

Mathematical modeling of dialectical emergent hybrid regimes in ecosystems

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Statement

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ABSTRACT. Traditional resilience theory often models complex systems as toggling between discrete alternative regimes, such as clear-water and turbid states in shallow lakes, each stabilized by internal feedback. While analytically powerful, this binary paradigm overlooks more nuanced dynamics observed in many real-world systems: the emergence of hybrid regimes that blend structural and functional elements of opposing regimes. These configurations are not transient midpoints, but stable, self-organized outcomes shaped by legacy effects, feedback recombination, and historical memory—a process that is fundamentally dialectical in nature. This paper proposes a conceptual scaffold for formalizing such dialectical dynamics using mathematical tools. Using shallow lakes as model systems, we show how established methods, including bifurcation and catastrophe theory, stochastic differential equations, agent-based models, network theory, and machine learning, can be reinterpreted to analyze the ontological distinctiveness, spatial organization, feedback structure and management implications of hybrid regimes. Rather than advancing a single unifying model, we provide a roadmap for adapting existing techniques to better capture the complexity of ecological transitions. In doing so, we open space for a richer, more process-relational understanding of resilience.

1. Introduction

Ecosystems are dynamic and complex, responding to external pressures in non-linear and often unexpected ways [1]. Understanding these dynamics has become increasingly urgent in the context of accelerating environmental change driven by human activity. Within the broader Earth system context, the theory of alternative stable states has emerged as a central framework in ecology for understanding how systems respond to disturbance [37]. Building on the concept of ecological resilience [22], this theory explores the conditions under which ecosystems can absorb shocks, persist in a given regime, or shift into an alternative configuration. Traditionally, two forms of resilience have been distinguished: engineering resilience, which emphasizes the rate at which a system returns to equilibrium following disturbance (recovery), and ecological resilience, which allows for the existence of multiple stable equilibria and focuses on a system’s capacity to maintain function despite variability [2, 3]. When a system crosses a critical threshold, whether due to

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slow degradation or sudden perturbation, it may undergo a regime shift, entering a qualitatively different state that may be difficult or impossible to reverse [6].

Mathematics has played a foundational role in formalizing the theory of alternative stable states. Ecosystem stability and regime transitions have been analyzed using tools from nonlinear dynamical systems, bifurcation theory, and stochastic processes [17, 26, 31, 42]. One of the most influential model systems in this field has been shallow lake ecosystems, which can exhibit abrupt transitions between clear and turbid water states in response to nutrient loading and vegetation loss [36]. These systems have served as empirical and theoretical examples of regime shifts, providing tractable cases for both mathematical modeling and experimental validation. The dynamics of shallow lakes are frequently illustrated using the classic ball-in-cup heuristic, where the system state is visualized as a ball resting in one of several potential wells [8]—see Figure 1. While this metaphor is conceptually useful and intuitively captures the idea of multiple attractors, it can oversimplify the complexity of real-world ecological transitions, which often involve overlapping processes, historical contingencies and hybrid states that do not conform to a binary model. Mathematics has the capacity not only to simulate system dynamics, but also to reveal new ontological categories—such as hybrid regimes—by formalizing configurations that lie between or beyond traditional binary categorizations of regimes and system states.

Empirical studies reveal that regime shifts are rarely clean bifurcations from one attractor to another. In shallow lakes, transitions from clear to turbid water regimes often leave behind seed banks that influence the likelihood of future recovery of submerged vegetation coverage in the turbid regime [36]. Similarly, in savannas, legacy effects from past grazing alter soil conditions and seed dispersal pathways [41], and coral reefs degraded by overfishing and warming retain structural remnants that shape coral recruitment dynamics after regime shifts [23]. Beyond these individual cases, meta-analyses and longitudinal studies show that hybrid or mixed regimes are widespread, including grassland–savanna mosaics [13, 21], forest–shrubland transitions, and coral–algae reef systems [18]. These cases reinforce

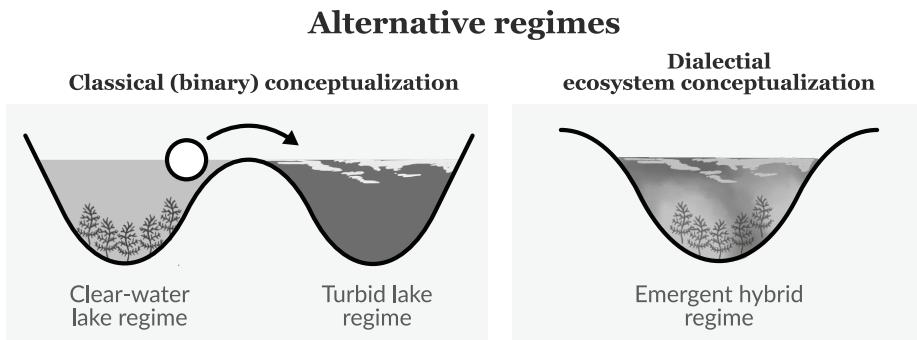


FIGURE 1. Schematic contrasting the traditional binary (rigid) conceptualization of alternative regimes with the more process-relational view of dialectical, higher-order regimes emanating from the synthesis of binaries.

the idea that regime transitions often produce intermediate or coexisting configurations, where historical legacies and novel feedbacks combine to form persistent, structurally complex systems. They suggest that regime transitions are not erasures of ecological history but rather integrations of it, generating emergent configurations that blend characteristics of past and present states. Such processes with the emergence of higher-order hybrid regimes have recently been conceptualized as “dialectical ecosystems” [5]—see Figure 1 and Figure 2.

Recognizing ecosystems as systems with interwoven and emergent hybrid regimes has significant implications for modeling and management. Moving beyond binary attractor models allows for the incorporation of memory effects (seed banks, ecological memory), feedback asymmetries (hysteresis, reinforcing vs. stabilizing feedbacks), and transitional dynamics (intermediate states, slow transitions, novel assemblages). In this light, conservation strategies must also evolve from restoring ecosystems to historical baselines – a frequently fruitless attempt – towards guiding adaptation and transformation processes that foster desirable hybrid regimes

