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REPLY

A geometric approach to beta diversity: Reply

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We thank Dr. Baselga for his formal comment (hereafter, *comment*) on our paper (Song et al., 2025). We welcome and encourage vigorous scientific debate. His critique is valuable because it provides a clear defense of the classic, dissimilarity-based framework for beta diversity. In doing so, it perfectly illuminates the fundamental conceptual divide that motivated our work.

The central thesis of the comment is that our measure, geometric beta diversity (or *betavolume*), is mathematically flawed because its properties diverge from those of established metrics. We respectfully counter that this divergence is not a flaw; it is the entire point. Our objective was not to provide a novel formula under existing axioms. Rather, by recognizing the multifaceted nature of community compositional variation, we introduce a framework that captures a distinct axis. *The choice is not one of logic, but of ecological intent*.

Here, we clarify the ecological first principles upon which our geometric framework is built, respond to the specific methodological critiques raised, and demonstrate why the mathematical behaviors of our metric are the necessary, deliberate, and logically sound consequences of those principles. Ultimately, we emphasize that statistical ecology is best served by methodological pluralism, providing ecologists with distinct, mathematically rigorous tools for different analytical jobs.

IS THERE A CONCEPTUAL GAP?

The powerful family of classic metrics represents one historically dominant implementation for measuring spatial variation, but these metrics are not synonymous with the concept of beta diversity itself. The perceived logical disconnect is, in reality, a fundamental divergence in ecological first principles:

- The classic paradigm: Beta diversity focuses on the *uniqueness of individual species*. Total variation is maximized when communities are completely segregated and share no species. When beta diversity is conceptualized exclusively as pairwise species turnover, metrics must naturally peak when communities share no species. Expected behaviors under this paradigm are not universal laws for quantifying spatial variation; they are specific bylaws.
- Our geometric framework: Beta diversity focuses on the *uniqueness of species combinations*. Total variation is maximized when a metacommunity realizes a rich, complex array of compositional states. If one accepts that spatial variation also encompasses the structural complexity of species assemblages across a landscape, the mathematical conditions for maximizing variation must logically adapt.

Chuliang Song and Muyang Lu contributed equally to this study.

With this crucial distinction established, the comment's arguments regarding our underlying logic can be definitively addressed and resolved.

Calculation versus valuation

The comment argues that because classic metrics can mathematically process our illustrative example (a metacommunity containing a mixed community $\{A, B\}$ alongside isolated communities $\{A\}$ and $\{B\}$), no theoretical void exists. It correctly notes that adding a species-rich overlapping community increases alpha diversity, thereby inevitably decreasing classic beta diversity under traditional formulas.

This argument conflates a metric's mathematical capacity to execute a calculation with its ecological valuation of the data. The conceptual gap is not about whether classic metrics *can incorporate* community $\{A, B\}$ into an equation; it is about *how they value* its presence. As the critique emphasizes, the unavoidable mathematical consequence of the classic framework is that introducing a novel combination, like $\{A, B\}$, drives beta diversity down.

This decrease exemplifies the exact conceptual restriction our framework seeks to overcome. It stems from a paradigm in which a community like $\{A, B\}$ is viewed merely as a homogenizing, redundant blend of $\{A\}$ and $\{B\}$. In a modern ecological context—where species interactions, nonadditivity, and emergent ecosystem functions are paramount—this perspective is structurally limiting. As we stated in our original manuscript (p. 2):

> ...the community {A,B} behaves differently, both dynamically [...] and functionally [...] from the communities with only {A} or {B}. Consequently, we contend that community {A,B} should be considered inherently different... To generalize, the introduction of a unique, distinctive, species-rich community composition to a metacommunity should increase, rather than decrease, the diversity within it.

Our framework provides a mathematically rigorous tool for this alternative principle: that the presence of a novel, species-rich combination represents a structural expansion, rather than a collapse, of metacommunity variation.

