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A hierarchical predictive theory of biodiversity change driven by environmental filtering of species traits: From environmental filtering to multi-scale dynamic integration

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Abstract
Current predictions of biodiversity change often rely on statistical correlations between species occurrences and environmental variables, or on single-scale species distribution models. Such approaches do not explicitly represent the causal chain that links environmental change, trait-based performance differences among organisms, and the resulting shifts in taxonomic, functional, and phylogenetic diversity. This study proposes the theory that environmental filtering of species traits is a central mechanistic link between environmental change and biodiversity dynamics, and that this link can be formalized through a trait filtering operator. The study proposes an original framework termed the Trait Filtering-Diversity Dynamics Hierarchy, abbreviated TF-DDH. The framework connects four organizational levels: individual fitness surfaces, population growth rates, community assembly, and regional species pools. At the core of the framework is a measurable mapping from environmental states and trait combinations to persistence probabilities. From this mapping, one can derive a filtering spectrum, trait sensitivity, and diversity change spectra. The study presents a set of quantitative methods to estimate the filtering operator, including hierarchical Bayesian models, structural causal models, and interpretable machine learning. It also describes simulation and empirical designs for testing the framework and illustrates how the framework can be applied to global change scenarios. The scientific significance of the approach is that it moves environmental filtering from a heuristic metaphor toward a formal, testable, and transferable predictive structure. The applied value is that it can improve early warning of biodiversity reorganization and guide trait-based conservation and restoration.

Keywords environmental filtering; functional traits; biodiversity change; predictive model; hierarchical theory; eco-evolutionary feedback; trait filtering operator; multi-scale integration.

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1 Introduction

1.1 Background

Global biodiversity is undergoing rapid reorganization, and in many regions decline, under the combined pressures of climate change, land-use change, biological invasions, and other anthropogenic disturbances (Sala et al., 2000; Pereira et al., 2010; Newbold et al., 2016; IPBES, 2019; Zhang, 2026a, 2027a). Predicting the direction and magnitude of biodiversity change has become a central challenge for ecology and conservation biology (Dawson et al., 2011; Urban, 2015; Zhang, 2026a-b, 2026f-h, 2027a). A large body of work has documented that local assemblages are changing in composition even when species richness remains relatively stable (Dornelas et al., 2014; Blowes et al., 2019; Antão et al., 2020). This pattern implies that predictions based only on species richness can miss important functional and phylogenetic reorganization. Consequently, there is growing demand for predictive models that are mechanistic enough to capture how environmental change reshapes the trait composition of communities and how those shifts translate into biodiversity change.

1.2 Limitations of existing approaches

Species distribution models are among the most widely used tools for predicting biodiversity responses to environmental change (Guisan and Thuiller, 2005; Elith and Leathwick, 2009; Zhang and Chen, 2011). These models typically estimate the relationship between species occurrence and environmental predictors, then project that relationship into future environmental scenarios. While useful, such models are often correlative at their core. They do not explicitly represent the demographic or performance-based processes by which environmental conditions favor some trait values over others (Guisan and Thuiller, 2005; Merow et al., 2014). Joint species distribution models extend this approach by modelling multiple species simultaneously and accounting for residual co-occurrence patterns (Pollock et al., 2014). However, even these models usually treat traits as covariates rather than as the central objects through which environmental filtering operates.

Community-level models and trait-based assembly models have made progress in connecting environmental gradients to community trait distributions (Shipley et al., 2006; Laughlin et al., 2012). For example, maximum entropy approaches can predict relative abundances from trait values and environmental conditions (Shipley et al., 2006; Sonnier et al., 2010). Dynamic vegetation models and trait-based ecosystem models link plant functional types or continuous trait distributions to ecosystem processes (Enquist et al., 2015). These approaches still face several challenges: (1) the concept of environmental filtering is frequently invoked as a metaphor rather than defined as an operational mapping (Kraft et al., 2015; Cadotte and Tucker, 2017). (2) Many studies focus on a single scale, such as local community assembly, while biodiversity responses emerge from processes operating from individuals to regional species pools (Leibold et al., 2004; Chase and Myers, 2011; Zhang, 2015, 2016, 2018). (3) Most models emphasize static trait-environment correlations and do not explicitly model temporal lags, thresholds, or eco-evolutionary feedbacks (Norberg et al., 2019; Harrison et al., 2020).

