological resilience from field data still faces important challenges regarding the type of attractors, the stochasticity and variability of ecosystem dynamics, and the dimensionality and instability of the basins of attraction.

3.1. Types of attractors and transient dynamics

While stable equilibrium points (at the bottom of the basins of attraction: Figure 1; Figure 2) are the simplest attractors to be characterized, other more complex attractors, such as cyclic dynamics, quasi-periodic oscillations, or strange attractors are also possible (Holling, 1973; Scheffer, 2009) (Figure 3a). Besides, the observed ecosystem states are not necessarily at equilibrium but can be subject to transient dynamics that can last from dozens to hundreds of generations (Hastings, 2004).

Identifying whether ecosystem behavior exhibits asymptotic or transient dynamics is an essential issue in assessing resilience and designing appropriate management practices (Francis et al., 2021). Some approximations addressed in Section 2 –using one specific pre-disturbance state as the baseline for assessing resilience– may imply serious simplifications of the system behavior, especially when long temporal data are not available and the reference is defined as the state immediately before the disturbance or the average value of the state variables (Lloret et al., 2011). In these approaches, the state used as the reference is implicitly assumed to be at equilibrium. However, this state could also correspond to a transient state impossible to recover. Besides, if the attractor is not a static stable state but a cycle or a more complex attractor, resilience could be underestimated. For example, one could define a specific state of a cyclic attractor as the reference and assume catastrophic changes if after the disturbance the system is in another state of the same cycle.

3.2. Stochasticity and variability of ecosystem dynamics

Although ecological dynamics are mostly driven by changes in a few dominant variables, small differences in environmental conditions or historical legacies may lead to great variability of secondary variables, and consequently, in the dynamics of the system state (Chapin et al., 2000; Peterson, 1998). Even in the absence of perturbations and under the same environmental conditions, it is unrealistic to assume that ecological systems perpetually remain within a steady state or follow the precise dynamics described by the attractor. Stochastic events, fluctuating variables (e.g., seasonality and normal weather conditions), and slow-changing conditions (e.g., local extinctions and colonization) prevent natural systems from establishing at the attractor and lead them to transient dynamics around the equilibrium (Hastings et al., 2021; Scheffer, 2009). As such, ecological attractors should not be represented by a single point (Figure 1) or trajectory (Figure 3a), but by a set of trajectories capturing the variability of ecosystem dynamics under certain environmental conditions (Figure 3b).

Among the approaches considered in Section 2, those based on probabilistic functions and ranges of variability consider the potential states that an ecological system can visit over time but overlook the characteristics of their dynamics (Figure 2). In this sense, the order or the speed at which ecological states succeed one another can have important implications. For example, whereas a gradual increase in the vegetation cover is a common process of primary ecological succession, the gradual loss of species abundance could indicate a regressive trajectory toward the degradation of an ecosystem (Alados et al., 2003).

3.3. Dimensionality of the basins of attraction

Evaluating the global dynamics of ecological systems requires considering the complex interacting network between their components (Mitchell, 2009). For example, the dynamics of plant communities depend on the interactions between individuals, which in turn vary with multiple environmental conditions, but also their size, spatial association, and the balance between competition and facilitation forces (Armas and Pugnaire, 2005; Callaway and

Lawrence, 1997). As such, the state space in which the domain of attraction is immersed is a multidimensional space whose axes are defined by the components of the studied ecological system and their interactions (e.g., species abundances) (Scheffer, 2009).

Such dimensionality of the basins of attraction is transferred to the ecological dynamics which, instead of being restricted to one dimension (i.e., one state variable whose value increases or decreases), can be expressed by the combination of changes in the state variables. Hence, resilience does not only depend on the magnitude of the disturbance but also its direction within the state space (Meyer, 2016; Scheffer, 2009). For example, an undisturbed ecosystem may fluctuate around a saddle point (Figure 3c). Whereas the system is very resilient to disturbances acting in one dimension of the state space, a small variation in the direction of the disturbance (i.e., affecting a different combination of state variables or their interactions) may push the system away from the original state.

Unfortunately, most studies evaluating engineering or ecological resilience adopt univariate approaches, considering the effects of only one driver of change on one state variable, and overlook the great complexity of ecological systems (Donohue et al., 2016).

3.4. Stability of the basins of attraction

Another factor leading to transient dynamics is the possible change of the shape of the basin of attraction due to press disturbances, such as climate change. On the one hand, ecological systems may gradually adapt to environmental changes, retaining the characteristic state variables and keeping the geometry of the basin of attraction (Carpenter et al., 2001; Gunderson, 2000). On the other hand, if the systems do not adapt to changes in external forces, the relationships between the state variables can change, and therefore, the geometry of the basin of attraction (Figure 3d). Such changes can occur smoothly and ecological systems may exhibit long transient dynamics. Alternatively, in the presence of alternative basins of attraction ('bistability'), ecosystem states can abruptly change when the level of pressure crosses a certain threshold (Scheffer and Carpenter, 2003).

Whereas some approaches, such as those based on historical ranges of variability or probability density functions, account for the stochasticity and multidimensionality of the data, they often assume the stability landscape and the immersed basins of attraction constant over time (Seidl et al., 2016). Changes in slow biotic or abiotic conditions may alter the geometry of basins of attraction and the whole stability landscape, making the historical reference states unattainable and unrepresentative of current conditions (Hobbs et al., 2009; McNellie et al., 2020). Thus, stability landscapes should be interpreted as "vibrating and wobbling structures" constantly affected by slow trends and stochastic fluctuations (Scheffer et al., 2015) and be calculated from data contemporary to the disturbances and drivers of change (Chambers et al., 2019).

