The Minimum Carbon Theory: A Physiological Basis for Species Coexistence

Lei Chen
College of Life Sciences, Sichuan University, Chengdu, China

Correspondence:
Email: lei.chen1029@gmail.com

Abstract

Understanding how species coexist and why diversity varies across regions remains a central challenge in ecology. Although existing theories such as niche theory, neutral theory, and modern coexistence theory have yielded important insights into species coexistence and diversity, their reliance on abstract parameters lacking direct physiological grounding limits empirical validation and constrains cross-scale integration. To address this limitation, the minimum carbon theory is proposed, defining C_{min} as the minimum net carbon gain required for survival, grounded in the first principle that autotrophic organisms must maintain a positive carbon balance to persist. Coexistence occurs when multiple species each sustain net carbon gains above their C_{min} under shared environmental regimes. The C_{min} theory provides a physiological foundation for understanding species coexistence and diversity, integrating existing ecological theories under the common constraint of carbon balance. Because carbon is the universal currency of life, the C_{min} can be applied across taxa and ecological scales, providing a broadly applicable framework for diverse domains, including biological invasions, ecosystem functioning, ecological stability, and evolutionary biogeography. In a biosphere increasingly shaped by global climate change, the C_{min} theory provides a unifying physiological lens on how individual carbon thresholds scale up to shape species diversity and ecosystem function.

Keywords: Minimum carbon theory, physiological threshold, species persistence, species coexistence, diversity patterns, ecosystem functioning

Introduction

Understanding how multiple species coexist within ecological communities remains one of the most fundamental and unresolved questions in ecology (Chesson 2000; Gravel et al. 2011). This challenge constrains our ability to explain diversity patterns and to predict ecosystem functioning and resilience under global climate change (Tilman et al. 2014). Despite decades of theoretical and empirical advances, a unified mechanistic theory capable of explaining species coexistence and diversity across heterogeneous environments remains elusive (Dybzinski and Tilman 2007; HilleRisLambers et al. 2012; Levine and HilleRisLambers 2009; Levine et al. 2017).

Over the past century, ecologists have sought to explain species coexistence and diversity patterns through process-based mechanisms, giving rise to several influential theories (Valladares et al. 2015). Classical niche theory emphasizes stabilizing mechanisms such as resource partitioning, which reduce interspecific competition and facilitate species coexistence (Dybzinski and Tilman 2007; Levine and HilleRisLambers 2009). In contrast, neutral theory assumes functional equivalence among species and attributes diversity to demographic stochasticity (Chave 2004; Hubbell 2011). Modern coexistence theory seeks to integrate these perspectives by quantifying the relative contributions of stabilizing and equalizing forces (Chesson 2000; Chesson 2018). Although these theories have provided important insights into species coexistence, they often depend on abstract parameters such as invasion growth rates and competition coefficients, which are difficult to quantify and test empirically in complex, long-lived, and multispecies systems (Adler et al. 2007; Chesson 2000; Gravel et al. 2011). This underscores the urgent need for a mechanistic theory of species coexistence that is both physiologically grounded and empirically testable (Kalyuzhny et al. 2014; Valladares et al. 2015).

At its core, ecology seeks to understand how organisms grow, persist, and interact with their environment under natural constraints (Begon and Townsend 2006; Ricklefs 2008). The survival of autotrophic plants ultimately depends on whether photosynthetic carbon gain outweighs the metabolic costs of maintenance, defense, and reproduction (Amthor 2000; Lambers et al. 2008; McDowell et al. 2008). The ability to persist physiologically under given environmental conditions is a prerequisite for community membership, allowing organisms to interact ecologically and enabling species to coexist. However, existing theories largely overlook the fundamental physiological basis of whether an organism can persist under specific environmental conditions (Gravel et al. 2011; HilleRisLambers et al. 2012; Tilman 2004). Therefore, rebuilding ecological theory from first-principles of plant survival is essential for understanding species coexistence and diversity.

Here, the minimum carbon theory (C_{min}) is proposed, in which species persistence is defined as maintaining net carbon gain above a critical physiological threshold. This threshold (C_{min}) indicates the minimum carbon gain required to sustain metabolic integrity and survival. Species persistence in a given environment depends on whether local carbon gain consistently exceeds its C_{min} threshold. The C_{min} is shaped by both plant traits and environmental resources, thereby defining its position in carbon niche space. Species coexistence occurs when multiple species can each meet their C_{min} under shared environmental conditions.

The C_{min} offers several key advantages over existing theories. First, the C_{min} provides a measurable physiological alternative to the abstract parameters that underpin many traditional coexistence theories. This facilitates physiologically based comparisons and empirical validation through experiments or field observations. Second, the C_{min} theory is not limited to autotrophic plants. This is because carbon is the universal currency of life, organisms from microbes to animals must maintain a positive net carbon balance to survive and reproduce (Gruner et al. 2008; Lambers et al. 2008; Lynch et al. 1986; Manzoni and Porporato 2009). Third, the C_{min} is inherently scalable. By defining species persistence through carbon-based physiological thresholds, it links individual performance to ecosystem function across taxa and environments. This cross-scale consistency enables C_{min} to be applied in explaining both local species coexistence and large-scale patterns of species distribution and diversity, while also enhancing predictions of ecosystem responses to environmental change.