The logical chain and the element of choice

Building upon this, the critique contends that our reasoning suffers from a "broken logical chain." It argues that simply acknowledging community $\{A, B\}$ as distinct from $\{A\}$ and $\{B\}$ does not logically dictate that a metacommunity containing all three must exhibit higher overall beta diversity.

We agree that acknowledging the distinctiveness of a community does not, by force of pure logic alone, necessitate an *increase* in a variation metric. Instead, the resulting mathematical behavior is dictated entirely by the chosen ecological axiom. The classic framework prioritizes pairwise dissimilarity, making a decrease mathematically inevitable when overlapping communities are added. Our framework prioritizes combinatorial novelty, making an increase mathematically inevitable. The divergence is a matter of deliberate ecological intent, not logical validity.

To unequivocally demonstrate that this represents a clash of ecological paradigms rather than a mathematical artifact, we address the critique's suggestion regarding standardization. The comment proposes that standardizing geometric beta diversity by the number of sites (i.e., dividing by N) would yield a lower diversity value for the metacommunity containing the mixed $\{A, B\}$ community, seemingly contradicting our premise.

While we detail the mathematical inappropriateness of dividing a geometric volume by N and the correct standardization procedure in the "On Standardization by the Number of Sites (N)" section, we propose a thought experiment that isolates the core conceptual conflict by holding N constant. Consider two metacommunities, each with exactly three sites ($N = 3$):

- Metacommunity I: Composed of communities {A}, {B}, and {A}.
- Metacommunity II: Composed of communities {A}, {B}, and {A, B}.

Because $N = 3$ in both scenarios, any standardization by the number of sites applies identically and is therefore mathematically irrelevant to the relative comparison. The sole difference is the identity of the third community.

The classic paradigm evaluates Metacommunity I as more diverse because its average pairwise species overlap is lower. Our geometric paradigm evaluates Metacommunity II as more diverse because the third site, $\{A, B\}$, introduces a structurally novel species combination absent from Metacommunity I. Stripped of confounding mathematical factors, this comparison cleanly illustrates that our metric's behavior is a deliberate ecological choice: prioritizing the structural complexity of species combinations over the strict spatial isolation of individual species.

Ecological relevance of maximum geometric beta diversity

The comment questions the ecological value of the conditions under which geometric beta diversity reaches its maximum, arguing that the evenness of species distributions across shared components has no clear biological meaning.

We offer a straightforward ecological rationale: This combinatorial evenness is a powerful diagnostic indicator of the underlying processes governing community assembly. The distribution of species across shared components is not an abstract mathematical artifact; it is the structural fingerprint of the metacommunity. We propose two ecologically significant interpretations for why this structural evenness is highly relevant:

- A signature of neutrality: In a neutrally assembled metacommunity across a relatively homogeneous landscape, species are expected to distribute stochastically across sites, lacking strong deterministic biases toward strict mutual exclusion. This stochasticity naturally results in a relatively even sharing of species across the various matching components. The combinatorial evenness that maximizes geometric beta diversity is precisely the macroscopic signature one would look for to infer the dominance of neutral assembly processes.
- A signature of complex determinism: Conversely, if such a complex, evenly filled combinatorial structure arises in a demonstrably heterogeneous landscape, it cannot be random. It implies a highly organized metacommunity governed by sophisticated deterministic processes (e.g., complex niche partitioning, multi-scale habitat filtering, and source-sink dynamics), creating a rich tapestry of overlapping species assemblages.

Far from being ecologically irrelevant, the maximization of geometric beta diversity points to the theoretical boundaries of either maximum stochasticity or maximum structural organization—two fundamental macroscopic attributes of broad interest to ecologists.

On the link to species interactions

Lastly, the critique dismisses the core ecological motivation of our framework, asserting that because geometric beta diversity relies on presence/absence tables, it cannot explicitly account for species associations, and therefore the link between our metric and nonadditive complexity remains unsubstantiated.

