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How biodiversity determines ecosystem stability at large scales? Multiscale diversity-stability cascade and the β diversity insurance hypothesis

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Abstract

The relationship between biodiversity and ecosystem stability has been studied intensively at local scales, but its extension to large spatial scales remains unresolved. This study develops a unified theoretical framework, the Multiscale Diversity-Stability Cascade (MDSC), to explain how biodiversity determines ecosystem stability across local, regional, and macroecological scales. The MDSC posits that large-scale stability is not the simple sum of local stabilities but emerges from a nonlinear cascade involving local α stability, spatial β asynchrony, and regional γ functional redundancy. β diversity acts as the pivotal variable, with a hump-shaped rather than monotonically positive effect on regional stability. This study introduces three operational concepts: stability conductance, scale resonance, and the diversity-stability landscape. Stability conductance measures the efficiency with which a change in β or γ diversity propagates to a change in regional stability. Scale resonance describes the amplification of regional variability when the spatiotemporal frequency of disturbances matches the intrinsic asynchronous oscillation period of the metacommunity. The diversity-stability landscape maps diversity configurations onto stability states and reveals thresholds, saddle points, and hysteresis. The study derives a hierarchical state equation and a simplified analytic module that links α, β, and γ components. The study proposes empirical strategies using global observation networks, remote sensing, Bayesian multiscale causal models, and spatially explicit simulations. The framework predicts that intermediate β diversity maximizes regional stability, that moderate landscape connectivity optimizes stability conductance, and that high β diversity reduces scale resonance. These results have direct implications for biodiversity conservation and global change early warning.

Keywords biodiversity; ecosystem stability; scale; β diversity; spatial insurance; metacommunity; multiscale cascade; stability conductance; scale resonance.

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1 Introduction

1.1 Scientific problem and background

Global environmental change is altering the composition and functioning of ecosystems at unprecedented rates (Cardinale et al., 2012; Isbell et al., 2017; Zhang and Liu, 2012; Zhang and Chen, 2011). One of the central concerns in ecology is whether and how biodiversity buffers ecosystem functioning against environmental fluctuations (McCann, 2000; Tilman et al., 2006; Loreau and de Mazancourt, 2013; Blowes et al., 2019; Zhang, 2026a-c, 2027a). The insurance hypothesis states that species diversity stabilizes ecosystem properties because different species respond differently to environmental variation, and their asynchronous fluctuations compensate each other (Yachi and Loreau, 1999; Loreau et al., 2021). This hypothesis has received substantial support from grassland experiments and local observations (Hector et al., 2010; Gross et al., 2014; Craven et al., 2018). However, most of this evidence comes from small plots or homogeneous local communities, where spatial processes are deliberately excluded or minimized (Gonzalez et al., 2020). At larger scales, ecosystems are spatially heterogeneous, connected by dispersal, and subject to disturbances that are partly synchronized across space (Wang and Loreau, 2014; Wilcox et al., 2017). It is unclear whether the mechanisms identified at local scales can be extrapolated directly to regions and continents.

Large-scale ecosystem stability is not merely an academic concern. Regional productivity stability underpins food security, carbon sequestration, and the provisioning of many ecosystem services (Isbell et al., 2015, 2018; Liang et al., 2016; Zhang, 2027b). Climate extremes such as droughts and heatwaves can synchronize ecosystem fluctuations over large areas, reducing the spatial insurance that normally stabilizes regional totals (Hautier et al., 2020). Understanding how biodiversity at multiple scales contributes to stability is therefore essential for predicting the consequences of biodiversity loss and for designing effective conservation strategies (May, 1972; Pimm, 1984; Chesson, 2000; Ives and Carpenter, 2007; Loreau, 2010; Mori et al., 2013; van der Plas, 2019; Gonzalez et al., 2020; Zhang, 2026b).

1.2 Limitations of existing explanations: scale gaps and mechanistic disconnects

Local studies have emphasized species richness, functional diversity, and compensatory dynamics as drivers of temporal stability (Tilman et al., 2006; Zhang, 2011, 2026a-b, 2027a; Isbell et al., 2015). The portfolio effect, in which statistical averaging across species reduces the variance of aggregate biomass, is a well-established mechanism (Doak et al., 1998). Species asynchrony and response diversity are the core processes underlying the insurance effect at local scales (Loreau and de Mazancourt, 2013; Craven et al., 2018). Yet these local mechanisms do not incorporate spatial heterogeneity or dispersal between patches.

At the regional scale, the spatial insurance hypothesis proposes that asynchronous dynamics among patches, coupled by dispersal, can stabilize the total regional ecosystem function (Loreau et al., 2003; Wang and Loreau, 2014). β diversity, which measures compositional differences among patches, is thought to promote spatial asynchrony because different species assemblages respond differently to environmental fluctuations (Dornelas et al., 2014; Wang and Loreau, 2016). Metacommunity theory provides a formal basis for understanding how dispersal and local interactions generate regional patterns (Leibold et al., 2004; Holyoak et al., 2005). However, metacommunity models often simplify environmental gradients and ignore global change drivers (Mouquet and Loreau, 2003). They rarely connect explicitly to γ diversity, evolutionary history, or macroecological constraints.

At the macroecological scale, γ diversity and regional species pools reflect long-term evolutionary and biogeographic processes (Whittaker, 1972; Jetz et al., 2019). Large-scale stability may depend on the functional redundancy embedded in the regional species pool, which provides a reservoir of response options under novel conditions (Zhang, 2015, 2016b; Loreau et al., 2021). Climate variability, disturbance regimes, and biogeographic history impose constraints that are absent from local experiments (Seddon et al., 2016).

Remote sensing studies have documented large-scale spatial patterns of ecosystem resistance and resilience to climate anomalies (De Keersmaecker et al., 2015; Forzieri et al., 2021), but linking these patterns to biodiversity remains challenging.

The three bodies of work have developed largely in parallel, with no unified causal chain connecting α, β, and γ diversity to stability at multiple scales. The field lacks a formal way to quantify how diversity at one scale transmits stability to the next scale. It also lacks a clear treatment of the nonmonotonic effects that may emerge when β diversity becomes too high or too low. The present study addresses these gaps.

1.3 Research objectives and core questions

The central question is how biodiversity determines ecosystem stability at large scales. Specifically, the following are asked. What are the relative contributions of α, β, and γ diversity to regional stability? Does the relationship between β diversity and regional stability follow a monotonic or hump-shaped form? How can we formalize the efficiency with which diversity changes at one scale propagate to stability changes at another scale? Under what conditions do disturbances synchronize with intrinsic community oscillations and amplify regional variability?

The study aims to construct a predictive and testable theory that links multiscale biodiversity to ecosystem stability. The theory should be sufficiently general to apply across terrestrial, freshwater, and marine ecosystems, and sufficiently operational to be tested with existing global data.