In this *Perspective*, the underlying physiological principles of the C_{min} theory are first outlined, followed by an explanation of how it provides a physiological foundation for species coexistence while reframing classic ecological theories, including niche theory, neutral theory, and modern coexistence theory. Extending beyond local coexistence, the C_{min} is then presented as a physiological framework for explaining large-scale diversity patterns and reframing macroecological theories, such as the species–energy hypothesis, water–energy dynamics, and the metabolic theory of ecology. Finally, five key domains are identified in which the C_{min} theory is broadly applicable, offering both mechanistic insight and predictive capacity. These include ecosystem functioning, climate change impacts on ecosystems, ecological stability, biological invasions, and evolutionary biogeography. Together, the C_{min} theory provides not only a general physiological basis for species coexistence and diversity, but also a unifying principle linking carbon balance to the structure and function of ecological systems.

Physiological principles underlying the C_{min} theory

The C_{min} theory is grounded in the core physiological principle that autotrophic plants must maintain a positive carbon balance to survive (Amthor 2000; Lambers et al. 2008; McDowell et al. 2008). Unlike cumulative measures such as carbohydrate pools or total biomass, flux-based metrics such as photosynthetic rate offer high temporal resolution, broad cross-taxon comparability, and strong compatibility with ecological models (Dietze et al. 2014; Litton et al. 2007). Therefore, the C_{min} is defined as the minimum rate of net carbon gain necessary to maintain metabolic function and ensure survival. This rate-based formulation also enables standardized comparisons of C_{min} across species and environments, providing a unified physiological lens for assessing survival limits under varying ecological conditions. Given the temporal variability of photosynthesis and respiration, C_{min} represents a mean net carbon gain rate integrated over biologically relevant timescales, rather than a momentary or daily flux. This integration smooths short-term fluctuations and captures the sustained carbon balance required for persistence. In fast-growing herbaceous plants, weekly to monthly integration windows may suffice. For long-lived woody species, particularly trees, averages across seasonal to interannual timescales more accurately reflect the threshold of carbon gain relevant to survival. This 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 (Lambers et al. 2008). When net carbon assimilation persistently falls below this threshold, plants fail to meet the energetic demands of maintenance, tissue turnover, and osmotic regulation, leading to progressive metabolic failure and eventual mortality (Lambers et al. 2008). This trajectory is consistent with well-documented cases of mortality driven by carbon starvation, supported by ample evidence across diverse stressors such as drought, frost, shading, and herbivory (Anderegg et al. 2012, 2015; Givnish 1988; Hartmann and Trumbore 2016; Herms and Mattson 1992; McDowell 2011; McDowell et al. 2008; Myers and Kitajima 2007; Sperling et al. 2015). By linking carbon balance to physiological viability, C_{min} provides a mechanistic and quantifiable criterion for species persistence (Figure 1).

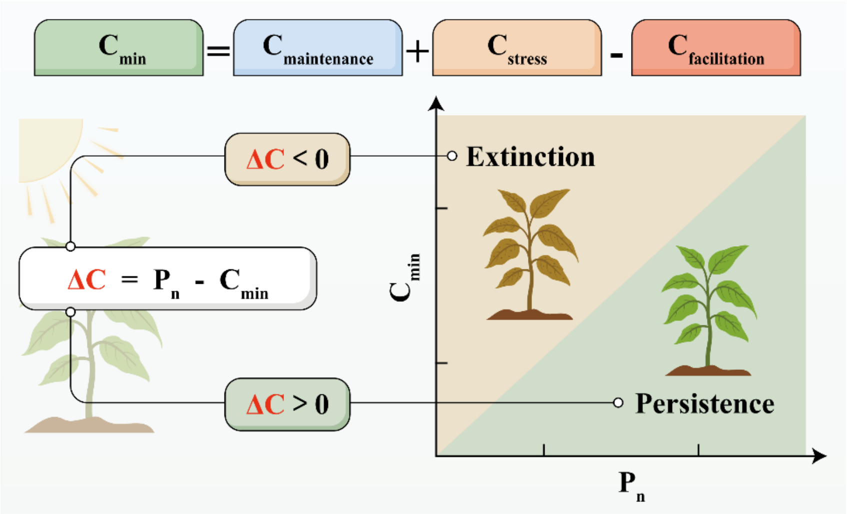

Figure 1 | Conceptual framework of the C_{min} theory. The C_{min} represents the minimum net carbon gain required to sustain metabolic function and survival. $C_{maintenance}$ denotes the baseline carbon demand for essential cellular maintenance through respiration, C_{stress} captures additional carbon costs imposed by abiotic or biotic stressors, $C_{facilitation}$ reflects reductions in demand arising from positive interactions, P_n and ΔC represent the net carbon gain and carbon surplus, respectively. A species can persist only when P_n exceeds its C_{min}, otherwise it faces extinction. Once C_{min} is met, surplus carbon (ΔC) can be allocated to growth and reproduction. Persistence is determined jointly by P_n and C_{min}, reflecting the fundamental trade-off between carbon acquisition and demand.

The C_{min} threshold can be formulized as:

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

where $C_{maintenance}$ denotes the baseline carbon demand required to sustain essential cellular functions through maintenance respiration; C_{stress} accounts for additional carbon demand imposed by abiotic factors such as drought and heat, or biotic factors such as competition and herbivory; $C_{facilitation}$ captures reductions in carbon demand resulting from positive biotic interactions, including mutualisms, neighbor shading, or microclimatic buffering; ε accounts for stochastic variation arising from individual heterogeneity and environmental noise. Because organisms may suppress structural growth while sustaining basic metabolism through dormancy or resource conservation under stressful conditions (Lambers et al. 2008; Ricklefs 2008), the component of C_{min} that excludes structural investment represents the minimal carbon requirement for physiological maintenance and survival (Lambers et al. 2008).

A species persists if $P_n > C_{min}$; otherwise, it fails to survive.

