Review

Not peer-reviewed version

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Posted Date: 11 March 2026

doi: 10.20944/preprints202603.0897.v1

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Review

Early Warning Signals in Ecological Time-Series

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Abstract

Ecosystems can undergo abrupt, often irreversible transitions between alternative states —phenomena termed critical transitions or regime shifts— with profound consequences for biodiversity, ecosystem services, and human well-being. Early warning signals (EWS) derived from time series analysis offer the prospect of anticipating such transitions before they occur, potentially enabling preventive management intervention. This review provides a comprehensive synthesis of EWS methods for ecological systems, encompassing theoretical foundations, statistical indicators, empirical applications, and emerging methodological frontiers. We examine the dynamical basis of EWS in critical slowing down theory, wherein systems approaching bifurcation points exhibit characteristic statistical signatures including rising autocorrelation, increasing variance, and spectral reddening. We present a systematic overview of proposed indicators (Table 1), discuss moving-window frameworks for their computation, and critically evaluate preprocessing requirements and sensitivity to analytical choices. Empirical applications across major ecosystem types—including lakes, coral reefs, grasslands, forests, and marine fisheries—reveal both successes and limitations, with EWS performance depending critically on data quality, transition mechanism, and system-specific dynamics (Table 2). We address recent advances including machine learning approaches, non-equilibrium thermodynamic indicators, multivariate extensions, and the important distinction between bifurcation-induced, noise-induced, and rate-induced tipping. We conclude with recommendations for specialists, emphasizing the integration of EWS within broader monitoring frameworks, systematic sensitivity analysis, and the interpretation of indicators as probabilistic assessments of changing resilience rather than deterministic predictions of imminent collapse.

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1. Introduction

The anticipation of abrupt, discontinuous changes in complex systems represents one of the most consequential challenges confronting contemporary science. Across disciplines ranging from climate science and ecology to epidemiology, neuroscience, and financial economics; dynamical systems exhibit the capacity to undergo rapid transitions between qualitatively distinct states, phenomena variously termed critical transitions, regime shifts, or tipping points [1,2]. In ecological contexts, such transitions carry profound implications: the collapse of productive fisheries, the eutrophication of clear-water lakes, the desertification of rangelands, and the die-off of coral reefs exemplify catastrophic reorganizations that may prove difficult or impossible to reverse on management-relevant timescales [3–5]. The development of methods capable of anticipating these transitions before they occur has accordingly emerged as a priority at the intersection of theoretical ecology, applied mathematics, and environmental policy.

 doi:10.20944/preprints202603.0897.v1

Since the dawn of civilization, humanity has devoted substantial intellectual resources to forecasting catastrophes of all kinds, encompassing natural disasters—floods, earthquakes, and eclipses—and, more recently, epidemics as well as economic and financial crises. Setting aside all attempts by diviners, oracles, chiromancers, and the like, the first scientific foundations of these endeavors are owed to the development of bifurcation theory by Henri Poincaré [6] as an essential component of dynamical systems theory, and subsequently to a branch thereof: catastrophe theory. This latter development is attributable to René Thom [7], who, in the 1960s and 1970s, formalized a mathematical apparatus that exhibited systems undergoing catastrophic changes in their response variables as a consequence of infinitesimal changes in a control parameter. Shortly thereafter, Christopher Zeeman [8] undertook the task to popularize catastrophe theory, while other researchers brought it to its complete formalization [9]. However, catastrophe theory fell into disuse, as it faced severe criticisms [10]. Later attempts to apply it to a wide variety of phenomena failed to find correspondence among the phenomena variables and the model variables and parameters

The theoretical foundation for early warning signals (EWS) of critical transitions rests primarily upon the phenomenon of critical slowing down (CSD), a generic property of dynamical systems approaching certain classes of bifurcations [11,12]. As a system approaches a fold (saddle-node) bifurcation, the most commonly invoked bifurcation type in ecological applications, the dominant eigenvalue of the linearized system approaches zero, causing the characteristic return time following perturbations to increase without bound [13]. This progressive loss of recovery capacity leaves characteristic statistical signatures in time series data: increasing temporal autocorrelation as the system retains memory of past states for longer periods, and increasing variance as perturbations accumulate faster than the system can dissipate them [13,14]. These signatures, along with related indicators including rising skewness, spectral reddening, and changes in higher-order moments, form the basis of the statistical EWS toolkit that has been developed and refined over the past two decades [15–17].

The intellectual lineage of EWS research extends to foundational work across multiple fields. In ecology, Holling's [18] distinction between engineering resilience (return time to equilibrium) and ecological resilience (magnitude of perturbation a system can absorb) established the conceptual framework, while Wissel [13] first articulated the connection between critical slowing down and approaching bifurcations. The explicit development of statistical early warning indicators for ecological regime shifts began in earnest with the seminal contributions of Scheffer et al. [1] and Carpenter and Brock [19], who demonstrated theoretically that rising variance could herald approaching transitions in lake ecosystems. Dakos et al. [15] subsequently showed that increasing autocorrelation preceded major climate transitions in paleoclimate records, catalyzing a substantial research effort that has sought to validate, refine, and extend these methods across diverse systems and scales [15,20] .

Despite the elegance of the underlying theory and the accumulation of supportive evidence from experimental, paleoclimate, and modeling studies, the translation of EWS from theoretical promise to operational forecasting tool remains incomplete. Several fundamental challenges constrain the practical utility of CSD-based indicators. First, the statistical power to detect early warning signals depends critically on data quality, time series length, sampling frequency, measurement error, and the magnitude of natural variability all influence detection probability [21,22] . Many ecological monitoring programs yield data of insufficient length or resolution for reliable EWS detection, and even high-quality records may produce ambiguous signals [23]. Second, not all ecological transitions arise through the gradual approach to bifurcation that generates classical CSD signatures. Noise-induced tipping, in which stochastic perturbations drive a system across a separatrix before the bifurcation is reached; rate-induced tipping, in which parameters change faster than the system can track; and transitions driven by acute external forcing may all occur without the characteristic slowing down that precedes bifurcation-induced transitions [24–26]. Third, even when detectable EWS precede a transition, they provide information only about the approach to instability, not about the precise

 doi:10.20944/preprints202603.0897.v1

timing, magnitude, or nature of the impending change [16,27]. The gap between detecting "something is changing" and predicting "what will happen and when" remains substantial.

Recent years have witnessed significant methodological advances that expand the EWS toolkit beyond its original foundations. Information-theoretic approaches, including Fisher information [28,29] and various entropy measures [30], offer alternative perspectives on system organization and stability. Multivariate extensions leverage covariance structure and eigenvalue dynamics to detect resilience loss in high-dimensional ecological communities [31,32]. Machine learning approaches, exemplified by deep neural networks trained on simulated tipping scenarios, can detect nonlinear precursors that escape low-order summary statistics [33,34]. Dynamic network biomarkers identify emergent modules of tightly correlated variables whose collective behavior diverges from the rest of the system prior to transition [35,36]. Non-equilibrium thermodynamic indicators derived from landscape-flux theory may provide earlier warnings than classical CSD-based metrics [37]. Spatial EWS complement temporal analysis, particularly in patterned ecosystems where changes in vegetation structure may presage collapse [38,39]. These developments collectively represent what may be termed a second generation of EWS methods—approaches that are multi-source, probabilistic, and explicitly designed to accommodate nonstationarity and observational limitations.

Several comprehensive reviews have addressed the EWS literature in recent years, and the present work builds upon, yet is distinctly positioned relative to, these prior syntheses. Scheffer et al. [14] and Dakos et al. [15] established the methodological foundations and empirical validation framework for CSD-based indicators; Clements & Ozgul [17] synthesized biological indicators of transitions; and, most recently, Dakos et al. [40] provided a cross-system audit of where, how, and which early warnings have been applied across climate, ecological, and human systems over the past two decades. These syntheses are broad by design, spanning Earth system tipping elements, socioeconomic systems, and biomedical applications.

The present review complements this body of work by pursuing three emphases that remain neglected in the existing literature. First, it restricts scope to ecological systems—lakes, coral reefs, grasslands, forests, and marine environments—enabling a mechanistically grounded, ecosystem-specific treatment of each transition type. Second, it integrates explicit methodological guidance on the analytical pipeline: windowing strategies, detrending and de-seasonalizing procedures, trend detection via Kendall's τ, and sensitivity analysis protocols (Section 3)—guidance essential for practitioners seeking to implement EWS in monitoring programs but underrepresented in narrative syntheses. Third, by anchoring each ecosystem section in the tipping-mechanism typology of Section 2.5, the review provides a principled framework for evaluating when CSD-based indicators are theoretically expected to perform—and when they are not—across mechanistically heterogeneous systems. Together, these emphases aim to provide ecological researchers and managers with a consolidated, method-focused reference grounded in ecosystem dynamics.

The present review provides a comprehensive synthesis of early warning signal methods for critical transitions in ecological systems, with particular emphasis on time series approaches. We pursue several objectives. First, we establish the theoretical foundations linking dynamical systems theory, bifurcation analysis, and the statistical signatures of critical slowing down (Section 2). Second, we present a systematic overview of proposed EWS indicators, including both classical CSD-based metrics and more recent developments, with attention to their mathematical formulations, data requirements, and known limitations (Section 3; Table 1). Third, we review empirical applications across major ecosystem types: lakes, coral reefs, grasslands, forests, and marine systems—evaluating the conditions under which EWS have succeeded, failed, or produced ambiguous results (Section 4; Table 2). Fourth, we discuss emerging methodological frontiers, including machine learning integration, multivariate extensions, and the critical challenge of prospective validation (Section 5). Finally, we offer recommendations for researchers and practitioners seeking to apply EWS in monitoring and management contexts, emphasizing the importance of methodological transparency, appropriate null model construction, and integration with mechanistic understanding.

Throughout, we maintain a perspective of informed pragmatism. Early warning signals represent neither infallible oracles nor theoretical curiosities without practical value, but rather tools whose utility depends critically on appropriate application, transparent reporting of uncertainties, and integration within broader frameworks of ecological understanding and adaptive management. As Anthropocene pressures accelerate and the prospect of crossing planetary boundaries becomes increasingly tangible [41], the capacity to anticipate critical transitions, even imperfectly, assumes growing urgency. Time-series-based early warning methods, continuously refined and thoughtfully applied, offer one of the most promising pathways toward this anticipatory capacity.

2. Theoretical Foundations of Early Warning Signals in Ecology

2.1. Critical Transitions, Resilience, and Tipping Points

A fundamental insight from dynamical systems theory is that many complex systems, including ecosystems, can exhibit multiple stable states under identical external conditions: a phenomenon termed multistability or alternative stable states [1,42]. Classic examples pervade ecology: shallow lakes may persist in either a clear-water state dominated by submerged macrophytes or a turbid state dominated by phytoplankton [43,44]; semi-arid rangelands can maintain either productive grassland or degraded bare-soil configurations [5,45]; coral reefs may exist as coral-dominated or macroalgae-dominated communities [4,46]; and forests can occupy either closed-canopy or open savanna states [47,48]. The existence of alternative stable states implies that ecosystem dynamics are governed not merely by external environmental forcing, but critically by internal feedback mechanisms that can maintain, or destabilize, particular configurations.

A *tipping point* (also termed critical threshold or bifurcation point) represents a critical value of an environmental driver or system parameter at which the current stable state loses its stability, precipitating an abrupt transition to an alternative state [2,14]. When such thresholds are crossed—whether through gradual environmental change (e.g., increasing nutrient loading, rising temperature) or acute perturbation (e.g., extreme drought, overharvesting)—the ecosystem may undergo rapid, discontinuous, and often unexpected reorganization [1,3]. These abrupt transitions, variously termed critical transitions, regime shifts, or catastrophic shifts in the ecological literature, are distinguished from smooth, continuous responses to environmental change by their nonlinear character and the disproportionate magnitude of ecosystem response relative to the incremental change in the driving variable [14,49].

From the perspective of dynamical systems theory, critical transitions in ecosystems are typically associated with local bifurcations, i. e. qualitative changes in the topological structure of a system's phase space that occur as parameters vary continuously [11,12]. The most commonly invoked bifurcation types in ecological contexts are the fold (saddle-node) bifurcation and the cusp catastrophe, both of which can generate the characteristic phenomenology of critical transitions: abrupt state changes, bimodality in state distributions, and hysteresis [1,50]. In a fold bifurcation, a stable equilibrium and an unstable equilibrium collide and annihilate as a control parameter crosses a critical threshold, leaving the system with no local attractor and forcing a rapid transition to a distant alternative state [11]. The cusp catastrophe extends this framework to two-parameter systems, yielding a bifurcation surface that predicts regions of bistability, critical thresholds, and the possibility of hysteresis loops [7,50].

Hysteresis, the dependence of the system's state not only on current conditions but also on its history, constitutes a particularly consequential feature of fold-type bifurcations in ecosystems [1,42]. When an ecosystem crosses a tipping point and transitions to an alternative state, returning to the original state typically requires reversing the driving parameter well beyond the original threshold value, often to substantially lower (or higher) levels [14]. This asymmetry between forward and backward transitions implies that regime shifts may be difficult or effectively impossible to reverse on management-relevant timescales, even if the original stressor is removed [3,51]. The potential for such irreversibility underscores the critical importance of anticipating approaching tipping points before they are crossed.

 doi:10.20944/preprints202603.0897.v1

2.2. Ecological Resilience: Definitions and Quantification

The concept of ecological resilience provides the theoretical foundation for understanding how ecosystems respond to perturbations and, critically, for anticipating when they may be approaching critical transitions. Holling's seminal distinction between "engineering resilience" (the rate of return to equilibrium following perturbation) and "ecological resilience" (the magnitude of perturbation a system can absorb before transitioning to an alternative state) established the conceptual framework that continues to guide resilience research [18,52]. In systems exhibiting alternative stable states, ecological resilience can be conceptualized geometrically as the size, depth, or width of the basin of attraction surrounding the current equilibrium in state space [1,53,54].

Mathematically, resilience near equilibrium is often quantified through the dominant eigenvalue of the system's Jacobian matrix evaluated at the equilibrium point [55]. For a system at a stable equilibrium, the dominant eigenvalue λ_1 is negative, and its magnitude $|\lambda_1|$ determines the rate at which small perturbations decay—larger magnitudes indicate faster recovery and hence greater local stability [15,56]. The reciprocal of $|\lambda_1|$ provides an estimate of the characteristic return time τ to equilibrium:

$$\tau = \frac{1}{|\lambda_1|} \tag{1}$$

As a system approaches a fold bifurcation, the dominant eigenvalue approaches zero from below, causing the characteristic return time to diverge—a phenomenon termed as *critical slowing down* [13,14,57]. This progressive lengthening of recovery times constitutes the fundamental dynamical basis for most early warning signals of approaching critical transitions.

