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The Niche–Energy–Time triadic synergy hypothesis (NET Hypothesis): A unified explanatory framework for determinants of species diversity

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Abstract

The geographical patterning of species diversity, most famously the latitudinal gradient, one of the oldest and most celebrated patterns in ecology, still lacks a unified mechanistic explanation. Existing hypotheses, including the species–energy hypothesis, the environmental heterogeneity hypothesis, the area hypothesis, neutral theory, metabolic theory, maximum entropy theory, and historical–evolutionary hypotheses, each capture a critical dimension of diversity generation. Yet none alone can explain why regions with identical energy inputs can differ so dramatically in species richness. After systematically reviewing these classical and cutting-edge theories, I propose a novel integrative framework: the Niche–Energy–Time triadic synergy hypothesis (NET hypothesis) in present paper. The NET hypothesis starts from three irreducible ultimate constraints: a thermodynamic constraint, available energy flux (*E*) sets the upper limit on the total biomass and number of individuals a community can sustain; a structural constraint, multidimensional niche space volume (*H*) determines the fineness with which that energy flow can be partitioned among species; and a historical constraint, the effective evolutionary and community assembly time (*T*) determines the degree to which that niche space has been filled. I argue that species diversity is an emergent outcome of these three constraints acting as a serial filter not a linear function of any single factor. I present the core mathematical structure of the NET hypothesis, demonstrate its logical necessity by deriving it from population energy allocation, the niche-width–species-number trade-off, and the macro-dynamics of speciation–extinction balance, and show its power to unify a wide range of classical diversity patterns, including the latitudinal gradient, elevational patterns, and island species–area relationships, as well as anomalous cases. The NET hypothesis does not overturn existing hypotheses but embeds energy, heterogeneity, area, and time into the *E*, *H*, and *T* dimensions, revealing the synergistic mechanisms by which they act as necessary but not sufficient conditions. It provides a testable, quantifiable, mechanistic foundation for predicting biodiversity change and guiding conservation planning.

Keywords species diversity; latitudinal gradient; niche theory; species–energy hypothesis; evolutionary time; metabolic theory; unified theory; macroecology.

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1 Introduction

1.1 The problem: the universality and persistent puzzle of species diversity geography

The uneven distribution of species diversity across the Earth's surface is one of the most striking and longest-studied macroecological patterns. From Alexander von Humboldt's early observations in the Andes, through Wallace's delineation of biogeographic realms, to modern quantitative analyses based on global databases, the decline in species richness from the equator to the poles, i.e., the latitudinal diversity gradient (LDG), has remained at the top of ecology's agenda (Hillebrand, 2004; Pontarp et al., 2019; Zhang, 2026). This gradient shows an impressive cross-taxon universality: terrestrial plants, mammals, birds, reptiles, amphibians, insects, and even marine organisms all exhibit broadly similar patterns (Willig et al., 2003; Mannion et al., 2014). Yet the LDG is far from the only macroecological pattern. Along elevational gradients, species richness often shows a mid-elevation peak or a monotonic decline, with complex underlying patterns (Rahbek, 1995; McCain & Grytnes, 2010). In island systems, the species–area relationship (SAR) has become one of ecology's most robust empirical laws, but the explanatory power of area per se is often confounded by habitat diversity, island age, and other factors (MacArthur & Wilson, 2001; Triantis et al., 2012). Ocean depth gradients, peninsula effects, and many other geographical patterns further enrich the complexity of the problem (Stevens, 1989).

Despite more than half a century of intensive research, a fundamental question remains unresolved: what ultimately determines the species diversity of a given region? More precisely, is there a minimal set of irreducible basic constraints whose synergistic action can, from first principles, deduce all of these macroecological patterns? This paper is organized around precisely this core question.

The difficulty stems from the intertwining of multiple causalities. Single-factor explanatory approaches, whether using energy variables such as mean annual temperature or net primary productivity (Currie, 1991; Hawkins et al., 2003), water–energy balance variables such as precipitation or actual evapotranspiration (O'Brien, 2006; Zhang and Chen, 2011), or environmental heterogeneity variables such as topographic relief and habitat diversity (Stein et al., 2014), often show significant explanatory power for specific taxa and regions but systematically fail when extrapolated across taxa and regions. Even more troubling is the high collinearity among these factors: tropical regions simultaneously enjoy high energy input, high water availability, high habitat complexity, and long-term climatic stability, making it extremely difficult to statistically separate their individual contributions (Rosenzweig, 1995; Gaston, 2000).

An even deeper theoretical difficulty is that even if we can statistically describe the spatial variation in diversity with high accuracy, we may not be able to explain it causally. In his seminal work, Currie (1991) found that actual evapotranspiration could explain more than 70% of the variation in richness of North American trees, mammals, birds, and reptiles, yet this correlation itself does not reveal the causal direction: does energy drive diversity, or does high diversity enhance ecosystem functioning and thus feed back onto energy flux? The rise of neutral theory further exacerbated this dilemma: Hubbell (2001) demonstrated that stochastic birth–death processes and limited dispersal alone could produce species abundance distributions remarkably consistent with observations, without invoking any niche differences or environmental variables. Metabolic theory entered from the opposite extreme: Brown et al. (2004) argued that biogeographic patterns of biodiversity are essentially macroscopic manifestations of the temperature dependence of individual metabolic rates. Yet Hawkins et al. (2007), in a global test of metabolic theory, found that the relationship between species richness and temperature was highly contingent on taxon and geographic region, lacking the universality predicted by metabolic theory. The coexistence of these competing theoretical frameworks indicates that a mechanistic consensus on macroecological diversity patterns is far from achieved.

Thus, the core question of this paper can be further sharpened: is there a minimal set of constraints, each irreducible to the others, whose nonlinear interaction suffices to unify the macroecological geography of species diversity? The answer I propose rests on three fundamental constraints, energy, niche space, and evolutionary time, and I argue that they constitute a complete basis for understanding the deterministic mechanisms of diversity.

1.2 Research objectives and significance

The objectives of this study have both theoretical and applied dimensions.

Theoretically, this study aims to transcend the traditional paradigm of listing factors and to establish a decisive theory of species diversity based on first principles. Specifically, I propose the Niche–Energy–Time triadic synergy hypothesis (NET hypothesis), arguing that available energy flux (E), multidimensional niche space volume (H), and effective evolutionary/assembly time (T) are the three irreducible ultimate constraints on species diversity, and I present the mathematical expression of their nonlinear interaction. This theoretical framework does not simply consider multiple factors simultaneously; it reveals the serial filter logic among them: energy provides the raw material of diversity, niche space provides the partitioning blueprint and evolutionary time determines the degree of realization. Any severe deficiency in a single dimension constitutes a bottleneck for diversity accumulation.

Methodologically, I construct a rigorous deductive pathway for the NET hypothesis: starting from the metabolic energy allocation of population growth, introducing the intrinsic trade-off between niche width and species number, and combining the macro-dynamic equilibrium of speciation and extinction, I demonstrate the logical inevitability of the NET core equation. I further propose operationalizable parameterization strategies—E quantified by remote-sensing net primary productivity (NPP) or actual evapotranspiration (AET), H estimated as the effective number of multivariate environmental principal components and their range of variation, and T represented by the geological time since the last major climatic disturbance or by phylogenetically weighted lineage ages, thus providing a clear path for empirical testing.

In application, the NET hypothesis offers a mechanistic guidance framework for biodiversity conservation. In the context of global change, human activities are impacting E (via land-use change altering productivity), H (via habitat homogenization compressing niche space), and T (via accelerated extinction disrupting long-term community assembly stability) at unprecedented rates and intensities. The NET framework makes it clear that protecting only energy (productivity) or area, while neglecting the maintenance of niche dimensionality and evolutionary history, cannot ensure the persistence of diversity. Conservation planning must attend to the integrity of all three dimensions simultaneously.

2 Comprehensive Review and Systematic Analysis of Existing Research

2.1 Environmental capacity hypotheses: diversity as a function of resources and space

2.1.1 The species–energy hypothesis and productivity hypothesis

The species–energy hypothesis is one of the oldest and most empirically tested theoretical approaches to explaining diversity gradients. Its core logic is deceptively simple: the more available energy a region has, the more individuals it can support (the more individuals hypothesis), thereby allowing more species to coexist at minimum viable population sizes (Wright, 1983; Srivastava & Lawton, 1998). Brown (1981) formalized this as the species–energy theory arguing that energy is the primary factor limiting species richness.

Empirical studies have provided strong, though not decisive, support. Currie (1991) found that species richness of four groups of North American vertebrates was highly correlated with actual evapotranspiration (AET). Hawkins et al. (2003), in a meta-analysis covering 85 global case studies, reported that water–energy variables outperformed other climatic and non-climatic variables in explaining species richness in 82 cases, explaining, on average, more than 60% of the variation when considered alone. Wright (1983), in a classic study of island birds, established a quantitative relationship between energy flux and species richness.

However, a core challenge to the species–energy hypothesis is the inconsistency in the shape of the species–productivity relationship. In their landmark review, Mittelbach et al. (2001) found that the relationship between species richness and productivity can take the form of monotonic increases, monotonic decreases, hump-shaped (unimodal) curves, or no significant pattern across spatial scales and systems, with no single universal relationship. Adler et al. (2011) further demonstrated that, at both global and regional scales, there was no clear relationship between net primary productivity and local (meter-scale) plant species richness, urging ecologists to look beyond productivity for other processes. Gillman and Wright (2014), from another angle, questioned the more individuals hypothesis suggesting that the energy–diversity relationship may not be mediated by individual numbers but may act directly via speciation rates.