1.3 Objectives and core questions

The core question of this paper is how environmental filtering of species traits can be formalized into a predictive theory of biodiversity change. The specific objectives are to review the theoretical foundations of trait-based community ecology, to define a measurable trait filtering operator, to build a hierarchical framework that links filtering at the individual level to diversity at multiple scales, to present quantitative methods for estimating filtering intensity and trait sensitivity, and to outline simulation and empirical tests.

1.4 Innovations

The study makes four main contributions: (1) it introduces the trait filtering operator as a formal mapping from environmental states and trait combinations to persistence probabilities. This moves environmental filtering from a loose metaphor to a computational object. (2) It proposes a multi-scale hierarchical framework, TF-

DDH, that connects individual fitness surfaces, population dynamics, community assembly, and regional species pools. (3) It integrates causal inference (Zhang, 2021a-c, 2027b), hierarchical Bayesian modelling, and interpretable machine learning into a unified estimation strategy. (4) It develops early-warning indicators based on shifts in community trait distributions and filtering spectra.

2 Theoretical Foundations

2.1 Evolution of environmental filtering theory

The idea that environmental conditions act as a sieve on species traits has deep roots in community ecology. Diamond (1975) discussed assembly rules as constraints on which species can coexist in a given environment. Grime (1977) proposed that environmental stress and disturbance select for distinct plant strategies, captured by the competitor, stress-tolerator, and ruderal framework. Keddy (1992) explicitly framed community assembly as the outcome of environmental filters that remove species lacking suitable traits. This perspective became influential because it offered a simple causal narrative: environmental gradients determine which trait values are viable in a given site, and species with those trait values are more likely to persist.

The environmental filtering metaphor was subsequently extended by trait-based community ecology, which treats functional traits as a common currency linking organisms to their environments (McGill et al., 2006; Violle et al., 2007). Functional traits are defined as measurable characteristics of individuals that influence performance through their effects on growth, reproduction, or survival (Violle et al., 2007; Zhang, 2026c-e, 2027b; Zhang and Qi, 2026). By focusing on traits rather than species identities, ecologists hoped to produce more general and transferable predictions (McGill et al., 2006). Early applications quantified the relationship between community-weighted mean traits and environmental gradients, often finding strong associations (Lavorel and Garnier, 2002; Ackerly and Cornwell, 2007). These associations were interpreted as evidence for environmental filtering.

At the same time, a critical literature emerged arguing that the environmental filtering metaphor can be misleading. Kraft et al. (2015) noted that observed trait clustering does not necessarily indicate filtering, because trait clustering can arise from competitive interactions, dispersal limitation, or phylogenetic conservatism. They proposed that filtering should be tested against null models and that the term should be restricted to cases where environmental conditions directly reduce the fitness of particular trait values. Cadotte and Tucker (2017) went further and asked whether environmental filtering should be abandoned as a concept. They argued that the term conflates several distinct processes, including abiotic constraints, biotic interactions, and historical effects. These critiques do not imply that environmental effects on trait distributions are unimportant. Rather, they imply that the concept requires more formal specification to be useful for prediction.

2.2 Trait-environment relationships

Global analyses have demonstrated that key plant traits covary with climate and soil conditions (Zhang, 2026f). The worldwide leaf economics spectrum captures a continuum from acquisitive leaves with high specific leaf area and high nitrogen content to conservative leaves with low specific leaf area and low nitrogen content (Wright et al., 2004; Reich, 2014). This spectrum is associated with gradients in temperature, precipitation, and soil fertility (Reich et al., 1997; Ordoñez et al., 2009). Wood density and plant height also show coordinated global patterns, forming a wood economics spectrum and a size axis that together with leaf traits describe much of the global variation in plant form and function (Chave et al., 2009; Díaz et al., 2016). Díaz et al. (2016) found that six major dimensions of plant variation capture the dominant axes of global functional diversity, and these axes are only partially aligned with environmental gradients. This result supports the idea that environmental filtering does not act on all traits equally, and that different environmental factors may filter different trait combinations.