4. Ecological Dynamic Regimes: a multidimensional, dynamical perspective of stable states

To reflect reality, stability landscapes should account for non-equilibrium dynamics at three hierarchical levels: first, the variability and stochasticity of ecological dynamics (Figure 3b); second, the long-term dynamical trends (i.e., the shape of the attractor or transient dynamics; Figure 3a); and third, the changes in the basin of attraction (Figure 3d). Finally, stability landscapes should account for multiple dimensions defined by the variability of the interactions between the state variables. Therefore, the stability landscape is defined as a multidimensional state space subject to temporal changes and capturing ecosystem dynamics through a set of trajectories fluctuating around some trend or average and responding to an intricate mix of internal processes and external forces (i.e., dynamic regimes).

A powerful approach in theoretical ecology addressing these issues is the one based on quasi-potential functions. Quasi-potentials allow assessing the stability of ecological systems through a surface (representing the stability landscape) that describes the dynamics of the system subject to low-intensity noise (Nolting and Abbott, 2016; Zhou et al., 2012). The empirical application of quasi-potentials depends on the previous definition and validation of a model based on stochastic differential equations. As these models are often difficult to parameterize, Suzuki et al. (2021) proposed reconstructing the stability landscape of ecological communities through a pairwise maximum entropy model based on species niches and interspecific interactions. In their approach, Suzuki et al. (2021) used the model to extract the probability of occurrence of multiple communities under certain environmental conditions. Then, they defined the stability landscape assuming that communities with low probability generally transition towards others with higher probability and similar species composition.

Alternatively, the behavior of dynamic systems can be reconstructed from non-parametric methods that infer dynamic patterns and state dependencies directly from the data. That is, without assuming specific data distributions, but still acknowledging that some dynamics are more representative of natural systems. Here, we focus on a recent framework based on ecological dynamic regimes (EDR framework; Sánchez-Pinillos et al., 2023). The EDR framework comprises a set of metrics and analyses to identify, characterize, and compare ecological dynamic regimes from empirical data based on the distribution of observed dynamics in a state space. In the EDR framework, the state space is defined by a matrix containing state dissimilarities in observed time series. Therefore, it can be applied to different ecological scales (e.g., populations, communities, ecosystems) and state variables (e.g., age classes, species abundances, functional traits) whenever their changes can be quantified through a dissimilarity metric. These characteristics make the EDR framework a good alternative to define new empirical indicators of ecological resilience (Section 5). Before that, we briefly review how the EDR framework can be used to reconstruct the stability landscape and characterize the basins of attraction.

4.1. The stability landscape in the EDR framework

The EDR framework considers the stability landscape as a multidimensional state space in which the basins of attraction are defined by the regions occupied by a set of ecological dynamics exhibiting analogous processes in the development, interaction, and reorganization of the state variables under certain environmental conditions and in the absence of perturbations (i.e., ecological dynamic regimes; EDR) (Figure 4a). In turn, ecological dynamics are represented as trajectories defined by a sequence of states (observations), such that each state is associated with a vector of coordinates in the state space capturing the relationships between state variables. Then, alternative EDRs are identified by clustering ecological trajectories with similar geometric characteristics in the state space. For that, it is important to use large data sets and check the data requirements and other technical details in the original publication (Sánchez-Pinillos et al., 2023).

To illustrate the definition of the stability landscape (Figure 4a), we used an artificial data set obtained by simulating the transition between communities dominated by a hypothetical species *1* towards the co-dominance of species *2* and *3* (EDR1) and the changes in communities dominated by species *6* to others dominated by species *4* (EDR2; Appendix A)

4.2. The attractors in the EDR framework

Within each EDR, attractors (and non-equilibrium dynamics) can be associated with the regions densely occupied by ecological trajectories and summarized in a set of representative trajectories (Sánchez-Pinillos et al., 2023). Similar to the approaches based on probability density functions to define alternative attractors, representative trajectories are based on the distribution and density of observed dynamics in the EDR. Therefore, they represent a characteristic sequence of ecosystem states toward which the system tends to evolve in the absence of disturbances. As representative trajectories do not assume a fixed distribution of the dynamics, they can be used to identify cycles, other more complex attractors, or common transient dynamics (Figure 4a). In Holling's words, the representative trajectories would represent "the referent trajectory containing only the cyclic properties of the system" excluding random forces that, together with the representative trajectories, "define the shape, size, and characteristics of the domain of attraction" (Holling, 1973). In contrast, the regions of the EDR that are most distant from the representative trajectories and have a low density of trajectories represent undetermined ecosystem dynamics in the boundaries of the dynamic regime or close to saddle attractors.

