

REVIEW

Explore before you restore: Incorporating complex systems thinking in ecosystem restoration

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Abstract

1. The global movement for ecosystem restoration has gained momentum in response to the Bonn Challenge (2010) and the UN Decade on Ecosystem Restoration (UNDER, 2021–2030). While several science-based guidelines exist to aid in achieving successful restoration outcomes, significant variation remains in the outcomes of restoration projects. Some of this disparity can be attributed to unexpected responses of ecosystem components to planned interventions.
2. Given the complex nature of ecosystems, we propose that concepts from Complex Systems Science (CSS) that are linked to non-linearity, such as regime shifts, ecological resilience and ecological feedbacks, should be employed to help explain this variation in restoration outcomes from an ecological perspective.
3. Our framework, Explore Before You Restore, illustrates how these concepts impact restoration outcomes by influencing degradation and recovery trajectories. Additionally, we propose incorporating CSS concepts into the typical restoration project cycle through a CSS assessment phase and suggest that the need for such assessment is explicitly included in the guidelines to improve restoration outcomes.
4. To facilitate this inclusion and make it workable by practitioners, we describe indicators and methods available for restoration teams to answer key questions that should make up such CSS assessment. In doing so, we identify key outstanding science and policy tasks that are needed to further operationalize CSS assessment in restoration.

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5. *Synthesis and applications.* By illustrating how key Complex Systems Science (CSS) concepts linked to non-linear threshold behaviour can impact restoration outcomes through influencing recovery trajectories, our framework Explore Before You Restore demonstrates the need to incorporate Complex Systems thinking in ecosystem restoration. We argue that inclusion of CSS assessment into restoration project cycles, and more broadly, into international restoration guidelines, may significantly improve restoration outcomes.

KEYWORDS

complex systems science, feedbacks, hysteresis, non-linearity, regime shift, resilience, restoration project cycle, threshold

1 | BACKGROUND

1.1 | Complex system science concepts in an era of restoration

A movement for ecosystem restoration has emerged in response to global land and water degradation and associated loss of biodiversity and ecosystem services (Nicholson et al., 2020; Strassburg et al., 2020). Restoration initiatives aimed at moving ecosystems from an undesired (i.e. degraded, damaged or destroyed) to a desired regime are booming worldwide (Chazdon et al., 2021; Gann et al., 2019). The United Nations (UN) responded to this momentum by launching the *UN Decade on Ecosystem Restoration 2021–2030*, which has encouraged further initiatives (Abhilash, 2021; FAO et al., 2021). By now, many useful guidelines and tools exist to steer the restoration community towards scientifically sound restoration, for example the *UNDER Principles and Standards of Practice for Ecosystem Restoration* (FAO et al., 2021, 2023), the Society for Ecological Restoration's *Principles and Standards* (Gann et al., 2019) and ITTO's *Guidelines for Forest Landscape Restoration in the Tropics* (ITTO, 2020).

Despite these clearly defined targets and guidelines (Di Sacco et al., 2021), restoration outcomes vary widely, with multiple failures to establish target ecosystems (Banin et al., 2023; Brancalion & Holl, 2020; Brudvig & Catano, 2021; Dudley et al., 2022). Examples of ecological failures, that is attributed to biotic and abiotic ecological constraints, include poor survival of planted or naturally regenerating trees in forest restoration (Banin et al., 2023; Christmann et al., 2023; Kodikara et al., 2017; Magaju et al., 2020), no population growth of targeted fish species in lake or coral reef restoration (Boström-Einarsson et al., 2020; Fox et al., 2019; Graham et al., 2013) and failure to restore non-turbid water conditions in lake restoration (Gulati et al., 2008; Jilbert et al., 2020; Søndergaard et al., 2007).

Undesired ecological outcomes in restoration may occur due to unexpected responses of ecosystem components to planned interventions. We argue that, as well as overly ambitious or unrealistic expectations, threshold behaviour due to complex system dynamics associated with ecological systems can explain unexpected restoration responses. In other words, ecosystem complexity itself poses constraints to restoration success (Munson et al., 2018; Van Nes

et al., 2016). Namely, natural ecosystems are Complex Systems, which are studied in the discipline of *Complex Systems Science* (CSS) and defined by eight emergent properties: heterogeneity, hierarchy, self-organization, openness, adaptation, memory, non-linearity and uncertainty (Appendix S1; Anand et al., 2010; Bullock et al., 2021; Filotas et al., 2014; Riva et al., 2022). Here, we emphasize three key concepts linked to the specific CSS property of non-linearity that we believe hold pivotal implications for restoration outcomes from an ecological perspective: *regime shifts (and potential hysteresis)*, *ecological resilience* and *ecological feedbacks*.

Non-linearity implies that ecosystems may show disproportionately large responses to environmental disturbances over time (e.g. drought, herbivory). In grasslands, for instance, herbivory may lead to slight declines in biomass in wet years, but the same levels of herbivory may also cause major declines in biomass and changes in vegetation composition in dry years (Stone & Ezrati, 1996). As a result of chronic environmental degradation, non-linearity can cause abrupt *regime shifts* in ecosystems, whereby they shift to an alternative stable state or regime by crossing a *critical (disturbance) threshold* (Table 1; Figure 1a; Dantas et al., 2016; Scheffer et al., 2001). An abrupt regime shift is reflected by a sudden, dramatic change in ecosystem state variables, for example lake waters shifting from clear to turbid due to eutrophication (Scheffer, 2001; Scheffer et al., 2001; Seidl & Turner, 2022), coral reefs shifting from coral- to algal domination (Graham et al., 2013) or forests shifting to savanna systems (or vice versa) due to changes in fire regime or dry season length (Figure 1b; Dantas et al., 2016; Fletcher et al., 2014; Oliveras & Malhi, 2016; Staver et al., 2011). After such a shift, restoration to the pre-degradation regime is likely slow and requires substantial reductions in the environmental pressures, possibly even to a level well below the one that led to the shift; a phenomenon called *hysteresis* (Table 1; Figure 1c; Muys, 2013; Selkoe et al., 2015; Staal et al., 2020). Thus, regime shifts, driven by non-linear behaviour in ecosystems, can influence recovery trajectories (Mayer & Rietkerk, 2004; Suding & Hobbs, 2009; Suding & Gross, 2006). Further, restoration trajectories will depend on whether or not a regime shift has already taken place in the ecosystem at the time when restoration interventions are applied, and if not, on how close to a critical threshold the ecosystem is at that time (Ghazoul et al., 2015; Ghazoul & Chazdon, 2017).

TABLE 1 Glossary (see Appendix S2 for extended glossary).

