The Minimum Carbon Theory: A Physiological Basis for Species Coexistence

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Abstract

Understanding how species coexist and why diversity varies across regions remains a central challenge in ecology. Although widely used theories such as niche theory, neutral theory, and modern coexistence theory have yielded key insights into coexistence and diversity, their reliance on abstract parameters lacking direct physiological grounding limits empirical validation and constrains cross-scale integration. To address this limitation, we propose the minimum carbon theory (c_{min}), grounded in the first principle that autotrophic organisms must maintain a net positive carbon balance to survive. The c_{min} defines the lowest rate of net carbon gain required for persistence, integrating the costs of maintenance respiration, and stress responses, offset by facilitative interactions that reduce metabolic demand. By linking species persistence to physiological carbon sufficiency, c_{min} provides a unified, mechanistic explanation for patterns of distribution, coexistence, and diversity across environmental gradients. Reframing existing theories, including niche differentiation, neutral dynamics, modern coexistence models, and macroecological hypotheses such as the energy–diversity and water–energy dynamics theories through the lens of carbon physiology, c_{min} offers a coherent mechanism to integrate previously fragmented ecological paradigms. Because carbon is the universal currency of life, the c_{min} can be applied across taxa and scales, unifying questions of invasion, ecosystem function, and ecological stability. In a biosphere increasingly shaped by climate stress, the c_{min} theory provides a physiologically grounded foundation for a unified theory of diversity, offering mechanistic insight into how individual carbon thresholds scale up to shape the structure and functioning of ecological systems.

Keywords: Minimum carbon requirement, physiological thresholds, species coexistence, diversity patterns, coexistence theory, ecosystem functioning

Introduction

Understanding how multiple species coexist within ecological communities remains one of the most fundamental and unresolved questions in ecology[1,2]. This challenge underlies our ability to explain diversity patterns, predict ecosystem functioning, and assess resilience under accelerating global change[3]. Despite decades of theoretical and empirical progress, a mechanistic theory that consistently explains patterns of species distribution, coexistence, and diversity across resource-limited and heterogeneous environments remains lacking[4-7].

Over the past century, several influential theories have been developed to address this problem[8]. Classical niche theory emphasizes stabilizing mechanisms, such as resource partitioning, that reduce interspecific competition and promote coexistence[4,5]. In contrast, neutral theory assumes functional equivalence among species and attributes diversity to demographic stochasticity[9,10]. Modern coexistence theory seeks to integrate these perspectives by quantifying the relative contributions of stabilizing and equalizing forces[2,11]. While these theories have offered key insights into species coexistence, they often rely on emergent or system-specific parameters, such as invasion growth rates or competition coefficients, which are difficult to quantify and empirically validate in complex, long-lived, and multispecies systems[1,2,12]. These theories also struggle to scale across taxa and climate regions, underscoring the need for a universal, mechanistic theory of coexistence[8,13].

At its core, ecology seeks to understand how organisms grow, persist, and interact with their environment under biophysical constraints[14,15]. The survival of autotrophic plants ultimately depends on whether photosynthetic carbon gain outweighs the metabolic costs of maintenance, defense, and reproduction[16-18]. However, current existing theory are largely decoupled from the physiological mechanisms that govern whether an organism can persist under given environmental conditions[1,7,19]. Therefore, rebuilding ecological theory from such first principles is essential for developing a coherent, scalable, and predictive understanding of species coexistence. Here, we introduce the minimum carbon theory (c_{min} theory), which reframes persistence as a problem of maintaining a net positive carbon balance. Each species is characterized by a minimum threshold of net carbon assimilation (c_{min}) required to sustain metabolic function and ensure survival. Whether a species can persist in a particular environment depends on whether the local carbon supply, determined by light, temperature, water, and nutrient availability, consistently meets or exceeds its c_{min}. The value of c_{min} reflects an integrated set of traits, including photosynthetic capacity, respiration rate, and resistance to biotic and abiotic stress. These traits shape a species' ability to sustain net carbon gain under variable environmental conditions, effectively defining its position in carbon niche space. Coexistence arises when species differ in carbon requirements and respond differently to environmental constraints.

This c_{min} theory offers several key advantages over existing theories. First, c_{min} is physiologically meaningful and empirically measurable, in contrast to abstract parameters used in traditional coexistence theories. It enables trait-based comparisons, integration into process-based models, and validation through experiments or field data. Second, the c_{min} concept is not limited to autotrophic organisms. Because carbon is the universal currency of life, organisms from microbes to animals must maintain a positive net carbon balance to survive and reproduce[16,20-22]. Third, the c_{min} is inherently scalable. By grounding species coexistence in carbon-based physiological thresholds, c_{min} bridges individual performance and ecosystem function across taxa and environments. This cross-scale coherence enables it to unify local coexistence dynamics with global diversity patterns and to predict ecosystem responses to environmental change.

In this perspective, we first outline the physiological underpinnings of c_{min} and its implications for species persistence. We then show how c_{min} provides a mechanistic foundation for species coexistence while reframing classic ecological theories, including niche theory, neutral theory, and modern coexistence theory. Extending beyond local dynamics, we demonstrate its potential to explain large-scale diversity patterns and to reinterpret macroecological hypotheses such as the energy–diversity hypothesis, water–energy dynamics, and the metabolic theory of ecology. Finally, we synthesize five key domains where the c_{min} theory demonstrates broad applicability and offers both explanatory and predictive power, including ecosystem functioning, climate change impacts, ecological stability, biological invasions, and evolutionary biogeography. Together, these applications position c_{min} not only as a general theory for understanding species persistence and diversity patterns, but as a unifying physiological principle linking organismal carbon balance to the structure, dynamics, and resilience of life on Earth.