4.3. Dynamic variability and stochasticity

The variability and stochasticity of the dynamics in the basin of attraction can be evaluated through three quantitative indicators based on the dissimilarities between ecological trajectories: dynamic dispersion, dynamic beta diversity, and dynamic evenness (Sánchez-Pinillos et al., 2023). Dynamic dispersion (dDis) quantifies the average dissimilarity between the trajectories of an EDR and another trajectory taken as a reference. Hence, dDis can be used to quantify how immersed the reference trajectory is within the other trajectories in the EDR. For example, a trajectory associated with a high dDis value might indicate that it is relatively isolated in the EDR and close to the boundaries of the basin of attraction (Figure 4b, Trajectory C). If the reference trajectory is the representative trajectory, dDis measures the overall dispersion of the trajectories in the EDR or, in other words, the dispersion or stochasticity of ecological dynamics in relation to the attractor (Figure 4a). Dynamic beta diversity (dBD) is a measure of the overall variability of the dynamics in the EDR and can also be interpreted as the variance of the basin of attraction. Finally, dynamic evenness (dEve) measures de regularity with which the ecosystem dynamics fill the EDR and indicates potential discontinuities within the basin of attraction.

5. Assessing ecological resilience based on ecological dynamic regimes

Assessing ecological resilience requires different analytical approaches depending on whether the stability landscape is affected by the disturbing agent or not. Theoretical ecologists distinguish between disturbances affecting the state variables or the parameters determining the behavior and relationships between the state variables (Beisner et al., 2003). In the first case, an extreme event of great intensity may push an ecological system to an alternative basin of attraction without changing the geometry of the basin of attraction (Figure 2a-b). In the second case, slow-changing conditions may affect the interactions between the state variables, leading the ecological system towards an alternative basin defined by different "parameters" or characteristic behaviors (Figure 2c-d).

For example, a wildfire of extreme severity may provoke the conversion of a forest area into a grassland dominated by shade-intolerant flammable grasses defining an alternative domain of attraction (Pausas and Bond, 2019). Whenever the environmental conditions (e.g., soil, climate) that allow the existence of both basins of attraction (forests and grasslands) remain constant, the stability landscape will not change. However, climate warming may promote the replacement of shade-tolerant tree species by grasses and shrubs better adapted to dry environments. As climate conditions become harsher, recursive feedback with fire and vegetation provokes the shrinking of the basin of attraction and the shift of forest systems to grasslands or shrublands.

We propose different ways to assess ecological resilience in real systems using ecological dynamic regimes as defined in the EDR framework. Based on the simulated data to reconstruct the stability landscape, we considered three scenarios potentially observed in nature: (*i*) Three communities in EDR2 (dominated by different proportions of species *6* and *4*) are affected by a pulse disturbance that removes 75% of the abundance of species *4*; (*ii*) all ecological communities describing the stability landscape are affected by a press disturbance that gradually increases the competitive ability of species *5*; and (*iii*) the three ecological communities of the first scenario are simultaneously affected by the press disturbance in the second scenario.

5.1. Resilience to pulse disturbances

The assessment of ecological resilience to pulse disturbances requires defining a stability landscape (a state space) including alternative basins of attraction (EDRs) under the same set of conditions. Once the stability landscape is defined from undisturbed trajectories, we can conduct a descriptive analysis of the dynamic patterns of disturbed ecological systems. Depending on the position of the post-disturbance states within the stability landscape, we can identify three potential responses (Figure 4b): *resistance*, if all post-disturbance states remain within the original dynamic regime (Trajectory B); *recovery*, if the system visits the margins of the dynamic regime and returns to the original basin of attraction (Trajectory C); and *shift*, if the system remains in an alternative dynamic regime after the disturbance (Trajectory A). Dynamic dispersion (dDis) taking the post-disturbance trajectory as the reference can be used to evaluate its membership in the original EDR (Figure 4b).

The geometry of post-disturbance dynamics can be more specifically described through four complementary indices (Table 1). *Resistance* captures the relative magnitude of the disturbance as a function of the immediate changes provoked in the system. *Amplitude* informs about the direction in which the system is displaced during the disturbance in relation to its impact and the proximity of the system to the representative trajectory. Positive values indicate that the disturbance displaces the system towards the boundaries of the EDR whereas negative values mean that the system is pushed towards the representative trajectory. *Recovery* quantifies the ability of the system to bounce back towards the representative trajectory following the relief of the disturbance (if positive) or move in the direction of the boundaries of the basin of attraction (if negative). Finally, *net direction* quantifies the proximity of the system to the representative trajectory some time after the release of the disturbance and in relation to the net change produced in the system. *Net direction* is analogous to *amplitude* in the sense that it captures whether the system is eventually displaced towards the attractor or the boundaries of the EDR. Altogether, these indices inform about the geometric characteristics of post-disturbance dynamics within the basin of attraction. Depending on the sign (positive, negative, or zero) of *amplitude, recovery,* and *net direction,* it is possible to interpret the overall dynamic of the system in relation to the attractor.

In the first scenario (Figure 4b), the three communities affected by pulse disturbances showed contrasting responses depending on the state of the system. The three communities were pushed towards the boundaries of the EDR ($A > 0$). However, the amplitude was lower for Trajectory B, which remained relatively parallel to the representative trajectory ($ND \approx 0$). Despite the high amplitude in Trajectory C, it quickly recovered towards the representative trajectory ($Rc = 0.47$) and even surpassed the pre-disturbance state in the direction of the representative trajectory ($ND < 0$). Finally, despite having the highest resistance ($Rt = 0.96$), the community corresponding to Trajectory A was unable to recover ($Rc < 0$) and changed towards a different attractor ($ND > 0$). These results contrast with those obtained in the third scenario (Figure 4d), in which the three communities affected by interacting disturbances showed similar patterns to Trajectory A, indicating the risk of compound press and pulse disturbances for the conservation of community dynamics.