These inconsistencies reveal a deep limitation of the species–energy hypothesis: energy is a necessary but far from sufficient condition for diversity. Two regions with identical energy flux can have vastly different diversity levels, with tropical deserts being a vivid example. This indicates that other dimensions play equally critical roles in regulating diversity.

2.1.2 The environmental heterogeneity hypothesis

The habitat heterogeneity hypothesis argues that diversity of the physical environment, including topographic complexity, soil type diversity, climatic variability, etc., allows more species to coexist by providing more dimensions of niche space (MacArthur, 1965; Stein et al., 2014). This hypothesis aligns with the internal logic of niche theory: each species occupies a unique *n*-dimensional hypervolume (Hutchinson, 1957), so the larger the total volume of niche space, the more species it can accommodate.

Tews et al. (2004) found that most studies supported a positive relationship between habitat heterogeneity and animal species diversity, but this relationship showed significant variation among species groups. Cramer and Willig (2004) tested the hypothesis in semi-arid ecosystems and found that habitat heterogeneity primarily affected diversity by altering the relative proportions of species in different habitat types rather than by changing species richness per se. Stein et al. (2014) noted that environmental heterogeneity is a universal driver of large-scale species richness patterns, but its effect is often confounded with area and energy: more heterogeneous regions also tend to have larger areas and higher energy fluxes.

It is noteworthy that habitat heterogeneity echoes the habitat diversity hypothesis in island biogeography. In island systems, area affects species richness not only through the area per se effect (larger islands support larger populations, reducing stochastic extinction risk) but also through the habitat diversity effect: larger islands typically contain more habitat types, thereby accommodating species adapted to different habitats (Simberloff, 1976; Triantis et al., 2012).

However, the environmental heterogeneity hypothesis also faces significant challenges. Firstly, which environmental gradients are relevant depends on the ecological characteristics of the study taxon, making heterogeneity a highly taxon-dependent concept. Second, the grain size of heterogeneity, i.e., the spatial scale of environmental variation, is closely related to how organisms perceive and utilize the environment, but this matching relationship is often neglected in macroecological studies. More importantly, even at identical levels of heterogeneity, the absolute diversity can differ by orders of magnitude due to historical factors such as the length of time a region has been colonized, pointing directly to the importance of the temporal dimension.

2.1.3 The area hypothesis and island biogeography

The relationship between area and species richness is one of the oldest and best-documented empirical patterns in ecology. Arrhenius (1921) and Gleason (1922) first proposed a power-law model describing this relationship: $S = cA^z$, where S is species number, A is area, and c and z are constants. MacArthur and Wilson (1963, 2001) elevated this empirical relationship to a theoretical framework with their equilibrium theory of island biogeography, positing that species richness on islands represents a dynamic balance between immigration and extinction, with area and isolation being the two key parameters regulating this balance.

The species–area relationship (SAR) has been widely verified across systems, from oceanic islands to terrestrial habitat fragments, from lakes to mountaintops. However, closer scrutiny of SAR mechanisms reveals that area is not a simple, unidimensional explanatory variable. Simberloff (1976) early on pointed out that the area per se hypothesis and the habitat diversity hypothesis are two logically distinct but empirically difficult-to-distinguish competing explanations. Recent research has further incorporated island age and geological dynamics: Whittaker et al. (2008) proposed the general dynamic theory predicting that species richness on oceanic islands follows a hump-shaped trajectory over the island's life cycle: young islands have few species, species accumulate as the island matures, and decline again as the island ages and undergoes erosion and subsidence. In a re-evaluation of the general dynamic theory, Steinbauer et al. (2013) showed that the peak in species richness occurs earlier than the peak in endemic species richness, and that area has a greater effect on total species richness than on the proportion of endemics.

Discussing the ecological and evolutionary drivers of the species–area relationship, Fine (2015) pointed out that the ecological mechanisms of the area effect (larger areas provide more individuals, lower extinction probabilities, and more habitat types) are intertwined with evolutionary mechanisms (larger areas may promote higher speciation rates and lower extinction rates), making it overly simplistic to classify area as merely an ecological or evolutionary factor.

2.2 Biotic regulation hypotheses: interspecific interactions and niche processes

2.2.1 Classical niche theory and the competitive exclusion principle

The concept of the niche is the cornerstone for understanding species coexistence. Hutchinson (1957) defined the niche as the multidimensional space of environmental conditions within which a species can maintain its population indefinitely (the *n*-dimensional hypervolume), providing a conceptual framework for the quantitative study of species–environment relationships. MacArthur and Levins (2001) proposed the limiting similarity theory, positing that the niche overlap among coexisting species has an upper limit, beyond which competitive exclusion will occur. This theory profoundly influenced community ecology for decades thereafter, establishing the core proposition that niche differentiation promotes diversity maintenance.

In his modern coexistence theory, Chesson (2000) refined this proposition into two classes of mechanisms: stabilizing mechanisms (niche differences that cause intraspecific competition to be stronger than interspecific competition) promote species coexistence; equalizing mechanisms promote coexistence by reducing fitness differences among species, thus slowing competitive exclusion (Zhang, 2011, 2014; Zhang et al., 2014). This framework provides an elegant conceptual system for understanding local-scale species coexistence.

However, classical niche theory faces the challenge of scaling up from local coexistence to large-scale geographical patterns. Observed niche differentiation patterns in communities can explain why certain species can coexist in a particular community, but they cannot directly explain why different regions differ by orders of magnitude in total species numbers. The niche dimensionality itself, as a container, the potential space that can accommodate species, is a variable shaped by environmental heterogeneity, climatic stability, and evolutionary history, rather than an independently given constant.

2.2.2 Neutral theory and its diversity predictions

Hubbell's (2001) Unified Neutral Theory of Biodiversity and Biogeography (UNTB) has been one of the most disruptive theoretical advances of the past two decades. The theory assumes that all individuals in a community are ecologically equivalent, having identical probabilities of birth, death, migration, and speciation, and that community dynamics are driven entirely by ecological drift and random dispersal. Under this extreme simplification, neutral theory successfully predicts multiple macroecological patterns, including species abundance distributions (SADs) and species–area relationships.

The strength of neutral theory lies in its role as a null hypothesis: it demonstrates that, at least under certain conditions, community patterns consistent with observations can be generated without invoking niche differences among species. Chave (2004) provided a systematic exposition of the mathematical foundations of neutral theory, noting that its success stems from the emergent properties of stochastic processes at large scales. However, neutral theory also faces serious empirical challenges. McGill (2003) showed that neutral models perform poorly in predicting species richness: there are often systematic deviations between observed and neutrally predicted species richness. Clark (2009) further pointed out that neutral theory cannot explain the non-random distribution of species along environmental gradients, nor the directional changes in community composition following environmental perturbations.

From the experience of neutral theory, we can extract an important theoretical lesson: stochastic processes (drift, dispersal limitation) are undoubtedly an important component of macroecological diversity patterns, but they are not strictly opposed to niche processes; rather, they may operate together at different relative importances across different spatiotemporal scales. Leibold and McPeek (2006) argued that the synthesis of niche and neutral perspectives, rather than an either-or choice, is the way forward for ecological theory development.

2.2.3 Niche construction, predation pressure, and the intermediate disturbance hypothesis

In addition to competition and drift, other dimensions of biotic interactions also participate in regulating diversity (de Araujo, 2019; Rana, 2020; Venkataiah and Ramesh, 2024). In their niche construction theory, Odling-Smee et al. (2003) emphasized that organisms are not merely passive occupants of niches but also active modifiers, through metabolic activities, behavioral choices, and ecosystem engineering effects, organisms alter their own and others' environmental conditions, thereby creating new niche space and modifying existing selection pressures. This feedback mechanism may be particularly pronounced in hyperdiverse tropical ecosystems: high species richness itself may, through niche construction, increase niche space dimensions, forming a positive autocatalytic loop.

The influence of predator–prey interactions on diversity is equally profound (Zhang, 2011, 2012, 2018; de Araujo, 2019; Rana, 2020; Venkataiah and Ramesh, 2024). In a classic experiment, Paine (1966) demonstrated that top predators could significantly increase overall community species richness by suppressing the abundance of competitively dominant species. The Janzen–Connell hypothesis focuses on the promotion of species coexistence by density-dependent host-specific natural enemies: the higher the density of conspecific individuals, the greater the probability of attack by specialized natural enemies, thereby providing living space for competitively inferior heterospecific individuals (Janzen, 1970; Connell, 1971). This mechanism is thought to play a key role in the maintenance of the exceptionally high diversity of tropical forests.

Connell (1978) proposed the Intermediate Disturbance Hypothesis (IDH), which integrates biotic and abiotic processes from another angle. The IDH predicts that species diversity is maximized at intermediate levels of disturbance frequency, post-disturbance time, or spatial scale, too little disturbance allows competitive exclusion to eliminate weak competitors, while too much disturbance allows only a few tolerant or rapidly colonizing species to persist. Roxburgh et al. (2004) critically examined the theoretical basis of the IDH, noting that the occurrence of a diversity peak at intermediate disturbance levels depends on the existence of a clear trade-off between competitive ability and colonization ability. However in a systematic review of empirical evidence for the IDH, Mackey and Currie (2001) showed that while supporting studies exist, they are far from universal. Fox (2013) further argued that the IDH should be understood as an occasional phenomenon under specific conditions, not a general law of community ecology.

Taken together, biotic regulation hypotheses, although fruitful in explaining local coexistence mechanisms, have inherent limitations in their applicability and generalizability. These hypotheses focus on how species coexist locally rather than why some regions can accommodate orders of magnitude more species than others. Bridging from local to regional scales, from mechanisms to patterns, requires a theoretical framework capable of cross-scale integration.