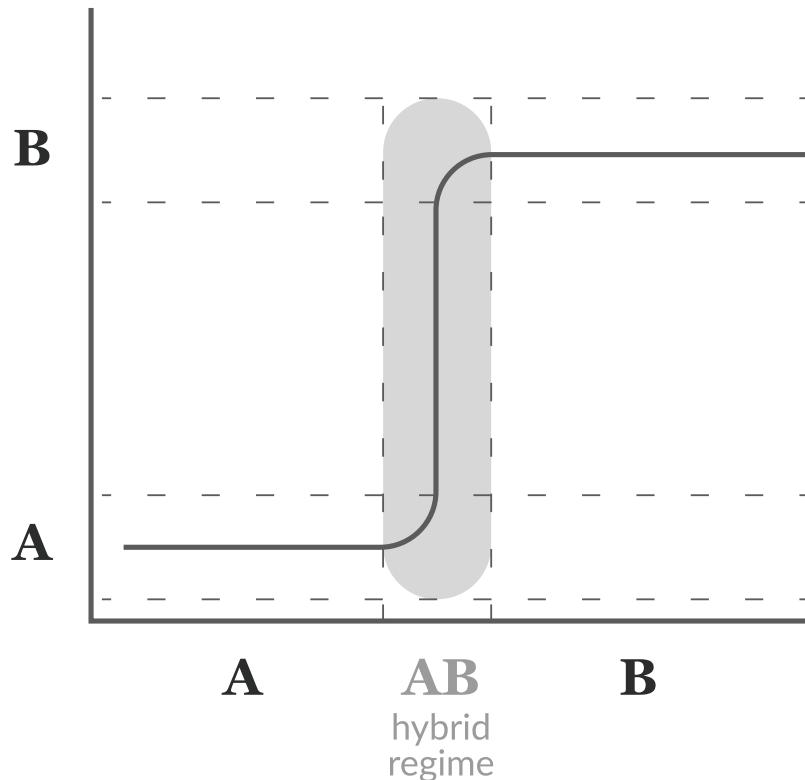


FIGURE 2. Conceptual diagram illustrating a change from a regime A to a regime B (left panel) and how a dialectical hybrid regime AB emerges from the synthesis of regimes A and B.

for human ecosystem service provisioning. This requires management approaches that embrace complexity and relational dynamics, while leveraging ecological memory and historical contingencies to reinforce resilience and sustain function under changing conditions [24, 29].

Examples of such adaptive strategies are emerging. Rather than halting the migration of coastal wetlands under sea-level rise, policies may instead facilitate their movement while maintaining core ecological functions [12]. Forests undergoing climate-driven change can support novel species assemblages that integrate legacy components that facilitate future adaptation potential [32]. Similarly, rather than restoring lakes to idealized clear-water states, managers might promote intermediate regimes with moderate vegetation and controlled turbidity [40]. In agroecosystems, blending traditional land-use practices with modern sustainability technologies can generate resilient, multifunctional landscapes [20].

This paper does not propose a single unifying model, but rather aims to provide a conceptual scaffold for future formal mathematical work, demonstrating how a suite of classical tools can be adapted to better represent emergent hybrid dynamics. By reframing alternative states not as discrete switches but as part of a continuous, process-relational change, resilience research can better capture the complexity of ecological dynamics in the Anthropocene. Ecosystems do not merely toggle between independent regimes; they evolve through intertwined transitions in space, time or both, shaped by history, structure, and feedback [5]. In this paper, we propose a mathematical framework for analyzing such emergent hybrid regimes. We first present propositions of emergent hybrid regimes that can be empirically tested. We then present mathematical tools that have been used in traditional regime shift research and resilience theory and then outline modifications that incorporate dialectical hybrid aspects (regime interdependence, ecological memory, and transitional structure), offering a more robust foundation for understanding and managing resilience.

2. Modeling resilience and regime changes

2.1. Propositions of emergent hybrid regimes. The following propositions are grounded in the dialectical ecosystem framework proposed by [5], which re-conceptualizes ecological change not as a binary shift between fixed regimes, but as a process of synthesis, integration, and transformation. Within this framework, hybrid regimes are not temporary anomalies or waypoints, but are often stable, emergent configurations that reorganize structural and functional elements inherited from historically distinct regimes.

To illustrate these ideas, we turn to shallow lake ecosystems that are among the most empirically studied and theoretically developed systems in regime shift ecology [36, 38]. While typically modeled as toggling between two alternative states (clear-water, macrophyte-dominated and turbid, phytoplankton-dominated) many lakes persist in long-lived intermediate configurations. These include structurally mixed or spatially heterogeneous states where features of both regimes coexist and interact in non-trivial ways. Scheffer et al. [38] emphasized that such states may arise near tipping points, while Bayley et al. [7] documented unstable oscillations in boreal lakes indicative of hybrid conditions. Rather than treating these configurations as transitional noise, we frame them as emergent regimes worthy of formal study.

The following propositions articulate a conceptual arc that begins with the ontological distinctiveness of hybrid regimes and progresses through their structural composition, feedback dynamics, and implications for management. Transitions between propositions are not mutually exclusive, but reflect different facets of a shared phenomenon: the persistence and self-organization of novel systems formed through integration of more than one regime. Many propositions describe co-occurring features (e.g., coexistence, emergent feedbacks, and memory effects), while others present testable claims about hybrid regime behavior. Anchored in the shallow lake model, they lay the foundation for formal modeling approaches in the subsequent section.

2.1.1. *Hybrid regimes are not transitional states but emergent syntheses of existing alternative regimes.* In some shallow lakes, long after an initial transition from a clear to turbid regime, a persistent hybrid state emerges, characterized by moderate water clarity, partial macrophyte cover, and intermittent algal blooms. Rather than occupying a midpoint, these states stabilize into a new attractor that resists collapse or reversion. This indicates ontological novelty rather than simple intermediate status [5].

2.1.2. *Hybrid regimes exhibit simultaneous coexistence of legacy structures.* Building on the previous point, hybrid systems often contain spatial or functional domains reflecting both predecessor regimes. Submerged vegetation may persist in protected zones while the open water remains dominated by phytoplankton [25]. These domains generate distinct, coexisting feedbacks, suggesting integration, not succession.

2.1.3. *Hybrid regimes manifest as either composites or spatial-temporal mosaics.* Coexistence may manifest as spatial mosaics (e.g., vegetated margins and turbid centers) or as temporal fluctuations (e.g., seasonal transitions between clearer and more turbid phases) [36]. The persistence of these configurations across time and space highlights the organizational complexity of hybrid regimes.

2.1.4. *The resilience of hybrid regimes is emergent and irreducible.* The resilience of a hybrid regime, i.e., its ability to maintain function under disturbance, cannot be reduced to the resilience of its source regimes. Hybrid systems respond differently to shocks, owing to newly formed feedback loops, reorganized thresholds and adaptive capacity [4]. For example, macrophyte patches in hybrid lakes may buffer sediment resuspension without fully suppressing algal dominance.

2.1.5. *Hybrid regimes are characterized by emergent feedbacks.* The coexistence of legacy components can generate novel feedback structures not present in either prior regime. In shallow lakes, partial macrophyte cover may suppress sediment disturbance enough to prevent collapse, while algal shading prevents full macrophyte expansion [43]. These mutually moderating dynamics form a distinct feedback architecture.

2.1.6. *Self-organization of hybrid regimes follows novel structural and spatial patterns.* Rather than reverting to clear or turbid archetypes, hybrid systems often self-organize into new configurations such as concentric vegetation bands, patch-dependent community types, or micro-gradients in resource availability. These patterns reflect restructured constraints and novel ecological equilibria [34].