5.2. Resilience to press disturbances

The assessment of ecological resilience to press disturbances or slow-changing conditions can be calculated through the temporal changes in EDRs (Figure 4c). The EDR framework includes a metric (d_{DR}) to measure the dissimilarities between two or more EDRs as a function of the relative position of the dynamics describing each EDR. Ecological resilience to press disturbances can be evaluated using approaches such as the one proposed by Bagchi et al., (2017). In particular, four potential responses (stability, abrupt nonlinear shift, reversible change, and gradual linear shift) can be identified depending on the variation of the dissimilarity between the initial and sequential states of the EDR. Complementarily, temporal changes in dynamic dispersion, beta diversity, and evenness metrics, as well as in representative trajectories, may help interpret the impact produced by the pressure (Sánchez-Pinillos et al., 2023). For example, the loss of biodiversity would lead to a homogenization of the dynamics, which would be reflected by a decrease in the value of dynamic dispersion and beta diversity. The decreasing value of dynamic evenness would indicate differences between the dynamics of two or more groups of ecological systems within the same basin of attraction. Although the results cannot be necessarily conclusive, low dynamic evenness is an indicator of alternative responses to the changing agent and the existence of bistability.

The implementation of these approaches can be limited by the length and amount of data required to define, first, the EDRs based on relatively long-term dynamics and, second, their changes over time. Alternatively, EDRs could be constructed from simulated data generated through mechanistic mathematical models or comparing EDRs for similar ecological systems affected by different sets of conditions (e.g., populations of the same species in different locations).

In the second scenario (Figure 4c), the comparison between disturbed and undisturbed EDRs showed that EDR2 was more severely affected ($dDR = 0.09$) than EDR1 ($dDR = 0.02$). Particularly, the effects of the press disturbance translated into a higher dynamic dispersion ($dDis = 0.36$) and diversity ($dBD = 0.10$) and slightly lower dynamic evenness ($dEve = 0.81$) than the undisturbed EDR ($dDis = 0.21;\ dBD = 0.07;\ dEve = 0.83$; Figure 4a), indicating potential transient dynamics towards a new equilibrium.

6. Conclusions and implications for biological conservation

Understanding the factors that influence ecological resilience to stochastic events and environmental changes is pivotal to biodiversity conservation in the context of global change and increasing anthropogenic pressure (CBD, 2022). Yet, it is equally important that inaccuracies in the concepts and assessment methods do not mislead the decisions of policy-makers and practitioners to design environmental policies and management plans (Donohue et al., 2016; Peterson et al., 2003).

From the point of view of biological conservation, promoting engineering resilience may seem a rational decision. However, management practices based on ‘command and control’ aim to maintain ecological systems in a particular static point, which may have negative consequences in the long term (Holling and Meffe, 1996). Depending on the components of the system affected by such interventions, the system may lose part of its intrinsic variability. For instance, the exclusion of disturbances of moderate intensity may provoke the spatial homogenization of the system, a reduction of functional diversity, and eventually, a greater vulnerability to future disturbances (Mori, 2011; Spies et al., 2006). Furthermore, it is possible that the target state to be preserved is not in equilibrium or is even far from it (Figure 4c). In that case, maintaining or restoring an ecosystem in a specific transitional or unstable state may require frequent management interventions that can be unaffordable in the long term (Francis et al., 2021; Hobbs et al., 2009).

The first step to enhance ecosystem resilience is to adopt a non-equilibrium perspective that recognizes ecosystem natural fluctuations (Connell and Sousa, 1983; Phillips, 2004). Here, we showed how the EDR framework can be employed to recreate generalized stability landscapes from empirical data (Section 4). Then, we proposed new ways to assess ecological resilience to pulse and press disturbances using dynamic regimes –rather than static states– as the reference (Section 5). Based on the behavior of disturbed systems within the stability landscape, we can obtain valuable information for two essential conservation strategies: prevention and restoration. Within a particular dynamic regime, the response of a system to a disturbance may depend on its state and the direction of the disturbance (i.e., the state variables or their interactions more severely affected). Whereas some post-disturbance trajectories remain in the original dynamic regime, others can change to an alternative regime (Figure 4b), involving a potential loss of biodiversity that, coupled with other environmental changes, may lead to irreversible changes and ecosystem collapse (Figure 4d) (Huang et al., 2023; MacDougall et al., 2013). The regions of the dynamic regimes in which disturbed trajectories show regime shifts (Figure 4b: Trajectory A) inform about the ecosystem components (state variables) that must receive more attention in the prevention plans (Lindenmayer et al., 2016). Similarly, the position of the disturbed state in the stability landscape can help decision-making regarding the feasibility of restoring the system. For example, an ecosystem in the original dynamic regime is expected to maintain its functionality and normal dynamics without much assistance ('helpful resilience'; Figure 4b: Trajectories B, C). In contrast, if the disturbed state has shifted to an alternative dynamic regime with very different dynamics and processes, the restoration of the system may require intensive management interventions ('unhelpful resilience'; Figure 4b: Trajectory A) (Standish et al., 2014).