Regime shift: (Carpenter et al., 2011; Dudney et al., 2018; Kéfi et al., 2013; Scheffer et al., 2012; Van Meerbeek et al., 2021; Van Nes et al., 2016) An ecosystem regime is an identifiable configuration with characteristic structure, functions and feedbacks. A regime shift is the change of an ecosystem from one regime or reference condition to an alternative regime as a result of non-linear (abrupt or smooth) responses of ecosystem state variables (e.g. biomass) to environmental pressures (Figure 1a)
Critical threshold (CT; or Critical transition or Tipping point): The point at which small disturbances can trigger large, abrupt changes in ecosystem state variable(s)
Early-warning signals (EWS): Generic indicators (e.g. critical slowing down) that mark loss of ecological resilience in a system, indicating that a regime shift is likely to occur
Hysteresis (or History-dependence): A phenomenon whereby the ecosystem degradation trajectory differs from the recovery trajectory: crossing the critical degradation threshold (CT2 in Figure 1a) results in a shift in the ecosystem regime from 1 (green) to 2 (red). To restore an ecosystem to regime 1, the environmental degradation pressure(s) (e.g. eutrophication) must be reduced to a lower threshold than the one which triggered the transformation of the ecosystem to an alternative regime (i.e. to CT1 instead of CT2)
Ecological resilience: (Dornelles et al., 2020; Dudney et al., 2018; Holling, 1973; Nicholson et al., 2020; Standish et al., 2014) A measure of the ability of ecosystems to absorb change and disturbances and still remain within critical thresholds of the same regime, that is maintain the regime
Helpful resilience: Resilience that helps to achieve the defined restoration aim. Higher helpful resilience of an ecosystem in regime 1 implies that a shift to regime 2 is less likely to occur under the same degradation scenario. This is considered helpful or desirable if the aim is to avoid regime shifts (Figure 1a)
Unhelpful resilience: Resilience that hinders the achievement of the defined restoration aim (Dudney et al., 2018; Standish et al., 2014). Higher unhelpful resilience of an ecosystem in regime 2 after a regime shift occurs implies that a shift back to 1 is less likely to occur, which is considered unhelpful or undesirable if the aim is to restore regime 1 (Figure 1a)
Ecological feedbacks: (Van Nes et al., 2016) Dynamic ecological interactions between (a)biotic factors (e.g. vegetation composition) and disturbance regimes (e.g. fire regime, grazing level) in an ecosystem that loop back to control system dynamics. Feedbacks can either dampen (negative or stabilizing feedbacks) or reinforce (positive or amplifying feedbacks) system change, thereby maintaining one regime or causing it to shift to an alternative one

A second concept that is intricately connected to non-linear behaviour of complex systems and thus to potential regime shifts, is the *ecological resilience* of degraded ecosystems to disturbances (Ghazoul et al., 2015; Ghazoul & Chazdon, 2017). Ecological resilience is a measure of the ecosystem's ability to absorb change and disturbance and still maintain the same regime (Appendix S1, Table S2). A decrease in resilience due to environmental degradation increases the likelihood of a regime shift to occur (i.e.

lower *helpful* resilience sensu Standish et al. (2014); Table 1; Folke et al., 2004; Rocha et al., 2015). On the other hand, ecosystems can be in a highly resilient alternative regime after prolonged degradation due to hysteresis, when the presence of ecological feedbacks maintain the degraded regime (i.e. higher *unhelpful* resilience sensu Standish et al. (2014); Table 1; Dornelles et al., 2020; Dudney et al., 2018; Staal et al., 2020). Both low resilience of the desired regime as well as high resilience of the undesired regime can hamper restoration performance (Magnuszewski et al., 2015; Standish et al., 2014).

A third concept that is tightly linked to non-linearity of complex (eco)systems are *ecological feedbacks*, that is dampening or reinforcing interactions between (a)biotic factors (e.g. vegetation composition) and disturbance regimes (e.g. fires) that loop back to control ecosystem dynamics (Table 1). These feedbacks can both maintain an ecosystem in a specific regime as well as cause it to shift to an alternative one and can thereby strongly influence degradation as well as recovery trajectories, thus influencing restoration outcomes (Hobbs et al., 2011; Scheffer et al., 2009; Verbesselt et al., 2016).

Importantly, potential *hysteresis* or history-dependence, is tightly linked to each of the three CSS concepts since this feature (i) can occur after a regime shift took place, (ii) reflects the new regime having a high unhelpful resilience and (iii) is governed by the presence of ecological feedbacks that maintain the new regime.

1.2 | CSS concepts in restoration guidelines

Most current restoration guidelines produced by international organizations do not sufficiently incorporate or operationalize CSS concepts linked to non-linear threshold behaviour (Appendix S2). While some guidelines include concepts of 'alternative ecosystems' (Gann et al., 2019; Appendix S2, Table S1), most do not. There is limited to no inclusion of concepts related to regime shifts, contrasting with frequent inclusion of the resilience concept (Appendix S2, Table S1: 298 × 'resilience' vs. 0 × 'regime shift' across all guidelines). Resilience, however, is rarely accompanied by a clear definition or concrete measurement tools, limiting its operational use in restoration practice. Further assessing the meaning of resilience in the guidelines, the focus is on restoring ecosystems that are resilient to all kinds of shocks (i.e. building *general resilience*), rather than on which ecosystem components should be resilient to which disturbances, and how to quantify and achieve this (i.e. building *specific resilience*; Dudney et al., 2018; Folke et al., 2010; Appendix S2, Table S2: 99% 'general' vs. 1% 'specific'). Through this focus on general resilience, the guidelines imply that resilience is always 'good', 'helpful' or 'desirable' in ecosystem restoration. However, this is not always the case, as resilience can be an unhelpful ecosystem feature, hindering successful restoration by reinforcing undesirable regimes, as we discuss above.

We argue that abrupt non-linear *regime shifts*, unhelpful *ecological resilience* and *ecological feedbacks* that maintain undesired

ecosystem regimes, can result in divergent, unexpected and unpredictable responses to restoration interventions, ultimately leading to undesired or 'failed' restoration outcomes (Krievins et al., 2018; Mayer & Rietkerk, 2004). Many restoration projects may involve degradation scenarios where a regime shift has not (yet) occurred, and resilience is still helpful, but we argue that the guidelines should be flexible and suitable to all degradation scenarios, including those where advanced degradation has already occurred. Hence, operationalizing these CSS concepts into the current guidelines and across restoration project cycles, can minimize or even avoid undesired outcomes, as well as potentially speed up the achievement of desired outcomes.

Importantly, the desired regime in restoration may not necessarily reflect the historic pre-degradation regime (Bardgett et al., 2021; Bullock et al., 2021; Crow, 2014; Gann et al., 2019). While historic regimes were traditionally the focus of 'ecological restoration', restoration stakeholders often now make a decision on whether their interventions should aim to 'Resist', 'Accept' or 'Direct' the increasingly unpredictable and unprecedented environmental changes that ecosystems are facing (Jackson, 2021; Lynch et al., 2022).

Furthermore, we acknowledge that ecological aspects alone are not sufficient to explain failed restoration outcomes (Elias et al., 2022; Maniraho et al., 2023). The process of successfully and efficiently restoring degraded ecosystems also relies on the trust and engagement of relevant stakeholder groups such as local communities and authorities, and on the social-economic and political settings such as functionality of the land tenure policies (Ahmmed et al., 2023; Metcalf et al., 2015; Petursdottir et al., 2013; Walters et al., 2021). Since we aim to demonstrate here how CS dynamics can explain some of the variation in restoration outcomes from an ecological perspective, instead of highlighting the various dimensions that may influence restoration outcomes, inclusion of social-economic factors are beyond the scope of our manuscript. That is, our framework (i) focuses on the ecological dimension of CS dynamics, which is nested within a broader social-ecological dimension (Nikinmaa, 2020) and (ii) assumes that restoration planning is being approached from a social-ecological perspective, that is the interventions are designed with careful consideration of social-economic as well as ecological dimensions (Crow, 2014; Elias et al., 2022; Lade et al., 2013; Maniraho et al., 2023; Nayak & Armitage, 2018).