Physiological basis of c_{min} theory

The c_{min} theory builds on the core physiological principle that autotrophic plants must maintain a net positive carbon balance over ecologically relevant timescales in order to survive [16-18]. We define c_{min} as the minimum sustainable rate of net carbon gain, quantified as the difference between photosynthetic assimilation and the total of respiratory and other carbon losses, that is required to support metabolic maintenance and ensure survival. Unlike cumulative metrics such as carbohydrate pools or total biomass, flux-based indicators like net carbon assimilation provide finer temporal resolution, improved comparability across taxa, and stronger integration with process-based models [23,24]. This flux-based perspective places c_{min} within a dynamic, mechanistic theory that is empirically measurable and ecologically interpretable across diverse species and environments.

Given the spatiotemporal variability of photosynthesis and respiration, c_{min} represents an average net carbon gain rate integrated over biologically relevant timescales, rather than a momentary or daily flux. This temporal integration smooths short-term fluctuations and captures the sustained carbon balance required for long-term persistence. In fast-growing herbaceous plants, daily to weekly integration windows may suffice. For long-lived woody species, particularly trees, monthly or seasonal averages more accurately reflect cumulative carbon dynamics relevant to survival. This flexible temporal scaling ensures that c_{min} remains both physiologically realistic and comparable across life forms and environmental regimes.

Functionally, c_{min} represents a physiological threshold below which an organism can no longer sustain essential metabolic functions[16]. When net carbon assimilation persistently falls below this level, plants fail to meet the energetic demands of cell maintenance, tissue turnover, and osmotic regulation[16]. Sustained deficits initiate cascading physiological dysfunction, ultimately leading to death. This trajectory aligns with the well-documented phenomenon of carbon starvation and is supported by evidence across a range of environmental stressors, including drought, frost, shading, and herbivory[18,25-32]. By directly linking environmental carbon supply to physiological viability, c_{min} offers a quantifiable and mechanistic criterion for persistence. The C_{min} threshold can be formulized as:

$$C_{min} = C_{resp} + C_{stress} - C_{facilitation} + \varepsilon$$

Here, C_{resp} denotes the baseline carbon cost of cellular maintenance and respiration. C_{stress} accounts for additional carbon demands imposed by abiotic (e.g., drought, heat) or biotic (e.g., competition, herbivory) stressors. $C_{facilitation}$ captures carbon cost reductions conferred by positive interactions, such as mutualisms or neighbor shading. The residual term ε represents stochastic variation due to individual heterogeneity and unmeasured environmental noise.

Therefore, species persistence depends on whether net photosynthetic carbon gain (P_n) consistently exceeds the minimum threshold (c_{min}); that is, a species persists if $P_n > c_{min}$, but faces local exclusion or eventual population collapse when this condition is not met.

A species persists if $P_n > c_{min}$; otherwise, it is excluded.

The threshold-based nature of c_{min} encapsulates a fundamental constraint on survival. When net carbon assimilation persistently falls below this physiological minimum, plants can no longer sustain essential metabolic processes, ultimately leading to carbon starvation and death[16]. Persistence is not simply a function of whether a species has a high or low c_{min}, but of whether its net carbon gain reliably exceeds this threshold under prevailing conditions. Both conservative species with low c_{min} and acquisitive species with high c_{min} can persist, provided that their carbon balance remains positive in their local environment. This context dependence reflects a core trade-off between carbon demand and carbon acquisition, which in turn structures species distributions across environmental gradients[15,33-35].

The c_{min} refers to the minimum net carbon gain required to sustain essential metabolic functions necessary for survival, without considering structural growth[16]. Under stressful environmental conditions, many organisms, including both plants and animals, can enter dormant or resource-conserving states in which structural growth ceases but metabolic maintenance continues[15–16]. The difference between Pn and c_{min} represents the carbon surplus available to the organism. Once the baseline metabolic costs are met, this surplus can be allocated to structural investment, such as the formation of new leaves, stems, or roots, as well as to reproductive efforts. In contrast, c_{min} marks the physiological threshold below which survival becomes unsustainable, as all assimilated carbon is consumed solely to maintain core metabolic functions.

Collectively, these features establish the c_{min} theory as a physiologically explicit foundation for predicting species persistence under constraint. Building on this foundation, the c_{min} theory offers a mechanistic perspective on how species coexist and how diversity patterns emerge along gradients of resource availability and environmental stress.

The c_{min} theory: Linking carbon balance to species coexistence

Deciphering the mechanisms that allow multiple species to coexist in resource-constrained environments remains a central pursuit in ecology[5,8]. Classical theories, including niche differentiation, negative density dependence, neutral theory, and modern coexistence theory, serve as foundational theories for understanding species coexistence[2,9,12]. However, they often rely on parameters that are difficult to quantify and remain disconnected from the physiological processes that ultimately determine survival[7,8]. The c_{min} theory bridges this gap by grounding species persistence in the fundamental carbon economics of autotrophs.

According to the c_{min} theory, species survival, growth, and reproduction depend on maintaining a sustained net positive carbon balance. Coexistence emerges when multiple species are able to meet their respective c_{min} thresholds under shared environmental conditions. Because c_{min} reflects an integrated suite of traits, such as photosynthetic capacity and stress tolerance, species differ in their minimum carbon requirements, resulting in distinct, physiologically defined carbon niches. This differentiation enables coexistence under overlapping but non-identical environmental regimes. As a result, communities can include both conservative species with low carbon demand and acquisitive species with higher carbon requirements.