The application of the EDR framework can be limited by the large amount of data required to infer the stability landscape. However, the increasing number of initiatives to generate and maintain long-term monitoring networks at large spatial scales (e.g., LTER, NEON) is bringing new opportunities to apply this approach in real ecosystems. Further, although the EDR framework ideally requires large data sets covering the temporal scale of the system, it admits dimensionality reduction techniques (to deal with the effects of the lack of data) and the use of short time series collected in multiple sampling units at different states (to recreate dynamic regimes) (Sánchez-Pinillos et al., 2023). Another important question to consider is the resolution of the data to generate the stability landscape. A high resolution (many ecological trajectories and short inter-state periods) is adequate for systems with quick dynamics. However, high-resolution data may lead to overfitted landscapes. In contrast, landscapes generated from low-resolution data could overlook topographic details of the basins of attraction, which may have important consequences in restoration projects (Peterson, 1998).

Because the EDR framework is in its early stages, future applications in real ecosystems affected by a range of pulse and press disturbances of different intensities and durations are essential to fully understand its significance in conservation science. In that sense, we hope our perspective inspires some of those applications to support practitioners and policy-makers with accurate information to avoid severe and undesirable ecosystem responses.

Glossary

Attractor: State or sequence of states to which an undisturbed dynamical system naturally approaches. It can be in the form of a static point, a cyclic sequence of states, or other more complex shapes.

Basin of attraction: A set of ecological states whose dynamics lead towards a given attractor in the absence of large perturbations.

Ecological dynamic regime: Ecosystems' fluctuations around some trend or average resulting from the interaction between internal processes and external forces that, in the absence of perturbations, keep the system within the basin of attraction.

Ecological resilience: Ability of ecological systems to tolerate disturbances and still maintain the same relationships between state variables (Holling, 1973).

Engineering resilience: Ability of ecological systems to recover to their reference condition upon disturbance (Pimm, 1984).

Non-equilibrium dynamics: Fluctuations of the ecosystem behavior as a response to its internal processes or external forces following or not a general trend or average.

Press disturbance: Continuous disrupting events affecting the structure of ecological systems or the physical environment over long periods (e.g., climate warming, land-use change).

Pulse disturbance: Discrete and relatively short event that disrupts the structure of ecological systems or the physical environment (e.g., wildfires, floods).

Stability landscape: Multidimensional state space subject to temporal changes and capturing ecological dynamics within and outside the basins of attraction under certain external conditions.

State space: Multidimensional space defined by the state variables and their interactions in which ecological dynamics can be represented by linking in chronological order the states of ecological systems.

State variables: A set of variables that completely describe the state of the system and from which it is possible to infer the system dynamics. Examples of state variables are individual size classes, species abundance, or nutrient concentrations.

Transient dynamics: Dynamical behavior of a system that is different from its long-term behavior (Hastings, 2004).

Vector field: In physics, multidimensional state space defined by a set of transition vectors that determines the path of a system as a function of its position within the space.

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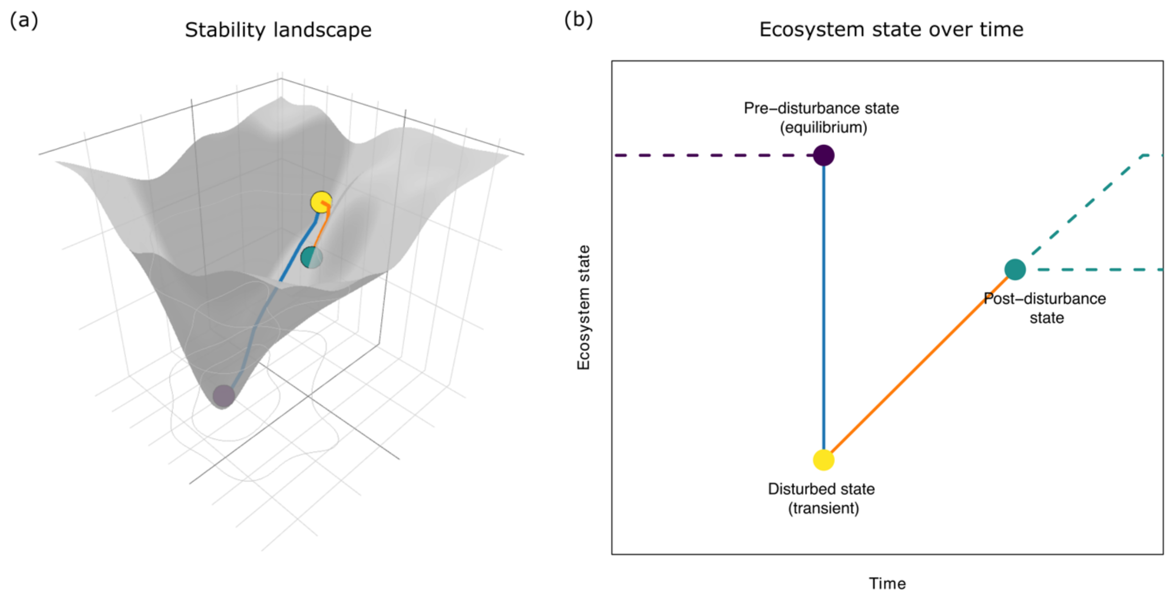

Figure 1. (a) Conceptual representation of the stability landscape when engineering resilience is considered. (b) Schematic visualization of the temporal variation of the ecosystem state before, during, and after a disturbance. From the perspective of engineering resilience, in the absence of disturbances, ecosystems remain in equilibrium (purple points). When it is disturbed, the system moves to a transient state within the basin of attraction (blue lines and yellow points) from which the system will gradually recover the original state or remain in a transient state (orange lines and green points).