In the following sections of our framework *Explore Before You Restore*, we demonstrate how regime shifts, ecological resilience and feedbacks influence recovery trajectories with examples from science and practice and then suggest how these concepts might be included in restoration practice. In doing so, we identify key science and policy tasks that are needed to operationalize these concepts into useful tools for the restoration community. Our framework follows a typical 6-step restoration project cycle (Table 3; Appendix S3, Table S1: Assessing, Planning, Implementing, Monitoring & Evaluating, Maintaining and Adaptive Management) and is, therefore, directly applicable for restoration practitioners, scientists and policymakers.

2 | HOW COMPLEX SYSTEMS SCIENCE CONCEPTS CAN HELP EXPLAIN RESTORATION TRAJECTORIES

Regime shifts, possibly coupled with high unhelpful resilience of the new regime in cases of hysteresis, can strongly influence recovery trajectories and thus determine which restoration interventions, ranging from simple to more complex, are needed to achieve desired targets (Figure 2; Mayer & Rietkerk, 2004; Selkoe et al., 2015; Suding & Hobbs, 2009). Namely, in ecosystems that have experienced an abrupt regime shift but with no evidence of hysteresis, reversing degradation to below the threshold level that led to the shift is likely sufficient to restore the system to the pre-threshold regime (i.e. reverse the shift) (Figure 2 middle scenario: halt degradation and/or additional interventions, Chazdon et al., 2021). For example, regeneration of native vegetation is sometimes constrained by invasive plant species in severely degraded tropical forests. Effective control of invasives, in these cases, may promote recovery of native species composition associated with the pre-threshold ecosystem regime (Brancalion et al., 2019; Douterlungne et al., 2013; Gratton & Denno, 2005).

By contrast, in ecosystems where hysteresis maintains the degraded regime through ecological feedbacks that strengthen unhelpful resilience (Table 2), restoration efforts need to do more than simply establish the environmental condition(s) that were prevalent before the shift. Disrupting the high unhelpful resilience of the new regime typically requires multiple, coinciding and often expensive, interventions (Figure 2 bottom scenario: halt degradation and additional interventions; Chazdon et al., 2021; Muys, 2013; Selkoe et al., 2015; Van Nes et al., 2014). For instance, after several decades of heavy grazing in terrestrial grasslands, palatable plants may essentially be absent, with natural recovery of these systems taking up to 100 years or longer due to hysteresis (Cipriotti et al., 2019). In arid ecosystems, increased aridity may then lead to desertification, making the possibility for vegetation recovery even lower, even where aridity levels subsequently decrease (Kéfi et al., 2007). Achieving successful restoration then requires a combination of interventions, such as reducing grazing, combined with measures such as reseeding with desirable well-adapted species, woody species control, soil erosion prevention and protection and soil water management (Table 2).

Furthermore, reduced helpful resilience of a system undergoing degradation, but which is still in the desired ecosystem regime, can also influence the restoration trajectory (with or without a pending regime shift) (Selkoe et al., 2015). Even though halting degradation will likely restore the desired regime (Figure 2 top scenario), reduced resilience can slow down recovery. For instance, abandonment of agricultural systems can create favourable conditions for tree regeneration to restore forests with generally little need for additional interventions (Figure 2; Boulton et al., 2022; Poorter et al., 2016; Rolim et al., 2017; Rozendaal et al., 2019). Reduced helpful resilience of these post-agricultural systems, however, driven by the intensity of the past agricultural land use and environmental changes and reflected by, for example a lack of seed sources or resprouting ability

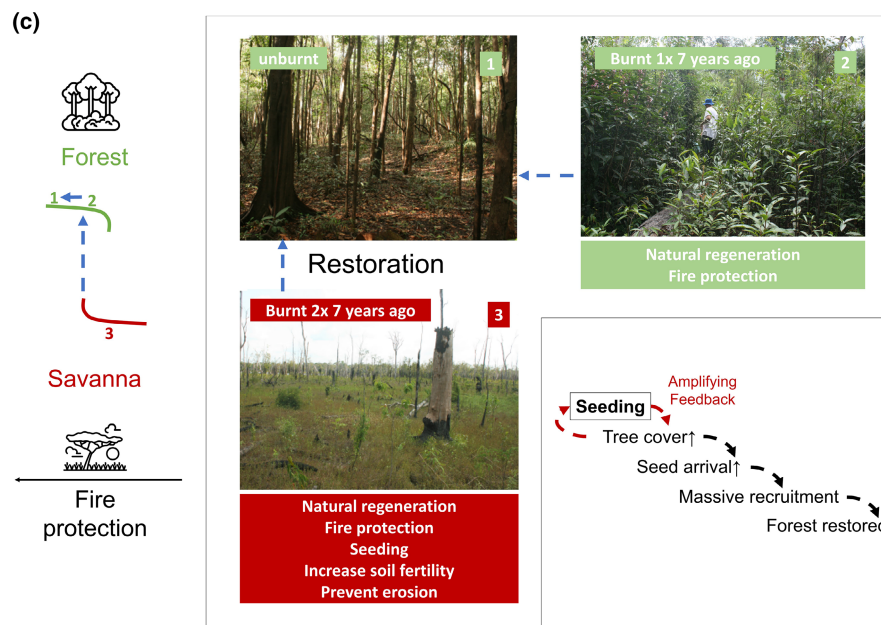
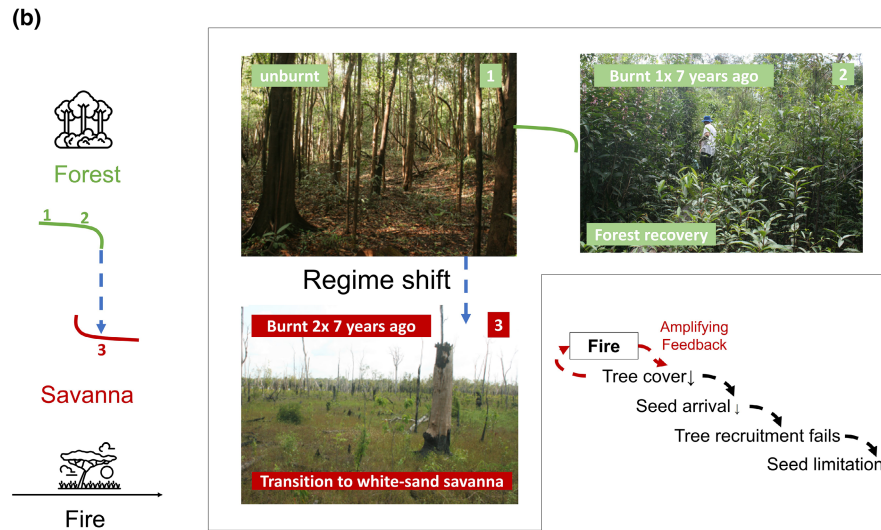
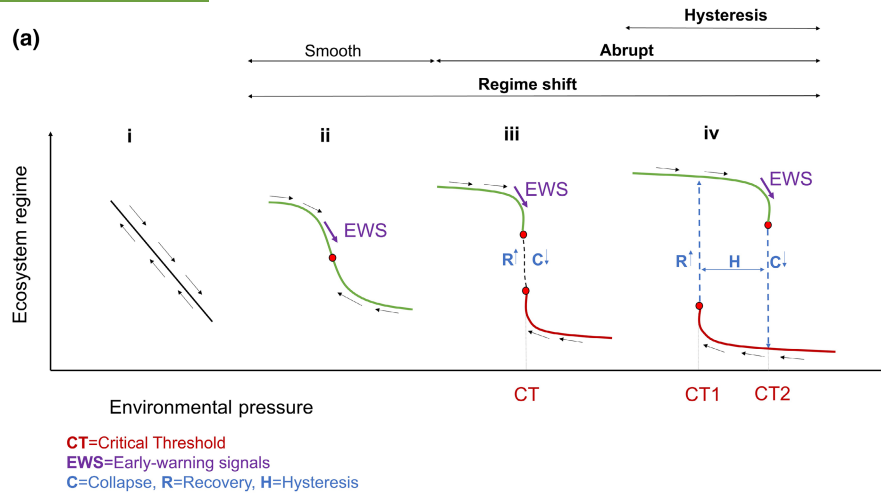