1.4 Research approach and main innovations

The study proposes the Multiscale Diversity-Stability Cascade (MDSC) framework. The framework decomposes regional stability into three interacting components: the weighted average of local α stabilities, the spatial asynchrony generated by β diversity, and the regional γ functional redundancy. The study argues that β diversity is the pivotal variable, but its effect on stability is hump-shaped rather than linear. The study introduce three new concepts. Stability conductance is the partial derivative of regional stability with respect to β diversity or γ redundancy. Scale resonance is the amplification of variability when the disturbance spectrum overlaps with the intrinsic asynchronous oscillation spectrum of the metacommunity. The diversity–stability landscape is a potential surface that maps diversity configurations onto stability states and can reveal thresholds, saddle points, and hysteresis.

The study presents the mathematical skeleton of the framework, derive a simplified analytical module, and outline empirical and simulation strategies for testing the predictions. The study is organized as follows. Section 2 reviews the literature and identifies theoretical gaps. Section 3 develops the MDSC framework and its core propositions. Section 4 describes methods for empirical testing. Section 5 presents expected patterns and model predictions. Section 6 discusses implications, limitations, and future directions. Section 7 concludes.

2 Theoretical Gaps

2.1 Local-scale diversity-stability mechanisms

The modern study of diversity and stability began with the observation that species-poor communities can fluctuate more than species-rich communities (MacArthur, 1955; Elton, 1958). Early theoretical work suggested that complexity could be destabilizing (May, 1972), but this result applied to randomly assembled systems and did not account for the statistical averaging of species fluctuations. The portfolio effect states that the variance of aggregate biomass declines as the number of independent or weakly correlated species increases (Doak et al., 1998). The insurance hypothesis adds a biological mechanism: species differ in their responses to environmental fluctuations, and these differential responses generate compensatory dynamics that reduce the temporal variability of total community biomass (Yachi and Loreau, 1999). This mechanism has

been formalized in terms of species covariance and the synchrony of species fluctuations (Loreau and de Mazancourt, 2013).

Long-term grassland experiments have provided strong support for the insurance effect. Tilman et al. (1996) showed that more diverse plots maintained more stable biomass across a drought, and Tilman et al. (2006) found that species richness increased the temporal stability of community productivity over a decade. Hector et al. (2010) demonstrated that population asynchrony and overyielding jointly explained the stabilizing effect of plant diversity in European grasslands. Gross et al. (2014) reanalyzed multiple biodiversity experiments and confirmed that species richness increases temporal stability primarily through species asynchrony rather than through the portfolio effect alone. Craven et al. (2018) showed that multiple facets of biodiversity, including functional and phylogenetic diversity, contribute to the diversity-stability relationship in grassland communities.

Local experiments also reveal important context dependencies. Nutrient enrichment weakens the stabilizing effect of diversity because it increases species synchrony and reduces complementarity (Hautier et al., 2014; Hautier et al., 2015). Climate extremes can reduce stability even in diverse communities if the extreme synchronizes species responses (Isbell et al., 2015). Nonetheless, biodiversity generally increases resistance to climate extremes and enhances recovery after disturbance (Isbell et al., 2015; Craven et al., 2016; Zhang, 2026a-d).

The main limitation of local studies is that they usually control or ignore spatial heterogeneity and dispersal. Local plots are relatively homogeneous, and the observed stability reflects within-community mechanisms only. Spatial processes that operate at landscape and regional scales cannot be captured by small plot experiments (Gonzalez et al., 2020).

2.2 Spatial and regional extensions

The spatial insurance hypothesis extends the insurance effect to heterogeneous landscapes. Loreau et al. (2003) showed theoretically that dispersal between patches with different environmental conditions can stabilize regional ecosystem functioning by allowing species to track favorable conditions. This mechanism is analogous to the portfolio effect but operates across space rather than across species. β diversity is central to spatial insurance because it reflects compositional differences among patches and hence the potential for different patches to respond differently to environmental fluctuations (Wang and Loreau, 2014; Wang and Loreau, 2016).

Metacommunity theory provides a formal framework for understanding how local interactions and dispersal jointly determine regional patterns (Leibold et al., 2004). The metacommunity concept unifies four perspectives: patch dynamics, species sorting, mass effects, and neutral dynamics (Holyoak et al., 2005). These perspectives differ in the relative importance of dispersal, environmental heterogeneity, and demographic stochasticity, and they have different implications for regional stability. Species sorting models predict that environmental heterogeneity promotes β diversity and spatial insurance (Mouquet and Loreau, 2003). Mass effects models predict that high dispersal can homogenize communities and reduce spatial asynchrony (Loreau et al., 2003). The storage effect and competition-dispersal trade-offs are additional mechanisms that can maintain diversity and stability in fluctuating environments (Chesson, 2000).

Empirical studies at regional scales have begun to test these ideas. Wang and Loreau (2014) developed a framework to partition ecosystem variability into α and β components and showed that β variability can make a large contribution to γ variability. Wilcox et al. (2017) used data from a long-term grassland experiment and found that asynchrony among local communities stabilized ecosystem function at the metacommunity scale. Hautier et al. (2020) showed that eutrophication reduced spatial asynchrony and destabilized grassland productivity at multiple spatial scales.

The relationship between β diversity and spatial asynchrony is not straightforward. High β diversity can arise from strong environmental sorting, which also increases the potential for asynchronous responses across patches (Wang and Loreau, 2016). However, if β diversity is too high, local communities may become too dissimilar, reducing functional redundancy within patches and increasing local extinction risk (Loreau et al., 2021). This suggests a possible nonmonotonic relationship, but this possibility has not been formalized.

2.3 Macroecological and global-scale constraints

At macroecological scales, γ diversity and regional species pools are shaped by evolutionary and biogeographic processes that operate over long time scales (Whittaker, 1972; Jetz et al., 2019). Regional species pools provide a reservoir of functional traits that may be critical for maintaining stability under novel environmental conditions (Loreau et al., 2021; Zhang, 2027c). γ diversity and functional redundancy can act as a long-term insurance mechanism because they increase the probability that some species will be able to tolerate future perturbations (Mori et al., 2013).

Global analyses of remote sensing data have revealed large-scale patterns of ecosystem stability. De Keersmaecker et al. (2015) quantified the resistance and resilience of global vegetation to short-term climate anomalies and found that these properties are related to vegetation cover and climate variability. Seddon et al. (2016) showed that ecosystem sensitivity to climate variability varies strongly across biomes and is influenced by biodiversity and land use. Forzieri et al. (2021) reported that European forests are becoming increasingly vulnerable to climate-driven disturbances, with implications for regional carbon stability.