Trait-environment relationships are not limited to plants. For many animal groups, body size, thermal tolerance, diet breadth, and dispersal ability are related to climatic gradients and habitat conditions (Foden et al., 2019; Mouillot et al., 2020; Zhang, 2026g). These relationships provide the empirical basis for the idea that environmental change will systematically favor certain trait values over others, thereby changing community trait distributions. However, most observed trait-environment relationships are correlational. They show that communities in warmer or drier places tend to have certain trait values, but they do not directly measure how environmental conditions reduce the persistence of species with unsuitable traits.

2.3 Existing models for biodiversity change prediction

Several classes of models are used to predict biodiversity change. Species distribution models estimate the probability of occurrence of species as a function of environmental variables and then project this function into future or novel environments (Guisan and Thuiller, 2005; Elith and Leathwick, 2009). These models can be fitted to large datasets and are operationally convenient, but they rely on the assumption that the realized niche can be inferred from current distributions and that this niche will remain stable under environmental change (Araújo and New, 2007; Thuiller et al., 2008). Joint species distribution models account for residual co-occurrence and can estimate environment-trait interactions when traits are included as predictors (Pollock et al., 2014; Norberg et al., 2019). However, they generally do not model individual performance or demographic filtering.

Trait-based assembly models make a more explicit link between traits and community structure. Shipley et al. (2006) used maximum entropy to predict relative abundances from trait values and environmental variables, demonstrating that a small number of traits can explain substantial variation in community composition. Laughlin et al. (2012) extended this approach by incorporating intraspecific trait variation, showing that models that ignore intraspecific variation can misestimate the strength of environmental filtering. These models typically assume that communities are at equilibrium with their environment, an assumption that is questionable under rapid environmental change.

Dynamic vegetation models simulate the distribution of plant functional types or continuous trait values based on physiological and demographic processes (Enquist et al., 2015). These models can in principle represent the demographic effects of environmental filtering, but they are computationally demanding and often require detailed parameterization. Hybrid approaches combine mechanistic demographic models with statistical species distribution models (Merow et al., 2014; Ehrlén and Morris, 2015). For example, integral projection models can link environmental conditions to individual growth, survival, and reproduction, and then scale up to population and range dynamics (Coulson, 2012; Merow et al., 2014). These approaches are promising but are usually species-specific and difficult to generalize to entire communities.

2.4 Gaps and directions

The existing literature reveals several gaps: (1) environmental filtering is frequently treated as a descriptive pattern rather than a formal process, which limits its predictive power (Kraft et al., 2015; Cadotte and Tucker, 2017). (2) Most models operate at a single scale, either individual, population, community, or regional, whereas biodiversity change is a multi-scale phenomenon (Leibold et al., 2004; Chase and Myers, 2011). (3) The response of biodiversity to environmental change is known to involve temporal lags, thresholds, and feedbacks, yet these dynamic features are rarely incorporated into predictive models (Norberg et al., 2019; Harrison et al., 2020; Zhang, 2026a-b, 2026h). (4) Taxonomic, functional, and phylogenetic diversity may respond differently to the same environmental change, but predictions typically focus on species richness (Mouillot et al., 2013; Tucker et al., 2017). A predictive framework is needed that integrates these elements.

3 Original Theoretical Framework: Trait Filtering–Diversity Dynamics Hierarchy

3.1 Core concepts

The framework is built on a small set of formal concepts (Appendix).

The trait filtering operator, or TFO, is defined as a mapping from an environmental state vector E and a trait combination matrix T to a persistence probability P. Formally,

$$P = F(E, T) + \varepsilon$$

where F is a function that may be nonlinear and asymmetric, and ε represents stochastic variation and historical contingency. The operator is intended to capture the direct effect of environmental conditions on the probability that an individual or species with a given trait combination persists in a given location over a defined time interval.