2.1.7. *Hybrid regimes retain measurable legacies while generating novel features.* Legacy features (e.g., macrophyte seed banks, benthic invertebrate communities) persist and are repurposed within hybrid dynamics. Macrophytes may shift from

being primary producers to functioning as sediment stabilizers. The system's history is not erased but embedded into its ongoing function [33].

2.1.8. *Transitions to hybrid regimes follow gradual, heterogeneous trajectories.* Unlike classic regime shifts, the emergence of hybrid regimes may occur slowly, unevenly, and without clear tipping points. In shallow lakes, this might involve years of creeping vegetation expansion or patch-wise turbidity decline. Such dynamics may lack traditional early warning indicators like critical slowing down [11, 14], further distinguishing transitions to hybrid regimes.

2.1.9. *Hybrid regimes require dialectical management.* Finally, hybrid systems challenge restoration goals aimed at returning to historical baselines [16]. Instead, management may adopt a dialectical approach, aiming to stabilize or guide hybrid regimes toward desirable functions; e.g., tolerating moderate turbidity, supporting partial macrophyte cover, or leveraging legacy structures for resilience [5].

2.2. Toward mathematical formalization of hybrid regimes. The propositions outlined above offer a conceptual progression for understanding hybrid regimes: beginning with their ontological distinctiveness, moving through their spatial and structural organization, characterizing their internal feedback dynamics, and ending with their implications for management. Rather than proposing an entirely new mathematical toolkit, our aim is to adapt existing modeling approaches from regime shift theory to reflect the distinct qualities of hybrid regimes as conceived within a dialectical ecological framework [5].

Traditionally, the mathematics of regime shifts has operated within a binary paradigm, simulating transitions between discrete stable states, such as the classic clear and turbid regimes in shallow lakes, using bifurcation theory [35], stability analysis [37], or stochastic models of critical transitions [26]. These methods have been immensely productive in identifying tipping points, early-warning signals, and thresholds for restoration. For instance, tipping points have been extensively studied through bifurcation theory, where small parameter changes lead to sudden qualitative shifts in system behavior [27]. Early-warning indicators such as increasing autocorrelation and variance near bifurcations have been formalized within the context of fast–slow stochastic systems, particularly in relation to critical slowing down [28]. However, univariate early-warning approaches (e.g., variance, autocorrelation) may have limited utility for exploring complex systems, especially when drivers are unknown. Conversely, multivariate methods (e.g., redundancy analysis, discontinuity analysis, Fisher information) can be used to capture complex ecosystem dynamics including abrupt and gradual transitions, cross scale dynamics and alternate regimes [44–47]. Thresholds for restoration and recovery have also been analyzed using potential landscape methods and large deviation theory, providing quantitative tools to estimate escape times from basins of attraction under stochastic forcing [9].

However, these approaches are often not designed for systems where legacy structures persist, novel configurations emerge, and multiple attractors co-occur in persistent tension. Hybrid regimes, by contrast, require a conceptual and technical shift: not in the invention of new methods, but in the reconfiguration of modeling logics to account for memory effects, spatial coexistence, emergent feedbacks, and gradual transitions that defy classical bifurcation behavior. While we highlight a selection of modeling strategies to illustrate how such a shift might be operationalized, these represent just a small portion of the broader mathematical landscape

available for engaging with complex ecological dynamics. To help orient such exploration, we propose a conceptual grouping of the propositions into four overlapping domains: (1) ontological distinctiveness, (2) spatial and structural organization, (3) system dynamics and feedbacks, and (4) management and transformation. These domains are not rigid categories but serve as heuristic lenses through which existing tools might be reinterpreted and recombined to more effectively engage with the complexity of hybrid regimes.

A. ONTOLOGICAL DISTINCTIVENESS (PROPOSITIONS 2.1.1, 2.1.2, 2.1.4)

This domain emphasizes that hybrid regimes are not transient intermediates but emergent attractors in their own right. They combine features of “parent alternate” (clear-water, turbid) regimes while maintaining structural coherence and distinct resilience properties. Existing approaches, such as multi-stable dynamical systems (e.g., cusp catastrophe models, fold bifurcations), could be adapted to model these conditions by incorporating memory terms or lag-dependent feedbacks, allowing the system to retain influence from past states. Additionally, state-dependent feedback asymmetries can be introduced into differential equations to prevent the system from fully reverting to or converging with either prior regime. Standard resilience metrics, such as return times, basin width, and cross-scale resilience [22, 39], remain useful but must be interpreted in light of the system’s hybrid nature, recognizing that resilience may emerge through the synthesis of opposing dynamics.

B. SPATIAL AND STRUCTURAL ORGANIZATION (PROPOSITIONS 2.1.3, 2.1.6, 2.1.7)

Hybrid regimes often express themselves spatially as mosaics or blended composites of legacy elements and new formations. To model this, existing spatially explicit approaches, such as reaction–diffusion models, cellular automata, and agent-based simulations, can be employed and expanded to capture fine-scale patchiness and emergent patterns. Variables encoding ecological legacies (e.g., macrophyte seed banks, sediment nutrient content) can be embedded as spatially heterogeneous parameters to simulate how historical configurations influence ongoing structure. Additionally, metrics like spatial autocorrelation, entropy, or patch dynamics may be used to quantify the degree of spatial integration or fragmentation in hybrid systems. These models do not need to break from prior spatial ecology frameworks but should be tuned to capture the coexistence of structure and novelty.

C. SYSTEM DYNAMICS AND FEEDBACKS (PROPOSITIONS 2.1.5, 2.1.8)

Hybrid regimes often follow gradual, heterogeneous transitions that are not well captured by classical models of abrupt critical transitions. Here, established modeling methods such as nonlinear interaction networks or coupled differential equations remain applicable, but must be adapted to simulate emergent feedback loops; that is, interactions between system components that arise only once legacy elements are recombined. Additionally, models should test for the presence or absence of critical

slowing down and other early-warning indicators (e.g., rising variance, autocorrelation) that are typically used to anticipate tipping points. Simulating hybrid regime emergence under varying levels of noise, external forcing, or parameter drift can reveal conditions under which these signals fail to materialize, thus distinguishing trajectories of hybrid regimes from canonical regime shifts.

D. MANAGEMENT AND TRANSFORMATION (PROPOSITION 2.1.9)

Hybrid regimes challenge the logic of restoration to a prior state and instead call for dialectical ecosystem management that works with adaptation and transformation, incorporating novelty rather than excluding it [5]. Existing tools from social-ecological systems modeling can be adapted to incorporate management levers (nutrient reduction, habitat buffers, species reintroductions) as dynamic variables within the system. Models that use multi-objective optimization can help identify trade-offs between competing goals such as water clarity, biodiversity, and productivity in hybrid regimes of lakes. Furthermore, adaptive management models that include learning loops and system monitoring can simulate how interventions evolve in response to shifting feedbacks and uncertainties. These approaches are not new but require reframing their objectives: from controlling a system's state to guiding its transformation.