Global biodiversity data sets have enabled tests of the diversity-productivity relationship at large scales. Liang et al. (2016) found a consistent positive relationship between tree species richness and forest productivity across the globe. Duffy et al. (2017) showed that biodiversity effects on productivity in natural ecosystems are comparable in magnitude to those of key abiotic drivers. These findings suggest that biodiversity can influence ecosystem functioning at large scales, but their implications for temporal stability remain less clear.

A key challenge is that global and regional studies often lack detailed species-level data, making it difficult to separate α, β, and γ components of diversity (Chase et al., 2019). Remote sensing provides information on ecosystem properties but not on species composition. Conversely, local biodiversity surveys provide species data but limited spatial and temporal coverage. Bridging this gap is essential for testing multiscale stability theory.

2.4 Deficiencies of existing theoretical models for scale extrapolation

Local models of diversity and stability typically ignore spatial heterogeneity and dispersal. They represent a single community in a homogeneous environment, and their predictions cannot be directly extended to regions where patches differ and exchange individuals (Loreau et al., 2003). Metacommunity models incorporate space but often simplify environmental gradients to one or two axes and assume constant dispersal rates (Leibold et al., 2004). They rarely include realistic global change drivers such as climate trends, land use change, or nutrient enrichment, and they rarely track γ diversity or evolutionary history (Mouquet and Loreau, 2003).

Global ecosystem models, such as dynamic global vegetation models, include climate and biogeochemical processes but typically represent biodiversity only crudely, often as plant functional types rather than species (Prentice et al., 2007). These models cannot capture the species-level mechanisms that underlie the insurance effect. Moreover, they generally do not distinguish between α, β, and γ stability components.

A unified framework that simultaneously includes α, β, and γ diversity, multiple stability dimensions, and realistic spatial structure is lacking. Such a framework is needed to understand how biodiversity determines stability at large scales and to predict responses to global change.

2.5 Key gaps

Four key gaps emerge from this review: (1) there is no quantitative decomposition of the causal chain from α to β to γ diversity and stability across scales. (2) The role of β diversity in large-scale stability is poorly characterized, especially the possibility of nonmonotonic effects. (3) There is no formal concept that describes the efficiency with which diversity at one scale propagates to stability at another scale. (4) There is no treatment of the resonance between disturbance scales and intrinsic community oscillation periods, which could amplify regional instability. These gaps motivate the theoretical framework developed in the next section.

3 Theoretical Construction: The Multiscale Diversity-Stability Cascade Framework

3.1 Basic definitions and logical starting points

3.1.1 Multidimensional stability

Stability is a multidimensional concept that includes temporal variability, resistance, resilience, and recovery (Pimm, 1984; Ives and Carpenter, 2007; Zhang, 2016a-b, 2018). Temporal variability is often measured as the inverse of the coefficient of variation of biomass or productivity. Resistance is the ability to withstand a perturbation without changing much (Zhang, 2016a). Resilience is the rate of return to the reference state after a perturbation. Critical slowing down refers to the increase in recovery time near a tipping point and can serve as an early warning signal (van Nes and Scheffer, 2007; Scheffer et al., 2009; Zhang, 2016b, 2026a, 2026c).

At large scales, stability must be considered not only in time but also in space. Spatial synchrony measures the correlation of fluctuations among patches and determines whether local fluctuations cancel out or amplify in the regional aggregate (Loreau and de Mazancourt, 2013; Wilcox et al., 2017). A central task is to understand how temporal and spatial components combine to produce stability at higher levels.

3.1.2 Scale decomposition of diversity

Whittaker (1972) introduced the classical decomposition of diversity into α, β, and γ components. α diversity is the diversity within a local patch, typically measured as species richness, functional diversity, or phylogenetic diversity. β diversity is the difference in composition among patches and can be measured using indices such as Bray-Curtis dissimilarity, functional β diversity, or phylogenetic β diversity. γ diversity is the total diversity of the region, representing the regional species pool and its functional redundancy.

These three components are not independent. γ diversity constrains the possible values of α and β diversity. β diversity reflects the spatial turnover generated by environmental heterogeneity, dispersal limitation, and historical contingencies. A central premise of the MDSC is that α, β, and γ diversity play distinct but interacting roles in generating stability at different scales.

3.1.3 Stability scales

The study defines three stability scales in parallel with diversity scales. Local α stability is the temporal stability of a single patch (Zhang, 2027d). Regional γ stability is the temporal stability of the sum of all patches in a region. Macroecological stability is the stability of aggregate ecosystem properties across multiple regions or continents. The MDSC focuses on how α stability, β asynchrony, and γ redundancy combine to determine γ stability.

3.2 Core theoretical propositions

Proposition 1: γ stability decomposition

Regional γ stability can be decomposed into three cascade components. The first component is the weighted average of local α stabilities, where the weights reflect patch contributions to regional biomass or productivity. The second component is β asynchrony, which measures the degree to which fluctuations in different patches are out of phase. The third component is γ functional redundancy, which captures the ability of the regional species pool to replace functions lost locally. These three components interact nonlinearly, so that γ stability is

not simply the sum of the three contributions.

Formally, we write

$$S_\gamma = F(\Sigma_i w_i S_{\alpha,i}, \varphi_\beta, R_\gamma, C, E)$$

where S_γ is regional stability, $S_{\alpha,i}$ is the stability of patch i, w_i is the relative weight of patch i, φ_β is a measure of β asynchrony, R_γ is γ functional redundancy, C is a spatial connectivity matrix, and E is the environmental disturbance covariance structure. The function F is nonlinear and may exhibit thresholds.

Proposition 2: β diversity dominance

At large scales, β diversity becomes a dominant driver of stability because it determines the potential for spatial insurance. High β diversity means that patches contain different species with different environmental responses, so that fluctuations are less synchronized across patches. This spatial asynchrony reduces the temporal variability of the regional aggregate. However, this effect has an upper limit because beyond a certain point, increasing β diversity reduces local functional redundancy and increases the risk of local extinctions. Thus β diversity is necessary but not sufficient for high regional stability.

Proposition 3: β diversity optimal interval hypothesis

The study proposes that the relationship between β diversity and regional stability is hump-shaped. When β diversity is very low, patches are compositionally similar, their fluctuations are synchronized, and spatial insurance is weak. When β diversity is very high, patches are so dissimilar that local functional redundancy declines, local stability decreases, and the regional species pool becomes fragmented. At intermediate β diversity, spatial asynchrony and local redundancy are jointly optimized, producing maximal regional stability. This hypothesis contrasts with the implicit assumption in much of the literature that more β diversity is always better for stability.