Beyond local stability metrics, alternative approaches to quantifying resilience include measures based on basin geometry (basin width, depth, or volume), potential energy landscapes, stochastic stability (mean first-passage times between basins), and information-theoretic quantities [58–60]. Each approach captures different aspects of system robustness and may exhibit different sensitivities to approaching transitions. Integrating multiple resilience metrics may therefore provide more robust early warning than any single indicator [17,20].

2.3. Critical Slowing Down: The Dynamical Basis of Early Warning Signals

Critical slowing down (CSD) refers to the phenomenon whereby a dynamical system's rate of recovery from perturbations decreases as it approaches a bifurcation point [13,57]. This slowing of internal dynamics constitutes the theoretical cornerstone upon which most statistical early warning signals are constructed [14,61]. The phenomenon arises generically near fold bifurcations because the linearized dynamics around equilibrium become progressively weaker as the equilibrium approaches the bifurcation point—the "restoring force" that returns the system to equilibrium diminishes, yielding increasingly sluggish dynamics [11,62].

For ecological systems subject to continuous stochastic forcing (environmental variability, demographic stochasticity), critical slowing down produces characteristic statistical signatures in time-series data that can serve as early warning signals [19,61]. The three most widely studied indicators are increasing standard deviation, increasing temporal autocorrelation and increasing variance:

2.3.1. Increasing Autocorrelation

As the characteristic return time τ increases, the system retains memory of past states for longer periods, manifesting as elevated autocorrelation at short lags [61,63]. For a discrete-time autoregressive process of order one (AR(1)), the lag-1 autocorrelation coefficient ρ_1 is related to the continuous-time return rate by:

$$\rho_1 = e^{-\Delta t/\tau} \tag{2}$$

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where Δt is the sampling interval [60,64]. As $\tau \to \infty$ near the bifurcation, $\rho_1 \to 1$, indicating that consecutive observations become increasingly similar and the time series exhibits progressively stronger temporal persistence. Empirically, rising AR(1) coefficients in sliding windows across time series have been detected prior to transitions in paleoecological records, experimental ecosystems, and contemporary monitoring data [20,61,65].

2.3.2. Increasing Variance

Slower recovery dynamics also imply that perturbations accumulate before the system can return to equilibrium, leading to increased variability in the state variable [14,19]. For a linear stochastic system driven by white noise with variance σ_ϵ^2, the stationary variance of the state variable σ_x^2 scales inversely with the return rate:

$$\sigma_x^2 = \frac{\sigma_\epsilon^2}{2|\lambda_1|} \tag{3}$$

As $|\lambda_1| \to 0$ near the bifurcation, variance diverges, reflecting the system's diminished capacity to regulate deviations from equilibrium [15,19]. Rising variance in sliding windows has been validated as an early warning signal in numerous theoretical, experimental, and empirical studies [19,66,67].

2.3.3. Increasing Standard Deviation

As a direct consequence of increasing variance near a critical transition, the standard deviation of the state variable σ_x also rises, providing a complementary early-warning signal [14,19]. Since $\sigma_x = \sqrt{\sigma_x^2}$, substituting Equation 3 yields:

$$\sigma_x = \frac{\sigma_\epsilon}{\sqrt{2|\lambda_1|}} \tag{4}$$

where σ_ϵ is the standard deviation of the noise forcing and λ_1 is the dominant eigenvalue of the linearised system. As the bifurcation is approached and $|\lambda_1| \to 0$, σ_x diverges, reflecting the system's diminishing capacity to buffer stochastic perturbations [57,63]. In practice, a rising trend in the standard deviation computed over sliding windows constitutes an indicator of critical slowing down that is often evaluated alongside AR(1) and variance, as the three statistics are not independent but can reinforce one another in empirical time series [20,60].

2.3.4. Some Additional Statistical Indicators

Beyond autocorrelation and variance, several additional statistical indicators have been proposed based on the expected dynamical changes near bifurcations. These include (among many others):

- **Skewness:** As the system approaches a tipping point, the state distribution may become increasingly asymmetric due to the nonlinear shape of the stability landscape, yielding rising skewness prior to transition [68,69].
- **Flickering:** In bistable systems near critical thresholds, stochastic fluctuations may occasionally drive the system across the separatrix into the alternative basin of attraction before returning, producing sporadic excursions visible as "flickering" between states [14,70].
- **Spectral reddening:** Critical slowing down shifts the power spectrum of fluctuations toward lower frequencies (longer wavelengths), a phenomenon detectable as increasing spectral density at low frequencies [15,71].
- **Conditional heteroscedasticity:** Increased sensitivity to perturbations near tipping points may manifest as greater variability in variance itself, detectable through ARCH/GARCH-type analyses [72].
- **Spatial indicators:** In spatially extended systems, critical slowing down can manifest as increased spatial correlation, increased spatial variance, and changes in spatial pattern structure (e.g., patch size distributions, connectivity) [5,39,73].

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A comprehensive review of EWS metrics can be found in the Section 3.

2.4. Scope, Limitations, and Applicability of CSD-Based Early Warning Signals

EWS grounded in critical slowing down occupy a specific and well-defined niche within the broader landscape of transition forecasting: they are designed to detect the fingerprints of *bifurcation-driven* (B-tipping) transitions, in which a slowly changing parameter gradually erodes the stability of a fixed point until the system loses it entirely. This specificity is a strength—it connects EWS directly to rigorous dynamical systems theory—but it is also a constraint, because ecological transitions can be generated by at least three other mechanistically distinct tipping types, each with its own relationship to CSD-based indicators (see Section 2.5).

Despite compelling theoretical foundations and mounting empirical support, the application of CSD-based EWS is subject to four important limitations that constrain their reliability for prospective prediction of ecosystem transitions [16,26,60]:

1. **Detection power is data-limited.** The statistical power to detect early warning signals depends critically on time-series length, sampling frequency, measurement error, and the magnitude of natural variability [16,21]. Short or noisy time series may yield high false-positive or false-negative rates, limiting operational predictive capacity [15,22].
2. **EWS are transition-mechanism specific.** Not all ecological transitions are preceded by detectable critical slowing down. Transitions driven primarily by external forcing (e.g., abrupt climate shifts, acute disturbances) rather than gradual erosion of resilience may occur without the slow approach to instability that generates classical EWS [74,75]. Transitions arising from noise-induced, rate-induced, or shock-induced tipping (N-, R-, and S-tipping; see Section 2.5) do not produce the characteristic statistical precursors of fold bifurcations [24,25].
3. **EWS signal instability, not timing.** Even when EWS are detectable, they provide information only about the approach to instability, not about the precise timing, magnitude, or nature of the impending transition [14,27]. Translating generic indicators into specific, actionable predictions remains a substantial challenge.
4. **High-dimensional complexity obscures signals.** Regime shifts in real ecosystems often involve complex, high-dimensional dynamics, spatial heterogeneity, multiple interacting stressors, and cascading effects across trophic levels—complexities that may obscure, amplify, or fundamentally alter the expression of critical slowing down [76,77].

These limitations underscore the importance of interpreting EWS as probabilistic indicators of changing resilience rather than deterministic predictions of imminent collapse, and of integrating statistical indicators with mechanistic understanding, experimental validation, and adaptive management frameworks [17,20,60].

2.5. A Typology of Tipping Mechanisms and Their EWS Signatures

The utility and reliability of any given early warning indicator depends fundamentally on the mechanism by which the transition is generated. Following Ashwin et al. [78] and Lenton et al. [79], four mechanistically distinct classes of tipping can be identified for a general stochastic dynamical system $\dot{x} = f(x;\mu) + \sigma\xi(t)$, where μ is a slowly evolving control parameter, σ is noise amplitude, and $\xi(t)$ is a stochastic forcing term. Identifying which class applies to a given system is a prerequisite for responsible EWS deployment.

2.5.1. B-Tipping (Bifurcation-Induced)

The deterministic skeleton $\dot{x} = f(x;\mu)$ undergoes a bifurcation as μ approaches a critical value μ_c. The most common case in ecology is the *fold* (saddle-node) bifurcation, in which two fixed points—one stable, one unstable—collide and annihilate as $\mu \to \mu_c$. The dominant eigenvalue $\lambda_1(\mu)$ of the Jacobian $Df(x^*;\mu)$ at the stable fixed point x^* satisfies $\lambda_1 \to 0^-$ as $\mu \to \mu_c$ (Equation 1). This eigenvalue convergence is the mechanism of CSD: the characteristic return time $\tau_r = -1/\lambda_1 \to \infty$, so

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perturbations decay increasingly slowly, inflating variance and autocorrelation in the observed process. CSD is a *necessary* consequence of B-tipping in systems well-described by a fold bifurcation, making it in principle detectable from time-series data [11,12]. Other bifurcation types (Hopf, transcritical, pitchfork) can also generate CSD, though the precise indicator dynamics differ: a Hopf bifurcation produces a complex conjugate pair of eigenvalues whose real part approaches zero, generating increasing oscillatory variance rather than a monotonic AR(1) rise [80].

2.5.2. N-Tipping (Noise-Induced)

The deterministic skeleton retains its stable fixed point ($\lambda_1 0$ throughout), but sufficiently large stochastic fluctuations can kick the system over the basin boundary into an alternative attractor [70]. Formally, the probability of an N-tipping event in time T follows a Kramers-type escape rate $P_{\text{esc}} \approx 1 - \exp(-T/\tau_K)$, where $\tau_K \propto \exp(\Delta V/\sigma^2)$ and ΔV is the depth of the potential well. Because λ_1 remains negative and bounded away from zero, *CSD indicators do not rise systematically before N-tipping events*. Indeed, an increase in σ that raises escape probability will inflate variance in a way that superficially resembles a CSD signal, generating false positives [81]. Distinguishing N-tipping from B-tipping based on time-series data alone is a fundamental inferential challenge [70].

A particularly insidious practical complication arises when the noise amplitude σ itself increases over time—for instance, due to rising environmental variability under anthropogenic forcing. In such cases, the stationary variance of the observed process (Equation 3) will inflate even though the dominant eigenvalue λ_1 remains bounded away from zero and no bifurcation is being approached. The resulting trend in variance is statistically indistinguishable from a genuine CSD signal, generating false positives that could trigger unwarranted management interventions. This σ-driven variance inflation is not merely a theoretical concern: increasing climate variability in precipitation, temperature, and disturbance regimes means that many ecological monitoring programs are likely operating under non-stationary noise conditions. Researchers should therefore complement variance-based indicators with return-rate estimates (e.g., from pulse perturbation experiments or drift-diffusion fitting), which are more directly tied to λ_1 and less sensitive to changes in forcing amplitude [57,82]. When experimental perturbations are not feasible, comparing variance trends against independent proxies of external forcing variability can help distinguish genuine resilience loss from noise-driven inflation.

2.5.3. R-Tipping (Rate-Induced)

A stable state can be lost if the control parameter $\mu(t)$ changes faster than the system can track it, even if the system would remain stable under quasi-static conditions at every instantaneous value of μ [19,25]. Formally, R-tipping occurs when the rate $|\dot{\mu}|$ exceeds a critical threshold that depends on the geometry of the co-dimension-1 stable manifold in the (μ, x) phase plane. Because λ_1 never approaches zero—the system is always formally stable relative to its current μ value—*no CSD signal is generated before R-tipping*. Temporal autocorrelation and variance may in fact remain approximately constant or even decrease slightly as the system tracks a moving attractor under rapid forcing. R-tipping is particularly relevant for ecological systems subject to rapidly intensifying anthropogenic pressures [19].

2.5.4. S-Tipping (Shock-Induced)

An abrupt, large-amplitude perturbation—independent of the system's proximity to a bifurcation—displaces the state variable directly into an alternative basin of attraction [70]. Examples include catastrophic coral bleaching following a single anomalous thermal event, or forest loss following a megafire. By definition, no precursory dynamics precede the event, and *no CSD signal is expected or observed*. Post-shock behavior (recovery rate, trajectory in state space) may yield retrospective information about resilience but cannot provide prospective warning.

doi:10.20944/preprints202603.0897.v1

3. Time Series Early Warning Methods

Several time-series measures have been proposed as early warning indicators for ecological systems. Typically, the strategy involves calculating these metrics on ecological time-series data, such as population abundance, biomass, and vegetation cover over time, and monitoring their trends. A systematic increase in any of these indicators indicates that the system approaches a critical threshold [15]. In this section, we summarize the most studied indicators, their theoretical foundations, and the expected behavior as the system approaches critical transitions (see Table 1).

Table 1. Common statistical indicators as early warning signals (EWS) based on time series analysis. Each indicator relates to theoretical changes expected when approaching a tipping point, assuming primarily internal variability (white noise forcing) and proximity to a catastrophic bifurcation exhibiting critical slowing down (CSD).

EWS Indicator	Mathematical Definition	Property Measured	Expected Change Before Transition	Limitations / Caveats
Lag-1 Autocorrelation (AR(1))	$\rho_1 = \frac{\sum_{t=1}^{n-1}(x_t - \bar{x})(x_{t+1} - \bar{x})}{\sum_{t=1}^{n}(x_t - \bar{x})^2}$	Temporal memory at lag-1. Inversely related to the return rate: $\rho_1 \approx e^{\lambda \Delta t}$.	**Increases** toward 1 as the bifurcation approaches, reflecting critical slowing down [14,15].	Sensitive to detrending method; false positives under non-stationary forcing; assumes linear dynamics near equilibrium.
Variance	$\sigma^2 = \frac{1}{n-1}\sum_{t=1}^{n}(x_t - \bar{x})^2$	Amplitude of fluctuations (2nd central moment). Often reported as σ or $CV = \sigma/\lvert\bar{x}\rvert$.	**Increases**. Reduced stability amplifies perturbations; flickering also elevates variance before collapse [83,84].	Confounded by changes in forcing magnitude; sensitive to outliers and noise non-stationarity.
Skewness	$\gamma_1 = \frac{\frac{1}{n}\sum_{t=1}^{n}(x_t - \bar{x})^3}{\sigma^3}$	Asymmetry of the distribution (3rd standardized moment).	**Typically increases**. Distribution becomes skewed toward the alternative regime. Flickering generates asymmetric tails. Sign depends on transition direction [68,84].	Highly sensitive to outliers; sign interpretation requires knowledge of system geometry; needs large samples.
Kurtosis	$\gamma_2 = \frac{\frac{1}{n}\sum_{t=1}^{n}(x_t - \bar{x})^4}{\sigma^4} - 3$	Tail heaviness (4th standardized moment). Measures frequency of extreme values vs. Gaussian.	**Increases**. Extreme fluctuations become more frequent; flickering produces heavy tails from stochastic jumps between attractors [68,84].	Extremely sensitive to outliers; requires very large samples; 4th moment has high variance.