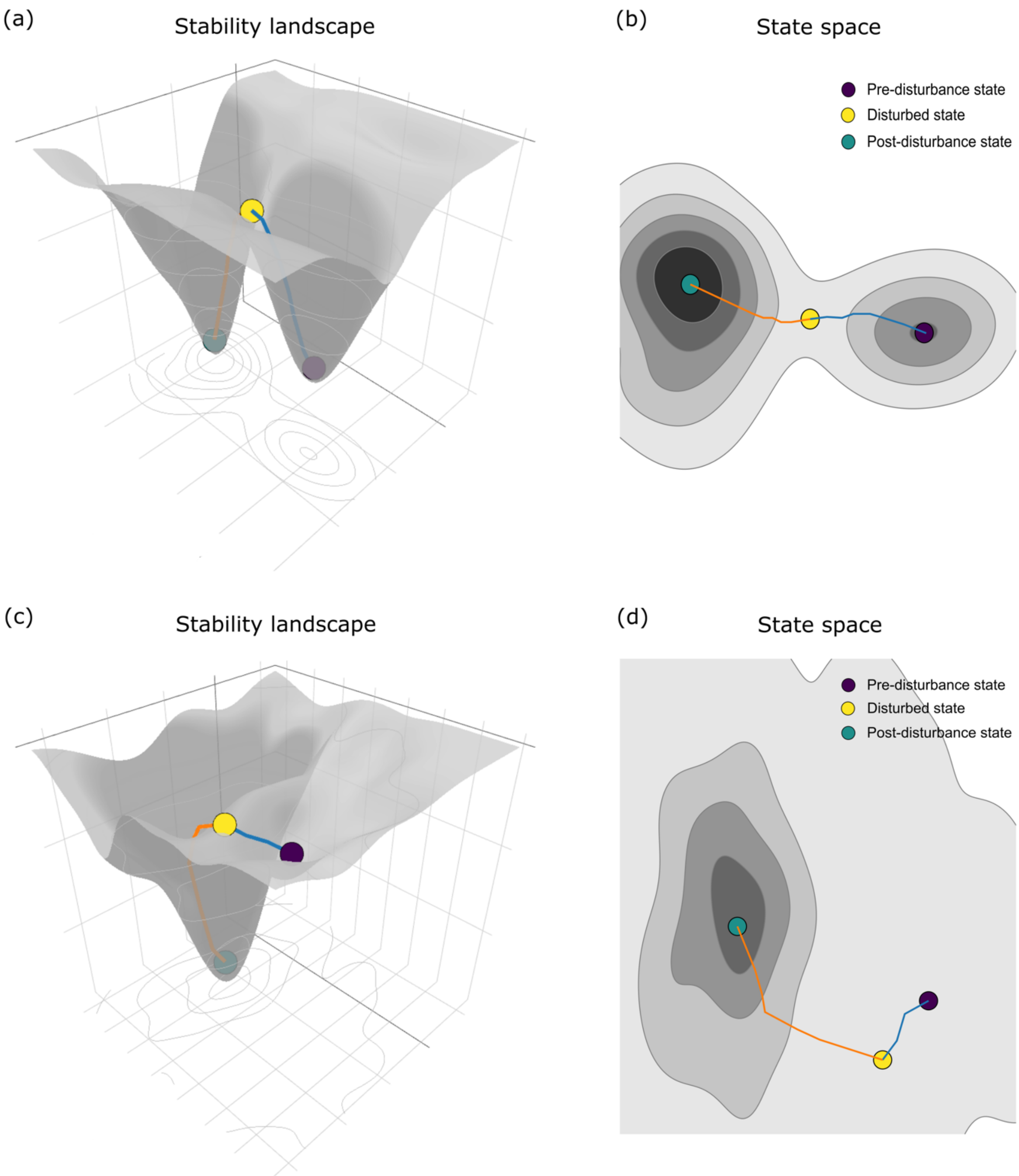

Figure 2. Hypothetical stability landscapes and their corresponding state spaces (representing the range of variability of ecosystem conditions based on probability density functions). (a, b) The loss of ecological resilience may be due to an extreme event that flips the system into an alternative basin of attraction. (c, d) Changing environmental conditions affecting the state variables may "erode" the basins of attraction, modifying the stability landscape and making ecosystems more vulnerable to disturbances of relatively low magnitude. Points represent ecosystem states before, during, and after the disturbance. Blue and orange lines represent the system trajectories caused by the disturbance and after the relaxation of the disturbance. In the state spaces, grey areas represent the distribution and variability of ecosystem states. The darkest areas represent the most common states and are assumed to be more stable and at the bottom of the basin of attraction.