Therefore, species persistence depends on whether net photosynthetic carbon gain (P_n) consistently exceeds the minimum threshold (C_{min}). A species can persist when P_n exceeds this physiological threshold, but fails to survive when it does not. The C_{min} captures a core physiological limit to survival. When net carbon assimilation persistently falls below the C_{min}, plants can no longer sustain essential metabolic processes, ultimately leading to carbon starvation and mortality (Lambers et al. 2008). Persistence depends not merely on whether a species has a high or low C_{min}, but on whether its net carbon gain consistently exceeds this threshold. Both conservative species with low C_{min} and acquisitive species with high C_{min} can persist, as long as they maintain a positive carbon balance. This reflects a fundamental trade-off between carbon acquisition and demand, shaping the conditions under which different strategies can sustain persistence (Reich 2014; Ricklefs 2008; Westoby et al. 2012; Wright et al. 2014).

$$\Delta C = P_n - C_{min}$$

The carbon surplus (ΔC), defined as the difference between P_n and C_{min}, arises only when net carbon gain exceeds the threshold for survival. Once this baseline requirement is met, surplus carbon can be allocated to structural growth and reproduction, including the formation of new leaves, fruits, and seeds.

In conclusion, the C_{min} offers a physiologically grounded alternative to traditional interaction-based theories, shifting the focus from emergent ecological processes to the underlying carbon constraints that determine species survival. It provides a physiological basis for predicting species persistence and for explaining the emergence of coexistence and diversity patterns across resources and stress gradients.

The C_{min} theory links carbon balance to species coexistence

Deciphering the mechanisms that enable multiple species to coexist within shared environments remains a longstanding and central challenge in ecology (Levine and HilleRisLambers 2009; Valladares et al. 2015). Classical theories, including niche differentiation, neutral theory, and modern coexistence theory, serve as conceptual foundation for understanding species coexistence (Adler et al. 2007; Chesson 2000; Hubbell 2011). However, they often depend on abstract parameters that are difficult to verify through experiments or field observations (HilleRisLambers et al. 2012; Valladares et al. 2015). The C_{min} addresses this gap by providing a physiologically grounded framework for species coexistence, rooted in the carbon economics of autotrophs.

According to the C_{min} theory, species survival, growth, and reproduction depend on maintaining a sustained positive carbon balance. Coexistence is physiologically possible when multiple species can consistently meet their respective C_{min} thresholds under shared environmental conditions (Figure 2). 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 support both conservative species with low carbon maintenance costs and acquisitive species with high carbon uptake capacities, as long as each maintains a positive carbon balance.

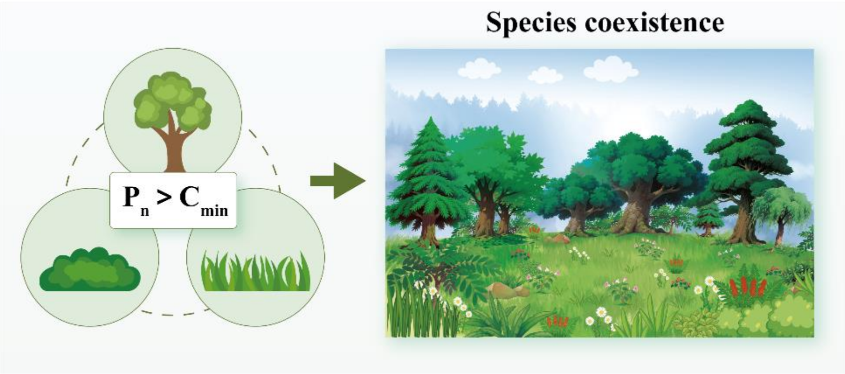

Figure 2 | Conceptual diagram of how C_{min} links carbon balance to species coexistence. P_n and C_{min} represent the net carbon gain and minimum carbon required to sustain metabolic function and survival, respectively. Coexistence occurs when species maintain P_n above their C_{min} thresholds under shared conditions. Variation in C_{min} defines distinct physiological carbon niches, facilitating coexistence under overlapping but non-identical environments.

To illustrate this mechanism, consider a simplified system in which two species compete for a finite carbon pool, *K*, representing the maximum carbon available to autotrophs. The *K* is similar to the classical concept of carrying capacity (Dushoff 2000; Seidl and Tisdell 1999), but it is grounded in the environmental carbon supply. Species A, characterized by a low C_{min}, exhibits lower metabolic demand and follows a more conservative carbon uptake strategy. In contrast, Species B has a higher C_{min}, requiring greater carbon input to sustain metabolic function and supported by a faster carbon acquisition rate. Under favorable environmental conditions, both species can maintain net carbon gains above their respective thresholds and coexist. However, as conditions become harsher and carbon availability declines, Species B is more likely to fall below its C_{min} and decline, while Species A continues to persist due to its lower carbon requirement. When carbon supply fluctuates over time, temporal niche partitioning may arise, with Species B dominating during resource-rich periods and Species A persisting through resources-limited periods. Coexistence thus depends on the match between carbon availability and species-specific C_{min} thresholds across spatial and temporal scales.

In conclusion, the C_{min} serves as a unifying axis of ecological differentiation, capturing trade-offs across multidimensional resource gradients. Thus, the C_{min} theory provides a mechanistically grounded, scalable, and testable explanation for coexistence. It connects individual-level carbon economics with population and community outcomes, and reconciles deterministic and stochastic mechanisms by emphasizing how physiological thresholds shape species coexistence under variable environmental conditions.