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EWS Indicator	Mathematical Definition	Property Measured	Expected Change Before Transition	Limitations / Caveats
Power Spectrum (Spectral Reddening)	$S(f) \propto f^{-\beta}$ Spectral exponent β from log-log slope.	Variance distribution across frequencies. Summarized by exponent β or low/high frequency power ratio.	**Shifts toward low frequencies**. Slow fluctuations dominate; spectrum reddens with $\beta \to -1$ (flicker noise) [61,71,85].	Requires long, evenly sampled series; confounded by trends; spectral leakage bias.
Entropy Indicators	Permutation: $H_p = -\sum_{i=1}^{m!} p_i \ln p_i$ Shannon: $H_S = -\sum_{i=1}^{k} p_i \ln p_i$	Complexity and regularity. Low entropy = predictable dynamics; high entropy = random behavior.	**Typically decreases**. More correlated dynamics reduce ordinal pattern diversity, indicating fewer accessible states and loss of resilience [30].	Depends on embedding parameters; may increase in some systems; interpretation is system-specific.
Detrended Fluctuation Analysis (DFA)	$F(s) \propto s^{\alpha}$ α: DFA exponent ($\alpha = 0.5$: white noise; $\alpha = 1$: critical).	Long-range correlations; scaling of fluctuations across time scales. Related to Hurst exponent.	**Increases** toward 1.0, indicating memory across multiple temporal scales typical of critical dynamics [15,86].	Requires very long series; sensitive to non-stationarities and detrending order; crossover effects complicate interpretation.
Return Rate	$\lambda = -\frac{\ln(\rho_1)}{\Delta t}$ Or $\lambda = 1/\tau_{\mathrm{rec}}$ from recovery time.	Rate of return to equilibrium after perturbation. Direct measure of dominant eigenvalue.	**Decreases** toward zero—the direct manifestation of critical slowing down [13,57].	Requires known sampling interval; assumes linear dynamics; experimental measurement needs controlled perturbations.

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EWS Indicator	Mathematical Definition	Property Measured	Expected Change Before Transition	Limitations / Caveats
Conditional Heteroskedasticity	GARCH(1,1): $\sigma_t^2 = \omega + \alpha_1 \epsilon_{t-1}^2 + \beta_1 \sigma_{t-1}^2$	Time-varying volatility; measures whether variance clusters in time (volatility persistence).	**Increases**. Variance becomes more dependent on recent fluctuations; $\alpha_1 + \beta_1 \to 1$ indicates persistent volatility [72].	Requires long series; model selection is non-trivial; assumes parametric volatility form.
Potential Analysis (Bimodality)	$BC = \frac{\gamma_1^2 + 1}{\gamma_2 + 3}$ $BC > 0.56$ suggests bimodality.	Shape of stability landscape; presence of alternative stable states.	**Bimodality increases**. Potential barrier between states decreases; distribution develops two modes [87].	BC is a rough heuristic; potential reconstruction assumes quasi-static equilibrium; sensitive to bandwidth.
Cross-Correlation	$\rho_{xy} = \frac{\mathrm{Cov}(x,y)}{\sigma_x \sigma_y}$	Linear association between system variables; synchronization and coupling strength.	**Increases**. Components become more coupled as all variables slow down together and respond coherently [15].	Requires multiple variables; sensitive to common drivers; does not distinguish direct from indirect coupling.
Dynamic Network Biomarkers (DNB)	$I_{\mathrm{DNB}} = \frac{\overline{PCC_d} \cdot \overline{SD_d}}{\overline{PCC_o}}$ where PCC_d denotes intra-module correlation, SD_d the standard deviation of the dominant module, and PCC_o the correlation with other modules.	Detects modules of highly correlated variables whose collective dynamics diverge from the remainder of the system prior to transition.	**Increases abruptly**. A subset of variables becomes highly correlated internally, exhibiting elevated variance and decoupling from the rest of the system [35,88,89] .	Requires high-dimensional data (omics, networks); identification of the dominant module may be ambiguous; assumes modular system structure.

Continued on next page

Table 1 – Continued from previous page

EWS Indicator	Mathematical Definition	Property Measured	Expected Change Before Transition	Limitations / Caveats
Criticality Index	$CI = \frac{\lambda_1}{\sum_{i=1}^{n} \lambda_i}$ where λ_1 is the largest eigenvalue of the covariance matrix and $\sum \lambda_i$ the total variance.	Fraction of variance explained by the first principal component; measures dominance of a single collective mode.	**Increases** toward 1. System dynamics become dominated by a single collective mode, indicating loss of effective dimensionality [90,91].	Sensitive to the number of variables; requires multivariate data; may be confounded by common external forcing.
Fisher Information	$FI = \int \frac{1}{p(x)} \left(\frac{\partial p(x)}{\partial \theta} \right)^2 dx$ Empirical estimation via changes in probability distribution.	Sensitivity of the system to changes in control parameters; quantifies the degree of order within the system.	**Decreases**. Reduced capacity of the system to distinguish between states; loss of order and increased uncertainty prior to collapse [28,29].	Empirical estimation requires discretization sensitive to bin selection; interpretation depends on the choice of control parameter.
Network Correlation	$\bar{\rho} = \frac{2}{n(n-1)} \sum_{i<j} \rho_{ij}$ Mean pairwise correlation among n system variables.	Global synchronization; average degree of coupling among system components.	**Increases**. All components respond more coherently to forcing due to generalized critical slowing down [15,92].	Does not distinguish direct from indirect correlation; sensitive to common drivers; requires multiple simultaneous time series.
Hysteresis	$H = \lvert x_{\text{forward}}(\theta) - x_{\text{backward}}(\theta) \rvert$ Difference between forward and backward trajectories in parameter space.	Irreversibility; path-dependence of system state. Indicates the presence of alternative stable states.	**Emerges or increases**. The system exhibits different transition thresholds depending on the direction of parameter change, confirming bistability [1,42].	Requires experimental manipulation of the control parameter in both directions; difficult to detect in observational systems; requisite time scales may be prohibitive.

3.1. Moving-Window Frameworks for EWS Detection

Early warning indicators derived from critical slowing down are most commonly computed within a moving-window framework, in which a statistical metric is repeatedly re-estimated on successive segments of the time series and its temporal trend is then quantified [14,15]. This approach transforms a univariate time series into a derived indicator time series, whose trajectory can reveal progressive changes in system dynamics as a critical transition is approached. The choice of window design fundamentally shapes both the sensitivity and reliability of early warning detection.

3.1.1. Rolling vs. Expanding Window Approaches

Two primary windowing strategies dominate the early warning literature, each with distinct statistical properties and ecological interpretations. In the rolling (sliding) windows approach, one fixes a window length w (typically expressed in time units or number of observations) and slides it forward, often with substantial overlap (e.g., advancing by a single time step), so that at each time index t the indicator is computed from the local segment $\{x_{t-w+1}, \ldots, x_t\}$. This design mimics prospective real-time monitoring because each estimate uses only the most recent w observations, discarding older data that may reflect different dynamical regimes [15]. The resulting time series of indicator values can then be tested for systematic trends (increases or decreases) that would be consistent with approaching a bifurcation.

Rolling windows offer high sensitivity to local changes in system dynamics, making them particularly effective at detecting late-stage acceleration in early warning metrics near a transition point [79]. However, this sensitivity comes at a cost: when w is small (e.g., $w < 50$ observations), variance in indicator estimates can be substantial, leading to noisy trajectories that obscure genuine trends and increase false-positive rates [15,22]. The choice of window size thus involves a fundamental trade-off between temporal resolution and estimation precision. Empirical guidelines suggest that w should be large enough to reliably estimate the desired statistic (e.g., at least 30-50 observations for variance or autocorrelation estimates) but small enough to track changes over the time scale of the hypothesized transition [15,20]. Some studies recommend setting w to approximately 50% of the total time series length as a starting point, though this heuristic should be validated against the suspected transition time scale [15].

In contrast, the expanding (growing) windows approach incrementally increases the window size over time, computing the indicator from a cumulative segment $\{x_1, \ldots, x_t\}$ or from a fixed start point after an initial burn-in period to establish baseline conditions [15]. By pooling progressively more data, expanding windows reduce estimator variance and can provide more stable trend estimates, particularly early in the monitoring period when rolling windows would be based on limited data. However, this cumulative design has a critical limitation: if the system undergoes gradual or multi-phase changes, early observations reflecting a stable regime can dilute or mask late-stage acceleration in early warning metrics [22,79]. Expanding windows may therefore be less sensitive to recent dynamical shifts and can produce misleading trends when regime changes are not monotonic.

Comparative studies on both simulated and empirical ecological time series suggest that rolling windows generally outperform expanding windows for detecting imminent transitions, particularly when the approach is gradual and window size is chosen appropriately [15,79]. Nevertheless, combining both approaches or using hybrid schemes (e.g., expanding windows with weighted observations favoring recent data) may provide complementary information for robust early warning assessment [22].

3.1.2. Overlap and Computational Considerations

The degree of overlap between successive windows is another important design choice. Maximum overlap (advancing by one time step) produces the smoothest indicator trajectories and finest temporal resolution but introduces strong serial autocorrelation in the derived time series, which violates independence assumptions in many trend tests and can inflate significance estimates [15,93]. Nonoverlapping windows eliminate this autocorrelation but drastically reduce the number of data points available for trend analysis, potentially missing short-lived signals. A practical compromise is to use moderate overlap (e.g., advancing by $w/4$ or $w/2$ observations), balancing temporal resolution against statistical assumptions, though the optimal choice remains context-dependent and should be evaluated via sensitivity analysis or simulation studies [20,22].

3.1.3. Trend Detection Methods

Once a time series of indicator values has been generated via moving windows, the next step is to assess whether it exhibits a significant temporal trend consistent with critical slowing down. The trend is most frequently quantified using Kendall's τ, a rank-based, non-parametric measure of monotonic association that is robust to non-Gaussianity, outliers, and nonlinear transformations of the data [15,93]. For a derived indicator series $\{y_1, \ldots, y_n\}$, Kendall's τ ranges from -1 (perfect negative trend) to $+1$ (perfect positive trend), with values near zero indicating no systematic temporal pattern. Statistical significance is typically assessed via permutation tests or asymptotic approximations, yielding a p-value that indicates whether the observed trend is stronger than expected under a null hypothesis of no temporal structure [15,93].

Kendall's τ is preferred over parametric alternatives such as Pearson correlation or linear regression slopes because ecological time series often violate normality assumptions, contain outliers from extreme events, and may exhibit nonlinear trends near bifurcations [93]. However, Kendall's τ is most powerful for detecting monotonic trends and may miss more complex patterns such as accelerating or decelerating changes [20]. Alternative approaches include fitting polynomial or exponential trend models, computing Spearman's rank correlation (which has similar robustness properties but slightly different power characteristics), or employing change-point detection methods to identify abrupt shifts in indicator levels [22,33]. Recent work has also explored machine learning classifiers that integrate multiple indicators and their trends to improve early warning performance [33].

3.1.4. Preprocessing: Detrending and De-Seasonalizing

Generic critical-slowing-down indicators such as lag-1 autocorrelation ρ_1 (AR(1) coefficient), variance σ^2, and related second-order statistics can be strongly biased by exogenous trends, seasonal cycles, or other forms of non-stationarity that are unrelated to proximity to a bifurcation [15]. For example, a time series with a deterministic upward trend will naturally exhibit elevated variance and autocorrelation even in the absence of critical slowing down, potentially generating spurious early warnings. Similarly, pronounced seasonality can inflate variance estimates and create periodic autocorrelation patterns that obscure genuine dynamical changes [22].

To mitigate these biases, window-based estimation is typically preceded by detrending or de-seasonalizing procedures. The most common approach applies a smoothing filter (e.g., Gaussian kernel smoothing, LOESS regression, or moving averages) to the original time series, then analyzes the residuals after subtracting the smooth trend [15]. The bandwidth of the smoothing filter should be chosen to remove low-frequency trends and seasonality while preserving the higher-frequency fluctuations that reflect critical slowing down; bandwidths that are too narrow leave spurious trends intact, while overly broad smoothing can remove genuine signals [15,22]. First-differencing (computing $\Delta x_t = x_t - x_{t-1}$) is an alternative detrending method that eliminates linear trends but can also remove or distort autocorrelation patterns, making it less suitable for early warning analysis [94].

For strongly seasonal data, preprocessing may involve fitting and removing seasonal components via classical decomposition, seasonal-trend decomposition using LOESS (STL), or more sophisticated state-space models that separate trend, seasonal, and residual components [20]. After preprocessing, early warning indicators are computed on the residual time series within each moving window, ideally isolating changes in system resilience from confounding temporal patterns. However, preprocessing choices introduce additional degrees of freedom that can influence early warning results, and sensitivity analyses should examine how conclusions depend on bandwidth selection, smoothing method, and differencing order [15,22].

3.2. Interpretation and Limitations of Window-Based EWS

A significantly positive trend in lag-1 autocorrelation, variance, or related metrics computed via moving windows is commonly interpreted as consistent with reduced stability and slower recovery rates as a system approaches a critical threshold [14,79]. The theoretical foundation rests on the prediction that near a bifurcation point, the dominant eigenvalue of the linearized system approaches zero, causing perturbations to decay more slowly and fluctuations to amplify [14,62]. However, several critical limitations must be acknowledged when interpreting window-based early warnings in ecological applications.

3.2.1. Specificity and Alternative Mechanisms

Increases in autocorrelation and variance are not unique to approaching bifurcations and can arise from multiple alternative mechanisms. Stochastic transitions driven by rare large perturbations (e.g., extreme weather events, invasive species arrival) can produce abrupt regime shifts without gradual loss of resilience, yet retrospective analysis may still reveal apparent early warning trends if the data are conditioned on the transition occurring [16,95]. Similarly, directional environmental change that drives the system toward a threshold can generate trends in indicators even if the transition itself is discontinuous or driven by external forcing rather than endogenous destabilization [60]. Changes in environmental variability (e.g., increasing climate extremes) can directly inflate variance estimates independently of system stability [22].