To illustrate this process, consider a simplified system where two species compete in an environment with a finite carbon pool, denoted as K, representing the maximum net carbon available to autotrophs. Species A, with a low c_{min}, exhibits high carbon-use efficiency and lower metabolic costs. Species B, by contrast, has a higher c_{min}, reflecting a faster growth strategy and higher carbon demands. During periods of high resource availability, such as under warm, moist, high-light conditions, both species may maintain positive net carbon gain above their thresholds and coexist. As conditions deteriorate (e.g., due to drought, shading, or nutrient limitation), carbon availability declines. Species B is more likely to fall below its c_{min} and decline, while Species A continues to persist. If carbon availability fluctuates over time, for instance, due to episodic increases in productivity, temporal niche partitioning may further facilitate coexistence, with Species B dominating during high-resource periods and Species A maintaining continuity across a broader environmental range. This scenario illustrates a central principle of the c_{min} theory: species coexistence depends on the alignment between species-specific carbon thresholds and the temporal dynamics of carbon supply.

Crucially, the carbon pool K functions analogously to the classical concept of carrying capacity[36,37], but is mechanistically grounded in environmental carbon supply. It reflects the system's capacity to support net carbon gain across all coexisting species, as governed by factors such as light availability, soil moisture, temperature, and nutrient status. Stable coexistence requires that the total community-level carbon demand, defined as the sum of each species' c_{min} times its population size, remains below K. When demand is lower than supply, multiple species may persist. However, when one species operates near its carbon limit while others remain below theirs, the outcome becomes dynamic, ranging from stable coexistence to periodic exclusion.

By integrating multiple environmental drivers into a single physiological parameter, c_{min} serves as a unifying axis of ecological differentiation. It captures trade-offs along multidimensional resource gradients and provides a tractable pathway for empirical testing. Gas exchange measurements, carbohydrate reserves, and stress-response indicators can be used to estimate c_{min}, linking physiology directly to species coexistence. In this way, the c_{min} theory establishes a mechanistically explicit, scalable, and testable theory of coexistence. It bridges individual carbon balance with population- and community-level outcomes, and unites deterministic and stochastic perspectives by highlighting how physiological thresholds mediate species viability under fluctuating environmental constraints.

Reframing existing coexistence theories through c_{min}

Niche theory

Classical niche theory holds that stable species coexistence arises from ecological differentiation, whereby species occupy distinct niches defined by divergent resource requirements or environmental tolerances[5,19]. This separation reduces interspecific competition and facilitates coexistence[5,19]. Tilman's R* theory formalizes this concept by proposing that the species capable of maintaining zero net population growth at the lowest concentration of a limiting resource will competitively exclude others[38,39]. Under single-resource limitation, stable coexistence is unlikely unless spatial or temporal environmental heterogeneity enables niche partitioning[38,39]. The resource ratio hypothesis further extends niche theory into a multidimensional resource space, where multiple co-limiting factors, such as temperature, light, water, and nutrients, jointly shape species coexistence[40,41]. Species differ in resource acquisition efficiency and physiological demand, and coexistence arises when environmental supply ratios fall between their respective optima, allowing each species to be limited by different resources[38,41]. Together, these concepts underscore how trade-offs in resource use and environmental conditions shape species coexistence.

Yet these ss often treat resource-use traits in abstract terms, remaining disconnected from the physiological mechanisms that govern survival[7,8]. The c_{min} theory offers a physiologically grounded reinterpretation of niche theory by integrating the effects of multiple resource limitations into a single threshold: the minimum net carbon assimilation rate required to sustain metabolism and ensure survival. Because photosynthesis is inherently co-limited by light, water, nutrients, and temperature, c_{min} captures an organism's overall environmental tolerance and resource-use strategy.

Species-specific variation in c_{min} arises from differences in photosynthetic capacity, leaf and hydraulic traits, respiratory costs, and stress-response mechanisms. These physiological attributes determine a species' ability to maintain a positive carbon balance across environmental gradients and thus define its viable niche space. Accordingly, c_{min} serves as a trait-based proxy for ecological niche position, translating the abstract concept of multidimensional niche differentiation into a measurable and mechanistically interpretable parameter. Under the c_{min} theory, coexistence is underpinned by quantifiable differences in carbon requirements among species, offering a testable alternative to inferred niche structure.

By rooting niche differentiation in the fundamental carbon economy of plants, the c_{min} theory enhances both the empirical tractability and predictive power of niche theory. It enables researchers to quantify ecological strategies through physiological thresholds rather than relying on inferred competitive hierarchies.

Neutral theory

Neutral theory hypothesizes that species within a community are functionally equivalent, exhibiting identical rates of birth, death, and dispersal[9,10,13]. Coexistence arises not from ecological differentiation, but through stochastic demographic drift[9]. While biologically unrealistic in its strictest form, neutral theory remains a powerful tool for interpreting diversity patterns, particularly in hyperdiverse and spatially structured systems such as tropical forests[42,43] and marine plankton communities[44,45].

The c_{min} theory offers a physiological interpretation of the conditions under which neutral dynamics may hold. In communities where coexisting species share similarly low c_{min} values, such as shade-tolerant understory plants in tropical forests or unicellular algae in nutrient-rich aquatic systems, the physiological thresholds required to sustain a positive carbon balance tend to converge. When environmental carbon supply consistently exceeds these low thresholds, all species can sustain net assimilation, reducing the strength of competitive exclusion. Under such conditions, species coexistence may be shaped by demographic stochasticity, dispersal limitation, and historical contingency, giving rise to neutral-like dynamics[9] despite underlying physiological constraints.