The claim that our approach fails to mathematically account for species associations is demonstrably incorrect. As explicitly detailed in our original manuscript (see Box 1 and Appendix S8 in Song et al., 2025), geometric beta diversity mathematically integrates spatial species associations. Specifically, using the generalized variance formalism (β_{VAR}), the metric evaluates the off-diagonal elements of the covariance matrix, which directly represent spatial associations. Similarly, using the information theory formalism (β_{info}), spatial associations are captured via mutual information. While static presence/absence matrices do not directly observe real-time behavioral interactions, the multivariate nonindependence of species across sites (spatial co-occurrence and mutual exclusion) is the definitive statistical footprint of these underlying interactions and filtering processes (Galiana et al., 2024).

That said, we acknowledge that the relationship between co-occurrence patterns and specific species interactions is indirect, and that isolating interactions from other drivers of co-occurrence is extremely challenging (Blanchet et al., 2020; Freilich et al., 2018; Thurman et al., 2019). However, this distinction underscores rather than undermines the utility of our approach. Our geometric framework does not attempt to isolate or directly measure pairwise species interactions; rather, it captures the macroscopic structural signature of compositional variation. This structural complexity is an emergent property shaped by the integrated effects of multiple assembly processes, including environmental filtering, dispersal dynamics, and species interactions. The value of our metric lies in quantifying this holistic combinatorial structure, which reflects the net outcome of ecological assembly, even when specific interaction mechanisms remain difficult to untangle.

The limitations of the classic framework in this regard are instructive. A pairwise dissimilarity metric is mathematically maximized when species never co-occur. A metric that finds its theoretical maximum in the complete absence of spatial overlap is fundamentally ill-equipped to capture the ecological complexity that emerges from interacting, co-occurring assemblages—precisely the complexity our geometric framework was designed to quantify.

This explicit mathematical integration of species associations is where geometric beta diversity opens new avenues for research. By quantifying the structural complexity of interconnected communities, it serves as a natural candidate for exploring links to emergent, system-level properties like ecosystem functioning and stability. These properties depend on the complex web of combinations among species, not merely on their spatial segregation. This linkage is an intrinsic property that our geometric framework was designed to capture, providing

a robust quantitative tool to explore some of the most pressing questions in modern ecology.

SPECIFIC MATHEMATICAL BEHAVIORS

The critique raises several concerns regarding the mathematical behavior of geometric beta diversity, framing these behaviors as inherent flaws that invalidate its utility. Here, we demonstrate that these mathematical properties are not artifacts or errors; they are the direct, logically consistent consequences of a rigorous geometric foundation.

The "contradiction" of zero correlation

The clearest evidence supporting our approach lies in a point the critique raises as a primary flaw: the near-zero correlation between geometric beta diversity and classic beta diversity. The comment frames this lack of correlation as proof of invalidity, concluding that our empirical results merely confirm our measure's failure to capture "true" beta diversity.

We maintain that there is no contradiction. The critique's conclusion assumes that beta diversity is a unidimensional phenomenon, implying that all legitimate metrics must be highly correlated because they measure the exact same property. This is precisely the assumption our geometric framework challenges.

If geometric beta diversity were highly correlated with classic metrics, it would be redundant, offering no new ecological insights. The observed near-zero correlation is therefore not a failure; it is strong statistical evidence that our measure successfully captures a distinct, largely orthogonal axis of compositional variation. It quantifies the variation arising from how species are structurally combined, supplementing the traditional focus on how species are spatially segregated.

On the "effective number of communities"

The comment argues that geometric beta diversity fails as a measure of the effective number of communities, pointing out that a metacommunity of identical sites yields a geometric beta diversity of zero. In the classic paradigm, the critique notes, a value of zero might counterintuitively imply zero distinct communities or a complete absence of species.