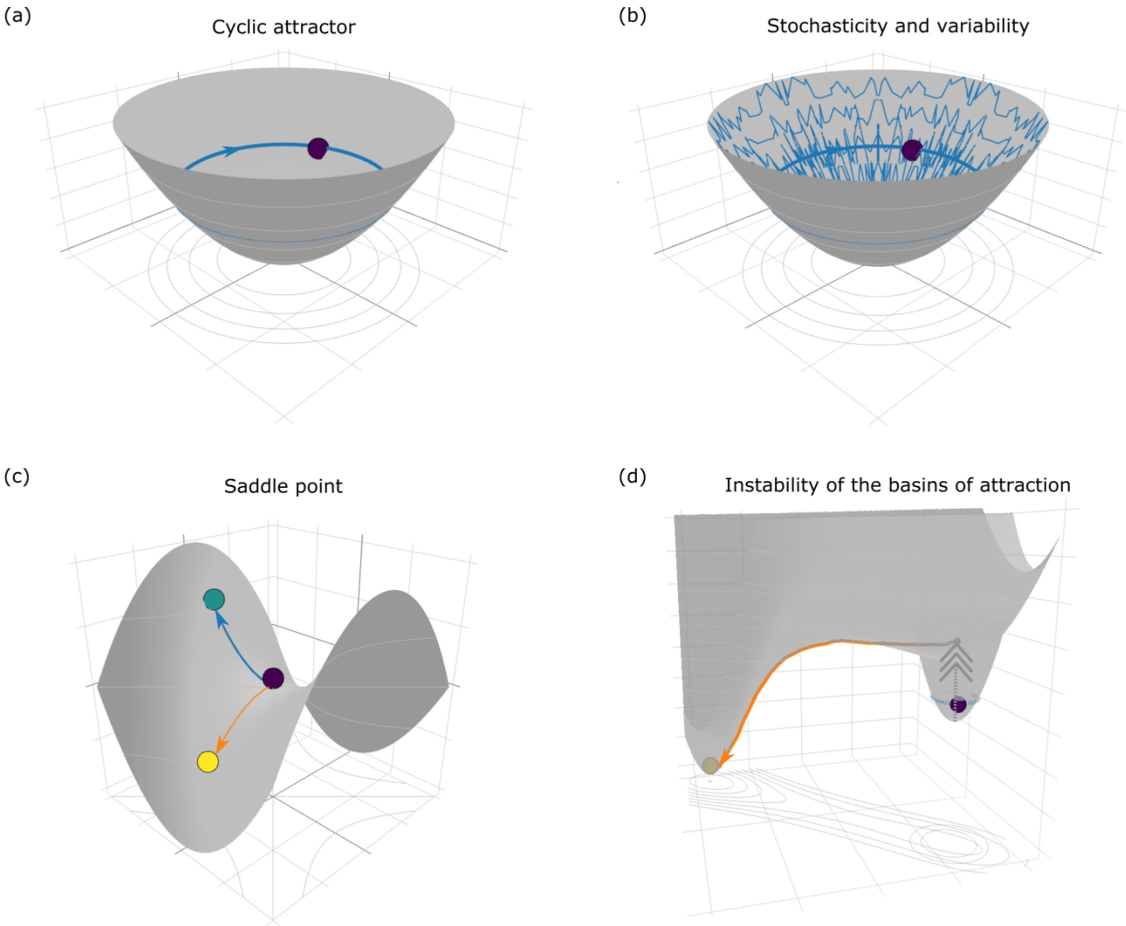

Figure 3. Challenges of quantifying ecosystem resilience. (a) Undisturbed ecosystems are not necessarily at stable equilibrium points but can show cyclic dynamics, other more complex attractors, or transient dynamics. (b) Ecosystems are characterized by great stochasticity and variability that make them fluctuate around some trend or average. (c) The effects of disturbances on ecosystems depend on the magnitude and direction of the disturbance in the state space (i.e., the effects on the resulting interactions between state variables). (d) Press disturbances may modify the geometry of the basin of attraction (grey arrows), affecting ecosystem vulnerability to other disturbances.