FIGURE 1 Conceptual graph of Complex System dynamics in ecosystems: That is (a) the presence of regime shifts in response to environmental pressures, with (b) an example of a regime shift in tropical forest ecosystems and (c) the trajectory to successful restoration (c). (a) From left to right: (i) linear response to environmental pressures, (ii–iv) non-linear response to environmental pressures with presence of regime shift, where transition to alternative regime is (ii) smooth so no presence of critical thresholds, vs. (iii–iv) presence of critical thresholds causing an abrupt regime shift to an alternative regime and (iv) exhibiting hysteresis, which implies that the alternative regime is highly resilient (Hu et al., 2022; Selkoe et al., 2015; Suding & Hobbs, 2009). After an abrupt regime shift (iii–iv), the ecosystem collapses 'C' from regime 1 to 2. Ecosystem Recovery 'R' occurs when the system is restored through the reversed abrupt pathway to regime 1. In the case of hysteresis 'H', the ecosystem collapse pathway differs from the recovery pathway due to high resilience of regime 2. (b) Photographic evidence of a regime shift in Amazonian floodplain forests (from Flores & Holmgren, 2021a, 2021b). When these forests are repeatedly burnt, tree growth rates slow down due to soil nutrient and seed dispersal limitations. After a first wildfire (2), these forests lose most of their seed banks. With time, seed banks are able to recover, that is forest recovery (1). After a second wildfire (3), burned forests persist in the open regime with a tree species composition, % sand and % herbaceous cover similar to white-sand savannas. These forests experience a regime shift to a white-sand savanna as reported by Flores & Holmgren, 2021b, due to the amplifying feedback of repeated fires on change in tree cover and seed availability (bottom right). (c) Forests burnt once in the floodplain landscape (2) need to be protected from wildfires to prevent recurring fires, which hinder natural forest recovery (1), while re-burnt forests (3) require additional assisted interventions (beyond natural regeneration and fire protection) to fully recover forest structure, diversity and functioning, such as seeding, soil fertility increases and soil erosion prevention. Particularly active seeding of well-adapted tree species in repeatedly burnt sites should increase tree cover, triggering recovery of the tree cover-seed availability feedback that restores the forest (bottom right).

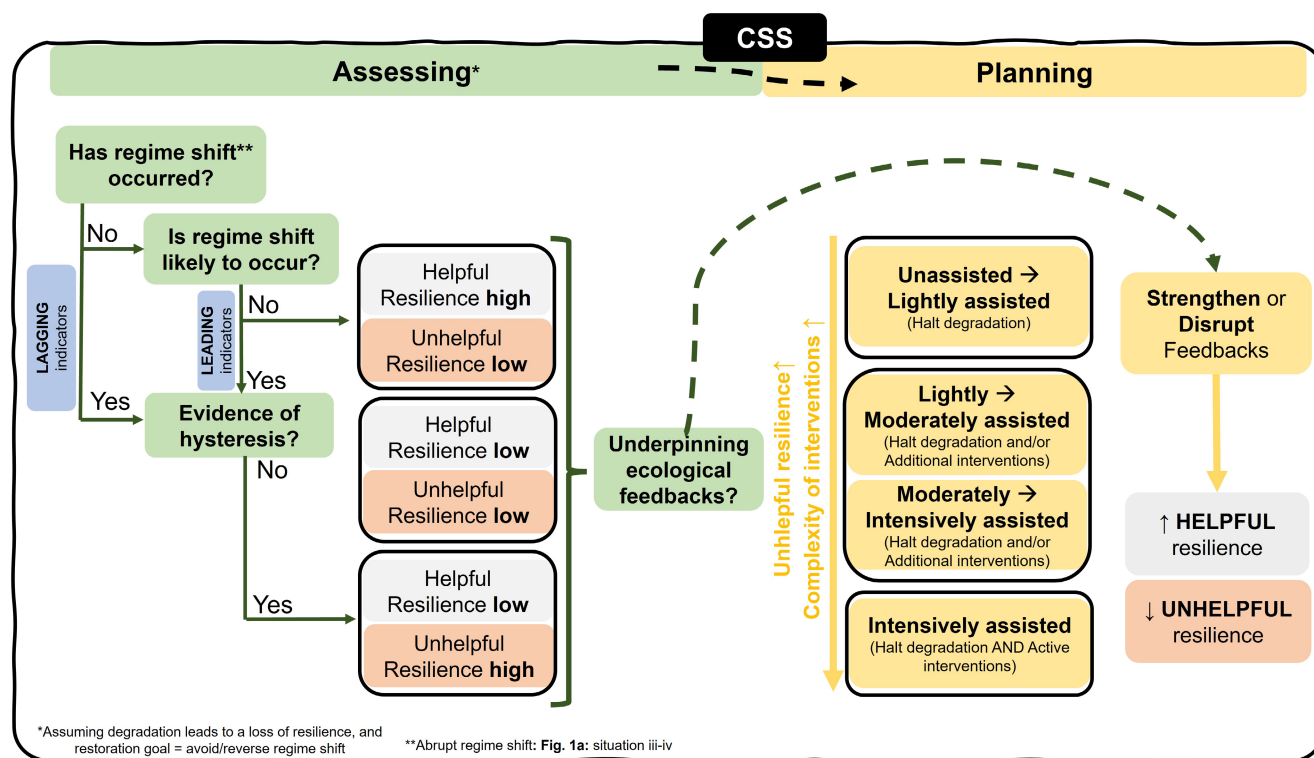


FIGURE 2 Incorporating CSS concepts in a restoration project cycle's Assessing and Planning phase. Key questions (green boxes) to incorporate in the CSS assessment phase in the restoration project cycle (left: *Assessing*) and guidance on how to prepare planned interventions for CSS assessment (right: *Planning*). The scheme assumes that degradation leads to a loss of helpful resilience potentially leading to an abrupt regime shift and that the aim of restoration is to avoid or reverse such shifts. Left: *Assessing*: Green boxes represent four questions to be answered by restoration teams during CSS assessment. Depending on the replies, three ecosystem regime scenarios arise: (i) no regime shift occurred (i.e. low unhelpful resilience in orange) and none expected (i.e. high helpful resilience in grey) (top scenario), (ii) pending regime shift (i.e. low helpful resilience), but no evidence of hysteresis (i.e. low unhelpful resilience) (middle scenario) and (iii) regime shift has occurred or is pending (i.e. low helpful resilience) and evidence of hysteresis (i.e. high unhelpful resilience) (bottom scenario). Lagging resilience indicators (blue) can be assessed to determine whether a regime shift has occurred, while leading indicators (blue) may signal a pending regime shift. Right: *Planning*: Yellow boxes represent suitable restoration interventions ranging from simple to more complex (top to bottom), with increasing evidence of regime shifts and hysteresis, that is increasing levels of unhelpful resilience (yellow arrow). The range of interventions are categorized according to the intervention continuum framework proposed by Chazdon et al. (2021) (unassisted, lightly, moderately and intensively assisted recovery). The interventions should act to strengthen or disrupt ecological feedbacks that increase helpful and decrease unhelpful resilience.