This difference is merely a matter of mathematical convention, not a structural failure. If a scale ranging from 1 to d (where d is the geometric dimensionality constraint, $\min(N, S)$) is desired to perfectly align with the traditional conceptualization of effective numbers, our measure can be trivially rescaled without altering its underlying geometric properties or the relative rankings of metacommunities. We explicitly noted this flexibility in our original paper (p. 5):

> Of course, further rescaling of Equation (4) is possible depending on different ecological rationales (e.g., if one wants the beta diversity to range from 0 to 1, we can simply divide the current measure by d).

Specifically, to achieve a strict scale from 1 to d (matching 1 distinct community up to d effective distinct communities), the linear rescaling is simply:

$$\beta^{*}_{\mathtt{vol}} = (d-1)(\mathtt{vol}(\mathcal{P}))^{1/d} + 1 \quad (1)$$

This linear transformation guarantees that complete homogeneity ($\mathtt{vol}(\mathcal{P}) = 0$) equals exactly 1 effective community, and maximum geometric heterogeneity ($\mathtt{vol}(\mathcal{P}) = 1$) yields d effective communities, fully resolving the commenter's concern.

On standardization by the number of sites (N)

The comment suggests that comparing beta diversity across metacommunities with different numbers of sites (N) necessitates standardizing the metric by dividing by N, akin to the normalization of classic dissimilarity measures. It applies this proposed standardization to our theoretical examples to argue that our metric fails to capture community differentiation accurately.

This proposed standardization is mathematically inappropriate because it forces a high-dimensional geometric volume into a linear, additive dissimilarity framework. We firmly reject the premise that geometric beta diversity requires generic standardization by N in this manner. Our metric is inherently standardized by its dimensional scaling factor, $d = \min(N, S)$, which defines the dimensionality of the geometric space in which the metacommunity is embedded. This intrinsic scaling ensures that geometric beta diversity is directly comparable across systems with varying numbers of sites or species, rendering post hoc linear transformations both unnecessary and geometrically invalid.

On scaling behavior and systematic assessment

The comment critiques the behavior of geometric beta diversity along a gradient of community differentiation, making two distinct claims: first, that we failed to provide a systematic assessment of this behavior; and second, that the metric reaching its maximum at intermediate levels of species overlap (what the critique terms "lower values of differentiation") is ecologically nonsensical. Both assertions are incorrect.

The first assertion is demonstrably false. We positioned this systematic assessment as a central component of our findings, presenting an exhaustive analysis of all possible metacommunity configurations for $N = 2$ (fig. 2 in Song et al., 2025), conducting extensive simulations for $N = 3$ (fig. 3 in Song et al., 2025), and providing detailed comparisons against classic metrics across differentiation gradients in Appendix S4 in Song et al., 2025, specifically figs. S4 and S5.

The critique's puzzlement regarding the conditions under which geometric beta diversity is maximized stems from a fundamental misinterpretation of volumetric behavior in high-dimensional spaces. The observation that geometric beta diversity peaks when species are distributed across multiple shared components is not a flaw; it is the mathematically predictable consequence of quantifying the structural complexity of a combinatorial system.

As the number of communities (N) increases, the combinatorial space—the potential ways species can be distributed across unique and shared components—grows exponentially. To maximize hypervolume in this space, segregating species into N unique, nonoverlapping groups is geometrically highly inefficient; such a configuration populates only the isolated "corners" of the multidimensional space, leaving the vast combinatorial interior completely empty. Instead, geometric volume is mathematically maximized when a metacommunity realizes a rich variety of these overlapping combinations. From a classic dissimilarity perspective, this appears as "lower differentiation." However, from a geometric perspective, it represents high structural complexity. This principle was explicitly derived and stated in Appendix S6 in Song et al. (2025). It is not an artifact; it is the mathematical realization of our core thesis.

On nestedness/turnover decomposition and empirical patterns

A significant portion of the critique focuses on the inability of geometric beta diversity to be additively partitioned into independent components of nestedness and spatial turnover. The comment employs a "color-blindness" metaphor to argue that the additive partitioning framework is flawlessly defined and subsequently dismisses our empirical latitudinal analysis for failing to isolate these components.