3.2.2. Conditional Sampling and Retrospective Bias

Many early warning studies analyze historical time series selected specifically because they ended in a known transition, introducing conditional sampling bias that can spuriously elevate indicator trends [16,95]. If only systems that transitioned are analyzed, one may observe rising indicators simply because fluctuations happened to be large near the transition (potentially contributing to it), rather than because of systematic slowing down. Prospective monitoring of systems that do not transition is essential to assess false-positive rates and calibrate expectations [20,22].

3.2.3. Window Size Sensitivity and Reporting Standards

The sensitivity of early warning detection depends critically on window size, overlap, preprocessing choices, and trend-testing methods, yet many studies report results for a single parameter combination without exploring robustness [22]. Best practices include conducting sensitivity analyses across a range of window sizes, reporting both positive and negative results, comparing multiple indicators, and validating findings against surrogate or null models that preserve key statistical properties of the data while removing hypothesized early warning signals (e.g., phase-randomized surrogates that maintain spectral properties but scramble temporal structure) [15,22,95]. Transparent reporting of methodological choices, null hypothesis specifications, and significance thresholds is essential for reproducibility and to avoid selective reporting of positive results [20].

3.2.4. Practical Recommendations

Given these limitations, window-based early warnings should be interpreted cautiously and embedded within broader monitoring frameworks that integrate mechanistic understanding, multiple lines of evidence, and explicit consideration of alternative hypotheses [22,60]. Combining multiple complementary indicators (e.g., autocorrelation, variance, skewness, spatial metrics), assessing their consistency, and contextualizing trends within ecological theory can strengthen inference [14,20,33]. Where possible, experimental manipulations or comparative studies across replicate systems can provide stronger causal evidence than relying solely on observational time series [22]. Ultimately, early warning signals are most useful when viewed as hypothesis-generating tools that warrant further investigation rather than as definitive predictors of imminent transitions.

In addition to generic CSD-based indicators, other statistical approaches exist. For example, the detection of increasing bimodality of frequency distribution of a variable – used as a signal – may indicate instability (i. e. the emergence of two basins of attraction)[96–98]. Another common signals is the visible flickering in the series: sudden oscillations between the typical values od two distinct states [70,84]. In such cases, metrics as the frequency of extreme events or persistence in alternating states can act as a warning. Furthermore, in spatial systems (e.g. vegetation cover), spatial indicators, such as increasing spatial variance, spatial auto-correlation or changes in patch patterns, have been proposed as spatial analogs of temporal EWS [15]. Although we focus here on time-series, it is worth noting that combining temporal and spatial signals can strengthen evidence of proximity to a transition.

3.3. Complementary Models and Approaches to Detect EWS

3.3.1. Methods Based on System Dynamics (Mechanistic Models)

One way to anticipate transitions is to employ explicit dynamic models of the system and analyze its stability in real time. Unlike purely empirical approaches (metrics described above), these methods attempt to infer dynamic parameters or fit simplified models to the data, thereby obtaining indicators more directly related to bifurcation theory. Some examples:

- **ARIMA/AR(ρ)** models with variable parameters: Fit an auto-regressive model to the series where the coefficients can change over time. For example, an AR(1) model $X_{t+1} = a_t X_t + b_t + \varepsilon_t$ allows the coefficient a_t to be estimated in each window, with an approach to 1 indicating a critical slowdown (very long return time) [15]. Extensions include threshold AR models, where different regimes are applied at different ranges of the variable.
- **Potential analysis (dynamic potential)**: This is a non-parametric approach that reconstructs the effective potential function of the system from the data distribution or a drift-diffusion estimate. The idea is to identify changes in the stability topography: for example, the appearance of a shallow or secondary minimum in the potential may signal a decrease in resilience. Tools such as potential analysis [87] detect multiple potential wells (indicating incipient alternative states) over time.
- **Nonparametric drift–diffusion estimation.** This approach consists of inferring the drift term $f(x)$ and the diffusion term $g(x)$ directly from the time series, assuming that the underlying dynamics follow a stochastic differential equation of the form

$$\frac{dx}{dt} = f(x) + g(x)\,\xi(t),$$

  where $\xi(t)$ represents a stochastic noise term . As the system approaches a critical transition, the derivative of the drift $f'(x)$—which is related to the dominant eigenvalue of the system—tends toward zero. Simultaneously, changes in the diffusion component may indicate emerging instabilities. Dakos *et al* [15] implemented a *drift–diffusion–jump* (DDJ) framework to distinguish between signals driven by critical slowing down and those caused by flickering in simulated ecological data [15]. Although powerful, these methods require relatively long time series data and rely on assumptions regarding the functional form of the system's dynamics.
- **Controlled experimental disturbances**: In systems that allow it (e.g., an experimental lake or a greenhouse pasture), the recovery rate can be measured directly by applying minor disturbances and observing the response. A decrease in the observed return rate is the most direct signal of proximity to a tipping point. For example, Veraart et al. [82] measured, in an aquatic microcosm, that population recovery after minor disturbances became increasingly slower as the transition was approached, demonstrating a loss of resilience.

In general, model-based approaches allow the integration of known theoretical information (equations, mechanisms) and offer more robust hypothesis testing (e.g., testing whether the data agree with a bifurcation model). They also facilitate significance testing through simulation (bootstrap of fitted models). However, they depend on the quality of the model fit and can fail if the real system does not conform to the model assumptions.

 doi:10.20944/preprints202603.0897.v1

3.3.2. Machine Learning Approaches

With the rise of data science, machine learning techniques have been introduced to detect subtle early warning patterns. One advantage is that machine learning (ML) algorithms can combine multiple indicators or extract non-obvious features from time series, potentially improving prediction accuracy. Some recent examples:

- **Classifiers trained on simulated data**: Large sets of synthetic time series with and without critical transitions can be generated (using simulated ecological models under various conditions), and a classifier (e.g., a neural network) can be trained to distinguish "near-tipping" time series from stable time series. EWSNet, developed by Bury et al. [23], is a convolutional neural network trained in this way, which learns to identify combinations of signals in univariate time series and to predict the probability of an impending transition. In tests, EWSNet has detected transitions in complex simulated data and some real data better than traditional individual indicators.
- **Models that integrate multiple indicators ("ensemble learning")**: Brett & Rohani [99] proposed combining various statistical indicators (e.g., RA, variance) as explanatory variables in a machine learning model (e.g., random forests or logistic regression) to predict a regime change. The premise is that different signals provide complementary information, and a trained algorithm can weigh them optimally. These models address the problem of deciding *a priori* which indicator to use; instead, they learn from training data which indicators or thresholds are most reliable.

4. Applications

In this section, we review notable examples where these methodologies have been applied to real ecosystems, including lakes, coral reefs, grasslands,and marine systems. These successful applications illustrate the opportunities and the challenges of searching EWS in empirical data.

4.1. Grasslands, Savannas, and Arid Ecosystems

Grasslands, savannas, and arid ecosystems represent paradigmatic systems for studying critical transitions, as they frequently exhibit abrupt shifts between productive vegetated states and degraded configurations under climatic stress or anthropogenic pressure [1,45]. These ecosystems collectively cover approximately 40% of the Earth's terrestrial surface and support the livelihoods of over two billion people, rendering their stability a matter of profound socioeconomic and ecological importance [100]. Desertification—the transition from semi-arid grassland to bare soil with sparse vegetation—constitutes a particularly consequential form of regime shift, with cascading implications for ecosystem services, food security, carbon sequestration, and regional climate regulation [5,45]. Theoretical vegetation models incorporating soil–water feedbacks, facilitation among plants, and grazing dynamics predict that these systems can undergo fold-type bifurcations, wherein gradual environmental deterioration leads to sudden, catastrophic vegetation collapse once a critical threshold is crossed [45,101]. The existence of alternative stable states implies that recovery following collapse may require substantially more favorable conditions than those that triggered the initial degradation, a phenomenon known as hysteresis [1,98]. These theoretical foundations suggest that early warning signals based on critical slowing down should, in principle, precede catastrophic desertification events, motivating substantial research effort toward their detection and validation.

4.1.1. Theoretical Foundations and Feedback Mechanisms

The theoretical basis for critical transitions in dryland ecosystems derives from scale-dependent feedback mechanisms that can generate and maintain alternative stable states [45,102]. Vegetation patches in water-limited environments modify their local environment in ways that enhance their own persistence: root systems improve soil structure and infiltration capacity, canopy shading reduces evaporative losses, organic matter accumulation increases water retention, and established plants facilitate seedling recruitment through nurse effects [100,102]. These positive feedbacks operate at local scales, creating favorable microsites within vegetation patches.

 doi:10.20944/preprints202603.0897.v1

Simultaneously, negative feedbacks operate at larger scales through resource competition. Vegetation patches deplete soil water from surrounding areas, inhibiting plant establishment in the inter-patch matrix and concentrating resources beneath existing vegetation [45]. The interplay between local facilitation and long-range competition generates the characteristic spatial patterning observed in many dryland ecosystems—banded vegetation ('tiger bush'), spotted patterns, and labyrinthine configurations—that reflect self-organized responses to water limitation [103,104].

Mathematical models incorporating these feedbacks predict that as environmental stress increases (reduced precipitation, elevated grazing pressure, or soil degradation), the system approaches a fold bifurcation. Near this threshold, the dominant eigenvalue governing vegetation dynamics approaches zero, generating critical slowing down that should manifest as rising autocorrelation and variance in vegetation cover time series [14,15]. Additionally, the spatial structure of vegetation is predicted to undergo systematic changes—increased spatial variance, altered patch-size distributions, and modified connectivity patterns—that may serve as complementary spatial early warning signals [38].

4.1.2. Spatial Early Warning Signals

A distinctive feature of EWS research in dryland ecosystems is the prominence of spatial indicators, reflecting the strong spatial organization imposed by scale-dependent feedbacks [38,39] . Kéfi et al. [5] provided seminal evidence that spatial vegetation patterns can serve as indicators of ecosystem degradation state. Analyzing vegetation cover data across a degradation gradient in Mediterranean arid ecosystems, they demonstrated that patch-size distributions deviated systematically from power-law scaling in degraded sites, suggesting that spatial pattern analysis could diagnose proximity to critical thresholds.

Subsequent theoretical work formalized the connection between critical slowing down and spatial pattern changes. As systems approach fold bifurcations, critical slowing down manifests not only in temporal dynamics but also in spatial structure: spatial variance increases as vegetation becomes patchier, spatial autocorrelation rises as patches become more clustered, and characteristic length scales shift as the dominant spatial modes change [39]. Kéfi et al. [38] provided a comprehensive methodological framework for computing spatial EWS, demonstrating their application to both simulated and empirical vegetation data.

The theoretical prediction that spatial patterns undergo systematic changes before desertification has received support from multiple empirical studies. In the Sahel region of Africa, analyses of vegetation pattern dynamics have revealed that degrading sites exhibit reduced patch connectivity, altered patch-size distributions, and increased spatial variance compared to stable sites. Importantly, these spatial changes may be detectable even when long temporal records are unavailable, offering practical advantages for monitoring programs in data-limited regions.

However, the relationship between spatial pattern and degradation state is not always straightforward. Multiple spatial pattern types (gaps, spots, bands) can be stable under identical environmental conditions, complicating the use of pattern type alone as a degradation indicator. Furthermore, some spatial pattern changes may reflect adaptive reorganization that enhances resilience rather than approaching collapse, and distinguishing these cases remains an active area of research.

4.1.3. Remote Sensing Evidence and Temporal Indicators

The advent of long-term satellite observation has enabled investigation of early warning signals across extensive arid and semi-arid regions, providing unprecedented opportunities to test theoretical predictions at landscape to continental scales [105]. Vegetation indices derived from satellite imagery—particularly the Normalized Difference Vegetation Index (NDVI) and related spectral measures—provide consistent, spatially comprehensive time series of vegetation productivity that can be analyzed for EWS.

Verbesselt et al. [106] conducted a landmark analysis of remotely sensed resilience across tropical and subtropical vegetation, including extensive savanna and dryland regions. Examining satellite vegetation index time series spanning 1982–2012, they quantified resilience through recovery rates

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following perturbations (primarily drought events). Their analysis revealed that in areas vulnerable to transition, the rate of vegetation recovery following rainfall deficits diminished over time—a direct manifestation of critical slowing down detectable in remotely sensed data. Crucially, areas showing declining recovery rates were more likely to subsequently experience permanent vegetation loss, providing prospective evidence that satellite-derived resilience indicators can anticipate degradation.

More recent analyses have extended these findings to African dryland ecosystems. Veldhuis et al. [107] demonstrated spatial slowing down in satellite vegetation patterns before desertification transitions in East African rangelands, with year-to-year changes in vegetation cover decreasing in areas approaching degradation thresholds—consistent with critical slowing down predictions. Similarly, Forzieri et al. [105] documented declining forest resilience globally using satellite observations, including pronounced resilience loss in semi-arid woodland systems approaching apparent tipping points.

Temporal EWS in dryland time series have also been investigated using traditional statistical indicators. Analyses of simulated vegetation dynamics under increasing stress have consistently shown rising autocorrelation and variance in vegetation cover preceding collapse [15,38]. At the landscape scale, remote sensing has facilitated the investigation of early warning signs in arid regions. Verbesselt *et al.* [106] examined satellite vegetation index time series in tropical forests and savannas, revealing that in areas vulnerable to transition (from savanna to desert or from forest to savanna), the rate of vegetation recovery following rainfall events diminished after years of recurrent drought. Similarly, more recent studies conducted in dry African ecosystems have identified spatial slowing, characterized by decreased year-to-year changes in cover, as well as reddening in the inter-annual fluctuations of primary productivity prior to sudden degradation events. Notably, Veldhuis *et al.* [108] provided evidence of spatial slowing down in satellite vegetation patterns before desertification transitions, thereby supporting theoretical predictions.

In temperate grasslands characterized by seasonal climates, it is challenging to discern ecological signals because of pronounced seasonal and successional variability. However, Clements and Ozgul [109] demonstrated that even biological traits, such as the average body size of herbivores, can shift prior to population collapse within grassland ecosystems. Specifically, a decrease in size variance, indicating a more homogeneous group of individuals, preceded significant reductions in some populations. This phenomenon is interpreted as a loss of demographic resilience.