The filtering spectrum is defined as the set of marginal effects of the TFO across different trait dimensions. For a trait axis z, the filtering spectrum can be obtained by integrating the TFO over the environmental state distribution and over the other trait dimensions. The filtering spectrum describes which trait dimensions are most strongly selected by a given environmental gradient.

Trait sensitivity is the local slope of the filtering spectrum with respect to an environmental variable. It measures how much the persistence probability changes when the environmental variable changes, for a given trait value. A high trait sensitivity means that small environmental changes produce large changes in the filtering of that trait.

The diversity change spectrum is the resulting pattern of change in taxonomic, functional, and phylogenetic diversity across spatial and temporal scales. It can be expressed as the rate and direction of change in different diversity components as functions of environmental drivers.

3.2 Basic assumptions

The theory rests on five assumptions: (1) traits are the direct targets of environmental filtering. Environmental conditions influence individual survival, growth, reproduction, and dispersal through their effects on trait performance (Violle et al., 2007; Laughlin and Messier, 2015; Zhang, 2026c-e, 2027b). (2) Filtering operates hierarchically across organizational levels. Individual-level fitness differences alter population growth rates, which in turn modify community trait distributions, which then change regional species pools through migration and extinction (Leibold et al., 2004; Vellend, 2010). (3) Filtering intensity and direction vary in space and time. Environmental gradients, disturbances, and resource pulses create non-stationary selection regimes (Chesson, 2000; Chase and Myers, 2011). (4) Ecological and evolutionary processes interact. Filtering can drive trait evolution, and trait evolution can modify filtering outcomes, producing feedbacks that affect long-term predictions (Hendry, 2017). (5) Taxonomic, functional, and phylogenetic diversity may respond asynchronously or even in opposite directions to the same filtering event (Mouillot et al., 2013; Tucker et al., 2017).

3.3 Hierarchical structure and mechanistic chain

The TF-DDH framework links four levels.

At the individual level, environmental conditions determine a fitness surface over a multidimensional trait space. This surface describes the expected fitness of an individual as a function of its trait values under a given environment (Laughlin and Messier, 2015). Environmental change moves or reshapes the fitness surface. Trait values that were previously near a local optimum may become suboptimal, reducing individual performance and persistence.

At the population level, the average fitness of individuals with different trait values determines population growth rates and carrying capacities. Species whose trait values are favored by the current environment tend to increase in abundance, while species with unfavored trait values decline. Intraspecific trait variation and phenotypic plasticity can moderate this response, because some individuals within a population may possess trait values closer to the new optimum (Violle et al., 2012; Laughlin et al., 2012).

At the community level, population dynamics interact with biotic filtering, including competition, facilitation, and trophic interactions (Zhang, 2015). These biotic processes can amplify or dampen environmental filtering. The community trait distribution moves toward an attractor jointly determined by abiotic and biotic filters (HilleRisLambers et al., 2012; Kraft et al., 2015). If environmental filtering is directional, the community trait mean shifts. If filtering is stabilizing, the trait variance decreases. If filtering is disruptive, the trait variance may increase.

At the regional level, local communities are connected through dispersal from a regional species pool. Species with trait values suitable for current environments can immigrate and maintain local diversity even after local extinctions. Conversely, if environmental change is widespread, the regional species pool itself may lose trait combinations, reducing gamma diversity and limiting the potential for future community reassembly (Leibold et al., 2004; Vellend, 2016). The hierarchical chain is completed by eco-evolutionary feedbacks: community trait shifts alter ecosystem functions such as productivity, litter quality, and microclimate, which in turn modify the environment experienced by individuals (Loreau et al., 2001; Hooper et al., 2005; Cardinale et al., 2012).

3.4 Multidimensionality and directionality of trait filtering

Environmental factors rarely act on a single trait in isolation. Drought, for example, may simultaneously filter hydraulic conductivity, specific leaf area, root depth, and seed mass (Díaz et al., 2016; Chave et al., 2009). Because traits are correlated through trade-offs and allometric relationships, selection on one trait often has indirect effects on others. The filtering spectrum is therefore a multidimensional object. The directionality of filtering can be directional, stabilizing, or disruptive. Directional filtering shifts the trait distribution mean and tends to reduce functional diversity. Stabilizing filtering narrows the trait distribution around an optimum and also reduces functional diversity. Disruptive filtering selects for extreme trait values and can increase functional diversity. The net effect on diversity depends on which trait dimensions are filtered and how those dimensions relate to the functional diversity metric used (Villéger et al., 2008; Laliberté and Legendre, 2010).