In sum, our contribution is not the development of a novel mathematical language, but a re-description of existing approaches in light of a new ecological ontology. Hybrid regimes, as emergent products of dialectical synthesis, require models that are sensitive to overlapping structures, feedback recombination, and complex temporal-spatial dynamics. The tools for this already exist within the mathematical ecology community; our aim is to redirect their focus and encourage their recalibration to a regime logic that is not binary, but integrative. While ordinary differential equations (ODE)-based approaches may be analytically tractable and ideal for identifying bifurcations and stability boundaries (e.g., Propositions 2.1.1–2.1.2), spatially explicit models such as agent-based simulations are better suited for empirically grounded questions involving patch dynamics and local feedbacks (e.g., Propositions 2.1.3, 2.1.6, and 2.1.7), especially when parameter heterogeneity and individual interactions are known from field data. In the following section, we illustrate how such recalibrated models have already been applied or can be adapted using shallow lake systems as a case study.

2.3. Case Studies. In this section, we present a series of case studies demonstrating how established modeling approaches from mathematical ecology and complex systems theory can be reinterpreted to address the distinctive properties of hybrid regimes. Each case study corresponds to one or more of the propositions outlined above and showcases how models can be used to explore features such as co-existence, emergent feedbacks, gradual transitions, and spatial heterogeneity. While not exhaustive, these examples reflect a range of techniques, including dynamical systems, stochastic processes, agent-based models, network theory, and machine learning that are especially well suited for probing the multiscale, feedback-rich nature of hybrid ecological systems. For each modeling approach, we provide a representative mathematical formalism to illustrate how dynamics of hybrid regimes, such as memory dependence, spatial feedback, or stochastic persistence, can be

encoded. These formalisms are not full model implementations but serve as entry points for theoretical and applied analysis.

2.3.1. *Nonlinear dynamical systems.* May's nonlinear models of competing species revealed how multiple stable equilibria can emerge from simple interaction rules [30]. To adapt these for hybrid regimes, modified systems of ODEs can incorporate memory effects (e.g., through time-lagged terms or hysteresis functions) to represent legacy-driven attractor landscapes. These models are ideal for conceptualizing how hybrid states stabilize as new attractors distinct from classical regimes. They are particularly useful when empirical parameter values are scarce but structural system logic is known. Consider the system

$$(2.1) \quad \frac{dx}{dt} = rx(1-x)(x-\alpha) + \int_0^t K(t-s)x(s) ds$$

where $x(t)$ is the system state at time t (e.g., turbidity, vegetation cover), r is a growth or feedback strength parameter, α is a threshold or tipping point between regimes, K is a memory kernel describing the weight of past states $x(s)$ on present dynamics (e.g., ecological memory), and the integral term introduces legacy effects or hysteresis via convolution with past system states.

The cubic polynomial $rx(1-x)(x-\alpha)$ defines a bistable system, where the state can settle into either of two equilibria (e.g., clear or turbid lake regimes). The additional integral term modifies the feedback structure by allowing past states to influence current trajectories, thereby enabling the system to stabilize in non-classical hybrid configurations. For instance, sediment seed banks or delayed nutrient cycling can stabilize partial macrophyte cover even under moderate turbidity, features of a hybrid regime not predicted by the classical model. These models are most useful when empirical detail is sparse but the underlying feedback architecture is well-understood, making them powerful conceptual scaffolds for theorizing attractors of hybrid regimes..

2.3.2. *Bifurcation Theory.* Bifurcation theory provides a powerful lens for understanding how gradual changes in system parameters can lead to abrupt transitions in state. Classical applications have emphasized the loss of stability at tipping points, often using saddle-node, transcritical, or Hopf bifurcations to model ecosystem collapses or flips between stable regimes. Kuehn offered a comprehensive framework for analyzing critical transitions in systems with fast–slow dynamics and stochastic perturbations, many of which are relevant to ecological resilience theory [26]. In the context of hybrid regimes, bifurcation theory offers additional value: it allows us to explore whether structurally distinct hybrid configurations emerge between classical attractors, or near points of attractor deformation (e.g., cusp points or codimension-2 bifurcations). These models are well suited for capturing ontological novelty, where hybrid regimes form new, low-dimensional attractors distinct from either legacy state.

Consider the two-timescale slow–fast dynamical system:

$$(2.2) \quad \begin{aligned} \varepsilon \frac{dx}{dt} &= f(x, y; \mu) \\ \frac{dy}{dt} &= g(x, y) \end{aligned}$$

where x is a fast ecological variable (e.g., turbidity or biomass), y is a slow variable encoding ecological memory or legacy (e.g., nutrient concentration, sediment load), μ is a bifurcation parameter, and $\varepsilon \ll 1$ separates timescales.

This canonical slow–fast system exhibits a fold bifurcation where small, gradual changes in the slow variable y or in the parameter μ can trigger sudden shifts in the fast variable x . When applied to shallow lakes, for example, x might represent water clarity and y the legacy nutrient content in sediments. Hybrid regimes may correspond to states lingering near the fold, stabilized by memory effects in y or by perturbations that prevent collapse.

In these systems, center manifold theory can be used to reduce dimensionality near bifurcation points and approximate stability of hybrid regimes under perturbation. This assumes that the system remains near a low-dimensional manifold where fast variables quickly relax to quasi-equilibrium while slow variables evolve gradually, an assumption often valid in ecosystems with legacy effects or path dependence.

The use of bifurcation analysis and slow–fast systems assumes that ecological dynamics operate on separable time scales, with fast-reacting processes (e.g., algal blooms) adjusting rapidly, and slow processes (e.g., sediment nutrient legacy or macrophyte recovery) evolving over longer horizons. This structure justifies singular perturbation techniques and enables metastable hybrid regimes to emerge in regions where fast-slow interactions create non-classical stability. However, in hybrid systems, the presence of feedback recombination and temporal heterogeneity may blur these time scales, requiring empirical justification or robust sensitivity testing.

In sum, bifurcation theory, particularly when extended with center manifold analysis, offers a way to explore the formation, persistence, and fragility of hybrid regimes at structural boundaries between classical attractors. It also enables the identification of quasi-stable hybrid points, which may be missed by traditional two-regime models.

2.3.3. Stochastic Differential Equations. Stochastic differential equations (SDEs) allow researchers to model how noise affects transitions between regimes. Wang and Qi used such models to simulate eutrophication dynamics under stochastic forcing [42]. For hybrid regimes, SDEs with state-dependent noise can reveal how stochastic persistence or noise-induced stabilization might allow hybrid states to emerge and persist. These models are suited for cases where empirical environmental variability (e.g., climate noise, nutrient pulses) is known, and system response under uncertainty needs to be evaluated.

