Configuration coefficients can mislead conservation inference from beta diversity in fragmented landscapes

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Abstract

Beta diversity informs reserve design and connectivity planning because compositional turnover links local assemblages to regional diversity. However, the conservation meaning of a beta-diversity pattern depends on the mechanism that generates it, not on the sign of a landscape-configuration coefficient alone. I use a recent Atlantic Forest tree beta-diversity analysis (Kramer et al. 2026, Global Change Biology, 32, e70855) as a worked case to show how a negative patch-number coefficient on total beta diversity can document a real landscape association without identifying fragmentation per se. In the dataset, habitat cover and patch number pass conventional collinearity screening but retain predictor geometry that limits same-amount, different-configuration contrasts. Patch number has a near-zero marginal correlation with total beta diversity yet becomes significant in the joint model, consistent with marginal-to-conditional amplification within a shared amount–configuration gradient. Under the alpha-corrected Raup-Crick response, patch number loses unique conditional support whereas spatial distance remains supported. Independent extraction across five operational extents further shows that explicit isolation, edge-exposure, interior-condition, and arrangement metrics do not provide convergent conditional support. The patch-number coefficient therefore documents a response- and metric-specific subdivision association, not an identified fragmentation-per-se mechanism. Conservation prescriptions such as several-small reserve design or corridor investment require mechanism-matched inference, response-estimand alignment, predictor separability, and biologically justified scale, not habitat-amount control alone.

Keywords: compositional turnover; connectivity; habitat fragmentation; landscape configuration; reserve design; SLOSS; statistical identification

Article impact statement: A patch-number coefficient on beta diversity cannot guide reserve or corridor decisions unless it identifies the fragmentation mechanism.

Beta diversity is the turnover in species composition among local assemblages that links local to regional diversity, and it is central to spatial conservation planning because local assessments can underestimate land-use biodiversity loss when regional turnover is high (Socolar et al., 2016, 2025). Where turnover is high, protected-area networks must capture that variation across multiple sites or lose species (Socolar et al., 2016), so beta diversity bears directly on the single-large-or-several-small (SLOSS) question (Fahrig et al., 2022) and on whether to invest in between-patch connectivity. Yet increased turnover does not by itself imply conservation benefit, because fragmented landscapes can show higher beta diversity while still losing landscape-scale diversity (Gonçalves-Souza et al., 2025). Habitat fragmentation is invoked as a driver of these patterns, and conservation studies increasingly treat landscape-configuration metrics — patch number, mean patch size, inter-patch distance — as evidence of how fragmentation reshapes beta diversity and, by extension, what conservation should do (Kramer et al., 2026). Yet the conservation significance of a beta-diversity pattern depends on the process that generates it. Turnover from dispersal limitation may warrant corridors, neutral turnover from rarity may warrant maximising protected area, and homogenisation may signal degradation (Socolar et al., 2016). The conservation action follows from the mechanism, not from the pattern alone.

The same logic applies one step upstream. Turnover, homogenisation, neutral sampling, dispersal limitation, and environmental filtering imply different conservation actions. A configuration coefficient used to explain beta diversity can inform conservation only if it identifies the spatial mechanism being invoked. A configuration coefficient documents an association, but need not identify the spatial-arrangement process that conservation inference attributes to it. Configuration coefficients on beta diversity can be read in opposite conservation directions. A positive coefficient may be interpreted as evidence that subdivision increases turnover because patches sample different environmental conditions or species pools, supporting landscape complementarity and several small reserves (Fahrig, 2017, 2020; Dambros et al., 2024); a negative coefficient may be interpreted as evidence that subdivision homogenises composition through isolation, edge exposure, or degradation, eroding distinctness (Kramer et al., 2026). Neither sign identifies its mechanism by itself. A positive coefficient does not establish that subdivision raises beta by environmental sampling rather than by confounding with habitat amount; a negative coefficient does not establish isolation-driven homogenisation rather than a subdivision contrast decoupled from isolation. The conservation meaning of a configuration coefficient depends on the process behind the beta-diversity pattern, and the coefficient must identify that process before its sign can carry a conservation verdict.

A recent Atlantic Forest tree-diversity analysis illustrates this identification problem. Kramer et al. (2026) report that number of forest patches is a significant negative predictor of total tree beta diversity across 95 landscapes and interpret this as evidence that fragmentation effects were separated from habitat amount and spatial distance. In observational landscapes generated by deforestation, however, configuration coefficients can be null, negative, or positive for reasons of predictor geometry rather than ecology (Ruffell et al., 2016; Martínez-Lanfranco, 2026a, b). They interpret the negative patch-number coefficient through generalist proliferation, edge exposure, habitat degradation, anthropogenic disturbance, specialist loss, and interaction between fragmentation and local degradation. Their earlier review supports this pathway in tropical and subtropical plant communities (Kramer et al., 2023). Whether the fitted coefficient identifies that pathway depends on response-estimand alignment, metric-mechanism correspondence, realised predictor geometry, and the spatial scale at which the proposed

mechanism is measured (Fletcher et al., 2007, 2018, 2023). Neither additive nor interaction amount control establishes these conditions (Martínez-Lanfranco, 2026a, b).