2.3 Historical and evolutionary hypotheses: time and speciation rate

2.3.1 The evolutionary time hypothesis and the "museum" hypothesis

The core assertion of the evolutionary time hypothesis is that species diversity is higher in the tropics because tropical ecosystems have maintained greater continuity and stability over long geological history, thus providing more time for species accumulation. Wallace (1878) had early noted this possibility, and Fischer (1960) systematically formulated it as the evolutionary time hypothesis. Stebbins (1974) proposed the tropical museum hypothesis further clarifying that the tropics act as a museum preserving more ancient lineages while simultaneously serving as a cradle continuously producing new species. Testing the museum versus cradle hypothesis in ants, Moreau and Bell (2013) found that the tropics simultaneously serve both functions—a refuge for ancient lineages and a generator of new species.

In a study of generic plant diversity in tropical Africa, Dagallier et al. (2019) identified the spatial distribution of cradles and museums noting that determining where species differentiated (cradles) and where they have persisted (museums) is crucial for understanding biodiversity distribution and conservation priorities. In their systematic review of evolutionary and ecological explanations for the LDG, Mittelbach et al. (2007) identified time-and-area hypotheses and diversification rate hypotheses as the two major evolutionary hypotheses for the origin of the LDG. The core argument of the former is that the tropical climate is older and historically occupied larger areas, providing more opportunities for diversification; the latter argues that speciation rates are higher or extinction rates lower in the tropics.

Fine and Ree (2006) provided empirical support for the time–area hypothesis. They found a significant positive correlation between current tree species diversity and a time-integrated parameter of area across geological epochs (Eocene, Oligocene, Miocene to present), indicating that the cumulative effect of historical area and time is an important factor shaping the contemporary latitudinal diversity gradient.

2.3.2 The tropical niche conservatism hypothesis

Wiens and Donoghue (2004) proposed the tropical niche conservatism hypothesis (TCH), which provides an elegant evolutionary explanation for the latitudinal diversity gradient. The logical chain of this hypothesis is as follows: (1) most biological lineages originated in tropical environments; (2) due to phylogenetic niche conservatism: the tendency of species to retain the climatic niche characteristics of their ancestors, many tropical-origin lineages find it difficult to evolve tolerance to temperate cold climates; (3) therefore, the tropics accumulate far more species than temperate regions, because temperate regions have been colonized only after a few lineages broke through the niche conservatism barrier. In an evaluation of the TCH, Kerkhoff et al. (2014) noted that its parsimony makes it a highly attractive mechanism for explaining large-scale diversity gradients, but it requires further phylogenetic testing.

An important strength of the TCH is that it simultaneously addresses both time and niche dimensionality: it not only points out the asymmetry in historical colonization time (limited time window for dispersal from the tropics to temperate regions) but also the constraint of niche evolution itself (niche conservatism limiting adaptation to non-tropical environments). However, the TCH encounters difficulties in explaining the rapid adaptive radiations of certain groups in high-latitude regions (e.g., conifers, salmonid fishes), which demonstrate that niche evolution is not always strictly constrained.

2.3.3 Macro-dynamics of speciation, extinction, and dispersal

From the perspective of macroevolutionary dynamics, the level of species diversity in a region is fundamentally determined by the relative balance of three rates: speciation, extinction, and dispersal (Briggs, 2013-2016). With his concept of the regional species pool, Ricklefs (2004) emphasized that the diversity of local communities is not merely the result of ecological processes but also the product of regional history—including long-term speciation, large-scale dispersal, and mass extinction events. Analyzing the fossil record, Jablonski et al. (2006) showed that the tropics have served not only as a diversity source (high speciation rates) but also as a diversity accumulator (low extinction rates) over multiple geological periods, jointly shaping today's latitudinal diversity gradient.

Mittelbach et al. (2007) further noted that the existence of a latitudinal gradient in speciation rates is itself a phenomenon yet to be explained. Dowle et al. (2013) proposed that a latitudinal gradient in molecular evolutionary rates, i.e., faster molecular evolution in the tropics, could accelerate the evolution of reproductive isolation and thus elevate speciation rates, providing a microevolutionary mechanistic basis for the LDG. However, decisive empirical support for this hypothesis is currently lacking.

2.4 Contributions and gaps of existing integrative attempts

2.4.1 Metabolic Theory of Ecology (MTE)

Brown et al. (2004) proposed the Metabolic Theory of Ecology (MTE), an ambitious attempt at unification. MTE starts from the quantitative relationship between individual metabolic rate and body temperature and body size, i.e., the Boltzmann–Arrhenius equation, and through scaling, derives multiple macro-patterns of populations, communities, and even ecosystems. On the diversity question, MTE predicts that species richness should be exponentially related to the inverse of environmental temperature, thereby reducing the latitudinal diversity gradient to the effect of temperature on metabolic kinetics.

However, the empirical challenges facing MTE cannot be ignored. In a global evaluation of terrestrial species richness gradients, Hawkins et al. (2007) found that the richness–temperature relationship was highly contingent on taxonomy and geography, lacking the universal response predicted by MTE. Testing MTE on elevational diversity gradients of amphibians and reptiles, Algar et al. (2007) similarly found that MTE predictions were supported only on some gradients. In their global evaluation of metabolic theory as an explanation for terrestrial species richness gradients, Hawkins et al. (2007) concluded that while there is evidence that temperature affects species diversity, its influence is not exerted through the single mechanism of temperature dependence of individual metabolic rates as MTE proposes.

The most critical gap in MTE is that it emphasizes only the thermodynamic constraint (temperature affecting metabolism and thus energy allocation) while treating the structure of niche space and the depth of evolutionary history as residual variables. Two ecosystems with identical temperatures can have drastically different diversity levels, for example, the tropical montane cloud forests on the eastern slopes of the Andes versus the Sahara Desert, a fact demonstrating that variation in metabolic rate alone is far from sufficient to predict differences in species numbers.

2.4.2 Maximum Entropy Theory of Ecology (METE)

Harte (2011) proposed the Maximum Entropy Theory of Ecology (METE), representing another form of unification attempt. METE applies the maximum entropy principle from statistical physics to ecology, arguing that, given a set of macroscopic constraints (total area, total number of individuals, total number of species, etc.), the state distribution of an ecosystem should be the one that maximizes entropy among all possible micro-configurations satisfying those constraints. METE has shown impressive accuracy in predicting species abundance distributions and species–area relationships (Harte et al., 2008; Zhang, 2012, 2016, 2018).

Harte and Newman (2014) further combined METE with MTE to derive equations of state linking species richness, energy flow, biomass, and abundance, successfully capturing the relationships among these state variables in 42 datasets. Gao et al. (2024) recently proposed that power-law distributions (Zhang, 2023, 2016, 2018), as predicted by maximum information entropy theory, could serve as a unified model of species abundance distributions, accurately describing the SADs of animals, plants, and microorganisms across all habitats and abundance scales.

However, the core limitation of METE is that while it successfully describes patterns, it does not fully reveal the causal mechanisms that generate those patterns. The maximum entropy principle is fundamentally a statistical inference method, not a causal process theory. As McGill (2010) noted in his review of unified theories, ecology already has at least six different unified theories, each emphasizing different underlying processes, from niche to neutral to metabolic, and this in itself is a problem, because the truly ideal unified theory in science should be unique. McGill suggested that geographic space, species traits, and time need to be incorporated into a unified theory to bridge the gap between theory and pattern.

2.4.3 Hierarchical frameworks and multi-factor integration

Jetz and Fine (2012) proposed a hierarchical framework that jointly incorporates historical area–productivity dynamics and contemporary environments, successfully predicting the latitudinal diversity gradient of global terrestrial vertebrates. A key innovation of this framework is its explicit recognition of the scales at which different factors operate: area and history operate at regional and biome scales, while productivity and temperature act at local scales. Belmaker and Jetz (2012) further tested this hierarchical framework in vertebrates.

In their review of the latitudinal diversity gradient, Pontarp et al. (2019) provided one of the most comprehensive integrative assessments in recent years. They emphasized that no single mechanism alone can explain the universality of the LDG, and that the joint action of multiple processes, including niche conservatism, speciation rate gradients, environmental energy constraints, and historical disturbances, is a more plausible explanation. They called for the development of integrative frameworks that can simultaneously encompass ecological and evolutionary dimensions, linking contemporary and historical processes.

Yet, even the most advanced integrative attempts still leave unanswered a fundamental question: what are the rules of interaction among energy, niche, and time? Do they act independently and additively on diversity, or do they synergize in a specific nonlinear manner? This is precisely the core theoretical gap that the NET hypothesis aims to fill.

3 Theoretical innovation: The Niche–Energy–Time triadic synergy hypothesis (NET hypothesis)

3.1 First principles and basic logic

The construction of the NET hypothesis is based on a core methodological stance: a decisive theory of species diversity must start from irreducible ultimate constraints, not from empirical correlations (Fig. 1). This stance draws inspiration from the first principles thinking paradigm in theoretical physics, starting from a closed set of basic constraints through rigorous deductive reasoning, to derive testable empirical predictions. I identify three irreducible constraint dimensions, none of which can be fully replaced or derived from the others:

Constraint 1: Thermodynamic constraint—available energy flux (*E*). The maintenance and proliferation of living systems consume free energy. The total amount of free energy that an ecosystem can capture and convert per unit time has a physical upper limit, which determines the maximum total number of individuals and total biomass that the system can sustain (Brown et al., 2004; Allen et al., 2007). Available energy flux is the raw material of diversity: given a minimum viable population size, the upper limit on total individual number sets a coarse upper bound on species richness. However, this constraint only sets a thermodynamic ceiling for diversity; it does not determine how energy is partitioned among species.