3.5 Temporal dynamics

Community trait distributions do not respond instantaneously to environmental change. There are several sources of lag. Species may persist for some time as remnant populations even when environmental conditions are no longer favorable, because demographic inertia and storage effects can buffer declines (Chesson, 2000). Recruitment limitation and dispersal limitation can delay the immigration of better adapted species (Leibold et al., 2004). When environmental filtering intensity crosses a threshold, communities may undergo abrupt state shifts, for example from forest to grassland, producing rapid changes in taxonomic and functional diversity (Scheffer et al., 2001; Zhang, 2016, 2026b). Historical contingency and priority effects can mean that the same environmental change produces different biodiversity outcomes depending on the initial trait composition and arrival order of species (Fukami, 2015). These dynamic features imply that time series models and non-equilibrium approaches are essential for prediction.

4 Methodological System

4.1 Data requirements and preprocessing

The estimation of the trait filtering operator requires four types of data. Trait data are available from global databases such as TRY and BIEN, which contain millions of trait records for plant species (Kattge et al., 2011; Kattge et al., 2020; Maitner et al., 2018). Community data come from plot networks, monitoring programs, and global repositories such as BioTIME and PREDICTS (Dornelas et al., 2018; Hudson et al., 2017). Environmental data include climate grids, soil layers, topographic variables, and land-use records. Phylogenetic data are needed for phylogenetic diversity and can be obtained from time-calibrated phylogenies and tools such as Phylomatic (Webb and Donoghue, 2005). Preprocessing must address intraspecific trait variation, missing trait values, and the harmonization of different trait sources (Violle et al., 2012; Kattge et al., 2020). Multiple imputation and hierarchical imputation using phylogenetic information are often appropriate (Blomberg et al., 2003).

4.2 Quantifying filtering intensity and trait sensitivity

Filtering intensity can be estimated from shifts in community trait distributions along environmental gradients. One common approach is to regress community-weighted mean traits and community trait variances against environmental variables, using either linear mixed models or gradient boosting machines (Ackerly and Cornwell, 2007; Breiman, 2001). However, community-weighted means confound environmental filtering with other assembly processes (Zhang, 2015). A more direct approach is to estimate the effect of environmental variables on the probability that a given trait value persists, using demographic or occupancy data. Hierarchical Bayesian models are well suited to this task because they can propagate uncertainty across levels and account for missing data (Gelman et al., 2013; Carpenter et al., 2017). Structural equation models can be used to test the hypothesized causal chain from environment to traits to diversity (Grace, 2009; Lefcheck, 2016). Machine learning models such as random forests and extreme gradient boosting can capture nonlinear interactions, and Shapley additive explanations can be used to extract trait-specific contributions (Lundberg and Lee, 2017; Chen and Guestrin, 2016).

The filtering spectrum can be estimated by evaluating the marginal effect of an environmental variable on persistence probability as a function of trait value. For example, if the TFO is fitted with a generalized additive model, the partial dependence of persistence probability on a trait under high versus low environmental stress gives the filtering spectrum for that trait dimension. Trait sensitivity is the derivative of this partial dependence with respect to the environmental variable.

4.3 Predictive model construction

A practical predictive workflow can combine several model components within a hierarchical Bayesian framework (Appendix). Let y_{it} denote the abundance or presence of species i at site t. Let z_i denote the trait values of species i, and let E_t denote environmental conditions at site t. A simple hierarchical model for the persistence probability p_{it} can be written as

$$\text{logit}(p_{it}) = \alpha + \beta_E E_t + \beta_T z_i + \beta_{ET} E_t z_i + u_i + v_t$$

where β_{ET} captures the interaction between environment and traits, u_i is a species random effect, and v_t is a site random effect. This interaction term represents the trait filtering operator. Extensions can include multiple trait dimensions, nonlinear effects, and spatiotemporal autocorrelation.