In grasslands and arid ecosystems, EWS are supported by modeling and remote sensing results; however, direct field time-series evidence is less prevalent than in lakes. Spatial indicators often provide more pronounced insights than temporal indicators, as exemplified by the formation of patchy vegetation patterns, which are considered an early warning sign of potential desertification. The integration of satellite data with on-site monitoring remains a promising approach for improving the early detection of degradation in these ecosystems. However, empirical validation using real vegetation time series has yielded mixed results. Génin et al. [110] developed the `spatialwarnings` R package to facilitate systematic computation of spatial EWS in vegetation data; while spatial indicators showed expected patterns in some datasets, others exhibited weak or inconsistent signals, highlighting the influence of data quality, environmental heterogeneity, and non-stationarity on EWS detection.

The heterogeneity of results across remote sensing studies reflects a broader challenge common to all temporal EWS analysis in drylands: non-stationarity, environmental gradients, and confounding land-use change can generate trends in AR(1) and variance unrelated to genuine loss of ecological resilience. These results reinforce the need to combine temporal indicators with spatial diagnostics and careful detrending of trends and seasonality [15,38] .

4.1.4. Savanna–Forest Transitions

Beyond desertification, dryland ecosystems encompass savanna–forest boundaries that can exhibit critical transitions in both directions [47]. The distribution of tropical vegetation between closed-canopy forest and open savanna states appears bimodal at intermediate precipitation levels, suggesting alternative stable states maintained by fire–vegetation feedbacks [47]. Forests suppress fire through

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shading (reducing grass fuel loads) and maintaining high canopy moisture, while savannas promote fire through continuous grass cover and seasonal drying. This feedback can maintain sharp boundaries between adjacent forest and savanna, with transitions between states occurring abruptly when thresholds are crossed.

Early warning signals for savanna–forest transitions have been investigated primarily through fire regime dynamics and vegetation structure indicators. Increasing fire frequency beyond historical ranges can progressively erode forest resilience by depleting seed banks, eliminating fire-sensitive species, and reducing canopy cover, potentially pushing the system toward savanna dominance. Time-series analyses of burned area dynamics in transitional forest–savanna ecotones have revealed that elevated interannual variability in fire extent often precedes vegetation state changes, consistent with theoretical expectations of increased variance near bifurcations [14].

Furthermore, shifts in the coupling between fire behavior and environmental drivers have been identified as potential indicators of declining forest resilience. In stable forest systems, internal feedback mechanisms—including high canopy moisture content, reduced understory fuel loads, and humid microclimatic conditions—buffer fire regimes against climatic fluctuations, dampening correlations between burned area and drought severity. As forests lose resilience and approach transition thresholds, this buffering capacity diminishes, resulting in increasingly tight coupling between fire extent and exogenous drivers. Empirical observations from Amazonian and African forest–savanna boundaries have documented this phenomenon, with increasing fire–climate correlations serving as harbingers of subsequent savanna encroachment.

4.1.5. Trait-Based and Demographic Indicators

Beyond aggregate vegetation indices, biological traits and demographic structure may shift prior to population collapse within grassland and savanna ecosystems, offering complementary indicators of declining resilience. Clements and Ozgul [109] demonstrated that trait-based indicators—including body size distributions of herbivore populations—can provide early warning of impending collapse. In their analysis, a decrease in body size variance (indicating demographic homogenization) preceded population collapse in grassland herbivores. This pattern reflects loss of demographic resilience: populations with diverse age and size structure can buffer environmental variability through differential responses among individuals, while homogenized populations lack this buffering capacity.

Similar principles may apply to plant communities, where diversity in functional traits (drought tolerance, rooting depth, phenology) confers resilience to environmental fluctuations. Declining functional diversity in grassland plant communities under chronic stress could potentially serve as an early warning signal, though this hypothesis remains less thoroughly tested than trait-based indicators in animal populations.

Demographic early warning signals have also been proposed for long-lived species in savanna ecosystems. Changes in tree population age structure—particularly reduced recruitment and loss of juvenile cohorts—may indicate declining population viability before changes in adult abundance become apparent. For slow-growing woody species, demographic indicators may provide earlier warning than aggregate biomass or cover measures, as changes in recruitment can precede detectable changes in standing biomass by years to decades.

4.1.6. Case Studies and Empirical Evidence

Several well-documented case studies illustrate both the promise and challenges of EWS detection in dryland ecosystems.

Sahel Greening and Degradation. The Sahel region has experienced dramatic vegetation changes over recent decades, including both degradation (1970s–1980s droughts) and partial recovery ('re-greening' since the 1990s). Analyses of satellite vegetation time series have revealed spatial heterogeneity in recovery patterns, with some areas showing sustained improvement while others remain degraded or continue declining. Preliminary analyses suggest that pre-drought spatial vegetation

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patterns differed between resilient and degraded sites, though confounding factors (soil type, land use history, topography) complicate interpretation.

Australian Rangelands. Long-term monitoring data from Australian arid rangelands have revealed episodic vegetation state changes associated with drought and grazing pressure. Analyses of these transitions have documented hysteresis—conditions required for recovery exceed those that triggered collapse—supporting alternative stable state dynamics. Systematic analysis of whether EWS preceded these documented transitions remains limited by data availability and the challenge of distinguishing gradual degradation from abrupt regime shifts.

Mediterranean Shrublands. Mediterranean ecosystems have provided important case studies for spatial EWS research. Degradation gradients across environmental or land-use intensity gradients offer space-for-time substitution approaches, wherein sites at different degradation stages are compared to infer temporal dynamics. These analyses have revealed systematic changes in spatial vegetation patterns along degradation gradients, supporting the potential utility of spatial EWS, though true prospective tests of predictive capacity remain rare.

Taken together, these case studies illustrate both the promise and difficulty of operationalising EWS in dryland systems. The Sahel, Australian rangelands, and Mediterranean drylands all provide evidence for hysteresis and spatial-pattern shifts across degradation gradients; however, truly prospective, out-of-sample evaluations of predictive EWS performance remain comparatively rare [107]. This gap between retrospective detection and genuine prospective prediction is one of the most pressing priorities for future research in this ecosystem type. Combining temporal indicators (AR(1), variance, recovery rates) with spatial diagnostics, and carefully treating non-stationarity and confounding environmental drivers, represents the most robust analytical pathway currently available [15,38].

4.2. Lakes and Freshwater Aquatic Systems

Shallow lakes are classic systems for studying critical transitions. The prototypical example is the change of a lake from clear water (dominated by macrophytes) to turbid water (dominated by phytoplankton) due to nutrient eutrophication. Scheffer et al. theorized that this system undergoes a fold bifurcation with hysteresis, and subsequent studies sought early warning systems (EWS) before the loss of clarity [43]. Wang *et al.* analyzed paleolimnological (sediment) data from a lake [70]. They found evidence of flickering years before the definitive transition to a turbid state: that is, fluctuations oscillating between clear and turbid conditions, reflected in greater variance and skewness in nutrient indicators. This flickering served as a robust early warning of the imminent collapse. On the other hand, controlled ecosystem-scale experiments have also been enlightening: Carpenter *et al.* manipulated a Wisconsin lake by gradually increasing piscivory pressure, leading to a regime shift. Using water quality and planktonic population data, they observed increasing variance and autocorrelation as the critical point was approached, which was consistent with the expected critical slowdown [65]. These findings highlight the utility of statistical indicators, such as variance and autocorrelation, in detecting critical slowing down prior to regime shifts. Moreover, they emphasized the importance of integrating empirical data and experimental manipulation to understand the resilience of ecosystems. These approaches provide valuable insights for developing effective management strategies to prevent undesirable ecosystem changes.

However, efforts to detect EWS in natural lakes have not always been consistently successful. A recent comprehensive study analyzed time-series data of phytoplankton and zooplankton from nine lakes worldwide, using various metrics (both univariate and multivariate) to identify early warnings preceding documented historical changes. The findings revealed that traditional signals (AR(1), variance) were only effective in predicting some change events, while in other instances, they either triggered false alarms or failed to detect any changes at all [23]. The study concluded that EWS has limited applicability to empirical lake data owing to complicating factors such as external noise, seasonal influences, and low temporal resolution, which obscure clear trend detection. In certain lakes, the observed transitions were non-critical (e.g., abrupt changes caused by point disturbances

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rather than bifurcations) and, as anticipated, did not show prior critical slowing [111]. Despite these challenges, the study also noted that combining methods (such as multivariate indicators and machine learning tools like EWSNet [112]) modestly enhanced predictive capacity, although no single method achieved high predictive certainty on its own.

In lotic ecosystems, such as rivers and streams, clear examples of EWS are less common because of the open nature of these environments. However, certain controlled trophic cascades in experimental streams have been reported to produce EWS. For instance, variations in dissolved oxygen levels and turbidity have been investigated as potential early indicators of hypoxia in eutrophic estuaries. Shallow lakes have effectively functioned as "natural laboratories" for validating EWS, demonstrating notable success in predicting water quality declines. Nevertheless, these studies underscore the practical challenges associated with the use of real-world ecosystem data. Factors such as the length of data records (many lakes have limited historical data) and external climatic influences, such as harsh winters and droughts, can obscure general trends.

4.3. Coral Reefs

Coral reefs can experience sudden shifts from being dominated by live coral to being overrun by macroalgae or other unwanted organisms such as debris or cyanobacteria. These regime changes are often triggered by disturbances such as bleaching events caused by thermal stress, overfishing of herbivores, or pollution, and pose a significant concern for tropical marine ecology [113–115].

Theoretical models suggest that coral reefs exhibit non-linear dynamics, including feedback loops. For example, healthy corals create conditions that favor their growth, such as high structural complexity and successful recruitment, whereas algal dominance hinders coral recovery. This dynamic can lead to alternative stable states—either a thriving coral reef or a degraded algae-dominated reef.

4.3.1. Empirical Evidence and Detection Challenges

However, one major challenge is the scarcity of long-term reef monitoring, which can be influenced by confounding factors such as hurricanes and ocean variability. Despite these challenges, some local time-series studies have reported subtle signs of such instability. For instance, prior to a decline in coral cover, an increase in the interannual variability of short algae (less than 5 cm) within the community was observed in the present study. This increase was interpreted as a sign of increasing instability. Similarly, some studies have noted increased temporal autocorrelation in coral cover measurements taken every few months just before mass mortality events, although these findings were not statistically significant [116].

Dakos et al. [60] proposed that generic indicators of CSD could be used as a basis to rank coral reefs by resilience, in the sense that reefs approaching a tipping point should already exhibit statistically detectable trends in variance and/or autocorrelation in relevant time series. In this framing, reefs “closer to the threshold” are expected to show increasingly persistent deviations from their baseline state, reflecting a weakening ability to recover from perturbations, whereas more resilient reefs should display comparatively stable fluctuation statistics. However, despite the conceptual appeal of this approach, dedicated empirical tests remain relatively scarce, and operationalizing CSD for reefs has proven difficult [117].

In the Great Barrier Reef (Australia), retrospective analyses of coral cover percentage data suggest that following repeated bleaching events, coral recovery slowed (a slowdown in cover dynamics) and spatial variance between sites increased before an algae-dominated regime was established in certain reef sections. This aligns with the expectation that spatially variable resilience can provide a signal (some patches collapse sooner than others, increasing variance between sites) [67,117].

4.3.2. Disturbance-Mediated Transitions and Hybrid EWS Approaches

While evidence from reefs continues to develop, there is cautious optimism that combining multiple indicators, such as the integrity of herbivorous fish food webs and fluctuations between coral and algae, could help predict a critical tipping point. For instance, a reduction in herbivore functional diversity, including the loss of keystone species, may serve as an early "biomarker" signaling that the ecosystem is at risk of losing control over algae growth. Integrative ecological web approaches, along with early warning systems (EWS), are currently being developed [115,118].

A central obstacle is that many reefs do not experience a clean, gradual drift toward collapse driven by a slowly changing control parameter—the canonical setting where CSD theory is most straightforward. Instead, reefs often respond to acute, pulse-like disturbances such as abrupt bleaching triggered by short-lived marine heatwaves, storm damage, or disease outbreaks. From a time-series perspective, these events behave less like the smooth "ramping" of a parameter and more like impulsive shocks superimposed on a noisy background. Such shocks can dominate the observed dynamics, masking or even breaking the assumptions under which classic CSD indicators are expected to rise monotonically. In other words, a reef may flip states because it is hit hard, not necessarily because it has been drifting slowly toward instability in a way that produces textbook early warning patterns.

However, the absence of a slow parameter drift does not imply the absence of informative precursors. Even under disturbance-driven dynamics, reefs can exhibit signatures of reduced stability that are consistent with the system moving closer to the boundary between alternative states. One such signature is *flickering*, in which the system intermittently visits an alternative regime before settling permanently. In the Caribbean, for instance, some sites have exhibited episodes of transient algal dominance in the years preceding a long-lasting shift to algae following major coral mortality. These brief algal blooms subsequently receded as corals partially recovered, indicating that the coral-dominated state was becoming increasingly fragile, and small perturbations were sufficient to push the system into an algal-like configuration, even if it could still "snap back" for a time. Interpreted through the lens of dynamical systems, flickering suggests that the reef's trajectory was increasingly influenced by the competing basin of attraction, with the system hovering near a threshold where either coral or algae could temporarily prevail over the other [70,84].

These considerations suggest a useful refinement to the original CSD-based classification idea: reef resilience assessment may benefit from combining classical CSD metrics (variance, autocorrelation) with transition-focused precursors, such as flickering and other indicators of bistability. This hybrid perspective acknowledges that reef degradation is often disturbance-mediated while still leveraging the broader principle that declining resilience leaves statistical fingerprints in ecological time series, even if those fingerprints are not always expressed as smooth, monotonic increases in variance and AR(1).

4.4. Marine Fisheries and Pelagic Ecosystems

Marine fisheries represent one of the most consequential domains for early warning research: stock collapses carry severe ecological and socioeconomic consequences yet have historically been detected only after irreversible demographic damage has occurred [119]. Pelagic ecosystems—the open-ocean communities of plankton, forage fish, and their predators—present a related but distinct challenge, in which abrupt community reorganizations are often driven by multi-decennial oceanographic forcing rather than by the gradual parameter drift that generates classical critical slowing down. Together, these systems test the boundaries of the EWS framework more severely than any other ecosystem type reviewed here, because the tipping mechanisms involved span the full typology of Section 2.5 : fold bifurcations in overexploited stocks, rate-induced and shock-induced transitions in plankton regimes, and multispecies reorganizations that combine elements of both.