Rather than contradicting neutral theory, the c_{min} theory refines its ecological scope. It suggests that functional equivalence may arise not from true ecological identity, but from convergence in carbon-based physiological demands under resource-saturated or demographically buffered conditions. In doing so, c_{min} bridges stochastic and deterministic perspectives on coexistence by identifying physiological thresholds that govern the emergence of neutrality. This theory offers a mechanistic basis for predicting when and where neutral-like patterns may arise, grounded in measurable traits of carbon acquisition and metabolic demand.

Modern coexistence theory

Modern coexistence theory (MCT) provides a unifying concept that reconciles niche and neutral processes by emphasizing the balance between stabilizing and equalizing forces[2,11]. Stabilizing mechanisms promote rare species recovery via niche differentiation, while equalizing mechanisms minimize average fitness differences to prevent exclusion[2]. Despite its conceptual elegance, MCT often relies on parameters, such as interspecific competition coefficients and invasion growth rates, that are difficult to quantify in natural systems [2,46].

The c_{min} theory offers a physiological foundation for quantifying both stabilizing and equalizing components of modern coexistence theory. Species-specific c_{min} values, defined as the minimum net carbon assimilation rate required for persistence, arise from the interplay between functional traits and environmental resource availability. Interspecific variation in c_{min} reflects ecological differentiation: species with lower c_{min} can persist under resource-poor or stressful conditions, whereas those with higher c_{min} require more favorable environments to maintain positive carbon balance. This divergence promotes niche partitioning and thus contributes to stabilizing coexistence.

In addition to trait-mediated differentiation, species coexistence can be further stabilized by frequency-dependent mechanisms. For example, the classical Janzen–Connell hypothesis suggests that rare species experience lower herbivory, pathogen pressure, and intraspecific competition near conspecific adults. From a c_{min} perspective, such rarity confers a physiological advantage: reduced enemy load and improved access to limiting resources enhance photosynthetic carbon gain and reduce metabolic costs, thereby lowering the realized c_{min} under favorable local conditions. This shift in carbon balance supports regrowth, storage, and reproduction, facilitating demographic recovery and promoting the persistence of rare species.

Also, c_{min} provides a physiologically grounded metric of intrinsic fitness differences, a core component of modern coexistence theory. Species with lower c_{min} thresholds possess a physiological advantage under resource-limited conditions, sustaining metabolic activity and survival. Conversely, species with higher c_{min} values tend to exhibit acquisitive functional traits, such as high photosynthetic capacity and rapid growth, which confer advantages in resource-abundant environments. This makes fitness asymmetries context-dependent, shaped by environmental variability rather than fixed competitive hierarchies. In stable or resource-enriched environments, species with high c_{min} values may maintain positive carbon balance and reproductive output, thereby avoiding rapid competitive exclusion.

By integrating both stabilizing and equalizing forces into a single, measurable physiological trait, the c_{min} theory makes the conceptual structure of modern coexistence theory empirically tractable. It allows coexistence mechanisms to be quantified through measurable physiological traits rather than inferred from demographic patterns. Rather than replacing MCT, the c_{min} theory reinforces and extends its explanatory scope by providing a mechanistic bridge between individual-level carbon economics and species coexistence across heterogeneous environments.

The c_{min} theory: Explaining species distributions and diversity patterns

The c_{min} theory provides a unifying physiological foundation for species coexistence by linking individual-level carbon balance to community dynamics. It reframes major coexistence theories within a single, testable paradigm rooted in carbon assimilation thresholds. By quantifying how environmental variation constrains survival and reproduction through measurable physiological limits, c_{min} offers predictive insights into species persistence across environmental gradients. This mechanistic perspective connects organismal physiology with macroecological patterns, enabling c_{min} to explain large-scale species distributions and diversity patterns across space and time.

Species distributions

The c_{min} theory roots species' geographic ranges in the fundamental carbon economics of autotrophs. For a plant species to establish, grow, and reproduce, it must maintain a consistently positive net carbon balance[16]. The c_{min} represents the minimum sustained net carbon gain required to avoid carbon starvation, defining a species-specific physiological threshold for persistence.

When local environmental conditions, such as temperature, precipitation, solar radiation, soil moisture, and nutrient supply, support carbon assimilation rates above this threshold, a species can persist and potentially expand its range. Conversely, when these factors suppress net carbon gain below c_{min}, long-term survival becomes physiologically unviable, regardless of dispersal ability or competitive traits. In this sense, c_{min} offers a first-principle explanation for why some species fail to colonize seemingly suitable habitats by revealing their inability to maintain a viable carbon balance under prevailing conditions.

By reframing species distributions in terms of carbon sufficiency, the c_{min} theory offers a physiological mechanism that defines the lower boundary of a species' fundamental niche. This shifts the core biogeographic question from “Where is a species found?” to

"Where can a species physiologically persist?" It enables researchers to translate complex climatic and edaphic gradients into testable physiological thresholds, advancing beyond correlative species distribution models toward mechanistic predictions grounded in plant function.