Constraint 2: Structural constraint—multidimensional niche space volume (*H*). Even if energy is abundant, if the environment is ecologically homogeneous (Zhang et al., 2015): all individuals face the same resource types and the same abiotic conditions, then competitive exclusion will lead to a few dominant species monopolizing resources, and high diversity cannot be realized. The number of niche dimensions and the span of each dimension determine the fineness with which energy flow can be partitioned among species (Hutchinson, 1957; MacArthur & Levins, 2001; Zhang, 2012, 2016, 2018; Rushdi and Alsalami, 2021). *H* is a function of both abiotic environmental gradients (e.g., the range of variation in temperature, moisture, and nutrient gradients) and biotic interaction networks (e.g., food web structure, symbiotic relationships, host specificity). The larger the niche space volume, the greater the possibility that energy flow can be "divided" along more dimensions, thus providing the structural basis for more species to coexist.

Constraint 3: Historical constraint—effective evolutionary and community assembly time (*T*). Abundant energy and broad niche space together provide the potential for diversity, but the realization of that potential requires time (Zhang, 2015, 2018). The formation of species (via the evolution of reproductive isolation) and their dispersal filling (via geographic migration) are rate-limited processes. Moreover, major environmental disturbances (e.g., glacial–interglacial cycles, large-scale volcanic activity, sea-level changes) may reset the diversity accumulation process of communities, making the effective assembly time much shorter than the absolute geological time (Jablonski et al., 2006; Fine & Ree, 2006). Thus, what determines diversity is not simply how long the region has existed but rather the continuous, cumulative time, under relatively stable environmental conditions, available for species to continuously form, immigrate, and persist (Zhang, 2015, 2016).

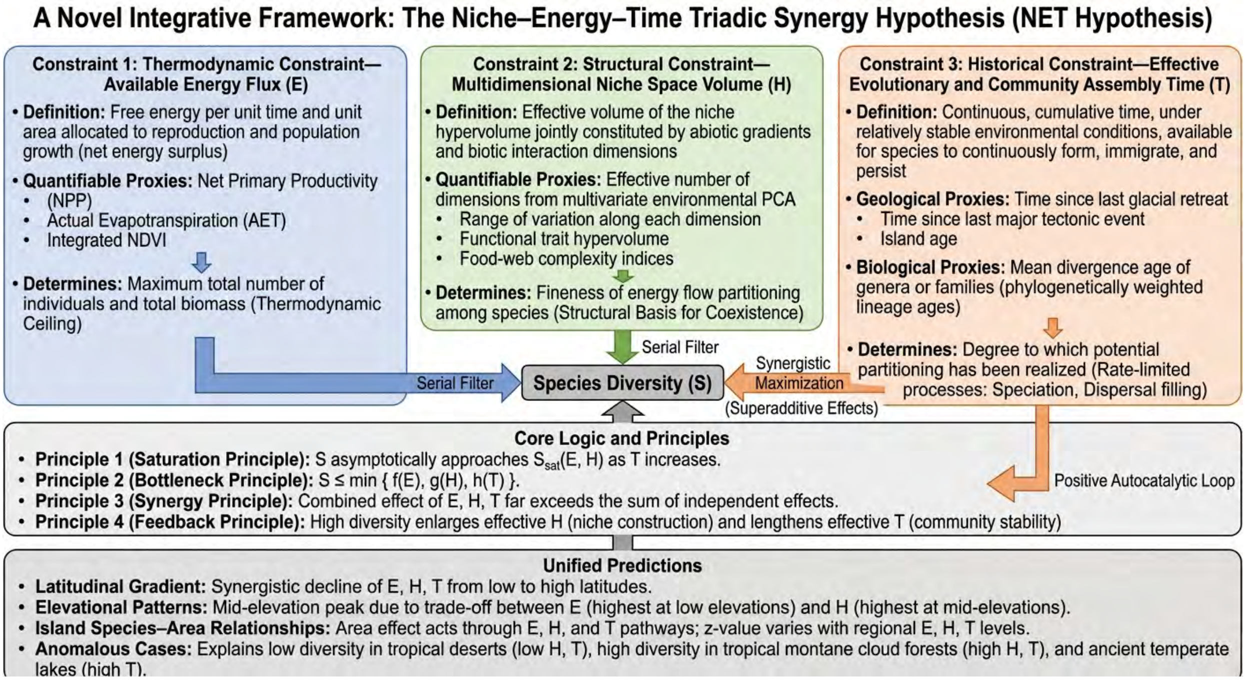

Fig. 1 The illustrated framework for the Niche–Energy–Time triadic synergy hypothesis (NET hypothesis).

The core logic of the NET hypothesis unfolds from this: species diversity is the emergent outcome of these three constraints acting as a serial filter. Energy determines the thermodynamic upper limit of "how much life" the system can support; niche space determines the structural possibility of in how many ways that energy can be partitioned; and evolutionary time determines to what degree that partitioning has actually been realized.

The relationship among the three is serial, not parallel—any severe deficiency in one dimension becomes a bottleneck for diversity, while the synergistic maximization of all three is the root cause of tropical hyperdiversity. This logic can be expressed as the following principles:

Principle 1 (Saturation Principle): For given E and H, as T increases, species richness S asymptotically approaches a saturation value $S_{\mathrm{sat}}(E, H)$ jointly determined by E and H. The rate at which speciation and immigration fill niche space decreases with time because available niches are progressively occupied.

Principle 2 (Bottleneck Principle): $S \leqslant \min \{ f(E), \mathrm{g}(H), h(T) \}$, i.e., diversity cannot exceed any of the energy maintenance limit, the niche accommodation limit, or the time realization limit.

Principle 3 (Synergy Principle): The effects of E, H, and T on S are superadditive, i.e., the marginal benefit of increasing one constraint is an increasing function of the levels of the other two. This means that when all three are simultaneously at high levels, their combined effect far exceeds the sum of their independent effects (Zhang, 2016).

Principle 4 (Feedback Principle): High diversity itself can, through niche construction, enlarge effective H, and through enhancing community stability, lengthen effective T, forming a positive autocatalytic loop (Odling-Smee et al., 2003; Zhang, 2016, 2018).

3.2 Precise definitions of core concepts

3.2.1 Effective energy flux (E)

Available energy flux (E) is defined as the free energy per unit time and unit area that an ecosystem can allocate to reproduction and population growth, representing the net energy surplus after deducting maintenance metabolism and heat dissipation. Quantifiable proxy variables include: net primary productivity (NPP, $\mathrm{gC \cdot m^{-2} \cdot yr^{-1}}$), actual evapotranspiration (AET, $\mathrm{mm \cdot yr^{-1}}$), and integrated normalized difference vegetation index (NDVI). E differs from total incident solar radiation in that it accounts for the actual regulation of photosynthetic energy conversion by limiting factors such as water and nutrients—precisely the core insight of the water–energy dynamics hypothesis (O'Brien, 2006).

3.2.2 Multidimensional niche space volume (H)

Multidimensional niche space volume (H) is defined as the effective volume of the niche hypervolume jointly constituted by abiotic gradients (temperature, moisture, light, soil chemistry, etc.) and biotic interaction dimensions (food web positions, symbiotic relationships, host specificity, etc.; Zhang, 2012, 2018). Drawing on Hutchinson's (1957) hypervolume concept and Blonder et al.'s (2014) hypervolume computational methods, H can be quantified as:

$$H = \int \int \ldots \int \ D(x_1, x_2, \ldots, x_n)\, dx_1 dx_2 \ldots dx_n$$

where D is an indicator function describing the density of available niches along each dimension (revealed by the distributions of actual species), and n is the effective number of niche dimensions (typically around 4–6; Hutchinson, 1957; Blonder et al., 2014). Empirically, H can be approximated by the effective number of dimensions from a multivariate environmental principal component analysis and the range of variation along each dimension. It is important to emphasize that H is not a static constant, i..e., it changes dynamically with climatic fluctuations, geological processes (e.g., orogeny creating new elevational gradients), and biological evolution (e.g., key innovations opening new adaptive zones).

3.2.3 Effective evolutionary and community assembly time (T)

Effective evolutionary and community assembly time (T) is defined as the continuous, cumulative time, since the last major environmental disturbance (sufficiently severe climatic or geological events to reset community diversity accumulation) during which species can form, immigrate, and persist with extinction rates remaining at relatively low levels. Geological proxies for T include: the time since the last glacial retreat (for temperate and high-latitude regions), the time since the last major tectonic event (for mountain ranges), or the age since island formation. Biological proxies for T include the mean divergence age of genera or families within the region (phylogenetically weighted lineage ages) (Jetz et al., 2012; Fine & Ree, 2006).

3.3 Theoretical formulation and mathematical structure

3.3.1 Core equation and its derivation logic

The core equation of the NET hypothesis can be expressed as:

$$S = k \cdot (E^{\alpha} \cdot H^{\beta} \cdot T^{\gamma}) / (1 + \varphi(E, H, T))$$

where

S is species richness (number of species in a region);
E is effective energy flux;
H is multidimensional niche space volume;
T is effective evolutionary–assembly time;
α, β, γ are positive scaling exponents, satisfying $0 < \alpha, \beta, \gamma < 1$ (diminishing marginal effects);
k is a positive normalization constant;
$\varphi(E, H, T)$ is a saturation feedback function reflecting self-inhibition of diversity.