4.4.1. Theoretical Basis for Tipping in Marine Systems

Fish stock dynamics can exhibit fold bifurcations when density-dependent recruitment processes interact with harvesting mortality. The canonical mechanism involves a dispensatory (Allee-effect) recruitment function: at low stock sizes, per-capita recruitment declines because mate-encounter rates fall, schooling anti-predator defenses erode, or cooperative spawning behavior is disrupted [1,69]. When a slowly increasing harvest rate erodes stock size toward the Allee threshold, the dominant eigenvalue of the linearized stock-recruitment system approaches zero from below, generating CSD

 doi:10.20944/preprints202603.0897.v1

in exactly the form described in Section 2.3. The associated EWS predictions are unambiguous: rising variance and autocorrelation in biomass or recruitment indices, increasing skewness toward low-biomass states, and slowing recovery rates following perturbations should all precede collapse.

A second, distinct mechanism operates through regime shifts in the broader marine ecosystem. In upwelling systems, semi-enclosed seas, and continental shelf ecosystems, multi-decennial oceanographic oscillations can abruptly reorganize productivity regimes, shifting the carrying capacity and recruitment environment for entire fish communities simultaneously [120,121]. These transitions often resemble rate-induced or shock-induced tipping—driven by rapid atmospheric forcing or sudden upwelling changes—rather than the gradual bifurcation approach that generates CSD. These indicators provide no reliable warning of R- or S-tipping events; this distinction has immediate practical implications for EWS design in fisheries and pelagic systems.

4.4.2. Empirical Evidence and Case Studies

Atlantic cod and North Atlantic groundfish. *(Retrospective.)* The collapse of Northwest Atlantic cod stocks in the early 1990s has been subjected to multiple retrospective EWS analyses. Examination of stock assessment time series spanning 1960–1992 documented rising interannual variance in recruitment indices and increasing lag-1 autocorrelation in spawning stock biomass in the decade preceding collapse, consistent with CSD predictions. However, Boettiger and Hastings [16] demonstrated that these apparent warning trends are statistically indistinguishable from noise expected under a null hypothesis of no approaching bifurcation when appropriate surrogate tests are applied. Because the analysis was conducted retrospectively on a series selected precisely because it ended in a known collapse, conditional sampling bias cannot be excluded as a partial explanation for the apparent signals. The cod case therefore illustrates both the theoretical plausibility of fisheries EWS and the inferential limitations that constrain their operational value when tested retrospectively without pre-specified null models.

Baltic Sea food-web reorganization. *(Retrospective; quasi-prospective.)* The Baltic Sea has provided one of the most thoroughly analyzed multispecies case studies for EWS in marine systems. Möllmann et al. [121] documented a major reorganization of the Baltic food web in the late 1980s, involving simultaneous regime shifts in cod, sprat, herring, and zooplankton communities driven by the interaction of fishing pressure and eutrophication. Subsequently, Lindegren et al. [122] applied CSD-based EWS to multivariate Baltic monitoring data and demonstrated that rising variance and autocorrelation in aggregate community indicators—particularly zooplankton biomass and fish recruitment composites—anticipated the reorganization by three to five years. Crucially, this analysis was structured as a quasi-prospective evaluation: indicators were computed on data available up to a pre-specified decision point, with the transition used as the validation event rather than the analysis target. This design provides stronger evidence for predictive validity than a purely retrospective analysis, though it falls short of a true prospective test because the transition outcome was known when the study was designed. The Baltic case is presently the strongest available evidence for operational EWS performance in a marine multispecies context.

North Pacific productivity regime shifts. *(Retrospective.)* Litzow and Mueter [120] assessed ecological regime shifts in the North Pacific, showing that abrupt, synchronized shifts in fish community structure were preceded by increasing temporal variance and spectral reddening in productivity indices. Hsieh et al. [123] showed that fishing pressure itself elevates interannual variability in exploited stocks, independently of proximity to a bifurcation. This finding creates a systematic false-positive risk specific to fisheries: the primary management action (fishing) directly inflates the primary EWS indicator (variance), a confounding effect with no direct analogue in lake, forest, or grassland applications. All analyses in this case were retrospective, relying on archived stock assessment records; no prospective or experimental evaluation has been conducted.

Global stock assessment survey. *(Retrospective.)* Vert-pre et al. [124] conducted the most comprehensive retrospective EWS analysis available, examining 230 fish stock time series from the RAM Legacy database for evidence of productivity regime shifts. Variance-based indicators correctly

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anticipated approximately half of documented collapses, but false-positive rates were substantial (approximately 40% of flagged stocks did not subsequently collapse). Anderson et al. [125] reached similar conclusions: EWS in fisheries have meaningful but limited predictive power, particularly for stocks subject to externally driven regime shifts rather than endogenous bifurcation dynamics. The retrospective design of both studies, and the fact that the stock assessment records used were themselves model-derived rather than directly observed, introduce inferential layers that limit conclusions about genuine predictive validity.

Peruvian anchovy and the Humboldt Current system. (Retrospective.) The collapse of the Peruvian anchoveta (*Engraulis ringens*) stock in the early 1970s, associated with the 1972–1973 El Niño event, represents one of the most dramatic fisheries collapses on record and provides an instructive contrast to the cod case. Unlike the Northwest Atlantic groundfish system, where chronic overharvesting gradually eroded stock biomass toward an Allee threshold consistent with B-tipping, the anchoveta collapse was primarily driven by the rapid shoaling of the thermocline and catastrophic reduction in upwelling productivity triggered by the El Niño anomaly, a dynamics consistent with S- or R-tipping rather than a gradual bifurcation approach [119]. Retrospective analyses of recruitment indices and sea surface temperature anomalies have not identified systematic pre-collapse trends in variance or autocorrelation that would constitute classical CSD signatures, consistent with theoretical expectations for externally forced transitions. The anchoveta case therefore illustrates the practical consequence of the B/R/S-tipping distinction (Section 2.5): deploying CSD-based EWS in upwelling systems subject to strong ENSO forcing carries a high risk of both false negatives (genuine collapses missed because no CSD signal precedes them) and false positives (elevated variance during La Niña recovery phases misinterpreted as resilience loss). This system-specific confounding underscores the need to incorporate oceanographic forcing indices as covariates when interpreting EWS indicators in eastern boundary current fisheries.

Pelagic plankton regime shifts. *(Retrospective.)* Hsieh et al. [123] documented that spectral reddening of climate-biological variability and rising variance in plankton indices preceded regime shifts in several pelagic systems, while Conversi et al. [126] provided a holistic synthesis demonstrating that synchronization of previously anti-phase population oscillations anticipated species-level collapses in open-ocean communities. Both analyses relied on long-term plankton monitoring archives (Continuous Plankton Recorder and equivalent programs), making them among the longest available marine time series. However, the dominant tipping mechanism in pelagic systems involves rapid atmospheric forcing and inter-basin oceanographic teleconnections that are more consistent with R-tipping than B-tipping—and, variance and autocorrelation are expected to perform poorly under R-tipping dynamics. The empirical detection of spectral reddening in these systems may therefore reflect changing external forcing rather than genuine CSD, a distinction that retrospective analyses cannot easily resolve.

4.4.3. Implications for Predictive Validity

Three lessons emerge from the marine and pelagic evidence that apply broadly to the EWS field. First, the distinction between endogenous B-tipping and exogenous R- or S-tipping is not merely theoretical: it determines whether CSD-based indicators have any predictive validity at all, and pre-classifying the likely tipping mechanism before deploying EWS is a prerequisite for responsible application [125]. Second, fishing pressure confounds variance-based indicators in a system-specific way that demands explicit null-model construction; any fisheries EWS analysis should compare observed trends against surrogates generated under a null hypothesis of a stable but heavily fished stock [17]. Third, no marine EWS study has yet achieved a true prospective test under operational conditions—one in which thresholds were pre-specified, decisions were made, and predictive accuracy was evaluated against subsequent outcomes. This gap is the central unresolved challenge in marine EWS, as it is across all ecosystem types reviewed here.

4.5. Pelagic Ocean Systems and Plankton Regime Shifts

Pelagic ocean ecosystems—the open-water environments dominated by plankton communities—have exhibited pronounced regime shifts that reorganize community structure, trophic relationships, and biogeochemical cycling across basin scales [126]. These shifts, documented in systems including the North Sea, North Pacific, and Baltic Sea, provide opportunities to examine EWS in large-scale marine ecosystems where transitions affect entire biological communities simultaneously.

4.5.1. Characteristics of Pelagic Regime Shifts

Unlike the localized transitions observed in lakes or coral reefs, pelagic regime shifts often involve coordinated changes across multiple trophic levels and large spatial scales. The 1980s regime shift in the North Sea, for example, involved simultaneous changes in phytoplankton, zooplankton, and fish communities that fundamentally altered ecosystem structure and persisted for decades [126]. Similarly, the Pacific Decadal Oscillation has been associated with basin-scale reorganizations of plankton communities and fisheries productivity.

These large-scale transitions pose both challenges and opportunities for EWS detection. On one hand, the spatial extent of changes provides multiple independent time series that can be analyzed for convergent signals. On the other hand, the involvement of climate forcing complicates attribution—distinguishing EWS of endogenous instability from responses to exogenous climate variability remains difficult.

4.5.2. Spectral and Statistical Indicators

Studies of pelagic regime shifts have employed spectral analysis alongside traditional statistical indicators. Spectral reddening—the shift of variance toward lower frequencies—has been detected in plankton time series preceding some documented transitions, consistent with critical slowing down causing slow fluctuations to dominate system dynamics [61,123].

Hsieh et al. [123] examined long-term plankton monitoring data from the California Current system, finding increased variance in zooplankton populations during decades preceding apparent regime shifts. However, they noted that fishing pressure on planktivorous fish could itself destabilize plankton communities, illustrating the challenge of separating natural dynamics from anthropogenic forcing.

4.5.3. Synchronization as an Early Warning Signal

A distinctive feature of approaching pelagic regime shifts may be increasing synchronization among previously independent population fluctuations. Prior to some documented transitions, populations that fluctuated out of phase began oscillating in concert, suggesting that the system was becoming dominated by a single collective mode [126]. This synchronization is consistent with theoretical expectations: as the dominant eigenvalue approaches zero near a bifurcation, all system components become increasingly responsive to the same slow mode of variability.

Conversi et al. [126] proposed that increasing correlation among ecosystem components could serve as an early warning signal for marine regime shifts, complementing single-variable indicators. Their "holistic" view of regime shifts emphasizes the importance of monitoring community-level properties rather than focusing exclusively on individual populations.

4.5.4. Implications for Ocean Monitoring

The detection of EWS in pelagic systems has implications for large-scale ocean monitoring programs. Long-term plankton surveys, such as the Continuous Plankton Recorder survey in the North Atlantic, provide the extended time series necessary for EWS analysis. Integration of EWS indicators into ocean observing systems could potentially provide advance warning of impending regime shifts with consequences for fisheries, carbon cycling, and marine ecosystem services.

However, the large spatial scales, complex forcing mechanisms, and limited mechanistic understanding of pelagic transitions mean that EWS in these systems should be interpreted cautiously. The

doi:10.20944/preprints202603.0897.v1

challenge of prospective prediction—demonstrating that EWS provide useful advance warning rather than merely retrospective confirmation—remains largely unmet for basin-scale ocean regime shifts.

4.6. Forests

Forests can exhibit critical transitions on large scales, such as the savannization of the Amazon (collapse from humid forest to dry savanna) under climate change or the mass mortality of boreal forests, converting them into steppes after droughts and pest outbreaks. Such changes often involve hysteresis (e.g., once a forest is lost, local aridity increases, preventing regeneration). Identifying ecosystem services (ESS) in forests is complicated by the longevity of trees and the slowness of dynamics, but there are notable studies. Verbesselt et al. (2016) used satellite Normalized Difference Vegetation Index (NDVI) time-series (1988–2012) to detect signs of resilience loss in tropical forests. They found that in areas of the Amazon that subsequently experienced permanent biomass decline, the NDVI showed increasing autocorrelation and variance approximately 2–3 years before the transition [106]. Following severe drought events, areas that did not recover showed "scars" in the series: greater persistence at low values (high AR) and anomalous fluctuations. This is one of the first examples of an EWS applied to forests on a continental scale.

The detection of EWS in forest ecosystems increasingly relies on time-series analyses of demographic structures, particularly age and size distributions, to anticipate critical transitions and regime shifts. Theoretical frameworks predict that as forest populations approach tipping points, characteristic changes in demographic structure will emerge, including the simplification of age-class distributions and the loss of recruitment cohorts [14**?**]. For instance, the persistent absence of seedlings and saplings following disturbance events may indicate regeneration failure, signaling that the system is approaching a critical threshold beyond which recovery to the original state is unlikely [127]. Empirical applications of these principles have been documented in diverse forest biomes. In boreal forests, prolonged recruitment gaps following fire disturbances have been interpreted as potential indicators of imminent state changes, where forests may transition to alternative stable states, such as shrublands or grasslands, rather than regenerating to their pre-disturbance condition [128]. Similarly, in Mediterranean ecosystems, time-series analyses of stand structures have revealed declining regeneration rates that precede drought-induced forest dieback events [129].

Beyond demographic indicators, complementary EWS metrics derived from time-series data have strengthened the predictive capacity for detecting approaching transitions in forest systems. Critical slowing down, the phenomenon whereby systems recover more slowly from perturbations as they approach bifurcation points, has been detected through increasing temporal autocorrelation and variance in tree growth chronologies and forest productivity indices [38,61]. Studies in temperate forests have demonstrated that rising autocorrelation in radial growth time-series can precede widespread mortality events by several years to decades, providing a potential operational window for management interventions [130]. Furthermore, analyses of remotely sensed vegetation indices across tropical and temperate forests have revealed spatial and temporal signatures consistent with approaching tipping points, including increased flickering between states and the propagation of recovery delays across landscapes [105,106]. Collectively, these findings underscore the utility of integrating demographic monitoring with time-series-based EWS approaches to enhance our capacity for forecasting critical transitions in forest ecosystems under accelerating global change pressures.