Reframing existing coexistence theories through the C_{min}

Niche theory

Classical niche theory holds that species coexistence arises from ecological differentiation, whereby species occupy distinct niches defined by divergent resource requirements or environmental tolerances (Levine and HilleRisLambers 2009; Tilman 2004). The niche differentiation reduces interspecific competition and facilitates coexistence (Levine and HilleRisLambers 2009; Tilman 2004). 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 (Tilman 1980, 1982). Under single resource limitation, stable coexistence is unlikely unless spatial or temporal environmental heterogeneity enables niche partitioning (Tilman 1980, 1982). 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 (Miller et al. 2005; Tilman 1985). Species coexistence occurs when environmental supply ratios allow each species to be limited by a different resource, thereby reducing direct competition and promoting niche differentiation (Miller 2005; Tilman 1982). Together, these concepts underscore how trade-offs in resource use and environmental conditions shape species coexistence.

However, both niche and resource partitioning remain abstract constructs, lacking explicit links to underlying physiological mechanisms (HilleRisLambers et al. 2012; Valladares et al. 2015). The C_{min} theory offers a physiologically grounded reinterpretation of niche theory by integrating the effects of multiple resource limitations into a single carbon-based physiological threshold. Species-specific variation in the 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 carbon niche space. Accordingly, the 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. Therefore, the C_{min} theory provides a physiologically grounded and testable alternative to inferred niche-based explanations.

Neutral theory

Neutral theory hypothesizes that species within a community are functionally equivalent, exhibiting identical rates of birth, death, dispersal and speciation (Chave 2004; Hubbell 2011; Kalyuzhny et al. 2014). Coexistence arises not from niche differentiation, but from stochastic drift balanced by extinction and immigration or speciation (Hubbell 2011). Although its strict assumptions are biologically unrealistic, neutral theory remains a powerful tool for interpreting diversity patterns, particularly in hyperdiverse and spatially structured systems such as tropical forests (Chave and Leigh Jr 2002; Condit et al. 2002) and marine plankton communities (Behrenfeld and Bisson 2024; Sloan et al. 2006).

The C_{min} theory offers a physiological interpretation of the conditions under which neutral dynamics may emerge. In some communities, coexisting species may share similarly low C_{min} values, reflecting convergent adaptation to resource-limited environments, such as shade-tolerant understory plants in tropical forests or unicellular algae in nutrient-rich aquatic systems. In tropical rainforests, the shaded understory provides a stable microenvironment that allows shade-adapted species with low carbon demand to persist under limited resource supply. This convergence in C_{min} reduces fitness differences and supports coexistence patterns that resemble ecological neutrality. Similarly, in highly productive systems characterized by rapid biomass turnover, such as algal or phytoplankton communities, convergence in carbon requirements may lead to apparent functional equivalence. In both cases, demographic stochasticity can reinforce neutral-like patterns, when species are constrained by similar physiological thresholds. This suggests that neutral-like patterns may emerge not from true ecological equivalence, but from convergence in carbon-based physiological requirements.

In summary, the C_{min} theory frames neutrality as a testable outcome grounded in physiological principles, enabling empirical evaluation of where functional equivalence is likely to emerge. Rather than contradicting neutral theory, it refines its ecological scope by proposing that neutral-like patterns may emerge from convergence in carbon-based physiological demands. Although cross-species data on C_{min} remain limited, this hypothesis can be tested in ecosystems where species are expected to share similar carbon thresholds. Therefore, the C_{min} theory offers a physiological lens to evaluate neutrality and explain patterns traditionally attributed to either niche differentiation or demographic stochasticity.

Modern coexistence theory

Modern coexistence theory provides a unifying concept that reconciles niche and neutral processes by emphasizing the balance between stabilizing and equalizing forces (Chesson 2000, 2018). Stabilizing mechanisms promote coexistence through niche differentiation, while equalizing mechanisms reduce average fitness differences to prevent competitive exclusion (Chesson 2000). Despite its conceptual elegance, modern coexistence theory often relies on abstract parameters, such as interspecific competition coefficients and invasion growth rates, that are difficult to quantify in natural communities (Chesson 2000; Letten et al. 2017). The C_{min} theory offers a physiological basis for quantifying both stabilizing and equalizing components of modern coexistence theory. The C_{min} is shaped by both functional traits and environmental resource availability. Interspecific variation in C_{min} defines a carbon-based niche axis that reflects functional differentiation among species and facilitates niche partitioning to promote coexistence.

Also, the C_{min} theory offers a physiologically grounded measure of intrinsic fitness differences. Species with lower C_{min} thresholds require less carbon to maintain survival and growth, providing an advantage under resource-poor conditions. In contrast, species with higher C_{min} often possess traits that enhance carbon acquisition, such as high photosynthetic rates and rapid resource uptake. These acquisitive traits may also offset high carbon requirements, enabling species with elevated C_{min} to persist in harsh or resource-limited environments. Fitness differences therefore arise from the balance between carbon demand and acquisition capacities. This trade-off framework provides a physiological basis for intrinsic fitness differences and elucidates how species coexist across heterogeneous environmental gradients.

By integrating both stabilizing and equalizing processes into a measurable physiological trait, the C_{min} theory enables modern coexistence theory to be empirically tested. It enables niche differences and average fitness asymmetries to be evaluated through physiological measurements rather than inferred from abstract assumptions. By shifting the focus from species interactions to the physiological constraints on species persistence, the C_{min} theory reframes major ecological theories, including the niche theory, neutral theory, and modern coexistence theory. Consequently, the C_{min} provides a unified and testable approach to understanding species coexistence and the maintenance of species diversity.