Proposition 4: Scale coupling and stability conductance

The efficiency with which local diversity translates into regional stability depends on dispersal rate, landscape connectivity, environmental heterogeneity, and functional complementarity (Zhang, 2027a, 2027d). The study introduces the concept of stability conductance, denoted τ, to quantify this efficiency. Stability conductance is defined as the partial derivative of regional stability with respect to β diversity or γ redundancy. A high stability conductance means that a small change in diversity at one scale produces a large change in stability at the next scale. Stability conductance is itself a function of spatial structure and environmental context.

Proposition 5: Scale resonance

When the spatiotemporal frequency of disturbances matches the intrinsic asynchronous oscillation period of the metacommunity, regional variability can be amplified. We can call this phenomenon scale resonance. Disturbances such as droughts, heatwaves, or pest outbreaks have characteristic spatial and temporal scales. The metacommunity also has an intrinsic spectrum of fluctuations generated by species interactions and dispersal. When these spectra overlap, even moderate disturbances can generate large regional fluctuations. Biodiversity can shift the intrinsic oscillation spectrum and thereby reduce the likelihood or severity of scale resonance.

3.3 New concepts

3.3.1 Stability conductance (τ)

Stability conductance is the rate at which a change in diversity at one scale propagates to a change in stability at a higher scale. For β diversity, we define

$$\tau_\beta = \partial S_\gamma / \partial D_\beta$$

where D_β is a standardized measure of β diversity. For γ redundancy, we define

$$\tau_\gamma = \partial S_\gamma / \partial R_\gamma$$

Stability conductance can be positive, negative, or zero depending on the region of the diversity-stability landscape. It is analogous to thermal conductance or electrical conductance in that it describes how efficiently a signal is transmitted through a hierarchical system.

3.3.2 Scale resonance

Scale resonance occurs when the disturbance frequency spectrum overlaps significantly with the intrinsic fluctuation spectrum of the metacommunity. The study defines a resonance index as the overlap integral between the normalized disturbance spectrum $P_{\text{dist}}(\Omega, k)$ and the normalized community response spectrum $P_{\text{comm}}(\Omega, k)$, where Ω is temporal frequency and k is spatial frequency. The resonance index is

$$R = \int \int P_{\text{dist}}(\Omega, k)\, P_{\text{comm}}(\Omega, k)\, d\Omega\, dk$$

A high resonance index indicates that disturbances and community oscillations share frequencies, which can amplify regional variability. Biodiversity can reduce R by broadening or shifting the community response spectrum.

3.3.3 Diversity-stability landscape

The diversity-stability landscape is a potential surface that maps each combination of α, β, and γ diversity onto a stability value. This surface can have multiple local optima, saddle points, and thresholds. Transitions between states can show hysteresis, meaning that the path of degradation may differ from the path of recovery. The landscape provides a visual and mathematical tool for identifying critical transitions and for designing management interventions.

3.4 Mathematical skeleton of the MDSC

3.4.1 Hierarchical state equation

The study represents the dynamics of regional biomass $B(t)$ as the sum of local biomasses $b_i(t)$ over N patches:

$$B(t) = \Sigma_i\, b_i(t)$$

The local biomass dynamics follow a stochastic differential equation (Zhang, 2026c) with environmental forcing, species interactions, and dispersal. A general form is

$$db_i/dt = r_i\, b_i\, (1 - b_i / K_i) + g_i(b_i, E_i(t)) + \Sigma_j\, d_{ij}\, (b_j - b_i) + \sigma_i\, xi_i(t)$$

where r_i is the intrinsic growth rate, K_i is carrying capacity, g_i describes the response to environmental variable E_i, d_{ij} is the dispersal rate from patch j to patch i, and xi_i is white noise with variance σ_i^2.

The regional stability S_γ is defined as the inverse of the coefficient of variation of B:

$$S\gamma = \mu_B / sd_B$$

where μ_B is the temporal mean and sd_B is the temporal standard deviation of B.

3.4.2 Asynchrony and covariance structure

The temporal variance of regional biomass can be written as

$$\mathrm{Var}(B) = \Sigma_i \mathrm{Var}(b_i) + 2\,\Sigma_{i<j} \mathrm{Cov}(b_i, b_j)$$

The first term is the sum of local variances, and the second term depends on spatial synchrony. β asynchrony φ_β can be defined as one minus the average pairwise correlation of local biomasses:

$$\varphi_\beta = 1 - \mathrm{average}_{i<j}\, \mathrm{Corr}(b_i, b_j)$$

When patches fluctuate independently, Corr is near zero, φ_β is near one, and the spatial insurance effect is maximal. When patches fluctuate synchronously, Corr is near one, φ_β is near zero, and regional variance is high.

3.4.3 Spatial network and cross-patch flows

The dispersal matrix $D = [d_{ij}]$ defines the spatial network. Landscape connectivity can be summarized by the second smallest eigenvalue of the graph Laplacian, known as algebraic connectivity. Moderate connectivity may optimize stability conductance because it allows rescue effects without homogenizing communities.

3.4.4 Simplified analytical module

To obtain tractable predictions, let's consider a simplified two-patch model with linearized dynamics and environmental noise. Let x_1 and x_2 be deviations of local biomasses from equilibrium. Assume

$$d\,x_1/dt = -a\,x_1 + d\,(x_2 - x_1) + e_1(t)$$
$$d\,x_2/dt = -a\,x_2 + d\,(x_1 - x_2) + e_2(t)$$

where a is the local return rate, d is the dispersal rate, and e_1, e_2 are environmental noises with variances σ^2 and correlation ρ. The regional biomass deviation is $X = x_1 + x_2$.

The variance of X is derived in the Appendix. The result is

$$\mathrm{Var}(X) = \sigma^2\,(1 + \rho) / a$$

This shows that regional variance decreases as the local return rate a increases and as the environmental correlation ρ decreases. β diversity influences rho: high β diversity means patches respond to different environmental drivers, reducing ρ and thus stabilizing the regional total. Dispersal d does not appear in this simple linearized result because it affects both the mean and the variance in a way that cancels for the sum. In more complex models with nonlinearity, dispersal modulates stability conductance.

The full derivation, including the effect of β diversity on ρ and the resonance calculation, is given in the Appendix.

3.5 Relations to other theories

The MDSC generalizes the insurance hypothesis to multiple scales. The local insurance effect operates through species asynchrony within patches, while the spatial insurance effect operates through patch asynchrony among patches. The MDSC combines both and adds the γ redundancy component. It also extends metacommunity stability theory by explicitly linking β diversity to spatial asynchrony and by introducing the concepts of stability conductance and scale resonance. Finally, the MDSC connects to the theory of critical transitions and early warning signals by interpreting the diversity-stability landscape as a potential surface with thresholds and hysteresis (Scheffer et al., 2009; Scheffer et al., 2012).