The numerator captures the basic driving effects of E, H, and T on diversity; the denominator's saturation term reflects the spontaneous deceleration feedback in diversity accumulation: as niche space fills, opportunities for new species formation or immigration decrease, extinction rates may rise, and speciation rates may decline with niche filling.

3.3.2 Derivation pathways

The NET core equation can be rigorously derived via three reasoning pathways:

Pathway A: Population energy allocation and niche-width–species-number trade-off

Consider an ecosystem with total available energy E. For each species i to maintain a minimum viable population, a minimum energy threshold $e_{\min,i}$ is required. Total individual number $N \approx E / \bar{e}$, where $\bar{e}$ is mean individual energy consumption (Brown et al., 2004). For a given energy, the maximum sustainable number of species $S_{\max}$ depends on the niche width allocated to each species. Let the average niche volume per species be v_i. Then:

$$\Sigma(v_i) \leqslant H \text{ (niche space constraint)}$$

If average niche width is forced to compress as species number increases, reflecting competition-induced niche compression, there exists an optimal species number such that each species' population is not below the minimum viable threshold. From this, a nonlinear relationship between S and E, H can be derived, and this relationship is modulated by T: the longer T is, the more likely species are to evolve narrower niches (higher niche specialization), thereby increasing the cutting precision of H.

Pathway B: Macro-dynamic equilibrium of speciation and extinction

From macroevolutionary dynamics, the net change in regional species richness can be expressed as:

$$dS/dt = \lambda(E, H, S) - \mu(E, H, S) + I - E_m$$

where λ is speciation rate, μ is extinction rate, I is immigration rate, and E_m is emigration rate. λ increases with E (more energy supports larger populations, reducing the extinction effect of genetic drift and possibly accelerating molecular evolution; Gillman & Wright, 2014), increases with H (more niche dimensions provide more directions for speciation), and decreases with S (saturation effect as niche space is filled). μ decreases with E (larger populations are less prone to extinction), decreases with H (more niche dimensions provide refuges), and increases with S (density-dependent extinction). Solving the equilibrium condition $dS/dt = 0$ yields the form of the NET core equation.

Pathway C: Information-theoretic maximization derivation

Viewing the community as an energy-dissipative structure, diversity can be regarded as the degree of differentiation of energy flow. Under the constraints of given E, H, and T, the community tends to maximize its information entropy (the diversity of configurations), but subject to the ecological limitation of the competitive exclusion principle. This maximization process yields an interior solution whose form is consistent with the NET equation. This derivation pathway conceptually connects the NET hypothesis with Harte's (2011) maximum entropy theory, while adding the explicit constraints of niche dimensionality and evolutionary time.

3.3.3 Choice of saturation function and mathematical properties

The specific form of the saturation function $\varphi(E, H, T)$ determines the predictive behavior of the NET equation. Based on theoretical considerations, I propose the following candidate form for empirical testing:

$$\varphi(E, H, T) = c \cdot S_{\text{cap}}(H, T) / E$$

where $S_{\text{cap}}(H, T)$ is the potential saturation species number determined by H and T. When $S << S_{\text{cap}}$, the saturation effect is negligible and S approximates proportionality to $E^{\alpha} \cdot H^{\beta} \cdot T^{\gamma}$; as S approaches S_{cap}, the saturation term dominates and the rate of diversity increase sharply decelerates. S_{cap} itself is an increasing function of H and T: the larger the niche space and the longer the evolutionary time, the higher the asymptotic saturation level.

An important mathematical property of the NET equation is its bottleneck amplification effect on regions with low E, low H, or low T. When any constraint dimension is severely deficient, even if the other two are abundant, S is still confined to a low level. This explains the low diversity of tropical deserts (high E, very low H) and Antarctic seas (certain E and H, but T near zero due to persistent ice cover).

3.4 Unified predictions generated by the NET hypothesis

3.4.1 Latitudinal gradient

The NET hypothesis provides the most integrative unified explanation for the latitudinal diversity gradient. Low-latitude regions have the highest diversity because E, H, and T simultaneously reach their maxima, producing a synergistic effect (Pontarp et al., 2019; Mittelbach et al., 2007). Specifically:

***E* maximized**: Tropical regions receive the highest annual net radiation, which, in moist tropical rainforest areas, translates into extremely high NPP (Hawkins et al., 2003).

***H* maximized**: The seasonal stability of tropical climates means that environmental gradients fluctuate little within and between years, but the complex topography of the tropics (e.g., eastern slopes of the Andes) and the long history of biological co-evolution (tens of millions of years) have created exceptionally fine niche partitioning (Kerkhoff et al., 2014).

***T* maximized**: Most tropical regions were not directly affected by continental ice sheets during the Quaternary glaciations, giving them effective evolutionary times far exceeding those of temperate and boreal regions (Fine & Ree, 2006).

Moving toward higher latitudes, *E* (decreasing energy input), *H* (increasing climatic seasonality and interannual variability compressing effective niche dimensions), and *T* (repeated Pleistocene glacial resets of community assembly) decline in concert, leading to a nonlinear decrease in diversity. The NET hypothesis predicts that the latitudinal gradient at the global scale should show a three-factor synergistic decline pattern, rather than a linear response to any single factor.

3.4.2 Elevational patterns

Elevational diversity patterns have long posed a challenge to single-factor theories because of the frequent occurrence of mid-elevation peaks (Rahbek, 1995; McCain & Grytnes, 2010). The NET hypothesis provides a natural explanation through the trade-off between *E* and *H*:

Low elevations: *E* is highest, but the environment is often relatively homogeneous (flat terrain, uniform climate), so *H* is limited. In tropical lowlands, this leads to moderate rather than the highest diversity, although energy is abundant, niche space is insufficient to accommodate more species.

Mid-elevations: *E* has declined somewhat but remains at a high level, while *H* increases significantly due to increased topographic complexity (slope variation, aspect variation, formation of temperature inversions, etc.). The optimal trade-off between *E* and *H* produces the mid-elevation diversity peak.

High elevations: *E* (low temperature limiting productivity), *H* (habitat types shrink to a few alpine types), and *T* (limited time since mountain uplift and frequent glaciation) all decline simultaneously, leading to a sharp decrease in diversity.

The NET hypothesis predicts that the position and magnitude of the mid-elevation peak should depend on regional topographic complexity and geological history: in ancient orogenic belts, the peak should be more pronounced and positioned higher, while in young orogenic belts it should be weaker (the differential effect of *T*).

3.4.3 Island species–area relationships

The NET hypothesis provides a richer mechanistic explanation for island species–area relationships than traditional theories. In the NET framework, the area effect acts on *S* through three pathways simultaneously:

***E* pathway**: Area correlates with catchment productivity and coastal effects; larger area generally means larger total energy flux (though note that per-unit-area *E* may be independent of total area).

***H* pathway**: Area correlates highly with habitat diversity (habitat diversity hypothesis); larger area often means more habitat types are included (Triantis et al., 2012).

***T* pathway**: Island age and geological dynamic history affect effective *T* (Whittaker et al., 2008; Steinbauer et al., 2013).

The NET hypothesis predicts that the *z*-value (the log-log slope of the species–area relationship) should vary systematically due to regional differences in *E*, *H*, and *T*. In regions with abundant *H* and *T* (e.g., tropical archipelagos), the area effect should be weaker (low *z*-value) because area is only one of many driving factors; in regions with limited *H* or *T* (e.g., temperate archipelagos or young volcanic islands), the area effect should be stronger (high *z*-value) because area becomes the primary constraint on niche space. This prediction provides a new perspective for understanding the global variation in *z*-values.

3.4.4 Explanation of anomalous cases

The NET hypothesis also provides a unified explanatory framework for anomalous diversity cases:

Tropical deserts: *E* is high (abundant solar energy), but *H* is extremely low (extreme water uniformity collapses effective niche dimensions), and *T* is limited by long-term arid instability. The low values of *H* and *T* in the NET equation constrain *S* through the bottleneck effect.

Tropical montane cloud forests: *E* is medium-high (lower than lowlands but supplemented by cloud water interception), *H* is extremely high (steep terrain plus stable cloud layers create exceptionally rich microhabitat gradients), and T is extremely high (long-term stable climate without glacial disturbance). The simultaneous medium-high levels of all three produce a synergistic amplification effect, explaining the exceptionally high diversity.

Ancient temperate lakes (e.g., Lake Baikal, Lake Tanganyika): Compared to young temperate lakes, ancient lakes have significantly higher T (tens of millions of years of continuous existence), allowing high diversity to accumulate even when E and H are at moderate levels. This is consistent with the independent role of T in the NET hypothesis.

4 Innovative Methodology: Theoretical Deduction and Multi-Scale Validation Framework

4.1 Theoretical deduction and mathematical model construction

The theoretical deduction of the NET hypothesis proceeds from three first principles, using progressively rigorous mathematical derivation (Appendix):

Step 1: Energy allocation and individual number upper limit. Based on the core relationship of metabolic theory, individual metabolic rate $I \propto M^{(3/4)} \cdot e^{-Ea/kT}$, where M is body mass, E_a is activation energy, k is Boltzmann's constant, and T is absolute temperature (Brown et al., 2004). For a given total community energy flux E_{total}, the maximum sustainable number of individuals $N_{max} = E_{total} / I_{min}$, where I_{min} is the minimum individual energy demand. This sets the thermodynamic upper limit for species richness.

Step 2: Niche partitioning and species number. In an H-dimensional niche space, the niche of species i can be characterized as a hyperellipsoid centered at μ_i with covariance matrix Σ_i. Coexisting species must satisfy the niche separation condition: for any $i \neq j$, the Mahalanobis distance $d_M(\mu_i, \mu_j) \geqslant \delta_{min}$ (limiting similarity). The maximum number of non-overlapping hyperellipsoids that can be packed into the H-space is the niche accommodation limit S_H. Clearly, S_H is a monotonically increasing function of H and increases as the average niche volume $\bar{v}$ decreases.