Diversity patterns

Beyond shaping individual distributions, the c_{min} theory offers insight into one of ecology's central puzzles: the global variation in species diversity. A classic example is the latitudinal diversity gradient, where diversity peaks in the tropics and declines toward the poles[47,48]. Although numerous hypotheses have been proposed, including the species–energy hypothesis, the water–energy dynamics hypothesis and the metabolic theory of ecology, these theories are largely correlative and lack grounding in physiological mechanisms[49-52].

The c_{min} theory fills this gap by identifying a shared physiological threshold that determines whether a species can maintain a positive carbon balance under given environmental conditions. In resource-rich environments such as tropical rainforests, abundant light, temperature, and moisture allow photosynthetic gains to far exceed c_{min} for a wide array of species. This broad "carbon viability envelope" enables the coexistence of diverse functional strategies, promoting both taxonomic and trait diversity.

In contrast, cold and dry environments impose stringent carbon constraints. Photosynthetic assimilation is reduced by stress, while maintenance and repair costs often remain constant or increase. Under such conditions, only species with exceptionally low c_{min} that maximize carbon-use efficiency or minimize carbon loss are able to persist. This physiological filtering narrows the viable species pool, contributing to the low taxonomic richness and functional convergence observed in high-latitude and high-elevation ecosystems.

By translating environmental conditions into species-specific physiological thresholds, the c_{min} theory provides a mechanistic explanation for large-scale diversity patterns. It predicts that species richness should peak in regions where environmental energy inputs allow many species to meet their carbon needs, and decline where only the most efficient species can survive. In doing so, c_{min} advances biogeography from correlative pattern recognition to a physiology-based explanatory theory. It provides a physiological lens for understanding and predicting diversity patterns across ecosystems and regions.

Reframing existing diversity theories through c_{min}

A key strength of the c_{min} theory is its ability to unify diverse diversity hypotheses through a common physiological mechanism, moving beyond traditional reliance on statistical correlations or phenomenological patterns[48,53,54]. By linking species persistence to the universal constraint of carbon balance, c_{min} offers a consistent physiological basis for mechanistically interpreting and empirically testing large-scale diversity patterns.

Energy–diversity hypothesis

The energy–diversity hypothesis suggests that environments with higher energy input tend to support greater species richness[55]. This pattern, widely observed across biomes and particularly pronounced in the tropics, is often attributed to enhanced resource availability, higher niche partitioning, and larger population sizes that reduce extinction risk [48,56]. However, despite its empirical consistency, the hypothesis remains largely correlative—describing what occurs without explaining how energy directly supports survival at the organismal level.

The c_{min} theory addresses this mechanistic gap by introducing a physiological threshold—the minimum net carbon gain required to sustain metabolism. In energy-rich environments, high light availability and favorable temperatures enhance photosynthetic assimilation, increasing the probability that a wide range of species, both acquisitive and conservative strategies, can surpass their c_{min} thresholds. As a result, more species are able to maintain viable carbon balances, expanding the pool of coexisting taxa.

Conversely, in low-energy environments such as high-latitude forests or alpine zones, photosynthetic gains are constrained by light and temperature, while baseline respiratory costs persist. This imbalance raises the likelihood that many species will fall below their c_{min} threshold. Only species with intrinsically low c_{min} achieved through high carbon-use efficiency or low maintenance costs are able to persist. Thus, by explicitly quantifying the physiological constraints imposed by energy availability, the c_{min} theory transforms the energy–diversity hypothesis from a correlative pattern into a mechanistic model of carbon viability.

This reframing provides a physiologically grounded explanation for global richness gradients: diversity peaks where environmental energy allows many species to meet their carbon requirements, and declines where only a few can. In doing so, c_{min} offers a physiological lens through which to evaluate how energy regimes structure the carbon economy and coexistence potential of entire communities.

Water–energy dynamics hypothesis

Extending the logic of energy-based explanations, the water–energy dynamics hypothesis proposes that species richness is co-limited by both energy input and water availability[50,57,58]. Yet, the physiological mechanisms linking these climate variables to species persistence remains unclear [53,54].

The c_{min} theory provides a mechanistic explanation by linking water and energy constraints to the carbon balance. Since photosynthesis depends on both light and water, limitations in either reduce carbon assimilation. Under warm and moist conditions, photosynthetic efficiency tends to be high while metabolic costs remain moderate, enabling many species to maintain carbon surpluses above their c_{min} thresholds. These surpluses support greater taxonomic and functional diversity. In contrast, cold or arid environments constrain carbon gain while increasing metabolic demand. Only species with exceptionally low c_{min} values can persist under such conditions, which act as physiological filters and restrict the range of viable strategies.

By linking hydrothermal conditions to physiological viability, the c_{min} theory explains how water and energy jointly define ecological boundaries. It reframes traditional climate–diversity correlations as outcomes of a carbon-based viability landscape, where environmental constraints shape the functional composition and diversity potential of entire floras.

Metabolic theory of ecology

The metabolic theory of ecology (MTE) hypothesizes that temperature and body size fundamentally regulate metabolic rates, and that these constraints scale up to influence individual growth, population dynamics, and species richness[51]. MTE has provided a powerful theory linking physiological rates to macroecological patterns, predicting, for instance, that warming accelerates metabolism and life-history processes[51,52]. However, the theory remains fundamentally rate-based, describing the speed of energy flow through organisms without considering whether the net energy gain is sufficient to sustain life[59,60].