4 Research Methods and Empirical Strategy

4.1 Data sources and scale hierarchy

Testing the MDSC requires data at multiple spatial scales. Long-term ecological research networks such as the US LTER, the International LTER, and the NutNet global grassland experiment provide local time series of species composition and productivity. The Forest Global Earth Observatory provides standardized forest plot data across continents. Remote sensing products such as MODIS and Landsat provide gridded time series of vegetation indices that can be used to estimate ecosystem stability at regional to global scales. The GEDI lidar mission provides high-resolution vegetation structure data. Environmental DNA and citizen science platforms such as iNaturalist and eBird provide species occurrence data that can be used to estimate β diversity. Flux tower networks and climate reanalysis products provide continuous environmental time series.

4.2 Variable operationalization

Stability is operationalized as the inverse of the coefficient of variation of productivity over time. Also compute the first-order autoregressive coefficient AR(1) and the recovery time after perturbations as complementary indicators. Critical slowing down is measured as the increase in AR(1) and variance before an abrupt shift (Ratajczak et al., 2018), following Dakos et al. (2012) and Zhang (2026a, 2026c).

α diversity is measured as local species richness, functional diversity based on trait databases, and phylogenetic diversity based on megaphylogenies. β diversity is measured using Bray-Curtis dissimilarity, functional β diversity, and phylogenetic β diversity. γ diversity is the regional species pool size, the volume of functional space, and phylogenetic diversity of the region.

Environmental covariates include climate variability from reanalysis products, land use and fragmentation from remote sensing, and dispersal ability estimated from species traits.

4.3 Causal inference and statistical modeling

The study proposes a multiscale structural equation model to test the causal paths from α, β, and γ diversity to γ stability. The model includes latent variables for spatial asynchrony and γ redundancy. Bayesian hierarchical models are used to propagate uncertainty across scales and to estimate stability conductance as a derived parameter. Natural experiments such as islands, habitat fragments, and climate gradients serve as quasi-experimental designs to infer causality. Instrumental variable methods can address reverse causality between diversity and stability.

4.4 Spatially explicit dynamic simulations

The study proposes a spatially explicit metacommunity model with individual-based local dynamics and explicit dispersal. The model simulates species with different environmental niches and dispersal abilities on a heterogeneous landscape. β diversity is manipulated by varying environmental heterogeneity and dispersal limitation. Disturbances are imposed with defined temporal and spatial spectra. The model is used to test the β diversity optimal interval hypothesis, to quantify scale resonance, and to estimate stability conductance. Simulation results are compared with empirical patterns to form a closed empirical-simulation loop.

4.5 Model selection, validation, and reproducibility

Here use leaveone-region-out cross-validation and Bayesian model comparison to select among competing models. Sensitivity analyses test the robustness of conclusions to alternative diversity metrics and stability indicators.

5 Empirical Analysis and Model Predictions

5.1 Global and regional multiscale stability decomposition

The study predicts that the decomposition of regional stability will show substantial contributions from all

three components, but with strong context dependence. In regions with high environmental heterogeneity and moderate connectivity, β asynchrony will dominate. In regions with low heterogeneity or high connectivity, local α stability will dominate. γ redundancy will become important under long-term environmental change, when the regional species pool provides replacement options.

5.2 Shape of the β diversity-stability relationship

The study predicts a hump-shaped relationship between β diversity and regional stability. Empirical tests should reveal an intermediate optimum, below which spatial insurance is insufficient and above which local redundancy declines. This pattern may be obscured in data sets with limited β diversity ranges, which could explain why previous studies have reported mixed results.

5.3 Determinants of stability conductance

Stability conductance is predicted to be highest at intermediate landscape connectivity and intermediate environmental heterogeneity. Very low connectivity prevents rescue effects and spatial insurance. Very high connectivity homogenizes communities and reduces spatial asynchrony. Stability conductance should also increase with functional complementarity among species and decrease with environmental correlation among patches.

5.4 Evidence for scale resonance

The study predicts that scale resonance occurs when the dominant period of environmental disturbances, such as multi-year drought cycles, matches the intrinsic recovery time of the metacommunity. Regions with low β diversity and low response diversity will have a narrower intrinsic fluctuation spectrum and therefore a higher resonance index. High β diversity should broaden the spectrum and reduce resonance.

5.5 Regional stability projections under global change

Based on the MDSC framework, The study predicts that the loss of β diversity will be more destabilizing at regional scales than the loss of γ diversity alone, because β diversity directly controls spatial asynchrony. Climate change that increases the spatial synchrony of disturbances will reduce spatial insurance and destabilize regional productivity. Land use change that fragments landscapes and reduces connectivity will lower stability conductance and increase the risk of scale resonance.

6 Discussion

6.1 Large-scale stability is not the simple sum of local mechanisms

The MDSC shows that regional stability emerges from the interaction of local stability, spatial asynchrony, and regional redundancy. This implies that local experiments, while valuable, cannot fully predict regional stability. A region can be stable even if local patches are unstable, provided that patches fluctuate asynchronously and are connected by dispersal. Conversely, a region can be unstable even if local patches are stable, if disturbances synchronize patch fluctuations.

6.2 Scale-dependent mechanisms of diversity-stability relationships

α diversity primarily stabilizes local patches through species asynchrony and the portfolio effect. β diversity stabilizes regions through spatial insurance. γ diversity provides long-term insurance through functional redundancy and evolutionary potential. The relative importance of these components shifts with spatial scale and environmental context. The study formalizes this as the scaled insurance hypothesis, which integrates previous local and spatial insurance ideas.

6.3 Multiple stable states, hysteresis, and degraded ecosystem recovery

The diversity-stability landscape can exhibit multiple local optima. A gradual loss of β diversity may push the system across a threshold beyond which regional stability collapses. Recovery may follow a different path, showing hysteresis. Declining stability conductance can serve as an early warning signal of an approaching

critical transition. Monitoring β diversity and spatial asynchrony may therefore provide operational indicators for ecosystem management.

6.4 New foundations for biodiversity conservation

Current conservation priorities often focus on local species richness or total species numbers. The MDSC suggests that β diversity and its spatial network are equally important for regional stability. Conservation planning should identify and protect the stability conductance network, meaning the spatial configuration of patches and corridors that maximizes spatial insurance. The β diversity optimal interval provides a quantitative management target: maintain β diversity within the range that maximizes stability, rather than simply maximizing β diversity everywhere.

6.5 Applications and early warning under global change

The MDSC can be used to build early warning systems for regional ecosystem instability. Remote sensing can track spatial synchrony and β diversity proxies in near real time. Deviations of stability conductance from its historical baseline can signal increasing vulnerability. Scale resonance can be predicted by comparing the spectra of climate disturbances and ecosystem fluctuations. These tools can support proactive management to avoid critical transitions.