Step 3: Time dynamics and saturation. The filling of niche space is a time-dependent process. Over time period T, the rate of speciation events is $\lambda(t)$, and $\lambda(t)$ decreases as the proportion of filled niches increases. Given an initial species number S_0:

$$S(T) = S_0 + \int_0^T [\lambda(t) + I(t) - \mu(t) - E_m(t)]\, dt$$

As $T \rightarrow \infty$, $S(T)$ asymptotically approaches the equilibrium value $S_{eq}(E, H)$ jointly determined by E and H.

Step 4: Coupled solution. By jointly imposing the constraints from Steps 1–3, the steady-state solution for species richness under the simultaneous constraints of energy, niche, and time yields the form of the NET equation.

4.2 Parameterization and operationalization pathways

To make the NET hypothesis empirically testable, I propose the following explicit parameterization strategies:

Quantifying E. Prioritize remote-sensing-derived net primary productivity (NPP) data products (e.g., MODIS MOD17A3, 1-km spatial resolution, annual time step), aggregated at the regional scale (e.g., 100 km × 100 km grid cells). Alternatives include actual evapotranspiration (AET) datasets (e.g., Global AET from MODIS/Terra) and integrated NDVI values. To enhance comparability, multi-source fused E estimates are recommended.

Quantifying *H*. Use a two-step approach: (1) Perform principal component analysis on a matrix of environmental variables for the study region (including temperature, precipitation, solar radiation, topographic relief, soil type diversity, etc.; Zhang and Chen, 2011) and take the number of principal components k accounting for >90% cumulative variance as an estimate of the effective number of niche dimensions n_{eff}. (2) Calculate the range (maximum minus minimum) of each principal component as the length of each dimension, and approximate H as the geometric mean of these lengths multiplied by n_{eff}. For biotic interaction dimensions, supplement with functional trait hypervolume analysis (Blonder et al., 2014) or food-web complexity indices.

Quantifying *T*. Use the continuous time since the retreat of ice sheets at the Last Glacial Maximum (LGM, ~21,000 years ago) as the baseline T value, with the following adjustments: (1) For tropical regions that never experienced Quaternary glaciation, use the time since the last major climatic transition of the Cenozoic (e.g., since the mid-Miocene climatic transition, ~14 Ma) as an upper bound estimate of T. (2) For active orogenic belts, adjust T by the time since the main uplift phase. (3) For islands, use their geological age directly. Alternatives include phylogenetically based estimates of mean genus-level or family-level divergence ages.

The NET diversity index.Define a standardized NET diversity index:

$$\textit{NET-index} = S_{\text{obs}} / S_{\text{NET}}(E, H, T)$$

where S_{NET} is the prediction of the NET equation fitted with global parameters. A *NET-index* < 1 indicates that regional diversity is below the NET expectation (suggesting possible additional diversity-limiting factors), while a *NET-index* > 1 indicates diversity exceeding the NET expectation (possibly reflecting positive autocatalytic effects or parameter estimation errors).

4.3 Numerical simulations and thought experiments

To verify the internal logical consistency of the NET hypothesis and explore its predictive behavior, I designed the following numerical experimental framework:

Experiment 1: Single-factor manipulation experiment.Generate artificial ecosystems in silico, independently manipulating E, H, and T while holding the other two factors constant, and observe the response pattern of S. NET predicts: (a) when H and T are abundant, the S–E relationship shows convex growth that eventually saturates; (b) when H is limited, increasing E has a weak effect on S, i.e., energy is abundant but has nowhere to be utilized; (c) when T is insufficient, S is far below the potential value allowed by E and H, reflecting a time lag effect.

Experiment 2: Latitudinal gradient simulation.Set E, H, and T all to decrease linearly with latitude (simulating an idealized gradient from the equator to the pole) and observe the emergent pattern of S. NET predicts that S decreases nonlinearly with latitude, with a slow decline at low latitudes (synergistic effect when all three factors are abundant) and an accelerating decline at mid-to-high latitudes (bottleneck effects begin to manifest). This prediction differs from the purely monotonic or purely exponential declines predicted by single-factor hypotheses.

Experiment 3: Disturbance and recovery simulation.Introduce periodic environmental disturbances into the NET model (simulating glacial–interglacial cycles) and observe the temporal trajectory of S. NET predicts that increased disturbance frequency will significantly reduce the mean level of S, and that the time required to recover to pre-disturbance levels increases with latitude (because E and H are lower at high latitudes, so speciation and immigration rates are slower).

5 Result Deduction: Unified Explanation of Classical Problems By The NET Hypothesis

5.1 Unified explanation of global terrestrial diversity macro-patterns

The NET hypothesis predicts that the macro-patterns of global terrestrial species diversity should be jointly shaped by the spatial covariation of the three fundamental fields of E, H, and T, rather than being a simple response to any single field. Specifically:

Tropical South America (the Amazon Basin), especially the tropical montane cloud forests on the eastern slopes of the Andes, represents the extreme of synergistic maximization of the three NET factors: *E* is extremely high due to high temperature and humidity; *H* is extremely large due to the complex topography and climatic stratification of the Andes; and *T* is extremely long due to long-term freedom from direct impacts of Quaternary continental ice sheets. NET predicts that species diversity in this region should be the highest on Earth's land surface, which is highly consistent with observations (Barthlott et al., 2007; Jenkins et al., 2013).

In contrast, the **boreal forest belt (taiga)** has low *E* (cold-limited productivity), low *H* (few tree species, homogeneous habitats), and low-to-moderate *T* (repeated Pleistocene glacial resets), resulting in significantly lower species diversity than the tropics, again consistent with NET expectations. The higher diversity of temperate broadleaf forests in eastern China and eastern North America can be understood as a compromise among *E* (moderately high), *H* (moderate topographic complexity), and *T* (affected by glaciation but for a shorter period than the taiga).

Significant differences in diversity within tropical Africa: the high diversity of the Congo Basin rainforest versus the relatively low diversity of East African savannas, can be largely explained by differences in *H*: the Congo Basin has finer habitat differentiation, while savannas, with their relatively homogeneous vegetation structure and strong seasonal hydrological fluctuations, have lower effective niche dimensionality.

5.2 Explanation of anomalous cases

As discussed earlier, the NET hypothesis provides a coherent explanation for a range of anomalous cases:

Tropical deserts are a crucial test case for the NET logic: here, *E* is high (intense solar radiation), but the extreme water scarcity drives effective *H* toward zero—all organisms must cope with a single dominant constraint of extreme aridity, leaving very limited space for differentiation along other niche dimensions. Moreover, the long-term instability of desert climates also limits the effective accumulation of *T*. The bottleneck effect of $H \to 0$ leading to $S \to 0$ in the NET equation directly explains the low diversity: something no single-factor energy hypothesis can account for.

Mediterranean-climate regions (e.g., the Cape Floristic Region of South Africa, southwestern Australia) represent another manifestation of the NET logic: *E* is moderate (seasonal drought limits annual productivity), *H* is moderate (mountainous terrain and soil heterogeneity provide some niche space), but *T* is exceptionally abundant in specific geological histories (long-term stable Mediterranean-type climate has allowed extensive local endemism to evolve). This *T* compensation mechanism explains the exceptionally high plant diversity, particularly the extremely high levels of endemism, in Mediterranean-climate regions.

Abyssal plains represent the combined effects of low *E* (no photosynthesis, relying on marine snow sedimentation), low *H* (extremely uniform physical environment), and uncertain *T*, resulting in species diversity that, although not low in absolute numbers (due to the immense area), is far lower per unit area than in shallow seas and shelf regions, consistent with NET predictions.

5.3 Scale-dependence and shape variation of the species–energy relationship

The NET hypothesis provides a comprehensive explanatory framework for the controversy over the shape of the species–energy relationship, whether it is monotonically increasing, hump-shaped, or nonsignificant. According to the NET equation, the shape of the species–energy relationship is not fixed but conditionally depends on the levels of *H* and *T*:

Scenario A (*H* abundant, *T* abundant): When both *H* and *T* are at high levels, increases in *E* can be finely divided and utilized across a broad niche space, producing a near-linear *S*–*E* growth relationship. However, as *S* approaches the saturation level allowed by *H*, the growth slope gradually slows, producing a concave relationship. This corresponds to observations in systems like tropical rainforests.

Scenario B (*H* limited, *T* abundant): When *H* is limited, increases in E initially bring rapid growth in *S*, because there are a few unoccupied niches to fill, but then quickly saturate due to the lack of additional niche dimensions, producing a steep saturation-type relationship. This corresponds to patterns in species-poor systems.

Scenario C (*H* abundant, *T* insufficient): When T is short (e.g., in post-glacial temperate regions), even if E and H are both high, S remains far below its potential equilibrium value. In this case, the S–E relationship may show a weak correlation because historical time, not current energy, is the limiting factor. This explains why some highly productive temperate regions do not have outstanding species richness.

Scenario D (*H* and *T* covary with *E*): In natural systems, E, H, and T are often positively correlated (e.g., along latitudinal gradients), which can cause the S–E relationship to appear hump-shaped, because when E is highest, H may decline due to heat stress or homogenization (e.g., at the edges of tropical deserts), or T may be shortened by increased disturbance frequency.