To scale from individuals to populations, demographic models can be used. Integral projection models describe how individual size or trait distributions change over time under environmental conditions (Coulson, 2012; Merow et al., 2014). The environment-specific survival and growth kernels of an integral projection model provide a direct estimate of the TFO at the individual level. The population growth rate λ is then

computed as the dominant eigenvalue of the kernel, and changes in λ across environments indicate population-level filtering.

To scale from populations to communities, trait-based assembly models can be coupled with the estimated TFO. For instance, one can specify that the relative abundance of species i in community c is proportional to $\exp(\gamma\, f(E_c, z_i))$ where f is the estimated filtering function and γ is a scaling parameter (Shipley et al., 2006; Sonnier et al., 2010). This produces predictions for community-weighted trait means and functional diversity under novel environments.

Uncertainty can be propagated through all levels using posterior predictive simulation (Gelman et al., 2013; Vehtari et al., 2017). Leave-one-out cross-validation and spatial block validation can be used to assess predictive performance (Vehtari et al., 2017; Roberts et al., 2017). Bayesian model averaging can account for structural uncertainty among alternative model formulations (Hoeting et al., 1999).

4.4 Model validation and uncertainty analysis

Validation should include temporal extrapolation, spatial extrapolation, and simulation-based recovery tests. In temporal extrapolation, the model is fitted to an early period and used to predict later diversity change. In spatial extrapolation, the model is trained in one region and tested in another with similar environmental gradients. Simulation-based validation is particularly important because the true filtering function is known by construction in simulated data, allowing direct recovery tests. Uncertainty decomposition should separate parameter uncertainty, model structural uncertainty, and scenario uncertainty. Approaches such as ensemble forecasting and Bayesian model averaging are useful for this purpose (Araújo and New, 2007; Hoeting et al., 1999).

5 Case Studies and Simulation and Empirical Tests

5.1 Simulation test

A first test of the framework can be conducted with individual-based community assembly simulations. The simulation generates a regional species pool with trait values drawn from a known multivariate distribution. Individuals are assigned to sites with known environmental gradients. Each individual has a survival probability given by a known TFO, such as a Gaussian fitness function over a single trait axis, with the optimum determined by the environment. After simulated recruitment, competition, and dispersal, community trait distributions are recorded over time (Zhang, 2015). The simulated data are then analyzed using the proposed estimation workflow to test whether the filtering spectrum, trait sensitivity, and diversity change can be recovered. Because the true TFO is known, this provides a strong test of identifiability and bias. Simulation experiments can vary the strength of filtering, the dimensionality of the trait space, and the amount of dispersal limitation to assess robustness.

5.2 Empirical gradient test

Natural environmental gradients provide independent validation. Elevation gradients and aridity gradients are particularly useful because they contain strong environmental variation over relatively short distances (Körner, 2007). Along such gradients, one can collect community composition, trait measurements, and environmental data. The TFO can be estimated from spatial turnover in trait distributions, and its predictions can be compared with observed patterns of alpha and beta functional diversity (Villéger et al., 2008; Laliberté and Legendre, 2010). A key test is whether the filtering spectrum inferred from spatial gradients can predict temporal changes when the gradient shifts under climate change. If the filtering operator is transferable, then the same trait-environment interaction should explain both spatial and temporal variation.

5.3 Global change scenario application

The framework can be applied at global scale using trait databases and community datasets. Future climate scenarios from global circulation models provide environmental projections (Zhang, 2026a-b; Zhang and Liu, 2012). The estimated TFO can be used to predict changes in community-weighted trait values and functional diversity in different biomes under scenarios for 2050 and 2100 (Thuiller et al., 2008; Guisan et al., 2017). Regions where filtering intensity is high and functional diversity is projected to decline can be identified as filtering-sensitive areas and prioritized for conservation. This type of analysis has been conducted for some taxa and regions, but the TFO framework provides a more unified and mechanistic basis for such projections (Foden et al., 2019; Mouillot et al., 2020).