TABLE 2 Examples of hysteresis (history-dependence) in ecosystem dynamics (a) and activities to promote successful restoration (b).

Regime shift	Disturbance	(a) Hysteresis: High unhelpful resilience of the degraded regime	(b) Successful restoration (if aim is to reverse the shift): Decrease unhelpful resilience and increase helpful resilience through halting degradation and additional interventions	Reference
Grassland or savanna → Rangeland or Desert	Overgrazing Drought	Heavy grazing in terrestrial grass-dominated ecosystems leads to a decreased grass-to-shrub cover ratio, replacement of palatable by non-palatable grasses and altered soil resources and nutrients, restricting recovery of palatable grasses and the grassy system ('Rangeland'). Increased aridity can then lead to desertification ('Desert'), restricting even more the grassy vegetation recovery	<i>Halt degradation:</i> reduce or eliminate grazing <i>Additional interventions:</i> reseeding with desirable, well-adapted species, woody species control, soil erosion prevention and protection, soil water management	Christensen et al., 2023; Cipriotti et al., 2019; Kéfi et al., 2007; Rietkerk et al., 2004; Searle et al., 2009
Tropical floodplain forest → White-sand savanna	Fire increase	Repeated wildfires in tropical floodplain forests decrease tree cover which leads to reduced seed dispersal and consequently seed availability, keeping tree cover low and hampering forest recovery	<i>Halt degradation:</i> fire protection <i>Additional interventions:</i> increase soil fertility, soil erosion prevention and protection, assisted natural regeneration, seeding	Flores et al., 2017; Flores & Holmgren, 2021a, 2021b
Coral reef → Algal-dominated reef	Fishing Eutrophication Warming	A combination of fishing, eutrophication and warming pressures results in algal dominance and low abundance of herbivore fish groups that feed on algae, preventing successful coral recruitment while outcompeting successfully recruited corals	<i>Halt degradation:</i> reduce fishing pressures and chronic nutrient input, global warming mitigation <i>Additional interventions:</i> introduce herbivore fish groups that feed on algae, thus reducing algal dominance, introduce fish species such as parrot and surgeon fishes that promote coral recruitment	Graham et al., 2013
Temperate forest Base buffer domain → Acidic buffer domain	Acidification	Acidification in temperate forests, for example through conversion of deciduous to acidifying tree species, leads to greater litter mass and accumulation of toxic exchangeable aluminium, as well as lower microbial functional diversity, earthworm biomass and base saturation. Slow recolonization speed of earthworms and strong retention of aluminium impedes recovery to the base buffering domain	<i>Halt degradation:</i> stop conversion from deciduous to acidifying species <i>Additional interventions:</i> plant tree species with nutrient-rich litter, liming, reintroduction of soil microbes or soil fauna	Contos et al., 2021; Desie et al., 2019; Desie, Van Meerbeek, et al., 2020; Desie, Vancampenhout, et al., 2020; Jansone et al., 2020
Grassland → Woodland	Fire decrease	During periods of fire suppression in prairie communities, increased tree cover (i.e. woody encroachment) results in canopy closure which leads to fewer fires, preventing grassland community recovery	<i>Halt degradation:</i> stop fire suppression <i>Additional interventions:</i> reintroduce high intensity fire regime, introduce grazers to limit tree regeneration	Anderson et al., 2000; Ratajczak et al., 2018
Tree-dominated rainforest → Liana-dominated rainforest	Light increase (tree cutting)	Lianas grow rapidly in response to increased light levels caused by heavy disturbance in many tropical and subtropical forests, for example from logging or cyclones. Since lianas compete heavily with trees in tropical rainforests, tropical forests with abundant lianas can show slower rates of tree growth and thus slow or arrested forest recovery following disturbance compared to those with few lianas	<i>Halt degradation:</i> stop deforestation <i>Additional interventions:</i> liana cutting	Ingwell et al., 2010; Lai et al., 2017; Marshall et al., 2020; Phillips et al., 2002

for native tree species or soil nutrient imbalances, can slow down regeneration (Broughton et al., 2022; Cramer et al., 2008; Flores & Holmgren, 2021a, 2021b; Lawrence et al., 2010; Styger et al., 2007, 2009; Verheyen, 2021). Here, additional interventions (e.g. litter addition, enrichment planting) might speed up recovery (Figure 2; Sansevero et al., 2017; Styger et al., 2007).

In sum, restoration practice should strengthen ecological feedbacks that increase helpful resilience, and at the same time weaken or disrupt those that increase unhelpful resilience. These feedbacks will ultimately determine the likelihood of an abrupt shift between ecosystem regimes (Figure 2; Hoffmann et al., 2012; Huang et al., 2018; Stevens et al., 2017). For instance, if the target regime is grassland, woody encroachment may shift it towards a forest regime. The reinforcing 'canopy closure feedback' (i.e. trees → canopy closure → more trees through less below-canopy grasses to fuel fires) would drive the shift towards a forest regime, while the 'open vegetation feedback' (i.e. grasses → fire → more grasses through increased fuel loads) would maintain the desired regime. The canopy closure feedback underpins unhelpful resilience because it reinforces the undesired regime (and should be weakened), while the open vegetation feedback underpins helpful resilience because it reinforces the desired regime (and should be strengthened). Reintroduction of fires or introduction of grazers will both weaken the canopy closure (decrease unhelpful resilience) and strengthen the open vegetation

feedback (increase helpful resilience) (Johnstone et al., 2016; Pausas & Keeley, 2014a, 2014b).

Restoration management and guidelines have mainly focused on general resilience, which stems from the common but incorrect assumption that resilience is always helpful or 'good' (Appendix S3, Table S2; McDonald, 2000; Nimmo et al., 2015; Standish et al., 2014). This point has likewise been raised in other socio-ecological disciplines (Dornelles et al., 2020; Oliver et al., 2018; Van De Leemput et al., 2014). The singular focus on increasing helpful resilience is likely not sufficient to address degradation scenarios with abrupt regime shifts and hysteresis, where the presence of high unhelpful resilience implies a need for more complex interventions to actively disrupt those ecological feedbacks maintaining the undesired regime (Table 2).

Based on the evidence and examples of how CSS concepts can influence recovery trajectories and how restoration teams can tailor their interventions, we argue that restoration guidelines should explicitly incorporate CSS assessments in the restoration project cycle (Table 3). In such CSS assessment, restoration teams should evaluate; (i) the likelihood of an abrupt regime shift to occur, (ii) evidence of hysteresis or high unhelpful resilience in the degraded system and (iii) the underpinning ecological feedbacks that must be strengthened and/or disrupted to maintain the system in or shift it to, the desired regime (Figure 2; Table 2).