This framework unifies the diversity of relationship shapes found by Mittelbach et al. (2001) within a single theoretical system, rather than treating them as mutually contradictory evidence. The prediction of NET is that if the variation in H and T is controlled in empirical analyses, the residual S–E relationship should show a monotonically increasing saturation pattern; uncontrolled confounding is precisely the source of the inconsistency in relationship shapes.

6 Discussion

6.1 Innovative contributions of the theory and its accommodation of existing frameworks

The core innovation of the NET hypothesis lies not in simultaneously considering multiple factors, which has been attempted many times in the literature (e.g., Jetz & Fine, 2012; Pontarp et al., 2019), but in revealing the synergistic logic among these factors: they do not contribute independently and additively to diversity but jointly determine the final level of diversity through a serial filtering mechanism. This logic places energy, niche space, and evolutionary time at mutually non-substitutable constraint levels: energy provides the raw material but cannot determine the blueprint; niche space provides the blueprint but cannot determine the degree of realization; time determines the "degree of realization" but cannot exceed the upper limits set by the first two.

Another innovation of the NET hypothesis is its inclusive embedding of existing theories. NET does not overturn the species–energy hypothesis, the heterogeneity hypothesis, the area hypothesis, or the time hypothesis; rather, it embeds them into the E, H, and T dimensions, respectively, and reveals the specific mechanisms by which they act as necessary but not sufficient conditions. For example, the core insight of the species–energy hypothesis, that energy limits the upper bound of diversity, is retained in the NET framework as the thermodynamic constraint of the E dimension, but its inability to explain diversity differences under identical energy is remedied by the introduction of the H and T dimensions. Similarly, the immigration–extinction balance logic of the equilibrium theory of island biogeography is absorbed as part of the dynamic processes within the T dimension, while the area effect is decomposed into the synergistic action of area on the three pathways of E, H, and T.

6.2 Comparison with other integrative frameworks

Compared to metabolic theory (MTE), NET retains MTE's fundamental insight about the energy constraint but confines it to one of three constraint dimensions rather than being the sole explanatory variable. MTE faces a fundamental difficulty in predicting diversity differences at the same temperature, for example, the Sahara Desert and the Congo Basin have comparable mean annual temperatures but vastly different diversity, and NET naturally resolves this difficulty through the introduction of the H dimension.

Compared to maximum entropy theory (METE), NET proceeds from a different philosophical stance: NET pursues a unification of causal mechanisms, while METE pursues a unification of statistical inference. The two are not contradictory but operate at different levels of analysis: METE describes the expected state of an ecosystem given macroscopic constraints, while NET seeks to identify and quantify those macroscopic constraints themselves. A potential integration direction is to use the *E*, *H*, and *T* identified by NET as constraint inputs for METE, and test whether the species abundance distributions derived by METE are consistent with observations. This would be an important topic for future cross-theoretical validation.

Compared to Hubbell's (2001) unified neutral theory, NET explicitly acknowledges the central roles of niche differences (the *H* dimension) and energy constraints (the *E* dimension) in shaping diversity, while treating random drift and dispersal limitation as filling processes operating within the framework given by *E*, *H*, and *T*. This perspective aligns with the current consensus in ecology that niche and neutral perspectives are complementary rather than opposed (Leibold & McPeek, 2006; McGill, 2010).

6.3 Deep implications of ecological and evolutionary feedbacks

Principle 4 of the NET hypothesis (the feedback principle) points to an important theoretical direction: diversity is not merely a passive product of *E*, *H*, and *T* but also actively modifies these constraints themselves through niche construction and community stability effects. The hyperdiversity of tropical rainforests may be precisely the product of this positive autocatalytic loop: high diversity leads to more complex niche structures (through niche construction), more complex niche structures accommodate higher diversity; high diversity enhances the community's buffering capacity against environmental fluctuations, lengthening effective *T*, further promoting diversity accumulation.

This feedback logic provides a mechanistic explanation for the phenomenon of self-maintenance of tropical hyperdiversity. If the positive feedback is strong enough, the geographical patterning of diversity may exhibit bistable characteristics: tropical regions locked into a high-diversity stable state, while temperate regions locked into a low-diversity stable state, such that even moderate changes in certain environmental conditions may not easily cause the system to cross the threshold between stable states. This perspective has profound implications for understanding the response of diversity to global change: if human activities weaken *E* (through land degradation) and *H* (through habitat homogenization), they may not only cause direct diversity loss but also trigger a reversal of positive feedback: once the system crosses a critical threshold, diversity may accelerate its decline and be difficult to recover even if external stressors are removed.

6.4 Limitations and future empirical directions

Although the NET hypothesis has internal logical consistency and broad explanatory power, its rigorous empirical testing faces several important challenges.

(1) The precise quantification of *H* remains an open methodological problem. The identification of effective niche dimensions is highly dependent on the choice of environmental variables and the threshold setting for relevance. Different taxonomic groups (e.g., plants, mammals, soil microorganisms) may perceive entirely different niche dimensions, and how to unify these taxon-specific *H* estimates and integrate them into a common NET framework is an urgent problem to be solved.

(2) The estimation of *T* has considerable uncertainty in regions lacking detailed geological records and phylogenetic data. The effective evolutionary time of a region may be complexly affected by multiple geological events and climatic fluctuations, and simply using the time since the last glaciation as *T* may underestimate the actual historical complexity. Integrating geological, paleoclimatic, and phylogenetic data to more precisely characterize the spatial variation of *T* is an important direction for future empirical research.

(3) Direct global-scale testing of the NET hypothesis requires large-scale cross-taxon data compilation. Ideally, reliable data on *E* (remote-sensing NPP or AET), *H* (multivariate environmental heterogeneity), *T* (geological/phylogenetic age), and *S* (multi-taxon richness) should be obtained simultaneously in a global grid

system, and the NET equation should be fitted and compared using hierarchical Bayesian modeling or structural equation modeling. Several global database projects already exist (e.g., the PREDICTS database: Hudson et al., 2017; the GIFT database: Weigelt et al., 2020; the BioTIME database: Dornelas et al., 2018) that provide a data foundation for such analyses, but cross-database integration still requires substantial standardization work.

(4) The human dimension of the NET hypothesis has not yet been incorporated into the current framework. Human activities are altering *E* (through land-use change and climate change), *H* (through habitat fragmentation and homogenization), and *T* (through accelerated extinction and introduction of alien species disrupting community assembly processes) at unprecedented rates and intensities. The future NET framework needs to evolve into a NET-H model that quantifies the impacts of human activities on the three fundamental constraints, thereby predicting and providing early warning of diversity loss in the context of global change.

(5) The NET hypothesis currently focuses primarily on species richness (α diversity); its predictive ability for beta diversity (community composition differences) and gamma diversity (total regional diversity) has not yet been fully explored. Extending the NET framework to the dimensions of beta and gamma diversity is a natural next step theoretically.

7 Conclusion

This paper started from one of the oldest and most central questions in ecology: what determines species diversity? and, on the basis of a systematic review of existing energy hypotheses, heterogeneity hypotheses, area hypotheses, neutral theory, metabolic theory, maximum entropy theory, and evolutionary–historical hypotheses, identified a fundamental gap in existing theories: the lack of a mechanistic framework that simultaneously encompasses energy, niche dimensionality, and evolutionary time, and that specifies the rules of their interaction.

To fill this gap, I proposed the Niche–Energy–Time triadic synergy hypothesis (NET hypothesis). The core proposition of the NET hypothesis can be summarized as: Species diversity is not determined by any single factor but is jointly sculpted by three irreducible ultimate constraints, available energy flux (*E*), multidimensional niche space volume (*H*), and effective evolutionary and community assembly time (*T*). The relationship among the three is serial filtering rather than additive: energy provides the raw material of diversity, niche space provides the partitioning blueprint and evolutionary time determines the degree of realization. Any severe deficiency in one dimension constitutes a bottleneck for diversity accumulation; the synergistic maximization of all three is the root cause of tropical hyperdiversity.

The NET hypothesis is not only a qualitative conceptual framework but also a mathematically formalizable and quantitatively testable theoretical system. The core equation, $S = k\,(E^{\alpha} H^{\beta} T^{\gamma}) / (1 + \varphi(E, H, T))$, and its derivation logic presented in this paper provide a formal basis for deducing classical diversity patterns from first principles. The NET hypothesis successfully and unifies the explanations of the latitudinal gradient, elevational patterns, and island species–area relationships, and also provides a coherent mechanistic explanation for anomalous cases such as tropical deserts and Mediterranean-climate regions.

For conservation biology, the message of the NET hypothesis is clear: protecting only energy (e.g., maintaining productivity) or only area (e.g., establishing protected areas), while neglecting the maintenance of niche dimensionality and evolutionary history, will not ensure the persistence of biodiversity. In the era of global change, the simultaneous assault by human activities on all three dimensions of *E*, *H*, and *T* may trigger positive feedback loops of diversity loss, leading to irreversible biodiversity crises. Conservation planning should proceed from the three-dimensional perspective of NET, comprehensively assessing and maintaining the energy base, the integrity of niche space, and the continuity of evolutionary history in target regions.

The NET hypothesis is still in an early stage of development. Future work will focus on: (1) developing and validating standardized quantification methods for H and T; (2) conducting direct statistical tests and model selection based on global multi-taxon data; (3) incorporating human impacts and beta/gamma diversity dimensions into the NET framework; and (4) exploring the deep mathematical connections between the NET hypothesis and maximum entropy theory and neutral theory, advancing toward a truly unified theory.