Understanding species distribution and diversity through the C_{min}

According to the C_{min} theory, spatial variation in carbon availability filters species according to their ability to maintain positive carbon balance above species-specific physiological thresholds. This allows the C_{min} to predict large-scale patterns of species distribution and diversity. Therefore, in addition to explaining local-scale species coexistence, the C_{min} theory offers a unified and physiologically grounded perspective for understanding large-scale species distributions and diversity patterns across environmental gradients (Figure 3).

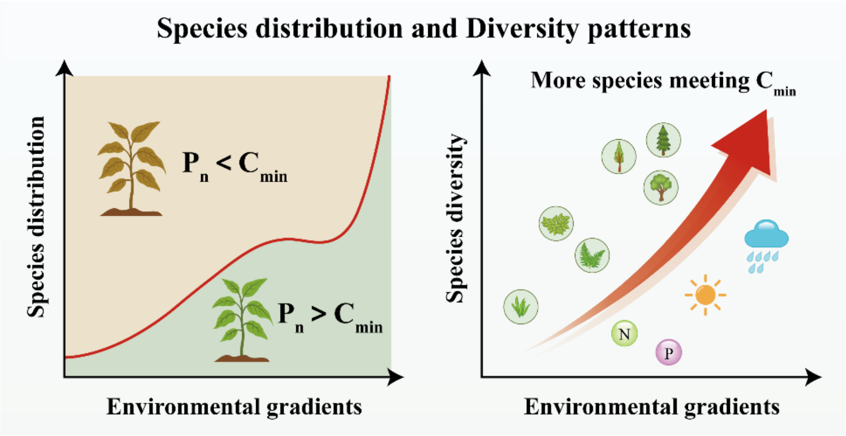

Figure 3 | Conceptual diagram of how C_{min} explain species distribution and diversity patterns. P_n and C_{min} represent the net carbon gain and minimum carbon required to sustain metabolic function and survival, respectively. A species can persist in a region only when local environmental conditions allow P_n to exceed its C_{min}. Under favorable conditions, abundant energy, water, and nutrients allow more species to meet this threshold, defining a broad carbon viability envelope that sustains high species diversity. In harsh environments, limited photosynthetic carbon gain and elevated stress-related costs make persistence contingent on lowering C_{min} or enhancing carbon acquisition to maintain a positive balance, and strong physiological filters reduce species diversity.

Species distributions

The C_{min} theory roots species' geographic ranges in the fundamental carbon economics of autotrophs. To establish, grow, and reproduce, a plant must maintain a positive net carbon balance (Lambers et al. 2008). The C_{min} defines the minimum carbon gain necessary to prevent carbon starvation and maintain survival, representing a species-specific physiological limit. When local environmental conditions such as temperature, precipitation, solar radiation, soil moisture, and nutrient availability support net photosynthetic carbon uptake consistently exceeds C_{min}, a species can persist and potentially expand its range. Conversely, when these factors suppress net carbon gain below C_{min}, persistence becomes physiologically impossible, regardless of dispersal ability or competitive traits. Thus, C_{min} provides a first-principles explanation for why some species fail to colonize seemingly suitable habitats, revealing their inability to sustain a positive carbon balance under prevailing conditions.

The C_{min} theory reframes species distributions through the lens of carbon thresholds, offering a physiological filter that sets the lower bound of a species' fundamental niche. This perspective shifts biogeographic inquiry from where species are currently observed to where they can physiologically persist. In contrast, traditional species distribution models rely largely on statistical correlations between species occurrences and environmental variables, often lacking explicit physiological foundations. Therefore, the C_{min} theory provides a mechanistic framework for predicting distributions grounded in the carbon economics of plants by linking environmental gradients to species-specific thresholds of carbon balance.

Large-scale diversity patterns

Beyond explaining individual species distributions, the C_{min} theory also offers a physiological perspective on large-scale diversity patterns. One of the long-recognized diversity patterns is the latitudinal gradient, with species richness peaking in the tropics and declining toward the poles (Mittelbach et al. 2007; Willig 2003). Although numerous hypotheses have been proposed to explain global diversity patterns, including the species-energy hypothesis, the water–energy dynamics and the metabolic theory of ecology, they are largely correlative and lack grounding in physiological mechanisms (Brown et al. 2004; Currie et al. 2004; Gillooly and Allen 2007; O'Brien 1998).

At low latitudes, abundant water and energy enable photosynthetic gains to greatly exceed C_{min} for a broad range of species. This wide carbon viability envelope accommodates diverse functional strategies, sustaining high taxonomic and trait diversity. In contrast, high-latitude environments constrain photosynthetic carbon gain while elevating stress-related carbon costs. Persistence under such conditions requires species to either reduce their C_{min} or enhance carbon acquisition to maintain a positive carbon balance. Only those capable of meeting C_{min} can survive, resulting in strong physiological filtering that narrows the species pool and contributes to the lower taxonomic and functional diversity characteristic of higher latitudes.

In summary, the C_{min} theory provides a physiological foundation for understanding large-scale diversity gradients. By grounding biogeography in plant physiological constraints, it moves beyond correlative patterns toward a predictive framework, offering new insights into how species diversity is structured across broad environmental gradients and how it may respond to environmental change.

Reframing existing diversity theories through the C_{min}

The C_{min} theory translates environmental gradients into physiological carbon thresholds, enabling mechanistic predictions of where and why diversity peaks or declines. The C_{min} theory also reframes existing diversity hypotheses (Fine 2015; Mittelbach et al. 2007; Rohde 1992) by grounding them in a shared physiological principle. It offers a mechanistic and testable foundation for predicting large-scale species diversity patterns, moving beyond descriptive correlations toward physiological explanation.