5.4 Time series dynamic analysis

Long-term monitoring data provide direct evidence on temporal dynamics. The BioTIME database compiles assemblage time series from many ecosystems and can be used to test whether trait-based measures respond to environmental change with the expected lags and nonlinearities (Dornelas et al., 2018). For example, repeated surveys in grasslands under experimental warming or nutrient addition can be used to estimate changes in community trait distributions over time and to compare these changes with predictions from spatial trait-environment relationships (Suding et al., 2008; Bjorkman et al., 2018). Such tests can reveal whether community trait shifts are delayed relative to environmental change and whether thresholds exist beyond which functional diversity collapses.

6 Discussion

6.1 Comparative advantages

The TFO framework has several advantages over conventional correlative models: (1) it represents environmental filtering as an explicit function linking environmental states and trait combinations to persistence probabilities, which makes the causal pathway testable and transferable (Kraft et al., 2015; Cadotte and Tucker, 2017). (2) It is hierarchical, connecting individual performance to population dynamics, community assembly, and regional diversity (Vellend, 2010; Leibold et al., 2004). (3) It can simultaneously predict changes in taxonomic, functional, and phylogenetic diversity, whereas species distribution models typically predict only species-level responses (Mouillot et al., 2013; Tucker et al., 2017). (4) It can incorporate eco-evolutionary feedbacks and non-equilibrium dynamics through its modular structure (Hendry, 2017; Fukami, 2015). These features are likely to improve prediction in novel environments, where species-level correlative models are known to be fragile (Guisan and Thuiller, 2005; Araújo and New, 2007).

6.2 Theoretical contributions

The framework contributes to ecological theory by converting environmental filtering from a metaphor into a formal object. The trait filtering operator and filtering spectrum provide a common language for describing how different environmental drivers select on different trait dimensions. The hierarchy clarifies how individual-level performance differences scale up to community and regional diversity change. The concept of trait sensitivity offers a measurable indicator of how strongly a given trait is filtered by a given environmental gradient. These concepts may also be useful for comparing filtering across taxa and ecosystems.

6.3 Limitations

Several limitations must be acknowledged. Trait data are incomplete for many taxa and regions, and missingness can bias estimates of filtering strength (Kattge et al., 2020; Violle et al., 2012). Intraspecific variation is difficult to capture fully at large scales, yet it can modulate community responses to environmental change (Laughlin et al., 2012). Distinguishing environmental filtering from dispersal limitation and demographic stochasticity remains a statistical challenge (Kraft et al., 2015; Vellend, 2010). Eco-evolutionary feedbacks require long-term genetic and phenotypic data that are rarely available (Zhang, 2026c-e; Zhang and

Qi, 2026). Finally, extreme climate states and novel ecosystems may fall outside the range of historical trait-environment relationships, limiting the reliability of extrapolation (Williams and Jackson, 2007). These limitations imply that the framework should be used with appropriate uncertainty quantification and tested against independent data.

6.4 Conservation and management implications

The framework has practical implications. It can identify which trait combinations are most sensitive to future environmental change and therefore which species and functional groups are most at risk (Foden et al., 2019). It can map filtering-sensitive areas where functional diversity is likely to decline rapidly, informing protected area planning and climate adaptation (Dawson et al., 2011; Urban, 2015; Zhang, 2026a-b, 2026f-g). It can guide ecological restoration by identifying trait values that are likely to persist under future conditions, rather than relying solely on historical reference communities (Suding et al., 2008; Funk et al., 2017). It can also support monitoring programs by providing trait-based early warning indicators, such as shifts in community trait skewness or rapid changes in trait sensitivity, that may precede species loss.

7 Conclusion

This paper has proposed a hierarchical predictive theory in which environmental filtering of species traits is the central mechanism linking environmental change to biodiversity dynamics. The theory formalizes filtering through a trait filtering operator and derives from it a filtering spectrum, trait sensitivity, and diversity change spectra. A multi-scale framework connects individual fitness surfaces to population growth, community assembly, and regional species pools. The paper has outlined a methodological system for estimating the filtering operator using hierarchical Bayesian models, structural causal models, and interpretable machine learning, and has described simulation and empirical tests. The approach is intended to improve prediction under global change by making the environmental filtering process explicit and testable. Future work should integrate genomic and phenomic data (Zhang, 2026c-e, 2027b; Zhang and Qi, 2026), develop real-time trait monitoring, and construct global maps of filtering spectra to improve the spatial and temporal resolution of biodiversity predictions.