The c_{min} theory complements and extends MTE by introducing a constraint-based criterion for survival. While elevated temperatures may increase both photosynthetic assimilation and respiratory demand, they do not guarantee a net carbon surplus[61,62]. In resource-limited or stressful environments, warming-induced drought may raise respiration[62,63], pushing species beyond their c_{min} threshold and increasing the risk of demographic decline. By embedding a physiological threshold into the logic of MTE, the c_{min} theory shifts the focus from metabolic rate to carbon sufficiency for survival. This is particularly valuable for forecasting climate-driven range shifts and extinction risk, providing a more comprehensive view of how warming reshapes diversity across spatial and functional gradients.

These physiological insights strengthen both the clarity and the broad applicability of the c_{min} theory. Rather than acting as an isolated theory, c_{min} provides a physiological link that helps clarify, refine, and connect existing diversity hypotheses through a shared focus on carbon balance. By focusing on a species' ability to maintain positive carbon gain, it links environmental energy and water supply to the metabolic conditions required for survival. As a measurable and comparable physiological threshold, c_{min} offers a common basis for understanding how energy, water, temperature, and diversity patterns vary across space and time. By placing species diversity in the context of carbon requirements, the c_{min} theory offers a more coherent and testable view of how diversity is shaped across ecosystems.

Universality and cross-taxon applicability of the c_{min} theory

Although initially developed to explore ecological dynamics in plant systems, the c_{min} theory provides a unified, mechanistic model with broad applicability across biological systems. At its core, c_{min} expresses a basic ecological principle: all organisms must maintain a positive carbon balance to support survival, growth, and reproduction[16,20-22]. Carbon functions as the central biological currency on Earth[64,65], and its acquisition, allocation, transport, storage, and remobilization govern the structure and function of all living systems[16,20-22]. In this sense, the principle captured by c_{min} transcends taxonomic boundaries, trophic levels, and modes of carbon acquisition.

In autotrophs such as vascular plants and algae, c_{min} defines the minimum net photosynthetic gain required to offset respiratory losses and endure abiotic and biotic stress. It sets the threshold for maintaining tissue integrity, supporting growth and reproduction, and ultimately persisting under given environmental conditions. As demonstrated in plants, chronic shortfalls below c_{min} lead to carbon starvation, physiological collapse, and mortality[16].

A similar principle applies to heterotrophs, including animals, fungi, and microbes, which rely on external carbon sources. In these organisms, persistence depends on achieving positive net energy intake through feeding, foraging, or symbiosis[66,67]. For heterotrophs, c_{min} can be interpreted as the minimum net energetic gain required to meet core metabolic demands such as cellular maintenance, thermoregulation, immune defense, and reproduction. Insects, for example, must meet developmental and immunological costs through consumption[68,69], in the same way that plants do through photosynthesis. Similarly, in microbial communities, the capacity to acquire and metabolize carbon substrates under nutrient-limited conditions determines both survival and competitive outcomes[70,71].

By reducing persistence to a balance between carbon or energy acquisition and loss, the c_{min} theory provides a first-principles basis for understanding environmental filtering, resource-mediated competition, and functional convergence across systems. It reframes species viability not as a taxon-specific attribute but as a universal physiological outcome shaped by environmental constraints. This cross-system comparability offers a coherent framework for investigating coexistence and diversity maintenance across trophic levels, taxonomic groups, and biomes.

The generality of c_{min} theory opens new opportunities for synthesizing diverse ecological subfields. In microbial ecology, it informs models of carbon use efficiency and community structure along resource gradients. In animal ecology, it offers a quantitative theory to assess energetic limits, habitat suitability, and stress-induced demographic thresholds. In food webs, c_{min} defines a physiological threshold for energy transfer, indicating that trophic interactions are limited not only by resource availability but also by whether each consumer's minimal energetic needs can be met within the trophic energy budget.

Together, these applications position c_{min} as a universal physiological filter that governs where, when, and which organisms can persist. Beyond its conceptual coherence, the c_{min} theory offers an empirically tractable and scalable tool for predicting ecological patterns across taxa, functional groups, and ecosystems. This shared metabolic axis connects individual physiological function to population dynamics, species distributions, diversity gradients, and ecosystem resilience. As a result, c_{min} enables a unified, process-based understanding of ecological structure and dynamics in a carbon-limited world—one increasingly shaped by climate change and resource constraints.

Ecological applications of the c_{min} theory

The c_{min} theory, grounded in the universal constraint that all organisms must sustain a positive net carbon balance, offers a mechanistic and scalable foundation for addressing fundamental ecological questions across spatial, temporal, and organizational scales. By linking physiological limits to emergent patterns, c_{min} connects individual tolerance with ecosystem responses in a carbon-constrained world. Here, we synthesize five domains in which c_{min} demonstrates distinctive explanatory and predictive power: (1) ecosystem functioning, (2) climate change impacts on ecosystems, (3) ecological stability, (4) biological invasions, and (5) evolutionary biogeography.

Ecosystem functioning

Ecosystem functioning emerges from the interaction between organismal traits and the biogeochemical processes they mediate, particularly those governing carbon, water, and nutrient cycles[72-74]. Traditional trait-based and process-based approaches have each contributed valuable insights into these dynamics, yet often operate in parallel, lacking a mechanistic bridge between organismal physiology and ecosystem-level outcomes[75,76]. The c_{min} theory bridges this gap by introducing a unified physiological metric that links functional traits to ecosystem processes: the minimum net carbon gain required for survival.

In ecosystems, plant traits, such as photosynthetic capacity, respiration rate, hydraulic efficiency, and nutrient-use strategy, determine key physiological processes, including carbon assimilation, water transport, and nutrient use efficiency[76]. These processes, in turn, shape how effectively individuals acquire and utilize environmental resources such as light, temperature, moisture, and nutrients[15,34]. Importantly, both trait expression and environmental resources supply jointly govern c_{min}, making it a dynamic threshold that captures the carbon costs of sustaining life under specific ecological conditions.