Consider the one-dimensional bistable system with multiplicative noise:

$$(2.3) \quad dx_t = [rx_t(1 - x_t)(x_t - \theta)] dt + \sigma x_t dW_t$$

where x_t represents the system state at time t (e.g., turbidity, macrophyte cover), θ is a critical threshold between regimes, r is the intrinsic feedback strength, σ is the amplitude of environmental noise, dW_t is the differential of a standard Wiener process (i.e., Brownian motion).

The deterministic component models classic bistability: the system has two attractors and one unstable threshold θ . The multiplicative noise term $\sigma x_t dW_t$ allows the influence of randomness to scale with the system state (e.g., stronger variability when biomass is higher). In hybrid regimes, noise may allow the system to hover near the threshold or oscillate between states, producing emergent behaviors such

as patchy vegetation or intermittent algal blooms. Importantly, the quasi-potential landscape associated with this SDE (derived from the Fokker–Planck equation) can reveal whether hybrid regimes form new stochastic wells, distinct from either clear or turbid regimes—a concept central to understanding the resilience of hybrid regimes.

2.3.4. Catastrophe theory. Scheffer et al. applied catastrophe theory to show how abrupt transitions could result from gradual parameter changes [37]. Fold and cusp catastrophes are relevant for modeling regime switches. For hybrid regimes, catastrophe theory can be used to study under what conditions two basins might partially merge or support structurally mixed states. This approach is well-suited for theoretical exploration and sensitivity testing, especially when a system is hypothesized to hover near multiple stable or semi-stable states.

Consider the cusp catastrophe potential function:

$$(2.4) \quad V(x; \alpha, \beta) = \frac{x^4}{4} - \frac{\alpha x^2}{2} - \beta x$$

where x is the state variable (e.g., turbidity, vegetation biomass), α, β are control parameters (e.g., nutrient loading, grazing pressure), and V defines a potential landscape in which the equilibria correspond to minima of V .

This function describes a landscape that can shift from monostable to bistable or multistable dynamics depending on parameter values. At certain cusp conditions, the system may allow intermediate or blended states to emerge between the classic equilibria. In hybrid regimes, this framework can help formalize scenarios where partial regime overlap or deformed attractor basins give rise to new quasi-stable configurations. Visualizing how the potential function changes with α and β provides insight into when hybrid dynamics are most likely to appear, and how small shifts in feedback structure or external forcing could destabilize them. While primarily used for structural diagnostics, this approach supports theoretical exploration of emergent attractors not present in classical two-regime models.

2.3.5. Agent-based models (ABMs). ABMs simulate behavior of individual agents (e.g., species, land users) and their interactions with the environment. Filatova et al. used ABMs to study land-use transitions in social-ecological systems [17]. For hybrid regimes, ABMs are especially useful for simulating how legacy patches, edge effects, and feedbacks at local scales lead to mosaic or composite system configurations. This method is highly compatible with empirical studies that track fine-scale spatial heterogeneity and are particularly useful in management scenarios requiring place-specific interventions.

Consider the spatial threshold rule for binary vegetation state:

$$(2.5) \quad v_{i,t+1} = \text{Prob} \left[\sum_{j \in N(i)} w_{ij} v_{j,t} + \eta_i(t) > \theta \right]$$

where $v_{i,t} \in \{0, 1\}$ is the binary state of patch i at time t (e.g., vegetated or bare), $N(i)$ is the set of neighboring patches, w_{ij} are interaction weights (e.g., dispersal or facilitation effects), η_i is a stochastic perturbation term, and θ is a patch-level threshold for state transition.

This formalism encodes local feedback rules that determine patch dynamics based on neighborhood influence, a typical setup in ecological ABMs. In hybrid regimes, such rules allow vegetated and non-vegetated areas to co-exist, reflecting

real-world spatial mosaics where legacy structures (e.g., seed banks, microtopography) support persistence. Over time, these rules generate complex emergent patterns, such as stable patchwork landscapes or shifting mosaics, that would be impossible to capture with continuous or aggregate models. This approach is highly adaptable to empirical datasets (e.g., aerial imagery, plot surveys) and is frequently used in adaptive management simulations to explore interventions under spatial heterogeneity.

2.3.6. Network theory & connectivity models. Network models represent system components (e.g., habitats, species, processes) as nodes and their interactions as edges. Dakos et al. demonstrated how network degradation can serve as an early warning of collapse [15]. In hybrid systems, feedback recombination and resilience can be assessed by examining changes in modularity, redundancy, and node centrality. Networks are especially useful for visualizing feedback architecture and can be grounded in empirical data where interaction matrices or habitat connectivity are available.

Consider the dynamic node equation:

$$(2.6) \quad \frac{dx_i}{dt} = f(x_i) + \sum_{j=1}^N A_{ij} \cdot g(x_j, x_i)$$

where x_i is the state of node i (e.g., species abundance, nutrient concentration, patch quality), A_{ij} is the adjacency matrix representing the presence and strength of interactions (edges) between nodes i and j , $f(x_i)$ describes internal dynamics of node i , and $g(x_j, x_i)$ is a function representing how connected nodes influence each other (e.g., facilitation, competition, dispersal).

This system models how each node's state evolves over time as a function of its own internal dynamics and its interactions with other nodes. For hybrid regimes, feedback recombination often involves non-trivial topology, such as when remnant nodes from one regime maintain connections in an emerging configuration (e.g., macrophyte patches connected by sediment stabilization in a mostly turbid lake). Metrics such as modularity, centrality, and clustering coefficient can be used to track how the network's architecture evolves, distinguishing hybrid regimes from simple regime flips. Network models also lend themselves to early-warning signal detection, especially by analyzing declines in connectivity or coherence as signs of weakening feedback structure prior to destabilization of hybrid regimes. This approach is especially useful when there is spatial or trophic interaction data available, or when hybrid regimes are suspected to involve distributed feedback effects across ecological scales (e.g., species networks, habitat fragmentation, or nutrient flows).

2.3.7. Machine learning & data-driven approaches. Machine learning (ML) approaches are increasingly used in ecology to uncover complex, nonlinear patterns in large observational or remote sensing datasets. Hampton et al. showed how deep learning could detect early signs of desertification by identifying weak signals preceding regime shifts [19]. For hybrid regimes, ML techniques are particularly valuable for detecting spatial-temporal complexity, emergent feedbacks, and slow transitions that may not be captured by mechanistic models alone. When combined with ecological theory, these tools can highlight novel indicators of regime mixing, or suggest thresholds and patterns where configurations of hybrid regimes are forming. ML approaches are particularly promising for adaptive management, where predictive algorithms support real-time monitoring and decision-making.