6.6 Limitations and future research

Several limitations must be acknowledged. Data on β diversity at regional to global scales remain incomplete, especially for non-plant taxa. Functional and phylogenetic β diversity metrics carry measurement uncertainty. The MDSC is a theoretical framework that requires extensive empirical testing across ecosystem types and latitudes. Long-term time series are scarce for many regions, and remote sensing proxies for diversity are indirect. Future work should integrate new biodiversity monitoring technologies, such as eDNA and acoustic monitoring, with satellite data. Model development should incorporate realistic dispersal and disturbance regimes, and empirical studies should test the β diversity optimal interval hypothesis explicitly.

7 Conclusion

7.1 Main findings

This study has developed the Multiscale Diversity-Stability Cascade framework. Regional stability can be decomposed into local α stability, β asynchrony, and γ functional redundancy. β diversity plays a dominant but nonmonotonic role, with an intermediate optimum for regional stability. Stability conductance quantifies how efficiently diversity changes propagate to stability changes across scales. Scale resonance describes the amplification of variability when disturbances match intrinsic community oscillations.

7.2 Theoretical contributions

The MDSC unifies local insurance, spatial insurance, and macroecological redundancy into a single causal framework. It introduces three new operational concepts: stability conductance, scale resonance, and the diversity-stability landscape. It proposes a testable β diversity optimal interval hypothesis that reconciles conflicting expectations in the literature.

7.3 Practical implications

The framework provides a basis for predicting regional ecosystem stability under global change. It suggests that conservation should protect β diversity and its spatial network, not only local richness. It offers quantitative indicators for early warning and management of ecosystem stability.

Appendix: Mathematical derivations and computational details

A.1 Variance decomposition in a two-patch linear model

Consider two patches with local biomass deviations x_1 and x_2 from equilibrium. The dynamics are

$$d\,x_1/dt = -a\,x_1 + d\,(x_2 - x_1) + e_1(t)$$
$$d\,x_2/dt = -a\,x_2 + d\,(x_1 - x_2) + e_2(t)$$

where a is the local return rate, d is the dispersal rate, and e_1, e_2 are environmental Gaussian white noises with variances σ^2 and correlation ρ.

Define the sum $X = x_1 + x_2$ and the difference $Y = x_1 - x_2$. Adding and subtracting the equations gives

$$dX/dt = -a\,X + e_1 + e_2$$
$$dY/dt = -\,(a + 2d\,)\,Y + e_1 - e_2$$

The variance of X is

$$\mathrm{Var}(X) = \mathrm{Var}(e_1 + e_2) / (2a) = (\sigma^2 + \sigma^2 + 2\,\rho\,\sigma^2) / (2a) = \sigma^2\,(1 + \rho) / a$$

Thus regional variance decreases as a increases and as ρ decreases. β diversity reduces ρ by making patches respond to different environmental drivers. This is the core spatial insurance effect in the linearized model.

A.2 Stability conductance calculation

Stability conductance is defined as $\tau_\beta = \partial\, S_\gamma / \partial\, D_\beta$. Using $S_\gamma = \mu_B / sd_B$ and the variance expression above with $\mathrm{Var}(B) = \sigma^2\,(1 + \rho) / a$, we can write

$$S_\gamma = \mu_B / (\sigma^2\,(1 + \rho) / a\,)^{1/2} = \mu_B\, a^{1/2} / (\sigma\,(1 + \rho)^{\,1/2})$$

If β diversity D_β reduces ρ, we can approximate $\rho = \rho 0 - k\,D_\beta$ for small changes, where $\rho 0$ is the correlation at zero β diversity and $k > 0$. Then

$$\partial\, S_\gamma / \partial\, D_\beta = \partial\, S_\gamma / \partial\, \rho * \partial\, \rho / \partial\, D_\beta$$

Then

$$\partial\, S_\gamma / \partial\, \rho = \mu_B\, a^{1/2} / \sigma * (\,-1/2\,)\,(1 + \rho)^{-3/2}$$

and $\partial\, \rho / \partial\, D_\beta = -k$. Therefore

$$\tau_\beta = k\,\mu_B\, a^{1/2} / (2\,\sigma\,(1 + \rho)^{3/2})$$

This expression shows that stability conductance is positive when β diversity reduces environmental

correlation, and it increases with local return rate and mean biomass, and decreases with environmental variability and correlation. It provides a simple operational formula for empirical estimation.

A.3 Scale resonance index

Let $P_{dist}(\Omega, k)$ be the normalized power spectral density of the disturbance, where Ω is temporal frequency and k is spatial frequency. Let $P_{comm}(\Omega, k)$ be the normalized power spectral density of the community response. The resonance index is

$$R = \int_0^\infty \int_0^\infty P_{dist}(\Omega, k)\, P_{comm}(\Omega, k)\, d\Omega\, dk$$

When the two spectra overlap strongly, R is large and regional variability is amplified. The community response spectrum can be estimated from time series of regional biomass using Fourier analysis. Disturbance spectra can be estimated from climate reanalysis or disturbance records. Computing R for different regions and diversity levels can test the scale resonance hypothesis.

A.4 Diversity-stability landscape construction

The landscape is constructed by simulating or estimating S_γ as a function of standardized α, β, and γ diversity. A potential function $V(D_\alpha, D_\beta, D_\gamma)$ can be fitted such that S_γ is a monotonic transformation of V. Thresholds and saddle points are identified by finding local maxima and minima. Hysteresis is tested by simulating forward and backward changes in diversity and comparing stability trajectories.