As the net outcome of trait–environment interactions, c_{min} provides a biologically interpretable measure of an organism's capacity to maintain a positive carbon balance. It therefore reflects not only the efficiency of resource use, but also the constraints imposed by environmental variability. In this sense, c_{min} serves as a proxy for multiple facets of ecosystem functioning, including primary productivity, carbon-use efficiency, and the coupling of carbon, water, and nutrient cycles.

Crucially, c_{min} is both physiologically grounded and methodologically tractable. It can be quantified at the level of individuals and scaled up to populations, communities, or ecosystems using a combination of gas-exchange measurements, remote sensing, and trait-based modeling. This scalability allows consistent integration of trait-based and process-based perspectives across spatial and temporal scales. By rooting ecosystem function in a shared physiological constraint, c_{min} enables robust predictions of functional shifts under climate variability, disturbance, and diversity change.

In sum, the c_{min} theory offers a first-principles axis for linking organismal carbon dynamics to emergent ecological outcomes. By capturing how variation in traits and environment shapes the metabolic viability of individuals, it provides a scalable and predictive lens for understanding and forecasting ecosystem function in a carbon-constrained biosphere.

Climate change impacts on ecosystems

Climate change is fundamentally destabilizing the balance between carbon acquisition and loss across ecosystems[62,77]. In many regions, particularly those nearing thermal or water-stress thresholds, respiratory carbon losses are increasing more rapidly than photosynthetic gains under warming conditions[78,79].Elevated temperatures amplify baseline metabolic costs, while prolonged drought, declining soil moisture, and atmospheric aridity suppress carbon uptake by constraining stomatal conductance and impairing biochemical photosynthetic efficiency [62,77]. Together, these stressors increase the minimum net carbon gain required for survival, tightening physiological constraints on species persistence.

The c_{min} theory offers a physiological lens for anticipating how climate stressors reshape ecosystem structure and function. By quantifying shifting carbon thresholds under warming and drying conditions, it identifies which species or functional groups are most vulnerable, and how their loss or decline may cascade into altered ecosystem processes. In particular, increases in c_{min} can reduce community-level carbon assimilation, weaken hydrological regulation, and disrupt nutrient retention, with downstream impacts on productivity, trophic structure, and biogeochemical coupling.

As climate extremes, such as droughts and heatwaves, become more frequent and intense[80-82], the balance between carbon supply and demand is increasingly disrupted. These events simultaneously depress photosynthetic input and elevate respiratory and stress-related carbon losses, further raising species' c_{min}. As thresholds rise, fewer taxa may maintain a positive carbon balance, leading to selective filtering of functional groups, shifts in dominance hierarchies, and reconfiguration of ecosystem structure. Over time, this reassembly can erode ecological functions such as resilience, carbon storage, and resource-use efficiency. By linking climate-induced changes in environmental conditions to physiological tipping points, the c_{min} theory enables predictive assessments of ecosystem vulnerability. It offers a unified, trait-based axis for projecting how altered carbon economics under climate change will reshape ecosystem structure, functioning, and service delivery.

Ecological stability

The c_{min} theory defines a carbon-based metabolic threshold that links individual physiological performance to survival under environmental stress. This tipping-point property makes c_{min} especially powerful for assessing ecological stability. When stressors such as drought, warming, or nutrient depletion reduce carbon gain or raise maintenance costs, organisms that cannot sustain a positive carbon balance fall below their c_{min}. This results in carbon deficits that suppress growth, impair function, and ultimately increase mortality[18,26]. As such physiological failures accumulate across taxa, they erode community composition, reduce functional redundancy, and destabilize critical ecosystem processes such as carbon storage and nutrient cycling. In this way, c_{min} provides a mechanistically grounded lens for tracing how localized metabolic imbalance can propagate into system-level instability.

Critically, c_{min} is inherently scalable. At the individual level, it reflects the balance between carbon supply and demand, determined by traits such as photosynthetic capacity, respiration rate, and allocation strategy. At broader scales, community- or ecosystem-level c_{min} can be derived by aggregating species-specific thresholds weighted by abundance or dominance. This enables direct comparison with available resource inputs, such as light, water, and nutrients, to assess how close a system operates to its collective carbon limit. As environmental change narrows the margin between available carbon and required c_{min}, ecosystems approach a critical zone of vulnerability where even small disturbances can trigger structural simplification and functional collapse.

Importantly, the c_{min} theory also allows explicit evaluation of stability across vertically stratified layers within ecosystems. In forests, for example, canopy, understory, and ground layers differ in their access to light, moisture, and nutrients, and thus exhibit distinct c_{min} values. Climate-driven changes in temperature or moisture may disproportionately elevate c_{min} in a specific layer, such as the shaded, water-limited understory, pushing it beyond what local conditions can support. If understory species are unable to meet their rising c_{min}, this can result in selective layer collapse, simplifying vertical community architecture and diminishing the system’s overall resilience and buffering capacity.

By uniting organismal metabolic constraints with emergent ecological dynamics, c_{min} also offers a physiologically explicit indicator of ecosystem stability. It supports early warning of systemic vulnerability, enables cross-biome comparisons of resilience, and bridges trait-based and process-based approaches for forecasting how ecosystems will respond to accelerating environmental change.