The realised predictor geometry limits cover-general same-amount, different-configuration contrasts (Appendix S1). In Kramer et al.'s 95 landscapes, habitat cover and number of patches have a Pearson r of −0.60 (Appendix S2) and pass standard variance-inflation screening. Standard collinearity diagnostics detect only linear dependence, whereas a diagnostic model confirms nonlinear threshold structure that leaves the high-cover, many-patches cell structurally empty (Appendix S1). Number of patches has a near-zero marginal correlation with total beta diversity ($r = -0.12$) yet achieves a significant standardised partial coefficient in Kramer et al.'s joint model ($\beta = -0.26$, $p = 0.01$; Kramer et al., 2026). This marginal-to-conditional amplification is consistent with estimation within a shared amount–configuration gradient. Thus, although the predictors pass a generic $r \leq 0.70$ screening rule, the realised geometry does not provide the independence needed for cover-general same-amount, different-configuration contrasts.

The clearest internal test is Kramer et al.'s own Raup-Crick analysis, introduced to account for alpha-diversity patterns that influence standard Bray–Curtis dissimilarity. Under the alpha-corrected index, neither habitat cover nor number of patches reaches significance in any selected model variant. Mean spatial distance is the only consistently supported predictor (their Appendix S7, standardised effect = 0.31, $p < 0.01$). The loss of patch-number coefficient support under Raup-Crick shows that its unique conditional contribution is specific to total beta diversity, even though its fitted-gradient alignment persists under the alpha-corrected response. This pattern is compatible with alpha-diversity- or abundance-sensitive pathways and does not identify a direct patch-configuration effect on alpha-corrected compositional dissimilarity. The patch-number structure coefficient is the correlation between the standardised predictor and the model's fitted linear predictor. It does not diminish under Raup-Crick; its unique conditional contribution attenuates while fitted-gradient alignment is preserved. The response correction therefore reorganises the balance between shared gradient alignment and unique partial contribution, rather than eliminating the patch-number association entirely.

Independent extraction reproduced the focal predictors and most of the published patch-number effect, so the central problem is attribution rather than measurement failure (Appendix S2). The interpretation also outruns Kramer et al.'s own fragmentation predictors. The mechanism implied by their interpretation requires subdivision to align with an isolation or reachability process. More patches can be interpreted as homogenising only if subdivision tracks shorter inter-patch distances and greater reachability (Fletcher et al., 2018), whereas greater nearest-neighbour distance should index dispersal limitation and compositional turnover (Myers et al., 2013). Yet after dropping mean patch size for its collinearity with habitat cover ($r = 0.94$), Kramer et al. retain two fragmentation dimensions that are empirically orthogonal. Patch number and nearest-neighbour distance correlate at $r = -0.04$, and an independent extraction reproduces this ($r = -0.11$). More patches therefore do not consistently track isolation across these landscapes, so the negative patch-number coefficient cannot be read as one side of a coupled subdivision–isolation gradient. Patch-number results, whether null or significant, are configuration-axis-specific and cannot be generalised to other spatial-pattern mechanisms without direct metric correspondence (Martínez-Lanfranco, 2026c). This analysis does not test cover-dependent effects on other configuration axes, but instead asks whether the reported patch-number coefficient identifies the fragmentation-per-se mechanism invoked to interpret it.

Only one of these decoupled dimensions receives support. Number of patches is retained and significant across Kramer et al.'s selected total-beta models, whereas nearest-neighbour distance, their explicit isolation metric, is absent from those models and non-significant under Raup-Crick (their Appendix S7: standardised effect +0.08 to +0.09, both $p > 0.1$). The supported signal is therefore a subdivision signal, not the subdivision-and-isolation pathway the Discussion invokes when it describes "small and isolated patches" and attributes homogenisation to isolation alongside edge exposure, degradation, generalist proliferation, and specialist loss. Patch number can estimate a subdivision contrast with habitat amount and landscape area held constant, but it cannot identify the broader fragmentation-per-se mechanism, because the isolation dimension that mechanism requires is both decoupled from patch number and unsupported in their own models.

Covariate extraction across five operational extents (25–400 km²; Appendix S3) corroborates this and tests whether other spatial pathways invoked by Kramer et al.'s interpretation rescue the fragmentation-per-se claim. Nearest-neighbour distance, edge coverage, and interior distance (interior forest depth) index isolation, edge exposure, and interior-condition pathways, respectively; none receives independent partial support for total beta diversity at any extent, even though nearest-neighbour distance and edge coverage show fitted-gradient alignment comparable to or greater than patch number in structure-coefficient terms (SC; Fig. 1). Metrics that align with the fitted response gradient therefore need not provide unique conditional support once habitat amount and spatial distance are included, and the edge-exposure pathway is no better identified than the isolation pathway.