Species–energy hypothesis

The species-energy hypothesis suggests that environments with higher energy input tend to support greater species richness (Clarke and Gaston 2006). This pattern, widely observed across biomes and particularly pronounced in the tropics, is often attributed to enhanced energy availability (Mittelbach et al. 2007; Pianka 1966). However, despite its empirical support, the hypothesis remains largely correlative, lacking a mechanistic explanation of how energy availability translates into species diversity. In high-energy environments, such as in tropical forests, high light availability and favorable temperatures enhance photosynthetic assimilation, a wide range of species, both acquisitive and conservative strategies, can surpass their C_{min} thresholds. As a result, more species are able to sustain a positive carbon balance, expanding the set of taxa that can coexist. Conversely, in low-energy environments, such as high-latitude forests or alpine zones, limited photosynthetic gains and elevated maintenance demands make it more difficult for species to sustain a positive carbon balance. This imbalance increases the likelihood that many species fail to meet their C_{min} threshold.

The C_{min} theory transforms the species–energy hypothesis from a correlative pattern into a mechanistic framework by explicitly quantifying the physiological constraints imposed by energy availability. It predicts that physiological filtering favors high diversity in environments where carbon demands are met by many species, and restricts diversity where only a few can persist. The C_{min} theory explains why high-energy environments promote greater coexistence, whereas low-energy systems impose stronger species filtering through carbon constraints.

Water–energy dynamics

Extending the logic of energy-based explanations, the water–energy dynamics proposes that species richness is co-limited by both energy input and water availability (Hawkins et al. 2003; O'Brien 1998, 2006). Yet, the physiological mechanisms linking these climate variables to species persistence remains unclear (Fine 2015; Rohde 1992). Since photosynthesis depends on both energy and water, limitations in either reduce carbon assimilation. Under warm and humid conditions, photosynthetic efficiency tends to be high while metabolic costs remain moderate, enabling many species to maintain carbon surpluses above their C_{min} thresholds. In contrast, cold or arid environments constrain carbon gain while increasing metabolic demand, less species can persist under such conditions, which act as physiological filters and reduce the species diversity. Thus, the C_{min} theory reveals how the joint availability of water and energy constrains carbon balance, thereby defining ecological boundaries and shaping large-scale patterns of diversity.

Metabolic theory of ecology

By predicting that temperature accelerates metabolic and life-history processes, the metabolic theory of ecology helps explain the tendency for species diversity to be higher in warmer environments, where elevated metabolic rates, faster resource turnover, and potentially greater rates of speciation prevail (Brown et al. 2004; Gillooly and Allen 2007). However, it remains fundamentally rate-based, focusing on how temperature and body size regulate the speed of energy flow through organisms, rather than quantifying whether the energy gain is sufficient to meet the physiological thresholds required for survival (Enquist et al. 2015; O'Connor et al. 2007).

The C_{min} theory complements and extends metabolic theory of ecology by introducing a constraint-based criterion for survival. Although elevated temperatures may increase photosynthetic carbon assimilation, they do not necessarily ensure a net carbon surplus (Atkin and Tjoelker 2003; Dusenge et al. 2019). Warming-induced drought may simultaneously reduce carbon input via stomatal closure and raise carbon demand through increased respiration associated with water stress and metabolic repair (Dusenge et al. 2019; Slot and Kitajima 2015), potentially pushing species beyond their C_{min} threshold and increasing the risk of mortality. By embedding a physiological threshold into the metabolic theory of ecology, the C_{min} theory shifts the focus from metabolic rate to carbon threshold 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 environmental gradients.

Together, these physiological insights strengthen the conceptual clarity and expand the ecological relevance of the C_{min} theory. Rather than standing alone, the C_{min} provides a unifying physiological foundation that clarifies, refines, and integrates existing diversity hypotheses through a shared framework of carbon balance. By linking environmental energy and water availability to the carbon requirements for persistence, the C_{min} theory provides a coherent and testable framework for explaining global diversity patterns.

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

At its core, C_{min} reflects a basic physiological principle: all organisms must maintain a positive carbon balance to support survival, growth, and reproduction (Gruner et al. 2008; Lambers et al. 2008; Lynch et al. 1986; Manzoni and Porporato 2009). Carbon functions as the central biological currency on Earth (Chapin III 1989; Falkowski et al. 2000), and its acquisition, allocation, transport, storage, and remobilization govern the structure and function of all living systems (Gruner et al. 2008; Lambers et al. 2008; Lynch et al. 1986; Manzoni and Porporato 2009). In this sense, the physiological principle captured by C_{min} transcends taxonomic boundaries, trophic levels, and modes of carbon acquisition.

In autotrophs such as vascular plants and algae, the 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, sustained carbon deficits below C_{min} lead to carbon starvation, physiological collapse, and ultimately mortality (Lambers et al. 2008). In heterotrophs, C_{min} represents the minimum net energetic gain from organic carbon compounds obtained from external sources, required to sustain core metabolic functions, including cellular maintenance, thermoregulation, immune defense, and reproduction. The C_{min} thus can also be applied to animals, fungi, and microbes, which rely on carbon-derived energy inputs to fuel metabolism and survival. In these organisms, persistence depends on maintaining a positive energy balance through feeding, foraging, or symbiosis (Karasov and Martínez del Rio 2007; Schmidt-Nielsen 1997). Animals, including insects, need to sufficient energy from organic carbon through feeding to support development and immune function (Hawkins et al. 1997; Schwenke et al. 2016), as plants acquire carbon via photosynthesis. Similarly, in microbial communities, the capacity to acquire and metabolize carbon substrates under nutrient-limited conditions, serving as both energy sources and structural building blocks, determines both survival and competitive outcomes (Hobbie and Hobbie, 2013; Toft and Andersson, 2010). Across trophic levels, C_{min} establishes a baseline constraint in which energy transfer depends on whether consumers can sustain carbon intake above their physiological threshold.