Biological invasions

Biological invasions restructure ecological communities by selectively favoring species capable of surviving and reproducing under altered environmental and competitive conditions[83,84]. Despite extensive research, the mechanisms underpinning biological invasions remain poorly resolved[85-87]. Prevailing hypotheses, including enemy release, increased competitive ability, novel weapons, and fluctuating resource availability, capture key invasion patterns but are often context-dependent, taxonomically constrained, and lack physiological grounding[88-91]. As a result, no general theory reliably predicts invasion success across ecosystems[85,92]. Yet, as with all organisms, the establishment and spread of invasive species ultimately depend on their ability to maintain a positive net carbon balance under novel environmental conditions. The c_{min} theory provides a mechanistic basis for addressing this challenge by linking invasion dynamics to the carbon economics of species persistence.

Successful invaders can achieve sustained carbon surpluses via two primary pathways: enhanced resource acquisition and reduced biotic resistance. Many invasive species possess acquisitive traits—such as high photosynthetic capacity, rapid growth rates, and efficient nutrient use—that elevate carbon gain across a wide range of environments[93-95]. Simultaneously, invaders frequently benefit from enemy release, encountering fewer herbivores, and competitors in their introduced ranges[96-98].This leads to lower carbon losses from defense and damage repair, effectively reducing their realized c_{min} thresholds under field conditions. Invasive species are therefore more likely to sustain positive carbon balances under variable or suboptimal conditions that may drive native species below their c_{min} thresholds. Moreover, some invaders may modify local resource dynamics or microclimates in ways that raise carbon costs for resident species, exacerbating metabolic stress and increasing the risk of local exclusion or collapse.

By explicitly accounting for both carbon inputs and losses, the c_{min} theory reframes invasion ecology from a trait-association paradigm to a predictive, physiologically explicit theory. It provides a common physiological currency for comparing invasion potential across taxa, environments, and disturbance contexts. This enables more accurate forecasting of invasion risk and informs management strategies such as early detection, biotic resistance enhancement, and restoration efforts focused on restoring favorable carbon balances for native species.

Evolution and biogeography

At macroevolutionary scales, variation in c_{min} reflects how different lineages have functionally adapted to long-term environmental constraints and resource regimes. In cold, arid, or nutrient-poor regions, natural selection likely favors conservative traits that minimize carbon loss[33,99,100], thereby lowering the threshold required for persistence. Conversely, in warm, humid, and resource-rich biomes such as tropical forests, many taxa have evolved acquisitive strategies characterized by high photosynthetic capacity and reduced investment in defense[100-102], enabling large carbon surpluses that support rapid growth, complex architectures, and diverse life histories.

The macro-physiological variation in c_{min} is unlikely to be randomly distributed across the tree of life. It may be shaped by historical niche constraints and trait inheritance, with closely related taxa tending to exhibit similar c_{min} values due to shared physiological limits. Spatial variation in c_{min} across species and ecosystems offers a physiological basis for interpreting major biogeographic patterns, including the latitudinal diversity gradient, regional endemism, and differences in species pools among biomes. The c_{min} theory thus offers a useful approach for exploring how long-term evolutionary history has shaped today's distribution of carbon-use strategies across different groups of organisms.

By integrating c_{min} with phylogenetic reconstructions, trait databases, and environmental datasets, researchers may be able to trace the evolutionary history of carbon-use strategies and quantify the physiological limits that shape species' biogeographic distributions. This approach provides a mechanistic basis for understanding how physiological constraints have contributed to diversity patterns across space and time. Ultimately, the c_{min} theory serves as a bridge between evolutionary history and contemporary biogeographic structure, offering new insight into how lineages could respond to future environmental change in a carbon-constrained world.

Conclusion

The c_{min} theory offers a physiologically grounded and quantitatively measurable threshold for species persistence, rooted in the fundamental principle that organisms must maintain a net positive carbon balance to survive. This simple yet universal constraint provides a powerful lens for explaining species coexistence under resource limitation and interpreting diversity patterns across broad spatial gradients.

Unlike existing ecological theories that often depend on abstract or system-specific parameters, c_{min} is built upon measurable biological processes that can be observed, quantified, and experimentally tested. Rather than replacing current theories, it provides a physiological foundation that reframes existing theories—including niche differentiation, neutral dynamics, energy–diversity relationships, and the metabolic theory of ecology—within a unified carbon economy. This integration not only clarifies the underlying carbon constraints that structure ecological systems but also bridges theoretical ecology with empirical validation.

The c_{min} principle is broadly applicable across the tree of life. Because carbon is the universal metabolic currency, this c_{min} extends beyond plants to animals, fungi, and microbes. Beyond taxonomic generality, c_{min} also facilitates connections across levels of biological organization. This cross-scale continuity provides a mechanistic link between organismal physiology and emergent ecological patterns, connecting trait-based strategies, environmental filtering, and ecosystem functioning. Consequently, the c_{min} can be applied to address a broad spectrum of ecological phenomena, including—but not limited to—ecosystem functioning, ecological stability, and invasion dynamics. Its mechanistic foundation enables a unified understanding of how physiological thresholds scale up to shape ecological outcomes under varying environmental conditions.

Taken together, c_{min} offers a unified theory with mechanistic clarity, empirical tractability, and wide applicability in ecology. By linking persistence directly to carbon thresholds, it establishes a strong foundation for advancing ecological theory and forecasting global change impacts. Integrating c_{min} more widely into ecological research provides a pathway to unify physiological mechanisms with large-scale ecological outcomes, improving our ability to anticipate diversity shifts and ecosystem responses under global change.

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