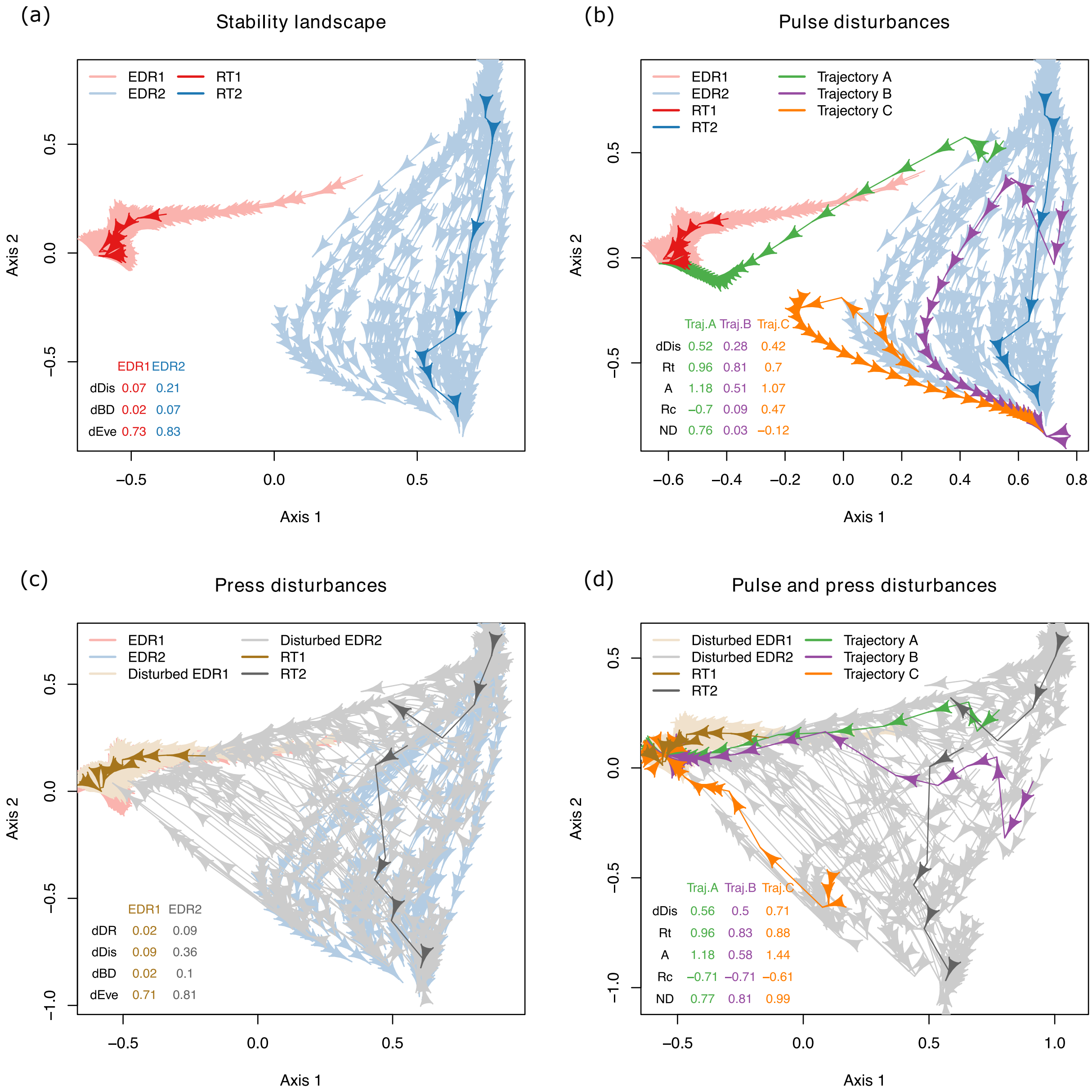

Figure 4. Representation of ecological dynamic regimes (EDR) defined by trajectories generated through general Lotka-Volterra models. (a) The stability landscape is represented by two alternative EDRs (EDR1, EDR2). Ecological dynamics are displayed as undisturbed trajectories showing the temporal variation of the state variables (species abundances) and their interactions. The variability of ecological dynamics is summarized by a representative trajectory in each EDR (RT1 and RT2) and the metrics of dynamic dispersion (dDis), beta diversity (dBD), and evenness (dEve). (b) Depending on the system state, a pulse disturbance may lead to different post-disturbance dynamics: resistance (Trajectory B), recovery (Trajectory C), or shift (Trajectory A). The indices of dynamic dispersion (dDis), amplitude (A), recovery (Rc), and net direction (ND) help identify the type of response in relation to the original EDR. Resistance (Rt) quantifies the immediate impact of the pulse disturbance. (c) Press disturbances may affect the geometry of the EDRs and their representative trajectories (RT1, RT2). The dissimilarity between undisturbed and disturbed EDRs (dDR) and the metrics dDis, dBD, and dEve inform about the impact and effects of the press disturbance in each EDR. (d) The combination of press and pulse disturbances may trigger the shift into an alternative EDR (Trajectories A, B, and C). Resilience indicators in (b) and (d) were calculated in relation to the undisturbed EDRs (a). All panels show the two first axes of the

state space generated via multidimensional scaling. Overall, axis 1 relates to the proportion of species *1* (positive), *2*, *3*, and *5* (negative); axis 2 relates to the proportion of species *6* (positive) and *4* (negative).

Table 1. Measures quantifying different components of post-disturbance dynamics in relation to the changes produced in the system and the relative position with the representative trajectory of the EDR.

Measure	Formula	Range*	Interpretation
Resistance	$Rt = 1 - d_{pre,dist}$	[0, 1]	Immediate response of the system to the disturbance (Sánchez-Pinillos et al., 2019). • Rt = 0; the dissimilarity between the pre-disturbance and the disturbed states is maximum. • Rt = 1; the pre-disturbance and the disturbed states are identical.
Amplitude	$A = \frac{d_{dist,RT} - d_{pre,RT}}{d_{pre,dist}}$ $\forall d_{pre,dist} > 0$	[-1, 1]	Direction of the system's dynamic during the disturbance. • A > 0; the disturbance pushes the system towards the boundaries of the EDR. • A < 0; the disturbance pushes the system towards the representative trajectory.
Recovery	$Rc = \frac{d_{dist,RT} - d_{post,RT}}{d_{dist,post}}$ $\forall d_{dist,post} > 0$	[-1, 1]	Ability of the system to evolve in the direction of the representative trajectory following the release of the disturbance. • Rc > 0; the system evolves towards the representative trajectory after the release of the disturbance. • Rc < 0; the system evolves towards the boundaries of the EDR after the release of the disturbance.
Net direction	$ND = \frac{d_{post,RT} - d_{pre,RT}}{d_{pre,post}}$ $\forall d_{pre,post} > 0$	[-1, 1]	Overall direction of the system's dynamic at the post-disturbance state in relation to the initial state. • ND > 0; the system is further to the representative trajectory than it was in the pre-disturbance state. • ND < 0; the system is closer to the representative trajectory than it was in the pre-disturbance state.

*Ranges assuming that the dissimilarity metric satisfies triangle inequality. $d_{i,j}$ quantifies the dissimilarity between two system states, i and j; *pre, dist,* and *post* refer to system states before, during (or immediately after), and following the release of the disturbance, respectively. *RT* refers to the representative trajectory. Note that *A, Rc,* and *ND* refer to the direction of the dynamics whereas the numerator of the indices quantifies the magnitude of the changes in relation to the representative trajectory.