TABLE 3 Restoration project cycle.

Assessing	• Drivers of degradation + Pre-degradation regime • Expected impact of climate change • Local and regional socio-economic context • Reciprocal engagement of local stakeholders • Complex Systems Science (CSS) Assessment - A Has regime shift occurred? Lagging indicators - B Regime shift likely to occur? Leading indicators - C Evidence of hysteresis? - D Underpinning ecological feedbacks of resilience?	Adaptive management • Re-evaluate objectives • Reiterate cycle to - A Maintaining or Ongoing management if objectives met - B Assessing if objectives not met
Planning	Visioning • Determine short-term, measurable objectives and longer-term goals Designing • Determine interventions to achieve objectives (Unassisted to Intensively assisted interventions) • Establish Key Performance Indicators (KPIs) to track performance • Tailor interventions to CSS assessment - A Determine complexity of interventions needed - B Strengthen and/or Disrupt feedbacks - C ↑Helpful and/or ↓ Unhelpful RESILIENCE	
Implementing	• Perform interventions	
Monitoring & Evaluating	• Track restoration performance through measured KPIs • Are the objectives being met? • Which constraints still remain?	
Maintaining	• Continue tracking restoration performance (M&E) • Continue restoration management	

Note: Our framework *Explore Before You Restore* suggests that key CSS concepts of regime shifts, ecological resilience and ecological feedbacks need to be incorporated in the project cycle to improve restoration outcomes. Suggested CSS aspects to be incorporated in the project cycle are in bold. Importantly, our framework assumes that restoration planning (i) carefully considers the social-economic dimensions (in addition to ecological ones) and (ii) is approached from a social-ecological perspective (Crow, 2014; Elias et al., 2022; Maniraho et al., 2023).

3 | CSS ASSESSMENT IN RESTORATION PRACTICE

Our framework follows a restoration project cycle which typically comprises six phases, including five distinct phases (Assessing, Planning, Implementing, Monitoring & Evaluation, Maintaining) and one phase that cuts across all others (Adaptive management) (Appendix S3). To incorporate CSS thinking in ecosystem restoration, we suggest that the *Assessing* phase is extended to involve four key questions related to CS dynamics in degraded systems (Table 3; Figure 2). These questions include (A) whether an abrupt regime shift has occurred or (B) is likely to occur, (C) where it has occurred, whether there is evidence of hysteresis (high unhelpful resilience of the degraded regime) and (D) which ecological feedbacks underpin helpful and unhelpful resilience (Figure 3). During *Planning*, restoration interventions should be tailored to the CSS assessment (Figure 3). Below, we provide an overview of indicators available to answer these questions during CSS assessment, based on currently available knowledge and tools. In doing so, we identify key outstanding science and policy tasks needed to further operationalize CSS assessment in restoration (Table 4).

3.1 | Question A: Has a regime shift occurred (lagging indicators)?

A critical question to ask is whether a prior abrupt regime shift has occurred to create the degraded ecosystem (Figure 2). If environmental

degradation has led to an abrupt regime shift, the degraded ecosystem will be substantially reorganized into a self-maintaining new stable regime (Figure 1a, scenario iii–iv). Importantly, a regime shift could also lead the system into a new unstable regime, resulting in a spiral of environmental degradation, for example failure of plant recruitment and growth leads to greater soil exposure and thence greater erosion and further vegetative failure. The complexity of restoration interventions will need to be greater after a regime shift to facilitate successful recovery (Figure 1; Table 2; Carpenter et al., 2008; Ghazoul & Chazdon, 2017; Suding et al., 2004).

To evaluate whether a regime shift has already occurred in the degraded system, restoration teams can use *lagging indicators of resilience*, which assess whether helpful resilience has decreased (Carpenter et al., 2008; Carpenter & Brock, 2006; Cowan et al., 2021; Ota et al., 2021; Scheffer et al., 2009). Such indicators are ecological attributes that develop over long periods of time in an ecosystem, hence reflecting a unique regime at a single point in time, and they can, therefore, indicate substantial reorganization of the degraded system (Berdugo et al., 2020; Cowan et al., 2021; Seidl & Turner, 2022). Lagging indicators in terrestrial vegetated ecosystems, for instance, are metrics describing the *above- and below-ground species diversity, dominance and composition, vegetation cover and structure and soil fertility* (Cowan et al., 2021). For lake ecosystems, typical indicators may be *nutrient* (e.g. Oxygen, Phosphorus) or *chlorophyll concentrations, pH, turbidity and species diversity* (Carpenter & Cottingham, 1997; Ortiz et al., 2020). Significant differences in these

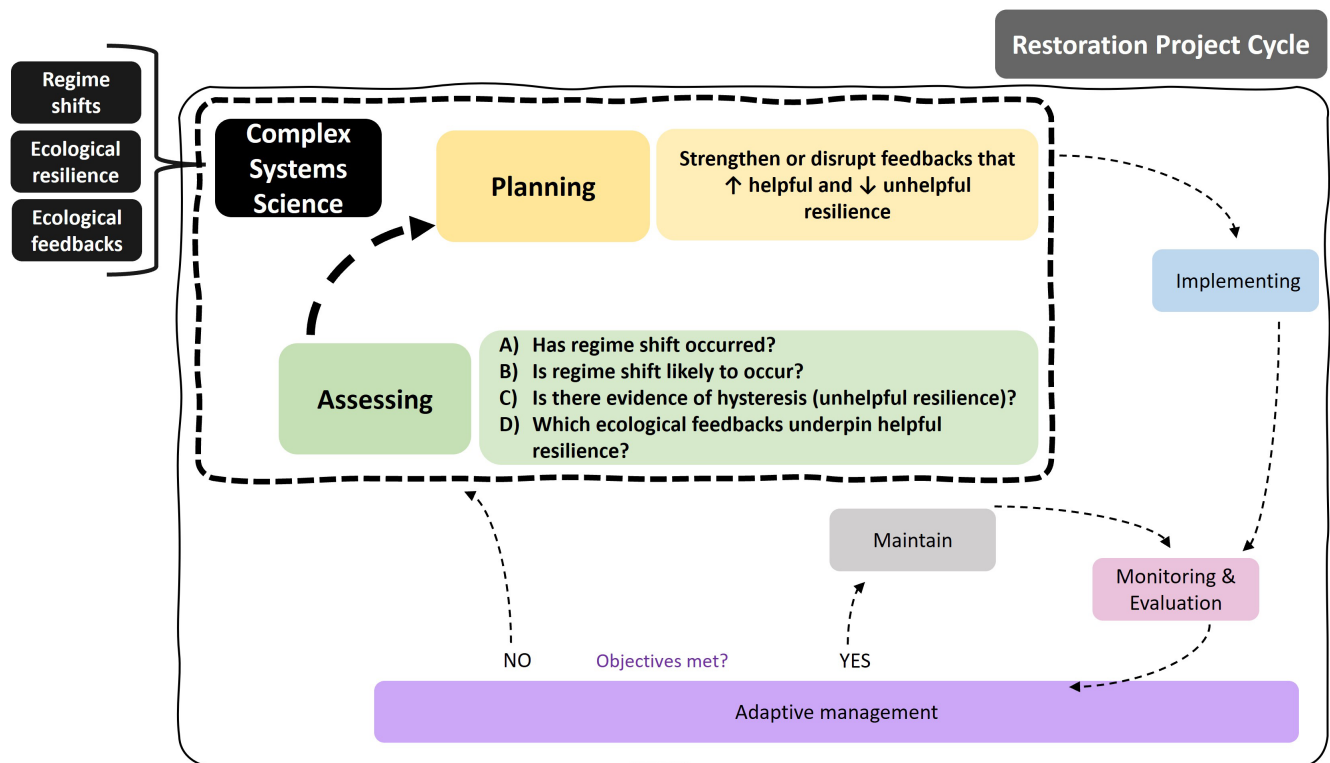


FIGURE 3 The different phases of a Restoration Project Cycle identified by scanning nine ecosystem restoration guidelines from international organizations published in the last decade 2012–2022 (Appendix S3). The details of each phase are explained in Table 3. Our framework suggests that three key elements of Complex Systems Science (top left) should be incorporated into the project cycle to improve restoration outcomes.