Consider the recurrent neural network architecture:

$$(2.7) \quad \begin{aligned} h_t &= \tanh(W_h h_{t-1} + W_x x_t + b) \\ \hat{y}_t &= \sigma(W_o h_t + c) \end{aligned}$$

where x_t is the input at time t (e.g., remote sensing index, nutrient load, vegetation cover), h_t is the hidden state vector (representing memory of past conditions), W_h , W_x , and W_o are weight matrices learned during training, b and c are biases, \hat{y}_t is the predicted output (e.g., probability of hybrid state, regime instability), σ is an activation function (e.g., sigmoid or softmax for classification).

This recurrent neural network (RNN) architecture is capable of modeling time series with memory and temporal dependencies, which are central to identifying hybrid regimes. For instance, it could be trained on long-term ecological monitoring data to predict the likelihood of regime blending or early signals of emergence of hybrid regimes. Unlike mechanistic models, ML methods do not require prior specification of interaction rules but can uncover hidden correlations and nonlinear structures from high-dimensional data. However, because ML models are often “black boxes,” their explanatory power is limited, making them most powerful when paired with theory-based approaches—e.g., using predictions to validate or refine formal dynamical models.

In hybrid regime modeling, ML can thus serve as a discovery tool, highlighting where traditional models might need revision or where new hybrid states may be emerging. Their use in real-time environmental monitoring, landscape pattern detection, and management prioritization is likely to grow as high-resolution datasets continue to accumulate.

2.3.8. Reaction diffusion systems (or PDE more generally). Partial differential equations (PDE) are well-suited to simulate regime shifts by capturing how local disturbances can spread or recede. Hybrid regimes, where different stable states co-exist, are modeled as stable pattern solutions of the PDE system. Front dynamics, which represent the movement of regime boundaries, are particularly informative for assessing resilience, as the speed and direction of these fronts can indicate whether an ecosystem is recovering or collapsing. PDE, particularly reaction-diffusion systems, provide a means to integrate spatial structure with nonlinear ecological dynamics, offering powerful tools for investigating resilience in heterogeneous landscapes.

Consider a general reaction-diffusion equation of the form

$$(2.8) \quad \frac{\partial u}{\partial t} = D \nabla^2 u + f(u, \mathbf{x}, t)$$

where $u = u(\mathbf{x}, t)$ denotes the density of a biological or ecological variable (e.g., vegetation biomass), D is the diffusion coefficient (which can be assumed to be constant or spatially/temporally heterogeneous), and $f = f(u, \mathbf{x}, t)$ represents local growth, mortality, and feedback processes.

The Laplacian ∇^2 models spatial dispersal or diffusion. Multiple stable states can emerge from nonlinearities in $f(u)$, allowing the system to model critical transitions or “tipping points.” Spatial patterns such as patchiness, bands, or fronts naturally arise in these systems and serve as indicators of proximity to regime shifts. PDE-based models have been applied to: (1) dryland vegetation patterns, showing transitions from striped to spotted patterns before desertification; (2) Invasive species dynamics, modeling how spatial spread interacts with native species’

recovery; (3) Coral reef systems, where algae-coral interactions result in spatial mosaics that shift under fishing pressure or warming. Such models help identify early warning signals of collapse, critical thresholds, and spatial refugia that enhance recovery capacity.

To assist readers in selecting appropriate modeling strategies for different aspects of hybrid regime analysis, we summarize the comparative strengths of the eight approaches in Table 1. The table contrasts analytical and numerical tractability, exploratory utility, and calibration potential, highlighting when a model is best suited for theoretical insight (e.g., bifurcation analysis, catastrophe theory) versus empirical application (e.g., SDEs, ABMs, machine learning). This comparison also underscores that hybrid regimes, given their complexity and multiscale nature, often require a modular or composite modeling strategy, drawing on multiple tools depending on system properties, data availability, and management needs.

3. Discussion and outlook

The framework developed in this paper offers a conceptual and methodological foundation for advancing the mathematical modeling of emergent hybrid regimes. By reinterpreting and extending tools from dynamical systems theory, stochastic modeling, network analysis, and machine learning, we aim to open a space for modeling the structural persistence, transitional memory, and feedback recombination that characterize hybrid regimes.

This contribution should be viewed not as finalized, but as an invitation to mathematical innovation. Several directions are particularly promising. First, center manifold theory could be employed to formalize the low-dimensional surfaces on which hybrid regimes may persist, especially near critical thresholds where classical bifurcation theory predicts regime transitions. In systems where slow variables (e.g., nutrient legacies, sediment composition) exert delayed effects, the dynamics may collapse onto manifolds that sustain configurations of hybrid regimes for extended periods. A concrete direction here is to explore the existence and stability of invariant manifolds in slow–fast systems with memory terms, potentially combining methods from geometric singular perturbation theory and integral delay equations.

Second, persistence theorems, originally developed to assess long-term coexistence in population models, could be extended to systems where elements of distinct regimes (e.g., macrophyte patches and phytoplankton blooms) coexist in tension. In such models, hybrid regimes could be framed as invariant sets with persistent subpopulations or state variables that do not dominate the system and never collapse to zero. One could develop sufficient conditions under which this form of bounded persistence occurs using Lyapunov-type functions or probabilistic permanence theorems.

Third, noise-induced transitions present opportunities for analyzing how stochastic fluctuations contribute to the formation or destabilization of hybrid regimes. Unlike bifurcation-driven tipping, where deterministic control parameters push the system across thresholds, stochastic models may exhibit quasi-stationary hybrid states stabilized by noise. Future work could formalize conditions for noise-supported metastability, particularly in systems where hybrid regimes occupy wide but shallow basins in the potential landscape. This direction aligns well with non-equilibrium statistical mechanics and could benefit from large deviation theory or stochastic bifurcation analysis.

A fourth opportunity lies in the application of topological methods, such as conley index theory or persistent homology, to classify the qualitative structure of hybrid regime dynamics. These approaches allow for the characterization of multi-attractor systems and the transitions between them without requiring a fully explicit model. For example, one could explore how feedback loops restructure as the system moves from binary attractors to configurations of hybrid regimes, or

Model type	Analytical tractability	Numerical tractability	Exploratory use	Empirical calibration potential	Typical use case
Nonlinear dynamical systems	High (for low dimensions)	High	Strong	Moderate (if structure known)	Conceptualizing hybrid attractors, stability structures
Bifurcation theory	High (near equilibrium)	Moderate	Strong	Moderate (with time-series data)	Identifying hybrid zones near tipping points
Stochastic differential equations (SDEs)	Moderate	High	Strong	Strong (with empirical noise data)	Evaluating stochastic persistence, noise-induced hybrid stability
Catastrophe theory	High	Moderate	Strong	Low	Mapping structural transitions, sensitivity analysis
Agent-based models (ABMs)	Low	High	Moderate	Strong (with landscape data)	Simulating patch mosaics, management intervention scenarios
Network models	Moderate	High	Moderate	Strong (with interaction matrices)	Analyzing feedback architecture, modularity, resilience metrics
Machine learning (ML)	Low (black-box models)	High	Weak (standalone)	Very Strong (large datasets needed)	Detecting early signals, high-dimensional pattern discovery
Reaction diffusion systems	Moderate to high	High	High	Moderate	Simulating spatial structure of ecological variables over

TABLE 1. Summary of modeling approaches for dialectical hybrid ecological regimes. Shown are eight modeling approaches discussed in the case studies, evaluating each method in terms of analytical and numerical tractability, theoretical exploratory power, and potential for empirical calibration.

how topological invariants signal the emergence of memory-induced loops in system phase space.