In summary, C_{min} establishes a unified physiological foundation for understanding environmental filtering, species coexistence, and diversity patterns across environmental gradients. By redefining species persistence as a universal outcome of carbon balance, rather than a taxon-specific trait, it enables cross-system comparisons that span taxonomic groups, trophic levels, and biomes. As a universal physiological filter, the C_{min} determines where, when, and which organisms can persist. Beyond its conceptual coherence, the C_{min} theory provides a first-principles, empirically tractable framework for understanding and predicting ecological structure and dynamics across the Earth's biomes.

Ecological applications of the C_{min} theory

The C_{min} theory, based on the first-principles that all organisms need to sustain a positive net carbon balance for persistence, provides a mechanistic and scalable framework for addressing fundamental ecological questions across levels of organization, space, and time. It bridges individual carbon dynamics and ecosystem responses, revealing how physiological thresholds shape large-scale patterns in a carbon-limited world. Beyond its explanatory power for species coexistence and diversity patterns, the C_{min} theory also serves as a broadly applicable framework across diverse ecological domains, including ecosystem functioning, climate change impacts on ecosystems, ecological stability, species invasions, and evolutionary biogeography.

Ecosystem functioning

Ecosystem functioning arises from the interaction between organismal traits and biogeochemical processes they mediate, particularly those related to carbon, water, and nutrient cycles (Chapin III et al. 2011; Ding et al. 2021; Faucon et al. 2017). Traditional trait-based and process-based approaches have contributed valuable insights into these ecosystem dynamics, however, lacking a mechanistic bridge between organismal physiology and ecosystem-level outcomes (Green et al. 2022; Zakharova et al. 2019). The C_{min} theory bridges this gap by introducing a unified physiological threshold that links functional traits to ecosystem processes.

In ecosystems, plant functional traits such as photosynthetic rate, respiration rate, xylem hydraulic conductivity, and leaf economic strategy regulate fundamental ecological processes, including carbon uptake, water fluxes, and nutrient cycling (Zakharova et al. 2019). These processes, in turn, shape how individuals effectively acquire and utilize environmental resources (Ricklefs 2008; Wright et al. 2004). Because both trait characteristics and environmental resource availability shape C_{min}, it captures how plant functional traits and environmental resource availability jointly influence ecosystem functioning. By scaling from individual carbon balance to ecosystems, C_{min} provides a unifying metric that links organismal physiology to ecological function and offers a general framework for understanding variation in functional traits and biochemical processes, which together determine the capacity of ecosystems to sustain functioning under changing environmental conditions.

Climate change impacts on ecosystems

Climate change is fundamentally disrupting the balance between carbon uptake and loss across ecosystems (Dusenge et al. 2019; Kirschbaum 2004). In many regions, especially those approaching thermal or water stress limits, warming accelerates respiratory carbon losses more rapidly than it enhances photosynthetic carbon uptake (Doughty and Goulden 2008; Duffy et al. 2021). Under warming conditions, prolonged soil and atmospheric drought further exacerbate carbon deficits by reducing stomatal conductance and depressing photosynthesis (Dusenge et al. 2019; Kirschbaum 2004). These stressors raise the C_{min} required for survival and intensify the physiological constraints on species persistence.

As climate extremes, such as droughts and heatwaves, become more frequent and intense (Chiang et al. 2021; Perkins-Kirkpatrick and Lewis 2020; Spinoni et al. 2014), they increasingly disrupt carbon balance and narrow the margin between carbon supply and the C_{min} required for survival. In the future, fewer taxa may be able to maintain a positive carbon balance, leading to selective filtering of functional groups, shifts in dominance hierarchies, and a reorganization of ecosystem structure, ultimately altering ecosystem functions. The C_{min} theory thus provides a physiological framework for anticipating how changes in carbon balance under climate change will reshape ecosystem structure and functioning.

Ecological stability

The C_{min} is defined as the minimum carbon threshold required for an organism to sustain physiological function and survive under environmental stress. This tipping-point property makes the C_{min} particularly well suited for assessing ecological stability. When stressors such as drought, heatwaves, or nutrient depletion reduce carbon gain or raise maintenance costs, organisms that cannot sustain a positive carbon balance fall below their C_{min}. This will result in carbon deficits that suppress growth, impair function, and ultimately increase the risk of mortality (Anderegg et al. 2015; McDowell et al. 2008). As physiological failure accumulates across taxa, it can erode community structure, reduce functional redundancy, and destabilize critical ecosystem functions. Thus, the C_{min} offers a mechanistically grounded framework for tracing how localized carbon imbalance can scale up to ecosystem-level instability.

Moreover, the C_{min} concept is inherently scalable. At the individual level, it reflects the balance between carbon supply and demand, shaped by resource availability and functional traits. At the community or ecosystem level, the C_{min} can be approximated by computing a community-weighted average of species-specific thresholds, based on their relative abundance, structural dominance, or contribution to ecosystem functioning. This community-weighted C_{min} represents the ecosystem's overall capacity to sustain a positive carbon balance, providing a scalable bridge from individual physiology to ecosystem-level carbon dynamics. This provides a means to evaluate how closely an ecosystem operates relative to its carbon threshold.