4.6.1. Fire Regime Dynamics as Early Warning Signals of Forest-to-Savanna Transitions

Fire regime dynamics are critical line of evidence for detecting early warning signals of impending state shifts in fire-prone forest ecosystems. In regions where forests and savannas represent alternative stable states, fire acts as a key driver in maintaining the boundary between these vegetation types, with the frequency, intensity, and spatial extent of burning determining which state predominates across the landscape [47,48]. Theoretical and empirical work has demonstrated that as forests approach critical thresholds, characteristic changes in fire regime behavior emerge that may serve as operational EWS. Specifically, increasing the fire frequency beyond historical ranges can progressively erode forest resilience by depleting seed banks, eliminating fire-sensitive species, and reducing canopy cover, ultimately pushing the system past a tipping point toward savanna dominance [131,132]. Time-series analyses of burned area dynamics in transitional forest-savanna ecotones have revealed that elevated interannual variability in fire extent often precedes vegetation state changes, which is consistent with the theoretical expectation of increased variance as systems approach bifurcation points [14,15]

Furthermore, shifts in the coupling between fire behavior and environmental drivers have been identified as potential indicators of declining forest resilience. In stable forest systems, internal feedback mechanisms, including high canopy moisture content, reduced understory fuel loads, and humid microclimatic conditions, typically buffer fire regimes against climatic fluctuations, dampening the correlation between burned area and fuel availability or drought severity [133,134] . However, as forests lose resilience and approach transition thresholds, this buffering capacity diminishes, resulting in an increasingly tight coupling between fire extent and exogenous drivers, such as accumulated fuel loads and seasonal moisture deficits [57]. Empirical observations from Amazonian and African forest-savanna boundaries have documented this phenomenon, with increasing correlations between burned areas and fuel connectivity serving as harbingers of subsequent savanna encroachment [48,133]. These findings highlight the diagnostic value of monitoring not only fire regime metrics *per se*, but also changes in the sensitivity of fire behavior to environmental forcing, to anticipate critical transitions in fire-mediated ecosystems under ongoing climate change and land-use intensification.

4.6.2. Remote Sensing Applications and Climate-Vegetation Feedbacks: EWS for Large-Scale Forest Collapse

Global vegetation models incorporating climate-forest feedbacks have provided compelling theoretical evidence that large-scale forest systems, particularly the Amazon basin, may exhibit detectable EWS years to decades before catastrophic collapse. These models integrate critical biophysical processes, including evapotranspiration regulation, precipitation recycling, and moisture-dependent fire dynamics, which generate positive feedback loops capable of driving abrupt transitions between forested and degraded states [2,135,136]. Model projections suggest that as deforestation and climate change progressively weaken these self-reinforcing mechanisms, characteristic EWS will emerge across spatial and temporal domains. Specifically, increasing spatial autocorrelation in seasonal drought patterns has been predicted as a precursor to basin-wide dieback, reflecting the loss of moisture recycling capacity and homogenization of water stress across previously heterogeneous landscapes [136,137]. Additionally, "flickering" dynamics, whereby satellite imagery reveals transient mosaics of intact forest patches alternating with degraded clearings, have been identified as potential signatures of bistability, indicating that the system oscillates between alternative attractors as it approaches a tipping point [14,15]. Recent analyses of long-term satellite records have detected such patterns in portions of the southeastern Amazon, where increasing dry-season severity and fire frequency have driven localized state changes consistent with the model predictions [138,139].

The operationalization of EWS detection through remote sensing platforms represents a particularly promising frontier for anticipating forest regime shifts at regional to continental scales. Despite the inherent inertia of forest ecosystems, which are characterized by long tree lifespans, slow demographic turnover, and lagged responses to environmental forcing, satellite-derived vegetation indices have demonstrated the capacity to capture subtle signatures of declining resilience before overt structural degradation becomes apparent [105,106]. Critical slowing down, manifested as the delayed recovery of vegetation greenness (e.g., NDVI, EVI) or above-ground biomass proxies following drought episodes or disturbance events, has emerged as one of the most robust and practically measurable indicators of approaching tipping points [61]. Time-series analyses of recovery rates across tropical, temperate, and boreal forests have revealed that declining resilience, quantified as lengthening return times to baseline conditions, often precedes widespread mortality and canopy loss by several years, providing a potential early detection window for management and policy intervention [105,106]. These advances underscore the transformative potential of integrating mechanistic vegetation models with satellite-based EWS monitoring frameworks to anticipate ecological tipping points under accelerating climate

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change, offering critical lead times for adaptation strategies aimed at averting regional-scale forest collapse and its associated impacts on the carbon cycle, biodiversity, and socioeconomic consequences.

Table 2. Summary of EWS reported across different ecosystem types and critical transitions.

Ecosystem (Transition)	Observed Early Warning Signals	Key References
Shallow Lake *(Eutrophication)*	Increasing lag-1 autocorrelation (AR(1)) and standard deviation in water quality parameters; flickering dynamics (oscillations between clear and turbid states) observed years before definitive regime shift; bimodal distribution of nutrient indicators preceding final collapse.	Wang et al. [70]
Experimental Lake *(Trophic Cascade)*	Progressive increases in autocorrelation and variance of phytoplankton density; decreased return rate from small perturbations measured *in situ* (critical slowing down); increased skewness in water transparency distribution prior to transition.	Carpenter et al. [65]
Semiarid Grassland *(Desertification)*	Increased spatial variance in NDVI; vegetation patch patterns becoming more connected (indicating spatial synchronization); rising temporal autocorrelation in productivity indices; reduced resilience manifested as slower recovery following drought events.	Kéfi et al. [5]; Veldhuis et al. [107]
African Savanna *(Herbivore Collapse)*	Increased interannual variance in population counts; shifts in age structure (reduced proportion of juveniles); elevated correlation among population dynamics of different herbivore species (synchronized decline across taxa).	Dakos et al. [140]
Coral Reef *(Algal Dominance)*	Elevated temporal persistence (AR(1)) in coral cover monitoring data; increasing interannual variance in macroalgal density; sporadic episodes of transient algal dominance (flickering) before permanent regime establishment; decline in herbivorous fish diversity.	Mumby et al. [46]; Dakos et al. [60]
Tropical Forest *(Amazon Savannization)*	Rising autocorrelation and variance in NDVI and evapotranspiration time-series; delayed recovery of vegetation greenness following droughts (critical slowing down detected via satellite); increased synchronization of fire activity across large areas; spatial flickering dynamics.	Verbesselt et al. [106]; Boulton et al. [139]
Boreal Forest *(Post-Fire Collapse)*	Repeated observations of reduced seedling density following fire events (declining resilience); increased variance among plots in regeneration rates; rising temporal autocorrelation in annual vegetation greenness indices prior to mass mortality events.	Carpenter and Brock [83]; Scheffer et al. [141]
Marine Fishery *(Stock Collapse)*	Increased interannual variability in recruitment; elevated autocorrelation in catch and biomass time-series; reduced resilience indices; demographic signals including decreasing proportion of young individuals years before collapse.	Biggs et al. [69]; Litzow et al. [120]
Pelagic Ocean *(Plankton Regime Shift)*	Spectral reddening of climate–biological variability (increased low-frequency power); rising variance in plankton indices in preceding decades; synchronization of previously anti-phase population oscillations before species collapse.	Hsieh et al. [123]; Conversi et al. [126]

[1] AR(1) = lag-1 autocorrelation coefficient; NDVI = Normalized Difference Vegetation Index. Flickering refers to transient oscillations between alternative states prior to permanent transition.

5. Perspectives on the Use of EWS in Ecology

The capacity to anticipate critical transitions in ecological systems before they occur represents one of the most consequential challenges in contemporary ecology. This section examines how early warning signals (EWS) derived primarily from time-series analysis are transforming our approach to ecosystem management, the methodological advances that are expanding the EWS toolkit, and the research frontiers that will shape the next generation of resilience diagnostics.

5.1. From Reactive Management to Anticipatory Risk Assessment

Conventional ecological monitoring has long operated in a reactive mode, detecting ecosystem deterioration only after critical thresholds have been crossed—a point at which recovery is often slow, expensive, or altogether infeasible. The EWS paradigm fundamentally reorients this approach by seeking to identify *loss of resilience* prior to regime shifts through the detection of statistical signatures of destabilization in time series data [14,60]. The theoretical foundation for this approach rests on the

 doi:10.20944/preprints202603.0897.v1

phenomenon of critical slowing down (CSD): as a system approaches a bifurcation point, its rate of recovery from small perturbations decreases, leaving characteristic imprints in temporal dynamics that can be quantified through indicators such as rising lag-1 autocorrelation and increasing variance [83].

The translation of this theoretical insight into operational practice is most naturally achieved through *resilience dashboards* embedded within routine monitoring programs. In such frameworks, CSD-based indicators are computed in rolling windows over time series and reported alongside uncertainty estimates derived from null model comparisons [60]. Crucially, these dashboards should not be conceived as binary alarm systems but rather as decision-support layers that integrate multiple lines of evidence: indicator trends extracted from temporal data, mechanistic understanding of pressures and feedbacks, and context-specific assessments of vulnerability. This parallels the evolution of meteorological forecasting, which translates complex model outputs into probabilistic risk communications rather than deterministic yes/no predictions.

For time-series-based EWS to inform governance effectively, however, careful attention must be paid to *operational thresholds*. Policy and management decisions typically require actionable categories (e.g., traffic-light risk levels), whereas temporal EWS outputs are inherently continuous and subject to noise. A productive direction therefore involves defining thresholds explicitly tied to management objectives—such as acceptable false alarm probabilities or expected loss functions—rather than relying solely on generic statistical significance. This naturally leads to the probabilistic and Bayesian decision frameworks discussed in subsequent sections, where uncertainty is treated as a first-class output and interventions are evaluated under explicit risk models [60].

5.2. Methodological Advances in Time-Series-Based EWS

The early EWS toolkit, centered on variance and autocorrelation computed from univariate time series, has undergone substantial expansion. This methodological evolution reflects two key recognitions: that no single indicator is universally reliable, and that many real-world transitions deviate from the classical CSD-at-a-bifurcation narrative. The advances described below constitute what may be termed a *second generation* of EWS methods—approaches that are multi-source, probabilistic, and explicitly designed to accommodate nonstationarity and observational limitations.

5.2.1. Multivariate Extensions for Complex Ecological Systems

Ecosystems are inherently multicomponent systems characterized by correlated species dynamics, functional redundancy, and cross-scale coupling. Resilience loss may therefore be distributed across communities and trophic levels in ways that are not strongly expressed in any single state variable. This observation has motivated the development of *multivariate* EWS approaches that synthesize information across multiple time series. A central insight is that destabilization may manifest as changes in covariance structure, shifts in dominant eigenvalues of community matrices, or alterations in coherence patterns that prove more sensitive than univariate summaries in high-dimensional settings [31,32]. These multivariate indicators leverage the full temporal structure of monitoring data while capturing emergent properties of community dynamics.

5.2.2. Probabilistic and Bayesian Decision Frameworks

A fundamental shift in EWS methodology involves moving from deterministic alarms to probabilistic risk statements. Rather than asking whether "an early warning signal is present," the operationally relevant question becomes: what is the probability of approaching a critical transition given the observed time series, and how does this probability change under alternative models and assumptions? This probabilistic perspective aligns more naturally with decision-making under uncertainty and provides a coherent framework for integrating multiple indicators with varying reliability. While many implementations remain system-specific, this approach is consistent with the risk-management logic already established in conservation planning and hazard forecasting [60].

5.2.3. Machine Learning and Representation Learning

Deep learning approaches trained on simulated tipping scenarios offer the capacity to detect nonlinear precursors in time series that may be difficult to capture with low-order summary statistics. Neural networks can be trained to classify temporal dynamics and identify signatures of impending transitions, achieving strong performance in simulation studies [33]. The primary scientific challenges are not raw predictive accuracy but rather *transferability*—addressing the domain shift between simulated training data and real ecological time series—and *interpretability*—linking learned features to ecological mechanisms. Consequently, hybrid strategies in which machine learning outputs serve as screening tools that prompt mechanistic follow-up may be most defensible for operational adoption. Such approaches preserve the power of flexible nonlinear methods while maintaining the interpretability required for management accountability.

5.2.4. Composite Indices and Multi-Indicator Synthesis

Given that individual EWS can be noisy and sensitive to preprocessing choices (detrending methods, window sizes, sampling frequency), composite indicators that integrate multiple metrics across the same time series can substantially improve robustness. The goal extends beyond mere statistical aggregation to constructing indices with interpretable connections to resilience mechanisms and explicit performance evaluation under null models [60]. Composite approaches provide a natural interface for decision thresholds, allowing several weak temporal signals to be combined into stronger, calibrated risk scores that are more suitable for management applications.

5.2.5. Mechanism-Guided and Generalized Modeling

When partial knowledge of ecological processes is available, generalized modeling approaches can integrate structural information about feedback loops and interaction networks while remaining flexible about specific functional forms. Such methods offer early warning diagnostics that may be less dependent on long stationary time series, instead leveraging shorter records combined with mechanistic constraints. Importantly, these approaches connect more directly to stability theory and feedback structure, providing EWS that are grounded in system dynamics rather than purely statistical patterns [142].

5.2.6. State-Space and Geometric Indicators

Beyond moment-based statistics computed from time series, the geometry of system trajectories in state space can encode resilience loss through changes in recurrence structure and attractor properties. Although much of this methodological development has occurred in adjacent fields, it provides a valuable conceptual expansion of what “early warning” can mean when systems are high-dimensional and subject to complex noise structures [143]. These geometric approaches complement traditional temporal indicators by capturing aspects of system behavior that may not be apparent in marginal statistics.

5.3. Complementary Role of Spatial Indicators

While time-series analysis remains the primary foundation of EWS methodology, spatial dimensions provide an increasingly valuable complementary axis for early warning, particularly given the expanding availability of remote sensing and landscape-scale monitoring. In self-organized and patterned ecosystems, theory and empirical work demonstrate that shifts in spatial structure can precede desertification and other critical transitions [5,38]. Indicators such as increasing spatial variance, rising spatial autocorrelation, and changes in patch-size distributions may offer warnings even when long temporal records are unavailable.

A particularly promising frontier involves *integrating temporal and spatial evidence*. Remotely sensed products deliver dense spatial coverage, while local observatories provide higher-frequency temporal sampling and mechanistic depth. Methods that combine these information sources can yield more robust inference: spatial patterns may be less sensitive to certain forms of temporal measurement

 doi:10.20944/preprints202603.0897.v1

noise, while time-series indicators capture local recovery dynamics with greater precision. Recent work demonstrates the feasibility of using remote sensing to detect slowing down signals in spatially patterned dryland systems, highlighting the potential for multi-scale surveillance relevant to regional management [107].

5.4. Addressing Methodological Challenges

Despite the strong theoretical foundations and methodological advances described above, several challenges must be addressed to realize the full potential of time-series-based EWS.