TABLE 4 Outstanding restoration science, practice, & policy tasks.

Theme	Task
Restoration Science-Practice	Extend the framework <i>Explore Before You Restore</i> • Operationalize resilience indicators (lagging, leading) into tools for ecosystem restoration • Develop practical methods to assess hysteresis • Extend ecosystem-, biome- and region- specific case study evidence on regime shifts and hysteresis in global databases and scientific literature • Support global restoration performance monitoring networks • Evaluate relationships between loss of resilience, abrupt regime shifts and restoration performance for different approaches (e.g. NR, ANR, Tree planting), bringing together different knowledge sources, that is western science, with Indigenous and Local Knowledge (ILK)
Restoration Policy	Operationalize CSS assessment into the Restoration Guidelines • Introduce the idea that (unhelpful) resilience can also hinder restoration • Translate CSS assessment in the restoration project cycle into practical and accessible language for the diversity of restoration teams • Target interventions that strengthen helpful resilience and weaken unhelpful resilience • Support global restoration performance monitoring networks

metrics between the degraded system, and either undisturbed controls (spatial comparison) or historic reference ecosystems (temporal comparison), at the time of restoration planning, can indicate that an abrupt shift towards a new stable regime has taken place, since the 'lagging' characteristic of these indicators implies that a new regime has already been in place for some time at the start of restoration (Figure 1a; Cowan et al., 2021).

For instance, humid Amazonian forests can shift to an alternative savanna state due to altered fire regimes (Barlow & Peres, 2008; Brando et al., 2014; Flores & Holmgren, 2021a, 2021b; Silvério et al., 2013). These vegetation state shifts are correlated with changes in vegetation structure and composition, biodiversity and ecosystem functioning that can be used as 'lagging' resilience indicators. For example, repeatedly burnt Amazonian blackwater floodplain forests lose tree cover, increase herbaceous cover and shift tree species composition from typically forest species towards an increasing abundance of white-sand savanna species (locally known as 'campinas'; Flores & Holmgren, 2021a). These vegetation shifts, from closed floodplain forests to white-sand savannas as fire occurrence increases, appear to be caused by both nutrient erosion (Flores & Holmgren, 2021a) and seed dispersal limitation (Flores & Holmgren, 2021b). Seed dispersal limitation could be caused by shifts in animal communities responsible for seed dispersal. For example, burnt forests and white-sand savannas show a lower abundance of omnivorous and frugivorous fish that are key seed dispersers for many forest tree species (Lugo-Carvajal et al., 2023). These complex changes in soil, plant and animal communities can be used as lagging indicators of resilience. Though these metrics may only provide an indication of regime shifts that happened at some point in the system's degradation history, for restoration this may already be instructive. We argue that it may be more important in ecosystem restoration to identify whether the degraded system finds itself in a new and undesired stable regime, which drivers of degradation have led to the regime, and what is causing the undesired regime to be maintained in the case of hysteresis, than to identify when exactly the regime shift took place.

3.2 | Question B: Is a regime shift likely to occur (leading or early-warning indicators)?

If the degraded system is not yet substantially reorganized, a shift may still be pending due to ongoing loss of helpful resilience (Boulton et al., 2022; Scheffer et al., 2001). Assessing the exact distance of an ecosystem to a critical threshold based on empirical data is not (yet) feasible and may always remain challenging (Davidson et al., 2023; Hillebrand et al., 2020; Van Nes et al., 2014). However, loss of helpful resilience over time, signalling a pending regime shift, can be evaluated through repeated measurements of *leading indicators of resilience* or *'early-warning signals'*, that is ecosystem attributes that specifically respond to environmental disturbances, such as tree growth or vegetation greenness which decrease due to drought or fire disturbances. Such leading indicators are useful to evaluate 'early-warning signals' that signal the vicinity of an abrupt shift (EWS, Table 1; Biggs et al., 2009; Carpenter et al., 2008; Cowan et al., 2021; Dai et al., 2012; Dakos et al., 2008; Forzieri et al., 2022).

Specifically, studies show that trends of slower recovery rates or of increased variability in these indicators in response to disturbances (i.e. *critical slowdown* or *flickering*, respectively), indicate that the ecosystem is approaching an abrupt shift (Carpenter et al., 2008; Dakos et al., 2015; Scheffer et al., 2001, 2009). For example, slower recovery of vegetation greenness related to successive droughts, and evaluated using remote sensing time series, has predicted tree mortality as the onset of a regime shift in different forest types (Boulton et al., 2022; Dakos et al., 2012; Liu et al., 2019; Verbesselt et al., 2016). Since leading indicators are useful to predict the likelihood of particular outcomes (Carpenter et al., 2008; Carpenter & Brock, 2006; Cowan et al., 2021; Ota et al., 2021; Scheffer et al., 2009), leading indicators of ecological resilience can thus be used to assess whether a regime shift might occur in the future in the context of CSS assessment.

Importantly, to assess a pending regime shift with leading indicators requires evaluating a rate of change, which is based on repeated measurements of the indicator over time. Repeated measurements in restoration could be extracted from, among others, indigenous

and local knowledge (ILK), repeated inventories and remote sensing (Falardeau et al., 2022; Pascual et al., 2017; Wheeler & Root-Bernstein, 2020). Gathering such data prior to restoration is generally not feasible for restoration teams, however, as it requires time and money and delays restoration on the ground. Therefore, project teams should realistically focus on incorporating repeated measurements of (the response of) leading indicators (e.g. species recruitment, biomass) to key disturbances in the ecosystem (e.g. fire, drought) in their M&E strategies. In this way, they can monitor possible changes in the response of the degraded ecosystem to disturbances from the restoration onset, which may signal a pending regime shift and adjust their interventions if they find indications for the latter.

3.3 | Question C: Is there evidence of hysteresis? Or which feedbacks underpin unhelpful resilience?

If a regime shift is likely to occur or has occurred, evaluating hysteretic behaviour in the degraded system is key, since greater restoration efforts are required to reverse the (potential) shift when hysteresis is present (Figure 2). Although trial treatments or driver reversal experiments allow quantification of hysteresis in the field by observing whether the system returns to a previous regime after halting or reversing the driver of degradation (Gann et al., 2019; McDonald, 2000; Ratajczak et al., 2018; Standish et al., 2014), these methods are again generally not feasible for teams on the ground because of a lack of time and money.