Appendix

A.1 Formal definition of the trait filtering operator

Let E be a vector of environmental variables measured at a site and time. Let T be a matrix whose rows correspond to species or individuals and whose columns correspond to trait values. The trait filtering operator is a function F that maps E and the trait vector z of a focal organism to a persistence probability p over a defined time interval:

$$p = F(E, z) + \varepsilon$$

where ε captures stochastic variation with mean zero. In the simplest logistic form,

$$\text{logit}(p) = \alpha + \beta_E^T E + \beta_z^T z + z^T \Omega E$$

where α is an intercept, β_E and β_z are main effect vectors, and Ω is a matrix of interaction coefficients. The interaction term $z^T \Omega E$ is the core of the filtering operator, because it represents how the effect of environment depends on trait values. If Ω has rank one, the interaction reduces to a single latent trait dimension that is most strongly filtered by a given environmental axis.

The filtering spectrum for trait dimension j is defined as

$S_j(e) = \partial F(E, z) / \partial z_j$ evaluated at $E = e$

integrated over the distribution of the other trait variables and over the environmental states of interest. This spectrum shows which trait values are favored or disfavored along an environmental gradient.

Trait sensitivity for trait j with respect to environmental variable k is

$TS_{jk} = \partial^2 F(E, z) / (\partial z_j \partial E_k)$

When this quantity is positive, increasing the environmental variable increases the advantage of larger trait values. When negative, larger trait values become increasingly disadvantageous.

A.2 Hierarchical Bayesian model for community trait change

At the community level, let Y_{it} be the abundance of species i at site t. A hierarchical model can be written as

$Y_{it} \sim \text{Poisson}(\lambda_{it})$

$\log(\lambda_{it}) = \mu + \theta_i + \delta_t + \beta^T E_t + \gamma^T z_i + z_i^T \Omega E_t$

$\theta_i \sim \text{Normal}(0, \sigma_\theta^2)$

$\delta_t \sim \text{Normal}(0, \sigma_\delta^2)$

where θ_i and δ_t are species and site random effects, respectively. The interaction matrix Ω captures trait filtering. Priors on Ω can be regularizing, such as a horseshoe prior, to avoid overfitting in high-dimensional trait spaces.

The model can be extended to functional diversity by predicting community-weighted trait means and Rao quadratic entropy from the fitted λ_{it}. These derived quantities can then be compared with observed values under cross-validation.

A.3 Simulation algorithm for recovery testing

A simple individual-based simulation proceeds as follows.

(1) Generate a regional pool of S species, each with a trait value z_i drawn from a normal distribution with mean μ_{pool} and variance σ_{pool}^2.

(2) Define an environmental gradient across L sites, with site l having environment E_l.

(3) Specify the true TFO as a Gaussian fitness function over the trait:

$w(z, E_l) = \exp(- (z - b\, E_l)^2 / (2\, \sigma_f^2))$

where b controls the strength of environmental filtering and σ_f controls the width of the filtering function.
(4) Initialize each site with an equal number of individuals from each species.
(5) In each time step, apply survival probability $w(z_i, E_l)$, then reproduce surviving individuals proportionally to their abundance, and finally apply dispersal at rate m from the regional species pool.
(6) Repeat for T time steps and record community trait means, variances, and species richness.

The recorded data are then fitted using the hierarchical Bayesian model described above. Recovery of the known parameter b and σ_f indicates that the estimation workflow can identify the TFO.

A.4 Data preprocessing steps

Trait data should be log-transformed when appropriate and standardized to zero mean and unit variance. Missing trait values can be imputed using phylogenetic imputation or multiple imputation by chained equations. Community data should be rarefied or modeled with observation error. Environmental variables should be checked for collinearity, and dimensionality reduction such as principal component analysis can be used when many correlated variables are present. All preprocessing choices should be reported and tested for sensitivity.

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