A.5 Sample code and data generation workflow

The sample code produces simulated datasets and implements the computational steps, including the two-patch model, stability calculations, stability conductance, scale resonance, diversity-stability landscape, and cross-validation with Bayesian model comparison.

```
<!DOCTYPE html>
<html lang="en">
<head>
    <meta charset="UTF-8">
    <meta name="viewport" content="width=device-width, initial-scale=1.0">
    <title>Multiscale Diversity–Stability Cascade – Simulator</title>
    <style>
        body {
            font-family: 'Segoe UI', Tahoma, Geneva, Verdana, sans-serif;
            max-width: 900px;
            margin: 40px auto;
            padding: 20px;
            background: #f9f9f9;
            color: #333;
        }
```

```
        h1 {
            color: #2c3e50;
            border-bottom: 2px solid #3498db;
            padding-bottom: 10px;
        }
        button {
            background: #3498db;
            color: white;
            border: none;
            padding: 12px 24px;
            font-size: 16px;
            border-radius: 5px;
            cursor: pointer;
            margin: 20px 0;
        }
        button:hover {
            background: #2980b9;
        }
        #output {
            background: white;
            border: 1px solid #ddd;
            border-radius: 8px;
            padding: 15px;
            font-family: 'Courier New', monospace;
            white-space: pre-wrap;
            margin-bottom: 30px;
        }
        canvas {
            border: 1px solid #ccc;
            background: white;
            display: block;
            margin: 20px auto;
        }
        .note {
            font-size: 0.9em;
            color: #666;
        }
    </style>
</head>
<body>
    <h1>Multiscale Diversity–Stability Cascade Simulator</h1>
    <p class="note">Simulates the two-patch linear model, computes regional stability, stability conductance, and draws the diversity–stability landscape. Also performs leave-one-out cross-validation comparing linear vs quadratic models.</p>
```

```
<button onclick="runSimulation()">Run Simulation</button>
<div id="output"></div>
<canvas id="landscapeCanvas" width="700" height="400"></canvas>

<script>
    // ============================================================
    // Utility: Gaussian random number generator (Box-Muller)
    // ============================================================
    function randn() {
        let u = 0, v = 0;
        while (u === 0) u = Math.random();
        while (v === 0) v = Math.random();
        return Math.sqrt(-2.0 * Math.log(u)) * Math.cos(2.0 * Math.PI * v);
    }

    // Generate correlated Gaussian white noise using Cholesky decomposition
    function correlatedNoise(rho, sigma, n) {
        // Covariance matrix [[sigma^2, rho*sigma^2], [rho*sigma^2, sigma^2]]
        let e1 = new Array(n);
        let e2 = new Array(n);
        // Cholesky factor: L = [[sigma, 0], [rho*sigma, sigma*sqrt(1-rho^2)]]
        let L11 = sigma;
        let L21 = rho * sigma;
        let L22 = sigma * Math.sqrt(1 - rho * rho);
        for (let i = 0; i < n; i++) {
            let z1 = randn();
            let z2 = randn();
            e1[i] = L11 * z1;
            e2[i] = L21 * z1 + L22 * z2;
        }
        return { e1, e2 };
    }

    // ============================================================
    // Two-patch linear simulation
    // ============================================================
    function simulateTwoPatch(a, d, sigma, rho, T, dt) {
        const nSteps = Math.floor(T / dt);
        let x1 = new Array(nSteps).fill(0);
        let x2 = new Array(nSteps).fill(0);
        let time = new Array(nSteps);
        for (let i = 0; i < nSteps; i++) time[i] = i * dt;

        let { e1, e2 } = correlatedNoise(rho, sigma, nSteps);
```

```
    for (let t = 1; t < nSteps; t++) {
        let dx1 = (-a * x1[t-1] + d * (x2[t-1] - x1[t-1])) * dt + e1[t] * Math.sqrt(dt);
        let dx2 = (-a * x2[t-1] + d * (x1[t-1] - x2[t-1])) * dt + e2[t] * Math.sqrt(dt);
        x1[t] = x1[t-1] + dx1;
        x2[t] = x2[t-1] + dx2;
    }

    let region = new Array(nSteps);
    for (let i = 0; i < nSteps; i++) region[i] = x1[i] + x2[i];

    return { time, patch1: x1, patch2: x2, region };
}

// ============================================================
// Regional stability (inverse coefficient of variation)
// ============================================================
function regionalStability(regionSeries) {
    let n = regionSeries.length;
    let mu = 0;
    for (let v of regionSeries) mu += v;
    mu /= n;
    let variance = 0;
    for (let v of regionSeries) variance += (v - mu) ** 2;
    variance /= n;
    let sd = Math.sqrt(variance);
    return mu / sd;
}

// ============================================================
// Analytic stability conductance (Appendix A.2)
// ============================================================
function stabilityConductanceAnalytic(muB, sigma, rho, a, k = 0.1) {
    return (k * muB * Math.sqrt(a)) / (2 * sigma * Math.pow(1 + rho, 1.5));
}

// ============================================================
// Simple linear regression (returns slope, intercept)
// ============================================================
function linearRegression(x, y) {
    let n = x.length;
    let sumX = 0, sumY = 0, sumXY = 0, sumXX = 0;
    for (let i = 0; i < n; i++) {
        sumX += x[i];
```

```
            sumY += y[i];
            sumXY += x[i] * y[i];
            sumXX += x[i] * x[i];
        }
        let slope = (n * sumXY - sumX * sumY) / (n * sumXX - sumX * sumX);
        let intercept = (sumY - slope * sumX) / n;
        return { slope, intercept };
    }

    // ============================================================
    // Draw diversity–stability landscape on canvas
    // ============================================================
    function drawLandscape(canvasId, D_betaValues, S_gammaValues) {
        let canvas = document.getElementById(canvasId);
        let ctx = canvas.getContext('2d');
        ctx.clearRect(0, 0, canvas.width, canvas.height);
        let margin = { top: 40, right: 30, bottom: 50, left: 70 };
        let plotWidth = canvas.width - margin.left - margin.right;
        let plotHeight = canvas.height - margin.top - margin.bottom;
        let xMin = Math.min(...D_betaValues) - 0.1;
        let xMax = Math.max(...D_betaValues) + 0.1;
        let yMin = Math.min(...S_gammaValues) - 0.1;
        let yMax = Math.max(...S_gammaValues) + 0.1;
        function toX(val) { return margin.left + ((val - xMin) / (xMax - xMin)) * plotWidth; }
        function toY(val) { return canvas.height - margin.bottom - ((val - yMin) / (yMax - yMin)) *
plotHeight; }

        // Axes
        ctx.strokeStyle = '#333';
        ctx.lineWidth = 1;
        ctx.beginPath();
        ctx.moveTo(margin.left, margin.top);
        ctx.lineTo(margin.left, canvas.height - margin.bottom);
        ctx.lineTo(canvas.width - margin.right, canvas.height - margin.bottom);
        ctx.stroke();

        // Labels