To assess hysteresis, restoration project teams should, therefore, evaluate whether the degraded system shows signs of strong ecological feedbacks at the local or landscape scale that act to maintain the undesired regime (unhelpful resilience). Such feedbacks can signal hysteretic behaviour (Figure 2; Table 2). In the case of the repeatedly burnt tropical floodplain forests, for example, lower tree cover due to wildfires in the degradation history of the system had led to a depleted seed bank, which leads to reduced seed dispersal and consequently lower seed availability and tree recruitment. This continues low tree cover and constrains forest recovery through these self-maintaining 'history-dependent' feedbacks between low tree cover and poor seed sources (Flores & Holmgren, 2021b). In many coral reefs, for instance, a combination of fishing, eutrophication and global warming has resulted in algal dominance and low abundance of herbivore fish groups that feed on algae. This feedback maintains the algal dominance and prevents successful coral recruitment through outcompeting successfully recruited corals (Graham et al., 2013). See Table 2 for more examples of hysteretic behaviour across different ecosystem types that can hamper successful recovery and thus impact ecosystem restoration.

3.4 | Question D: Which feedbacks underpin helpful resilience?

Besides feedbacks that maintain the undesired regime and indicate hysteresis by underpinning unhelpful resilience (question C),

feedbacks that maintain the desired regime and thus underpin helpful resilience must be identified as well to facilitate successful ecosystem recovery. In the example of a shift from the floodplain forest to a more open savanna ecosystem regime, feedbacks that would promote tree cover, such as assisted natural regeneration or seeding, underpin helpful resilience and could help force a shift to the desired forest regime. Intervening in this feedback is key to strengthening helpful resilience, in addition to weakening unhelpful resilience through, for example disrupting feedbacks that maintain the savanna regime by means of fire protection (Flores et al., 2016; Flores & Holmgren, 2021a, 2021b; Table 2 'Additional interventions').

Similarly, in the example of a shift from the coral- to the algal-dominated regime in degraded coral reefs, intervening in the feedbacks that promote coral recruitment and underpin helpful resilience, for example by introducing parrot- and surgeon fishes, can help force a shift to the desired coral regime (Graham et al., 2013). At the same time, disrupting the feedbacks that maintain the algal domination, which underpin unhelpful resilience, for example by introducing herbivore fish species that feed on the algae, will help to force the same shift (Graham et al., 2013, Table 2 'Additional interventions').

In sum, if restoration teams include CSS assessments in their restoration project cycles, they can adequately determine the complexity of required interventions based on the presence or likelihood of regime shifts and evidence of hysteresis (Figure 2, Planning). Further, they can target their interventions to specifically disrupt feedbacks that underpin unhelpful resilience and strengthen those that underpin helpful resilience. While collecting information about regime shifts, hysteresis and feedbacks may, in practice, be challenging, costly and time consuming, we reiterate that it can greatly improve restoration outcomes (Magnuszewski et al., 2015; Maxwell et al., 2017; Qiu et al., 2022; Xiao et al., 2020), possibly saving resources in the long run.

4 | OUTSTANDING TASKS

Answering questions A and B from the previous section assumes restoration teams select measurable and feasible indicators that are: (i) comparable to relevant reference systems across time or space and (ii) responsive to the key disturbance(s) in their ecosystem(s) (for question B) (Cowan et al., 2021). Despite promising prospects of specific resilience indicators and methods to detect regime shifts (Andersen et al., 2009; Boulton et al., 2022; Lenton, 2011), operationalization of these methods into clear recommendations and tools to use across different ecosystem types remains a key outstanding task for the scientific community (Table 4; Selkoe et al., 2015). Specifically, we identify the development of practical tools and methods to assess ecological resilience loss, abrupt regime shifts and hysteresis in degraded systems as outstanding tasks, as these are, to our knowledge, non-existent. The lack of scientific consensus on the usefulness and applicability of regime shifts in ecology likely also hampers this operationalization (Higgins et al., 2023; Hillebrand et al., 2023). Further, a

helpful platform where restoration teams can explore whether ecosystems from similar climates and degradation settings have experienced a regime shift, is the online database www.regimeshifts.org (Biggs et al., 2009; Stockholm Resilience Centre, 2022). This evidence-based catalogue should, however, be extended, as more scientists and practitioners assess regime shifts across different ecosystems and biomes (Table 4). Similarly, data-driven networks where teams can share their M&E restoration performance data (e.g. <https://globalrestorationobservatory.com/>) should be encouraged to facilitate global monitoring of restoration performance as we progress in the UNDER (Ladouceur & Shackelford, 2021). Further, scientifically testing the hypotheses brought forward in our framework, that is that the loss of helpful resilience and presence of abrupt regime shifts significantly influence restoration performance, remains another outstanding task (Table 4). Importantly, this should be done while bringing together different knowledge sources, that is western science, with Indigenous and Local Knowledge (ILK) (Falardeau et al., 2022; Wheeler & Root-Bernstein, 2020), as well as considering the broader social-ecological dimension of CS dynamics and ecosystem restoration (Appendix S1, Table S2; Folke et al., 2010; Nikinmaa, 2020). For restoration policy-makers, we encourage them to step away from common assumptions on helpful 'general' resilience and instead introduce the concept of unhelpful resilience and further incorporate CSS assessment into their guidelines (Table 4). A crucial step towards CSS incorporation will be to start 'learning-by-doing' (Kato & Ahern, 2008; Walters & Holling, 1990), that is apply the proposed CSS assessment in real-life restoration projects, tailor the restoration strategies to it, and monitor and evaluate the remaining constraints and effectiveness (Table 3). Importantly, such inclusion of CSS assessment in restoration should be done through translating the key concepts in practical and comprehensible language that are accessible to a wide diversity of restoration teams, for example also those teams with limited or no scientific expertise.

AUTHOR CONTRIBUTIONS

Sybryn L. Maes, Bart Muys and Michael P. Perring conceived the ideas; Sybryn L. Maes, Rachel Cohen, Michael P. Perring, Jean-François Bastin and Bart Muys co-organized the resilience workshop in October 2021 which lay the foundations for this manuscript, and in which all co-authors except George Gann actively participated; Sybryn L. Maes led the writing of the manuscript and designed all figures and tables. Sybryn L. Maes, Michael P. Perring, Rachel Cohen, Festus K. Akinnifesi, Aida Bargués-Tobella, Jean-François Bastin, Marijn Bauters, Paulo N. Bernardino, Pedro H. S. Brancalion, James M. Bullock, David Ellison, Adeline Fayolle, Tobias Fremout, George D. Gann, Hadgu Hishe, Milena Holmgren, Ulrik Ilstedt, Grégory Mahy, Christian Messier, Catherine L. Parr, Casey M. Ryan, Moutar Sacande, Mahesh Sankaran, Marten S. Scheffer, Katharine N. Suding, Koenraad Van Meerbeek, Hans Verbeeck, Bruno J. P. Verbist, Kris Verheyen, Leigh A. Winowiecki and Bart Muys contributed critically to the drafts and gave final approval for publication. Milena Holmgren and Aida Bargués-Tobella (1), Paulo N. Bernardino

(2) and Adeline Fayolle (3) corrected the Spanish, Portuguese and French abstract, respectively.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest. Kate Parr is an associate editor of *Journal of Applied Ecology*, but took no part in the peer review and decision-making processes for this paper.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Extended glossary.

Appendix S2: Problem statement.

Appendix S3: Restoration project cycle.

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