Appendix

Detailed Derivation of the NET Core Equation via Asymptotic Analysis of a Two-Timescale Diversification–Assembly System

This appendix provides the full mathematical derivation of the Niche–Energy–Time (NET) equation

$$S = k\ \frac{E^{\alpha} H^{\beta} T^{\gamma}}{1+cH^{\beta}T^{\gamma}/E}, \qquad \text{(A.1)}$$

which serves as the foundational quantitative statement of the NET hypothesis in the main text. The derivation proceeds in three stages: (1) We construct a deterministic model for the fast dynamics of species richness $S(t)$ given a fixed niche-time potential M. (2) We prove that this fast dynamics possesses a globally stable equilibrium $S^{*}(M)$ that takes exactly the functional form required by the NET hypothesis. (3) We introduce the slow dynamics of the niche-time potential M itself, showing that M grows over the effective evolutionary-assembly time T as $M(H,T) = H^{\beta}T^{\gamma}$. The observed species richness is then obtained by substituting this slow variable into the fast equilibrium, a standard adiabatic elimination procedure.

A.1 Fast dynamics: energy- and niche-limited diversification

Consider a region characterised by a constant effective energy flux E (in energy per unit time per unit area, e.g. NPP) and a fixed multidimensional niche space volume H. Over ecological time scales, the regional species pool adjusts through *in situ* speciation and immigration (jointly termed ‘origination’) and extinction. We treat the niche-time potential M, the maximum number of species that could eventually be differentiated given H and the time already elapsed, as a slow variable that is effectively constant on the time scale of the fast dynamics.

Let $S(t)$ denote the number of species present at time t. The origination rate (species per unit time) is modelled as

$$O(E, M) = b\, E^{\alpha} M, \qquad \text{(A.2)}$$

where $b>0$ is a constant and $\alpha \in (0,1)$ is a scaling exponent. Equation (A.2) posits that the total rate at which new species are added to the region is proportional to the available energy flux (raised to a power that reflects thermodynamic and metabolic constraints; Allen et al., 2007) and to the still-unrealised niche potential M. The linear dependence on M captures the idea that a larger potential pool of distinct niches provides more independent directions along which new species can arise. The rate is assumed to be independent of the current number of species S because speciation and immigration draw upon a much larger external or genetic pool; competitive interactions affect persistence, not the raw input of novel forms.

The total extinction rate (species per unit time) is taken to be

$$D(S; E, M) = d_1 S + d_2\, (M/E)\, S, \qquad \text{(A.3)}$$

where d_1, d_2>0. The first term, d_1S, represents a baseline per-capita extinction risk that is independent of energy and niche saturation. The second term, $d_2\,(M/E)\,S$, captures the increase in extinction probability when many potential niches compete for a finite amount of energy: as the ratio (M/E) grows, the average population size that can be supported for each realised species shrinks, amplifying stochastic extinction (Wright 1983; Hurlbert & Stegen 2014). The form is chosen to be linear in both S and (M/E), consistent with a first-order approximation of density-dependent resource limitation.

The fast dynamics of S is therefore governed by the ordinary differential equation

$$O(E,M) - D(S; E, M) = b\,E^{\alpha}\,M - d_1S - d_2\,(M/E)\,S. \qquad \text{(A.4)}$$

Equation (A.4) is a linear first-order equation that can be solved explicitly. Its unique equilibrium, obtained by setting $dS/dt = 0$, is

$$S^{*}(E,M) = b\,E^{\alpha}\,M\,/\,(d_1 + d_2\,M/E). \qquad \text{(A.5)}$$

To analyse stability, write the deviation from equilibrium as $x = S - S^{*}$. Then

$$dx/dt = -\,(d_1 + d_2\,M/E)\,x,$$

which is globally exponentially stable because the damping coefficient $d_1 + d_2\,M/E > 0$ for all $M \geq 0$. Hence, for any initial species richness, $S(t)$ converges monotonically and exponentially to $S^{*}(E,M)$ on a characteristic time scale

$$\tau_{\text{fast}} = 1/\,(d_1 + d_2\,M/E). \qquad \text{(A.6)}$$

Provided that ecological and microevolutionary processes (population establishment, competitive sorting) operate faster than the slow accumulation of niche-time potential, the observed species richness will be well approximated by the equilibrium value $S^{*}(E,M)$. We formalise this separation of time scales below.

A.2 Slow dynamics: accumulation of the niche-time potential

The niche-time potential M quantifies the total number of distinct ecological niches that could in principle be occupied given the environmental complexity H and the effective assembly time T. We conceptualise M as evolving on geological time scales through a cumulative process of niche discovery and refinement.

Consider the rate at which new niche dimensions or sub-niches are explored during adaptive radiation. If the exploration of niche space is an undirected, diffusion-like process in a high-dimensional hypervolume, the number of distinct regions visited by evolving lineages after time T scales as a power of T (Hughes et al. 2013). Moreover, the larger the underlying niche volume H, the more rapidly new niches can be differentiated. A simple phenomenological model that captures these features is the differential equation

$$dM\,/dT = \phi\,H^{\beta}\,\gamma\,T^{\gamma-1} \qquad \text{(A.7)}$$

where $\phi > 0$ is a constant, β describes how strongly the niche volume accelerates differentiation, and $\gamma \in (0,1]$ is the temporal scaling exponent. Integrating (A.7) with the initial condition $M(0)=0$ (a completely reset community) yields

$M(H,T) = \phi H^{\beta} T^{\gamma}$. (A.8)

The linear dependence $M \propto T^{\gamma}$ with $\gamma < 1$ reflects diminishing returns in niche discovery as the most accessible niches are occupied first; the limiting case $\gamma = 1$ corresponds to a constant rate of niche differentiation. The proportionality to H^{β} captures the well-established role of environmental heterogeneity in generating niche diversity (Stein et al. 2014). Equation (A.8) is the explicit form of the niche-time potential that we will insert into the fast equilibrium.

A.3 Adiabatic elimination: the NET equation

Because the fast time scale τ_{fast} (years to centuries) is typically orders of magnitude shorter than the slow time scale over which M changes (tens of thousands to millions of years), the system obeys an adiabatic approximation: the species richness S remains permanently close to the instantaneous equilibrium $S^{*}(E,M(T))$ as M slowly increases. Substituting (A.8) into (A.5) gives

$S(E,H,T) = bE^{\alpha}(\phi H^{\beta} T^{\gamma}) / (d_1 + d_2 (\phi H^{\beta} T^{\gamma})/E)$. (A.9)

Dividing numerator and denominator by d_1 and defining the lumped constants

$k = b\phi/d_1$, $c = d_2 \phi/d_1$,

we obtain the NET core equation in its final form

$S(E,H,T) = k E^{\alpha} H^{\beta} T^{\gamma}) / (1 + c H^{\beta}T^{\gamma}/E)$. (A.10)

Equation (A.10) is exactly the expression presented in Section 3.3 of the main text, with the niche-time saturation potential identified as $S_{\text{cap}}(H,T) = \phi H^{\beta} T^{\gamma}$ and the saturation function $\varphi(E,H,T) = c S_{\text{cap}}(H,T)/E$.

A.4 Asymptotic behaviour and limiting cases

The mathematical properties of (A.10) elucidate the three-way synergy that underlies the NET hypothesis.

1. Small niche-time potential ($cH^{\beta} T^{\gamma} << E$):

$S \approx kE^{\alpha} H^{\beta} T^{\gamma}$

Diversity is proportional to the product of all three factors, with no single one dominating. This regime characterises young or recently disturbed regions where niche space has not yet been filled.

2. Large niche-time potential ($cH^{\beta} T^{\gamma} >> E$):

$S \approx (k/c) E^{\alpha+1}$

Diversity becomes limited purely by energy; additional niche-time potential cannot further increase species richness. This regime corresponds to ancient, climatically stable systems (e.g. tropical rainforests) where energy is the ultimate bottleneck.

3. Energy-dominated regime ($E\to\infty$ for fixed H, T):

$S\to (k/c) E^{\alpha}(H^{\beta} T^{\gamma}) / (H^{\beta} T^{\gamma}/E) = (k/c) E^{\alpha+1}$

confirming that even unlimited energy cannot overcome a finite niche-time potential—the extra energy would be partitioned into ever smaller populations, eventually hitting extinction thresholds (Principle of Bottleneck).

4. Scaling collapse of the latitudinal diversity gradien

In tropical regions, E, H, and T are simultaneously large, and the denominator saturates. In high latitudes, all three are small, and the numerator dominates. The transition between these regimes generates a nonlinear decay of diversity with latitude that is steeper than any single-factor model predicts, consistent with empirical meta-analyses (Hillebrand 2004; Pontarp et al. 2019).

A.5 Generality and robustness

The derivation above employed a deterministic, lumped-parameter description. The essential structure of (A.10) is, however, robust to a wide range of microscopic assumptions. For instance, if the origination rate saturates at high M as $O = b\, E^{\alpha}M / (1 + M/M_0)$, the same algebraic form emerges after rescaling. If extinction contains an additional nonlinear term $\propto S^2$, the equilibrium equation can still be rearranged into the form (A.10) for an appropriate effective M. More importantly, the same functional relationship can be recovered from a spatially explicit neutral-niche hybrid model in which the probability of a new species establishing is proportional to the product of energy-dependent carrying capacity and niche-availability (see Supplementary Information of Jetz & Fine 2012 for a related construction). The power-law temporal scaling T^{γ} can also be derived from a stochastic adaptive radiation model with a declining speciation rate, where the expected number of species after time T grows as T^{γ} (Gavrilets & Vose 2005). Thus, while the details of the underlying biological processes will vary among clades and regions, the overarching mathematical structure, a saturating function of the product of the three fundamental constraints, appears to be a universal attractor for the dynamics of diversified life.

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