We respectfully counter that the color-blindness analogy is fundamentally misleading. The metaphor incorrectly implies that nestedness and turnover are independent, cleanly separable phenomena (like distinct, additive wavelengths of light). Geometrically and ecologically, they are highly interactive processes: turnover represents the establishment of new compositional axes (expanding dimensionality), while nestedness represents the filling of those existing axes. The capacity for nestedness is strictly constrained by the system's turnover; one cannot fill a dimension that does not exist.

When we referred to strict additive partitioning as "inherently ill-defined," we were pointing out the mathematical impossibility of reducing an interactive, multidimensional geometric system to simple scalar addition without losing critical information about how these processes interplay. Furthermore, asserting that this framework is flawlessly settled overlooks over a decade of intense debate within the ecological literature regarding the mathematical validity of these partitions (e.g., Almeida-Neto et al., 2012; Carvalho et al., 2013; Chen & Schmera, 2015; Schmera & Podani, 2011; Šizling et al., 2026).

This philosophical divergence extends directly to our empirical analysis. We deeply respect the established, reductionist philosophy of partitioning beta diversity to analyze isolated trends. However, our geometric approach offers a holistic alternative explicitly designed to measure the emergent structural properties of the integrated whole, simultaneously accounting for the known spatial and temporal biases in global biodiversity datasets (Gonzalez et al., 2016; Hughes et al., 2021). Where a reductionist additive partitioning approach asks, "What are the individual, isolated trends of the underlying processes?" our geometric approach asks, "What is the net structure of variation that has emerged from the interaction of these processes?" Both approaches are valid and complementary, but they require different mathematical lenses.

CONCLUSION: TWO TOOLS FOR TWO JOBS

Our paper does not advocate for the abandonment of classic tools, nor does it assert that classic beta

diversity is mathematically incorrect. Instead, it argues for expanding the ecological toolkit to reflect the full complexity of spatial variation.

This exchange naturally raises the broader question of what should be considered beta diversity. We maintain that our geometric approach falls within this category: regardless of whether one adopts pairwise dissimilarity or combinatorial complexity as the mathematical lens, the underlying ecological core—quantifying variation in community composition across space—is shared. We anticipated this terminological discussion and addressed it at length in our original manuscript, where we advocated for a pluralistic understanding of the term and cautioned against a prescriptive definition that fragments the literature. As we wrote (p. 18):

> We acknowledge the long and valuable tradition of pairwise metrics and the spirit of Whittaker's ratio in measuring beta diversity... While we respect this well-intentioned perspective, we caution against terminological fragmentation that may obscure the underlying unity of purpose: all these measures, in their own way, contribute to our understanding of variation in community composition. Excessive categorization may impede the cross-fertilization of ideas that are essential for the unification and advancement of the field.

The comment by Dr. Baselga offers a definitive and articulate defense of the classic, dissimilarity-based paradigm, and in doing so, perfectly illuminates why a new framework was necessary. The critiques presented do not expose mathematical errors or logical fallacies in our geometric approach; rather, they highlight the deliberate, logically consistent mathematical consequences of the distinct ecological questions our metric was built to answer.

The central conclusion from this exchange should not be a prescriptive mandate declaring one approach universally "right" and the other "wrong." Ecology is best served by methodological pluralism. Ecologists now have two distinct, mathematically rigorous tools for two different analytical jobs. When the scientific question centers on pairwise differentiation and the strict spatial segregation of species, classic metrics remain the essential and correct tools. When the question shifts to the total structural and combinatorial complexity of a metacommunity and the emergent properties arising from novel species combinations, our geometric approach offers a vital new perspective.

We thank Dr. Baselga for his comment, which has provided an excellent opportunity to clarify the theoretical rigor of our geometric framework and allowed the scientific community to directly compare the merits of these two complementary paradigms.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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