At the same time, it is essential to acknowledge the limits of formal modeling when applied to dialectical dynamics. Synthesis, as used in this framework, draws on philosophical notions of transformation that may resist reduction to conventional equations. Dialectical shifts involve qualitative changes in identity, feedback structure, and function, features often emergent and nonlinear in ways that defy closed-form solution. Thus, while formal models provide generality and analytic rigor, they risk oversimplifying the historical contingencies and context-dependence of real ecosystems [5]. Navigating this trade-off between abstraction and realism is a core challenge of ecological mathematics.

As a result, interdisciplinary approaches are vital. Mechanistic models could be coupled with machine learning techniques trained on long-term ecological data to detect early hybridization signals. For instance, deep learning models might identify shifts in spatial-temporal signatures of vegetation and turbidity that suggest hybrid regime formation, while formal models provide interpretability and testable hypotheses. Moreover, experimental mesocosms and field manipulations could serve as platforms to validate theoretical predictions, such as the presence of emergent feedback loops, slow transitions, or spatial mosaics predicted by dialectical ecosystems theory.

While this paper focuses on scaffolding current tools to accommodate hybrid regimes, a longer-term goal is to cultivate a broader dialectical mathematics of ecosystems. Such a framework would move beyond equilibrium-based paradigms to embrace synthesis, contradiction, and emergence as formal properties of ecological systems. This might involve developing new classes of models that allow structural recombination of feedbacks, formalize ontological shifts in state space (e.g., attractor bifurcation into blended manifolds), or use topological data analysis to represent transitions in processual, rather than state-based, terms. A dialectical mathematics would not aim for a single predictive model but rather a family of formalisms capable of expressing the open-ended, memory-dependent, and relational dynamics that characterize ecosystems under transformation. This opens a space for further theoretical innovation at the intersection of dynamical systems, mathematics, and ecological complexity.

In sum, this framework invites mathematical engagement with a class of ecological phenomena that has long eluded formalization. By shifting from binary to dialectical regime logic we provide not only a reinterpretation of existing models, but also a foundation for new ones. The challenge now is to build on this scaffold with formal, empirical, and trans-disciplinary tools that can illuminate the complex and evolving fabric of hybrid ecosystems and social-ecological systems.

References

- [1] C.R. Allen, D.G. Angeler, A.S. Garmestani, L.H. Gunderson, and C.S. Holling, *Panarchy: Theory and application*, *Ecosystems* **17** (2014), 578–589.
- [2] C.R. Allen, D.G. Angeler, B.C. Chaffin, D. Twidwell, and A.S. Garmestani, *Resilience reconciled*, *Nat. Sustain.* **2** (2019), no. 10, 898–900.
- [3] D.G. Angeler and C.R. Allen, *Quantifying resilience*, *J. Appl. Ecol.* **53** (2016), no. 3, 617–624.
- [4] D.G. Angeler, H.B. Fried-Petersen, C.R. Allen, A.S. Garmestani, D. Twidwell, W.C. Chuang, and C.L. Wonkka, *Adaptive capacity in ecosystems*, *Adv. Ecol. Res.* **60** (2019), 1–24.
- [5] D.G. Angeler and J.E. Maybee, *Dialectical ecosystems: Theory and applications*, *Adv. Ecol. Res.* **72** (2025), 39–90.
- [6] D.L. Baho, C.R. Allen, A.S. Garmestani, H.B. Fried-Petersen, S.E. Renes, L.H. Gunderson, and D.G. Angeler, *A quantitative framework for assessing ecological resilience*, *Ecol. Soc.* **22** (2017), no. 3, 17.
- [7] S.E. Bayley, I.F. Creed, G.Z. Sass, and A.S. Wong, *Frequent regime shifts in trophic states in shallow lakes on the Boreal Plain: Alternative “unstable” states?*, *Limnol. Oceanogr.* **52** (2007), no. 5, 2002–2012.
- [8] B.E. Beisner, D.T. Haydon, and K. Cuddington, *Alternative stable states in ecology*, *Front. Ecol. Environ.* **1** (2003), no. 7, 376–382.
- [9] N. Berglund and B. Gentz, *Noise-induced phenomena in slow-fast dynamical systems: A sample-paths approach*, Springer Science & Business Media, 2006.
- [10] B.T. Bestelmeyer, G.S. Okin, M.C. Duniway, S.R. Archer, N.F. Sayre, J.C. Williamson, and J.E. Herrick, *Desertification, land use, and the transformation of global drylands*, *Front. Ecol. Environ.* **13** (2015), no. 1, 28–36.
- [11] C. Boettiger and A. Hastings, *Quantifying limits to detection of early warning for critical transitions*, *J. Royal Soc. Interface* **9** (2012), no. 75, 2527–2539.
- [12] S.M. Borchert, M.J. Osland, N.M. Enwright, and K.T. Griffith, *Coastal wetland adaptation to sea level rise: Quantifying potential for landward migration and coastal squeeze*, *J. Appl. Ecol.* **55** (2018), no. 6, 2876–2887.
- [13] V.D.L. Dantas, M. Hirota, R.S. Oliveira, and J.G. Pausas, *Disturbance maintains alternative biome states*, *Ecol. Lett.* **19** (2016), no. 1, 12–19.
- [14] V. Dakos, S.R. Carpenter, W.A. Brock, A.M. Ellison, V. Guttal, A.R. Ives, and M. Scheffer, *Methods for detecting early warnings of critical transitions in time series illustrated using simulated ecological data*, *PLoS ONE* **7** (2012), no. 7, e41010.
- [15] V. Dakos, S.R. Carpenter, E.H. van Nes, and M. Scheffer, *Resilience indicators: prospects and limitations for early warnings of regime shifts*, *Phil. Trans. R. Soc. B* **370** (2015), no. 1659, 20130263.
- [16] C.M. Duarte, D.J. Conley, J. Carstensen, and M. Sánchez-Camacho, *Return to Neverland: Shifting baselines affect eutrophication restoration targets*, *Estuaries Coasts* **32** (2009), no. 1, 29–36.
- [17] T. Filatova, J.G. Polhill, and S. Van Ewijk, *Regime shifts in coupled socio-environmental systems: Review of modeling challenges and approaches*, *Environ. Model. Softw.* **75** (2016), 333–347.
- [18] N.A. Graham, J.E. Cinner, A.V. Norström, and M. Nyström, *Coral reefs as novel ecosystems: embracing new futures*, *Curr. Opin. Environ. Sustain.* **7** (2014), 9–14.
- [19] S.E. Hampton, C.A. Strasser, J.J. Tewksbury, W.K. Gram, A.E. Budden, A.L. Batcheller, and J.H. Porter, *Big data and the future of ecology*, *Front. Ecol. Environ.* **11** (2013), no. 3, 156–162.
- [20] C. Hawes, P.P. Iannetta, and G.R. Squire, *Agroecological practices for whole-system sustainability*, *CABI Rev.* (2021). <https://doi.org/10.1079/PAVSNNR202116005>.
- [21] M. Hirota, M. Holmgren, E.H. van Nes, and M. Scheffer, *Global resilience of tropical forest and savanna to critical transitions*, *Science* **334** (2011), no. 6053, 232–235.
- [22] C.S. Holling, *Resilience and stability of ecological systems*, *Annu. Rev. Ecol. Syst.* **4** (1973), 1–23.
- [23] T.P. Hughes, M.J. Rodrigues, D.R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, and B. Willis, *Phase shifts, herbivory, and the resilience of coral reefs to climate change*, *Science* **317** (2007), no. 5839, 1737–1742.