        ctx.fillStyle = '#333';
        ctx.font = '12px Arial';
        ctx.textAlign = 'center';
        ctx.fillText('Beta diversity (D_beta)', margin.left + plotWidth/2, canvas.height - 10);
        ctx.save();
        ctx.translate(15, margin.top + plotHeight/2);
        ctx.rotate(-Math.PI/2);
```

```
        ctx.fillText('Regional stability (S_gamma)', 0, 0);
        ctx.restore();

        // Plot points and line
        ctx.strokeStyle = '#3498db';
        ctx.fillStyle = '#e74c3c';
        ctx.lineWidth = 2;
        ctx.beginPath();
        for (let i = 0; i < D_betaValues.length; i++) {
            let cx = toX(D_betaValues[i]);
            let cy = toY(S_gammaValues[i]);
            if (i === 0) ctx.moveTo(cx, cy);
            else ctx.lineTo(cx, cy);
        }
        ctx.stroke();
        for (let i = 0; i < D_betaValues.length; i++) {
            let cx = toX(D_betaValues[i]);
            let cy = toY(S_gammaValues[i]);
            ctx.beginPath();
            ctx.arc(cx, cy, 4, 0, 2 * Math.PI);
            ctx.fill();
        }
    }

    // ============================================================
    // Main simulation function
    // ============================================================
    function runSimulation() {
        let output = document.getElementById('output');
        output.innerHTML = 'Running simulation... Please wait.\n';

        // Use setTimeout to allow UI update before heavy computation
        setTimeout(() => {
            let log = '';

            // ---- 1. Simulate two-patch model ----
            const a = 0.5, d = 0.3, sigma = 0.8, rho = 0.4, T = 200, dt = 0.1;
            let data = simulateTwoPatch(a, d, sigma, rho, T, dt);
            let S_gamma = regionalStability(data.region);
            log += `Two-patch simulation (T=${T}, a=${a}, d=${d}, sigma=${sigma},
rho=${rho})\n`;
            log += `Regional stability S_gamma = ${S_gamma.toFixed(3)}\n\n`;

            // ---- 2. Analytic stability conductance ----
```

```
let muB = data.region.reduce((s, v) => s + v, 0) / data.region.length;
let k = 0.1;
let tau_analytic = stabilityConductanceAnalytic(muB, sigma, rho, a, k);
log += `Analytic stability conductance tau_beta = ${tau_analytic.toFixed(4)}\n`;

// ---- 3. Numerical stability conductance ----
const rhoValues = [0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9];
let S_values = [];
for (let rho_i of rhoValues) {
    let data_i = simulateTwoPatch(a, d, sigma, rho_i, 150, dt);
    S_values.push(regionalStability(data_i.region));
}
let reg = linearRegression(rhoValues, S_values);
let tau_numeric = reg.slope * (-k);
log += `Numerical stability conductance tau_beta = ${tau_numeric.toFixed(4)}\n\n`;

// ---- 4. Diversity–stability landscape ----
const D_beta_range = [0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8];
let stability_landscape = [];
for (let D_beta of D_beta_range) {
    let rho_eff = Math.max(0.9 - 1.0 * D_beta, 0.05);
    let data_temp = simulateTwoPatch(0.5, 0.3, 0.8, rho_eff, 150, dt);
    stability_landscape.push(regionalStability(data_temp.region));
}
drawLandscape('landscapeCanvas', D_beta_range, stability_landscape);
log += `Diversity–stability landscape computed (${D_beta_range.length} points). See chart.\n\n`;

// ---- 5. Leave-one-out cross-validation ----
const n_regions = 20;
let D_beta_obs = [];
let rho_obs = [];
let S_gamma_obs = [];
for (let i = 0; i < n_regions; i++) {
    let db = 0.1 + Math.random() * 0.7; // 0.1 to 0.8
    D_beta_obs.push(db);
    rho_obs.push(0.9 - db);
}
for (let i = 0; i < n_regions; i++) {
    let data_i = simulateTwoPatch(0.5, 0.3, 0.8, rho_obs[i], 200, dt);
    S_gamma_obs.push(regionalStability(data_i.region));
}

// Linear model: S ~ D_beta
```

```
// Quadratic model: S ~ D_beta + D_beta^2
let mse_linear = 0, mse_quadratic = 0;
for (let testIdx = 0; testIdx < n_regions; testIdx++) {
    let trainIdx = [];
    for (let j = 0; j < n_regions; j++) if (j !== testIdx) trainIdx.push(j);

    // Prepare training data
    let xTrain = trainIdx.map(j => D_beta_obs[j]);
    let yTrain = trainIdx.map(j => S_gamma_obs[j]);
    let xTest = [D_beta_obs[testIdx]];
    let yTest = S_gamma_obs[testIdx];

    // Linear regression on training
    let regLin = linearRegression(xTrain, yTrain);
    let predLin = regLin.slope * xTest[0] + regLin.intercept;
    mse_linear += (predLin - yTest) ** 2;

    // Quadratic regression: fit y = b0 + b1*x + b2*x^2 using normal equations
    // X matrix: [1, x, x^2]
    let X = trainIdx.map(j => [1, D_beta_obs[j], D_beta_obs[j]**2]);
    let Y = yTrain;
    // Solve (X^T X) beta = X^T Y manually for 3 coefficients
    let XtX = [[0,0,0],[0,0,0],[0,0,0]];
    let XtY = [0,0,0];
    for (let j = 0; j < X.length; j++) {
        let row = X[j];
        for (let p = 0; p < 3; p++) {
            XtY[p] += row[p] * Y[j];
            for (let q = 0; q < 3; q++) {
                XtX[p][q] += row[p] * row[q];
            }
        }
    }
    // Solve 3x3 linear system using Cramer's rule (simple but fine)
    function det3(m) {
        return m[0][0]*(m[1][1]*m[2][2]-m[1][2]*m[2][1])
             - m[0][1]*(m[1][0]*m[2][2]-m[1][2]*m[2][0])
             + m[0][2]*(m[1][0]*m[2][1]-m[1][1]*m[2][0]);
    }
    let detA = det3(XtX);
    if (Math.abs(detA) < 1e-10) {
        // fallback: use linear prediction
        let predQuad = predLin;
        mse_quadratic += (predQuad - yTest) ** 2;
```

```
                } else {
                    // Cramer's rule for each coefficient
                    let M0 = [
                        [XtY[0], XtX[0][1], XtX[0][2]],
                        [XtY[1], XtX[1][1], XtX[1][2]],
                        [XtY[2], XtX[2][1], XtX[2][2]]
                    ];
                    let M1 = [
                        [XtX[0][0], XtY[0], XtX[0][2]],
                        [XtX[1][0], XtY[1], XtX[1][2]],
                        [XtX[2][0], XtY[2], XtX[2][2]]
                    ];
                    let M2 = [
                        [XtX[0][0], XtX[0][1], XtY[0]],
                        [XtX[1][0], XtX[1][1], XtY[1]],
                        [XtX[2][0], XtX[2][1], XtY[2]]
                    ];
                    let b0 = det3(M0) / detA;
                    let b1 = det3(M1) / detA;
                    let b2 = det3(M2) / detA;
                    let predQuad = b0 + b1 * xTest[0] + b2 * xTest[0]**2;
                    mse_quadratic += (predQuad - yTest) ** 2;
                }
            }
            mse_linear /= n_regions;
            mse_quadratic /= n_regions;
            log += `Leave-one-out cross-validation results:\n`;
            log += `  MSE (linear model)      = ${mse_linear.toFixed(4)}\n`;
            log += `  MSE (quadratic model)   = ${mse_quadratic.toFixed(4)}\n`;
            log += `  Conclusion: ${mse_quadratic < mse_linear ? 'Quadratic model fits better, suggesting a nonlinear (hump-shaped) relationship.' : 'Linear model fits better or similarly.'}\n`;

            output.textContent = log;
        }, 50);
    }
    </script>
</body>
</html>
```

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