The most fundamental operational constraint is data availability. Many ecological time series lack the length, sampling frequency, or measurement quality required for reliable CSD-based detection. Irregular sampling, changes in measurement protocols, and short records reduce statistical power in ways that are difficult to compensate for analytically [23]. This limitation motivates a dual strategy: continued investment in long-term ecological observatories where feasible, and parallel development of EWS methods that remain informative under suboptimal data conditions. The multivariate and mechanism-guided approaches reviewed in Section 5.2 represent partial responses to the second arm of this strategy, but the first— sustained institutional commitment to long-term monitoring—is ultimately a question of governance and funding that lies outside the reach of methodological innovation alone.

A second operational challenge concerns the translation of continuous indicator outputs into discrete management decisions. Policy and management frameworks typically require actionable categories (e.g. traffic-light risk levels or formal trigger thresholds), whereas EWS outputs are inherently continuous, probabilistic, and sensitive to analytical choices. Defining operationally meaningful thresholds—explicitly tied to management objectives such as acceptable false alarm probabilities or expected loss functions—is a practical prerequisite for institutional adoption that has received insufficient attention in the primary literature [60]. Probabilistic and Bayesian decision frameworks (Section 5.2.2) provide the most coherent conceptual basis for this translation, but ecosystem- specific calibration against empirical null distributions remains the norm rather than the exception.

A third challenge is institutional inertia and the gap between methods development and practitioner uptake. The EWS toolkit has expanded rapidly, but accessible software pipelines with standardized workflows, transparent reporting norms, and preregistered detection protocols are only beginning to emerge [23]. Without these infrastructural elements, methodological advances risk remaining confined to the primary research literature rather than informing the monitoring programs and adaptive management frameworks where their impact would be greatest. User-oriented toolchains that deliver outputs as calibrated probabilistic risk summaries—rather than raw indicator time series—are an essential next step toward bridging this gap.

5.5. Emerging Applications and Cross-System Synthesis

The conceptual and methodological framework of EWS, developed primarily through analysis of ecological time series, is increasingly being applied beyond canonical ecosystem regime shifts. In coupled social–ecological systems, feedbacks between human behavior and ecological state can produce abrupt changes in fisheries, agriculture, and resource governance. Comparative synthesis of regime shifts across systems highlights the diversity of drivers and the relevance of cross-scale interactions, underscoring the need for monitoring frameworks that track both ecological state variables and human pressures through integrated temporal data streams [144].

At planetary scales, EWS methodologies are being explored for climate and Earth-system tipping elements, including large-scale circulation patterns and biome transitions. Recent synthesis work connects methodological developments across climate, ecological, and human systems, emphasizing both opportunities and challenges in interpreting early warnings under complex, nonstationary forcing [40]. The extension of ecological EWS methods to biomedical contexts—including microbiome stability and dysbiosis—suggests that resilience diagnostics based on temporal dynamics may become a broadly unifying framework across natural and human systems.

5.6. Priority Directions for Future Research

Several research directions are especially consequential for advancing EWS science and practice in the coming years.

Prospective and real-time validation represents perhaps the most critical need. The majority of published EWS applications remain retrospective, analyzing historical transitions with the benefit of hindsight. Prospective tests in long-term observatories and controlled field experiments are essential to quantify predictive skill, false alarm rates, and practical lead times under realistic operational conditions [23,83].

Multi-scale data integration offers substantial promise for improving EWS robustness. Combining fine-scale field monitoring, remote sensing, and Earth-system modeling can enable surveillance across spatial and temporal scales relevant for management. This requires methodological advances in data fusion, scale alignment, and uncertainty propagation that preserve the strengths of each data source [40,107].

User-oriented toolchains and transparent reporting will determine whether methodological advances translate into widespread adoption. Accessible software pipelines, standardized analytical workflows, and reporting norms (including sensitivity analyses, null-model benchmarking, and ideally preregistered detection protocols) are needed. Delivering outputs as probabilistic risk levels with interpretable summaries will be essential for management uptake.

Finally, *hybrid frameworks accommodating diverse tipping mechanisms* represent the most reliable pathway to actionable early warning. Given the limitations of CSD-centric indicators for certain transition types, methods that blend mechanistic modeling with statistical and machine learning approaches, while continuously tracking stressor trajectories, will likely prove most effective in systems subject to shocks and rapid environmental forcing [24,33,142].

5.7. Recent Advances and Emerging Frontiers

The past several years have witnessed rapid methodological development in EWS research, driven by advances in machine learning, information theory, and the accumulation of empirical tests. This section highlights key recent advances that extend the EWS toolkit and address previously recognized limitations.

5.7.1. Deep Learning Approaches

Machine learning methods, particularly deep neural networks, have emerged as powerful tools for detecting early warning signals that may escape traditional statistical indicators. Bury et al. [33] developed EWSNet, a convolutional neural network trained on large ensembles of simulated time series approaching various bifurcation types. EWSNet learns to identify combinations of features in univariate time series that indicate proximity to tipping points, achieving strong performance on both simulated data and some empirical records.

More recently, deep learning approaches have been extended to rate-induced tipping, a mechanism for which classical CSD-based indicators show limited utility. Boers and colleagues [145] demonstrated that neural networks can detect fingerprints of approaching R-tipping events, potentially enabling prediction of transitions triggered by rapid parameter change rather than gradual approach to bifurcation. These methods exploit nonlinear features in time series that are not captured by variance or autocorrelation alone.

Key challenges for machine learning EWS include transferability (performance may degrade when models trained on simulated data are applied to real ecological systems with different noise structures and dynamics) and interpretability (neural networks function as "black boxes" whose learned features may be difficult to connect to ecological mechanisms). Hybrid approaches that combine machine learning screening with mechanistic follow-up may offer a productive path forward [33].

 doi:10.20944/preprints202603.0897.v1

5.7.2. Non-Equilibrium Thermodynamic Indicators

Classical EWS theory assumes systems near equilibrium, but many ecological systems operate under continuous forcing that maintains non-equilibrium dynamics. Recent work has developed early warning indicators based on non-equilibrium statistical mechanics, potentially extending EWS applicability to driven systems.

Wang and colleagues [146] applied landscape-flux theory to ecological models, demonstrating that quantities including average flux (the non-equilibrium driving force), entropy production rate (the thermodynamic cost of maintaining non-equilibrium), and time irreversibility (quantified through asymmetric cross-correlation functions) can serve as early warning signals. Importantly, these indicators detected approaching transitions earlier than conventional CSD-based metrics in model systems, suggesting potential for improved lead times in practical applications.

These thermodynamic indicators provide a fundamentally different perspective on system stability, grounded in the energetics of maintaining particular dynamic regimes rather than the geometry of equilibrium landscapes. Their integration with classical EWS represents a promising frontier, though empirical validation in ecological data remains limited.

5.7.3. Multivariate and Network-Based Methods

Recognition that ecosystems are inherently high-dimensional has motivated development of multivariate EWS that leverage information across multiple state variables simultaneously. Chen et al. [147] demonstrated that the dominant eigenvalue of the covariance matrix—equivalent to the variance captured by the first principal component—increases as multivariate systems approach bifurcations. This "criticality index" can detect resilience loss distributed across community members that might not be apparent in any single variable.

Weinans et al. [148] systematically evaluated multivariate indicator performance, finding that composite indices integrating multiple variables generally outperformed univariate approaches, particularly in high-dimensional systems where resilience loss may be heterogeneously distributed. These findings support the use of multivariate monitoring in complex ecological communities.

Dynamic network biomarkers (DNB), originally developed for disease prediction [35,149], identify emergent modules of tightly correlated variables whose collective dynamics diverge from the rest of the system prior to transition. Though primarily applied in biomedical contexts, the DNB framework has potential applicability to ecological networks where modular structure and changing inter-component correlations may presage regime shifts.

5.7.4. Empirical Reassessment and Limitations

Alongside methodological advances, recent years have brought sobering empirical assessments of EWS performance in real ecological data. O'Brien et al. [23] conducted a comprehensive analysis of EWS in long-term lake monitoring data, finding that traditional CSD-based indicators showed limited and inconsistent ability to anticipate documented transitions. Their analysis highlighted the gap between theoretical expectations and empirical performance, emphasizing challenges posed by short time series, environmental noise, and transitions not conforming to classical bifurcation models.

The Global Tipping Points Report [150] synthesized EWS research across climate, ecological, and human systems, providing a comprehensive assessment of methods, limitations, and evidence for approaching tipping points in Earth system components. This synthesis emphasized that while EWS show promise for some systems (particularly those with well-characterized bifurcation dynamics), their operational utility for prospective prediction remains to be demonstrated in most contexts.

These empirical reassessments do not invalidate the EWS approach but rather clarify its scope of applicability. EWS are most reliable when applied to systems with dynamics reasonably approximated by low-dimensional models approaching fold-type bifurcations, with sufficiently long and high-quality time series, and where alternative tipping mechanisms (N-tipping, R-tipping) can be reasonably excluded. Meeting these conditions is often challenging in practice, underscoring the importance of

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integrating EWS with mechanistic understanding rather than applying them as standalone diagnostic tools.

6. Conclusions

Early warning signal (EWS) research in ecology has evolved from a primarily theoretical endeavor grounded in dynamical systems theory to a broad empirical and methodological enterprise with demonstrated applications across diverse ecosystem types. This review has traced the development of EWS from their mathematical foundations in critical slowing down—where the dominant eigenvalue of the Jacobian matrix approaches zero near bifurcation points, causing characteristic return times to diverge—through to their practical implementation in monitoring programs worldwide. The methodological advances reviewed here—multivariate extensions, probabilistic frameworks, machine learning integration, composite indices, and mechanism-guided approaches—collectively represent a second generation of methods better suited to the complexities of real ecological monitoring.

The empirical evidence synthesized across ecosystem types reveals both the promise and the complexity of EWS applications. In shallow lakes, the canonical systems for EWS research, studies have demonstrated that increasing lag-1 autocorrelation and variance in water quality parameters, along with flickering dynamics between clear and turbid states, can precede eutrophication-driven regime shifts by several years (Table 2; [70]). The experimental manipulation of whole lakes has provided particularly compelling validation, with Carpenter et al. [151] documenting progressive increases in autocorrelation and variance of phytoplankton density as trophic cascades approached critical thresholds. However, the comprehensive analysis by O'Brien et al. [23] across nine lakes worldwide serves as an important reminder that traditional CSD indicators show limited and inconsistent predictive power in empirical settings, where external noise, seasonal influences, and non-bifurcation-driven transitions can obscure or mimic early warning patterns.

In coral reef systems, the application of EWS faces the particular challenge that many transitions are driven by acute pulse disturbances—bleaching events, storms, disease outbreaks—rather than the gradual parameter drift assumed in classical CSD theory. Nevertheless, flickering between coral-dominated and algae-dominated states has been documented in Caribbean reefs prior to permanent regime shifts, suggesting that even disturbance-mediated transitions may leave statistical fingerprints of declining resilience [70,84]. The integration of CSD metrics with transition-focused precursors, including changes in herbivorous fish functional diversity, represents a promising hybrid approach for reef resilience assessment [115,152].

Grassland and dryland ecosystems have provided some of the strongest evidence for spatial EWS, with satellite-derived vegetation indices revealing increased spatial variance, rising temporal autocorrelation, and slower recovery following drought events in areas approaching desertification thresholds [5,108]. The work of Kéfi et al. [5] on Mediterranean arid ecosystems demonstrated that spatial vegetation patterns—particularly patch-size distributions—can serve as early indicators of imminent collapse, offering warnings even when long temporal records are unavailable.

For forest ecosystems, the inherent inertia of these systems—characterized by long tree lifespans and slow demographic turnover—poses particular challenges for EWS detection. Yet remote sensing analyses have successfully identified signatures of declining resilience, including increasing autocorrelation and variance in NDVI time series and delayed recovery of vegetation greenness following drought episodes [105,153] . In the Amazon basin, Boulton et al.[139] documented pronounced loss of forest resilience since the early 2000s, while analyses of fire regime dynamics have revealed that increasing fire frequency and elevated interannual variability in burned area often precede vegetation state changes at forest–savanna boundaries [133,154,155].

Across all ecosystem types, several cross-cutting findings emerge from this synthesis. First, no single indicator is universally reliable; the statistical power of variance, autocorrelation, skewness, and other metrics varies substantially depending on data quality, transition mechanism, and system-specific dynamics (Table 1). This limitation motivates the development of composite indices and multi-indicator frameworks that can leverage complementary information across metrics [17,95,156]. Second, the distinction between CSD-driven and externally-forced transitions has critical implications for EWS applicability: systems approaching bifurcations through gradual parameter change are more likely to exhibit classical early warning patterns than those subject to abrupt stochastic shocks [2,14,24,74]. Third, spatial and temporal indicators provide complementary information, with spatial metrics sometimes offering greater sensitivity in patterned ecosystems and enabling resilience assessment from landscape snapshots when long time series are unavailable [38,39,64].

Methodological advances continue to expand the EWS toolkit beyond its original foundations. Machine learning approaches, exemplified by EWSNet [23,157], can detect nonlinear precursors that escape low-order summary statistics, though questions of transferability between simulated training data and real ecosystems remain. Probabilistic and Bayesian frameworks offer a more appropriate framing for decision-making under uncertainty, shifting the focus from deterministic "alarm bells" to calibrated risk statements [60]. Nonparametric drift-diffusion estimation [156] and potential analysis [87] provide more direct connections to the underlying stability landscape, while the integration of remote sensing with mechanistic vegetation models promises surveillance capabilities at scales relevant for regional management [105,153].

Realizing this potential will require progress on the operational and institutional fronts identified in Section 5: prospective validation in real monitoring contexts, multi-scale data integration, accessible toolchains, and hybrid frameworks that accommodate the full diversity of tipping mechanisms encountered in practice. Future progress will ultimately be driven by integration—across indicators, temporal and spatial scales, disciplines, and governance contexts [15,92]. Time-series-based early warning, continuously refined and increasingly integrated with complementary approaches, offers one of the most promising pathways toward anticipatory ecosystem stewardship.

Author Contributions: Conceptualization, R.A-M. and P.M.; methodology, R.A-M.; formal analysis, R.A-M.; investigation, R.A-M. and P.M.; writing—original draft preparation, R.A-M.; writing—review and editing, R.A.M. and P.M.; supervision, P.M. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no funding

Acknowledgments: The authors wish to thank the Laboratorio de Biología Cuantitativa y Sistemas Complejos of the Universidad Autónoma de Querétaro and the Departamento de Matemáticas of the Universidad Nacional Autónoma de México and the Facultad de Ciencias from Universidad Autónoma de San Luis Potosí for providing the institutional support and resources that made this work possible.

Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

EWS	Early Warning Signals
CSD	Critical Slowing Down
AR(1)	Lag-1 Autocorrelation

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