- [24] J.F. Johnstone, C.D. Allen, J.F. Franklin, L.E. Frelich, B.J. Harvey, P.E. Higuera, and M.G. Turner, *Changing disturbance regimes, ecological memory, and forest resilience*, *Front. Ecol. Environ.* **14** (2016), no. 7, 369–378.
- [25] S. Kosten, G. Lacerot, E. Jeppesen, D.D.M. Marques, N. Mazzeo, and M. Scheffer, *Effects of submerged vegetation on water clarity across climates*, *Ecosystems* **12** (2009), no. 7, 1117–1129.
- [26] C. Kuehn, *A mathematical framework for critical transitions: Bifurcations, fast–slow systems, and stochastic dynamics*, *Phys. D: Nonlinear Phenom.* **240** (2011), no. 12, 1020–1035.
- [27] Y.A. Kuznetsov, *Elements of Applied Bifurcation Theory*, Applied Mathematical Sciences, vol. 112, Springer, New York, 1998.
- [28] S.J. Lade and T. Gross, *Early warning signals for critical transitions: a generalized modeling approach*, *PLoS Comput. Biol.* **8** (2012), no. 2, e1002360.
- [29] M. Mancilla García, T. Hertz, M. Schlüter, R. Preiser, and M. Woermann, *Adopting process-relational perspectives to tackle the challenges of social-ecological systems research*, *Ecol. Soc.* **25** (2020), no. 1, 29.
- [30] R.M. May, *Thresholds and breakpoints in ecosystems with a multiplicity of stable states*, *Nature* **269** (1977), no. 5628, 471–477.
- [31] R.M. May and G.F. Oster, *Bifurcations and dynamic complexity in simple ecological models*, *Am. Nat.* **110** (1976), no. 974, 573–599.
- [32] B.J. Palik, P.W. Clark, A.W. D’Amato, C. Swanston, and L. Nagel, *Operationalizing forest-assisted migration in the context of climate change adaptation: Examples from the eastern USA*, *Ecosphere* **13** (2022), no. 10, e4260.
- [33] M.A. Palmer and D.C. Richardson, *Provisioning services: A focus on fresh water*, The Princeton Guide to Ecology, 2009, pp. 625–633.
- [34] M. Rietkerk and J. van de Koppel, *Regular pattern formation in real ecosystems*, *Trends Ecol. Evol.* **23** (2008), no. 3, 169–175.
- [35] S. Rinaldi and M. Scheffer, *Geometric analysis of ecological models with slow and fast processes*, *Ecosystems* **3** (2000), 507–521.
- [36] M. Scheffer, S.H. Hosper, M.L. Meijer, B. Moss, and E. Jeppesen, *Alternative equilibria in shallow lakes*, *Trends Ecol. Evol.* **8** (1993), no. 8, 275–279.
- [37] M. Scheffer, S. Carpenter, J.A. Foley, C. Folke, and B. Walker, *Catastrophic shifts in ecosystems*, *Nature* **413** (2001), no. 6856, 591–596.
- [38] M. Scheffer and E.H. van Nes, *Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size*, *Hydrobiologia* **584** (2007), 455–466.
- [39] S.M. Sundstrom, D.G. Angeler, A. Garmestani, J.H. Garcia, and C.R. Allen, *Transdisciplinary application of cross-scale resilience*, *Sustainability* **6** (2014), no. 10, 6925–6948.
- [40] D. van Wijk, M. Chang, A.B. Janssen, S. Teurlincx, and W.M. Mooij, *Regime shifts in shallow lakes explained by critical turbidity*, *Water Res.* **242** (2023), 119950.
- [41] B.H. Walker and I. Noy-Meir, *Aspects of stability and resilience of savanna ecosystems*, *Annu. Rev. Ecol. Syst.* **13** (1982), 395–409.
- [42] B. Wang and Q. Qi, *Modeling the lake eutrophication stochastic ecosystem and the research of its stability*, *Math. Biosci.* **300** (2018), 1–13.
- [43] M. Zhu, G. Zhu, L. Nurminen, T. Wu, J. Deng, Y. Zhang, and B. Qin, *The influence of macrophytes on sediment resuspension and the effect of associated nutrients in a shallow and large lake (Lake Taihu, China)*, *PLOS ONE* **10** (2015), no. 6, e0127915.
- [44] D.G. Angeler, O. Viedma, and J. Moreno, *Statistical performance and information content of time lag analysis and redundancy analysis in time series modeling*, *Ecology* **90** (2009), no. 11, 3245–3257.
- [45] T. Eason, A.S. Garmestani, C.A. Stow, C. Rojo, M. Alvarez-Cobelas, and H. Cabezas, *Managing for resilience: an information theory-based approach to assessing ecosystems*, *J. Appl. Ecol.* **53** (2016), no. 3, 656–665.
- [46] T.L. Spanbauer, C.R. Allen, D.G. Angeler, T. Eason, S.C. Fritz, A.S. Garmestani, K.L. Nash, and J.R. Stone, *Prolonged instability prior to a regime shift*, *PLoS ONE* **9** (2014), no. 10, e108936.
- [47] C.P. Roberts, D. Twidwell, J.L. Burnett, V.M. Donovan, C.L. Wonkka, C.L. Bielski, and C.R. Allen, *Early warnings for state transitions*, *Rangeland Ecology & Management* **71** (2018), no. 6, 659–670.

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