Furthermore, the C_{min} theory enables explicit evaluation of stability across vertical layers within ecosystems. In forests, for instance, the canopy and understory layers differ in their access to light, temperature and water, and thus exhibit distinct C_{min} values. Asymmetric increases in C_{min} across forest layers may arise from climate-driven shifts in temperature or water availability, driven by differences in local microclimate and resource access. If species in a given layer fail to meet their elevated C_{min}, selective collapse may occur, leading to a simplified vertical structure and reduced ecosystem resilience and buffering capacity. As a physiologically grounded metric of ecosystem stability, the C_{min} can be used to detect early signs of ecosystem vulnerability, enable cross-biome comparisons of resilience, and forecast ecological stability under climate change.

Biological invasions

Biological invasions restructure ecological communities by favoring species capable of surviving and reproducing under altered environmental and competitive conditions (Sax et al. 2007; Strayer et al. 2006). Despite extensive research, the mechanisms underpinning biological invasions remain debated (Cassini 2020; Courchamp et al. 2017; Daly et al. 2023). Existing hypotheses such as enemy release, enhanced competitive ability, novel weapons, and fluctuating resource availability capture key invasion patterns but are often context-dependent, taxonomically limited, and lack a physiological foundation (Blossey and Notzold 1995; Callaway and Ridenour 2004; Davis et al. 2000; Liu and Stiling 2006). Consequently, no general theory currently exists that can reliably predict invasion success across taxa and regions (Catford et al. 2009; Daly et al. 2023). However, as with all organisms, the establishment and spread of invasive species ultimately depend on their capacity to persist under novel environmental conditions. The C_{min} theory links this persistence to the carbon economics of survival, offering a unified physiological framework for predicting invasion success across taxa, environments, and regions, and laying the foundation for a general theory of biological invasions.

Successful invaders often maintain sustained carbon surpluses through two primary pathways: enhanced resource acquisition and reduced biotic resistance. Many invasive species exhibit acquisitive traits such as high photosynthetic capacity, rapid growth and efficient nutrient use, which promote carbon gain across diverse environmental conditions (Hussner 2009; McDowell 2002; Pattison et al. 1998). Simultaneously, invaders frequently benefit from enemy release, encountering fewer herbivores, and competitors in their introduced ranges (Colautti et al. 2004; Germain et al. 2020; Maron and Vilà 2001). This reduces carbon losses from defense and damage repair, thereby lowering their realized C_{min} thresholds under novel conditions. Because of lower carbon demand or enhanced carbon assimilation, invasive species are more likely to maintain positive carbon balance under environmental stress, promoting disproportionate reproductive success and range expansion relative to native species.

By integrating carbon acquisition and demand into a unified framework, the C_{min} theory provides a physiological basis for understanding biological invasions. It establishes a common carbon currency to assess invasion potential across taxa and regions. The C_{min} theory improves predictions of where and when invasions are most likely to occur, and informs targeted interventions such as early detection, strengthening native resilience, and restoring environmental conditions that support positive carbon balance in native species.

Evolutionary 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-limited environments, natural selection likely favors conservative traits that minimize carbon costs (Diaz et al. 2016; Reich 2014; Wright et al. 2001), thereby lowering the threshold required for persistence. Conversely, in warm, humid, and nutrient-rich biomes such as tropical forests, many taxa have evolved acquisitive strategies characterized by high photosynthetic capacity and reduced allocation to defense (Diaz et al. 2016; Sterck et al. 2011), leading to great carbon surpluses that support rapid growth, complex architectures, and diverse life histories.

Phylogenetically structured variation in carbon thresholds is unlikely to be randomly distributed across the tree of life. Instead, it may reflect historical niche conservatism and trait inheritance, with closely related taxa tending to exhibit similar C_{min} values due to shared physiological constraints. Spatial variation in C_{min} is closely associated with broad biogeographic patterns, including latitudinal diversity gradients, regional endemism, and biome-level differences in species pools. These patterns are likely shaped by the interplay between physiological constraints and environmental filters. Consequently, the C_{min} theory provides a powerful framework for exploring how long-term evolutionary history has shaped the present-day distribution of carbon-use strategies across the tree of life.

Conclusion

Understanding species coexistence and diversity patterns remains a central challenge in ecology. These patterns have traditionally been attributed to a suite of ecological processes, including competition, facilitation, resource partitioning, and dispersal limitation. The C_{min} theory introduces a distinct perspective by shifting the focus from process-based mechanisms to the physiological constraint on species persistence. The C_{min} theory offers a physiological foundation for understanding coexistence, whereby it occurs when each species maintains net carbon gain above its C_{min} under shared environmental conditions.

The C_{min} theory also provides new insight into large-scale diversity patterns observed across climatic and geographic gradients. In contrast to theories built on abstract or context-dependent assumptions, the C_{min} theory is rooted in physiological principles that are observable, quantifiable, and empirically testable. The C_{min} also reframes existing coexistence and diversity theories by grounding them in the common physiological constraint. This integration clarifies how carbon constraints shape ecological systems and strengthens the link between theoretical predictions and empirical observation in ecology. Because carbon is fundamental to all life, the C_{min} concept is broadly applicable across the tree of life, extending beyond plants to animals, fungi, and microbes. By bridging individual physiology with large-scale ecological outcomes, the C_{min} provides a unified framework applicable across diverse domains, including ecosystem functioning, ecological stability, and invasion dynamics.

In summary, the C_{min} provides a physiologically grounded, empirically testable theory for understanding species persistence, coexistence, distribution and diversity patterns across environmental gradients. By placing carbon balance at the center of ecological understanding, the C_{min} theory establishes a physiological foundational for explaining how physiological thresholds shape species diversity and ecosystem dynamics. Consequently, fully integrating the C_{min} into ecological research will not only improve predictions of species responses to climate change, but also enhance our ability to anticipate shifts in ecosystem structure, function, and resilience in an increasingly carbon-limited world.

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