The fitted-gradient structure also shifts with the response estimand. Interior distance has near-zero alignment under total beta diversity ($SC \approx 0.00$ to -0.02) but strengthens substantially under Raup-Crick ($SC = -0.30$ to -0.41), while its partial coefficient remains unsupported throughout. The landscape dimensions aligned with fitted compositional variation therefore differ between the two responses, without establishing an interior-depth effect that is merely underpowered or that either response is uniquely correct.

The patch-number coefficient therefore documents a real, response- and metric-dependent landscape association. The absence of convergent conditional support across explicit isolation, edge-exposure, interior-condition, and arrangement metrics, together with the reorganisation of fitted-gradient alignment across response estimands and operational extents (Fletcher et al., 2018), means that, from these analyses, the association cannot be attributed to fragmentation per se, whether conceived as a specific mechanism or as a diffuse aggregate configuration effect. A partial patch-number coefficient cannot be converted into a general fragmentation-per-se construct simply because no single mechanism explains it: a diffuse fragmentation effect defined as whatever remains after habitat amount is included would be an unidentified residual category, which is precisely the inferential step this analysis questions.

The patch-number coefficient remains informative, but its fragmentation-per-se interpretation does not hold across Kramer et al.'s own decoupled fragmentation dimensions, response estimands, or operational extents. A directionally reproducible association documents that Atlantic Forest tree composition varies along landscape subdivision gradients, consistent with habitat amount or broader landscape condition being reflected in tree composition, not separable in the realised predictor space of these landscapes. The retained spatial-distance effect under Raup-Crick is an interpretable spatial-assembly signal, not merely a statistical control, and

Atlantic Forest tree composition is structured by both environmental and spatial components (Zwiener et al., 2020).

Sufficient fragmentation-per-se inference requires demonstrated predictor separability, response-estimand alignment, metric-mechanism correspondence, and explicit evaluation of scale dependence (Fletcher et al., 2023; Valente et al., 2023; Martínez-Lanfranco, 2026a, b). Studies demonstrating such convergence provide stronger evidence than an additive partial coefficient alone (Fletcher et al., 2018). These analyses do not show that fragmentation is ecologically irrelevant in Atlantic Forest tree communities; they show that no fragmentation-per-se effect is identified by the reported coefficient. The Kramer et al. (2026) patch-number coefficient documents a total-beta association along a landscape-subdivision gradient, but it does not support fragmentation-per-se inference in any empirically specified form.

Conservation decisions inherit this identification gap. An underidentified configuration coefficient documents association without naming the spatial-arrangement process, so it cannot resolve decisions that turn on which process is operating. Favouring several small reserves over a single large one requires subdivision to generate conservation-relevant turnover rather than habitat amount or sampling artefact, and the coefficient establishes no such thing in either sign (Fahrig et al., 2022). Connectivity investment meets the same obstacle, since the case for corridors rests on dispersal limitation as the turnover-generating mechanism (Socolar et al., 2016), and an isolation metric decoupled from the supported subdivision signal leaves that mechanism unidentified. The same decoupling surfaces in the case reanalysed here. In Kramer et al.'s conservation discussion, the recommendation that smaller patches may serve as stepping stones rests on the spatial-distance pathway, whereas the questioned patch-number coefficient is a subdivision signal that loses unique conditional support under the alpha-corrected response. Their conservation prescription thus follows the mechanism that remains identified, not the fragmentation-per-se reading of the patch-number coefficient.

The point transfers to any fragmented system in which configuration metrics inform reserve design or connectivity planning. The prescription follows from the mechanism, and a coefficient must identify the mechanism before it can carry a prescription. Habitat-amount control is necessary but insufficient. Inference also rests on a mechanism-matched configuration metric, a response estimand aligned with the proposed process, and a biologically justified operational scale (Fletcher et al., 2018, 2023; Martínez-Lanfranco, 2026a, b, c). Configuration coefficients stay informative about how composition varies across landscapes. They mislead only when their sign is read as a fragmentation-per-se verdict, and through that verdict as a conservation prescription the coefficient does not support.

Acknowledgements: None.

Author contributions: J.A. Martínez-Lanfranco conceived the study, designed and performed all analyses, and wrote the manuscript.

Data and code availability: Reanalysis code, computed tables, and figures are archived at Zenodo: https://doi.org/10.5281/zenodo.20635343. The analyses use publicly available data and code from Kramer et al. (2025, 2026) (Zenodo: https://doi.org/10.5281/zenodo.16761037) and publicly available Atlantic Forest spatial products via the *atlanticr* R package.

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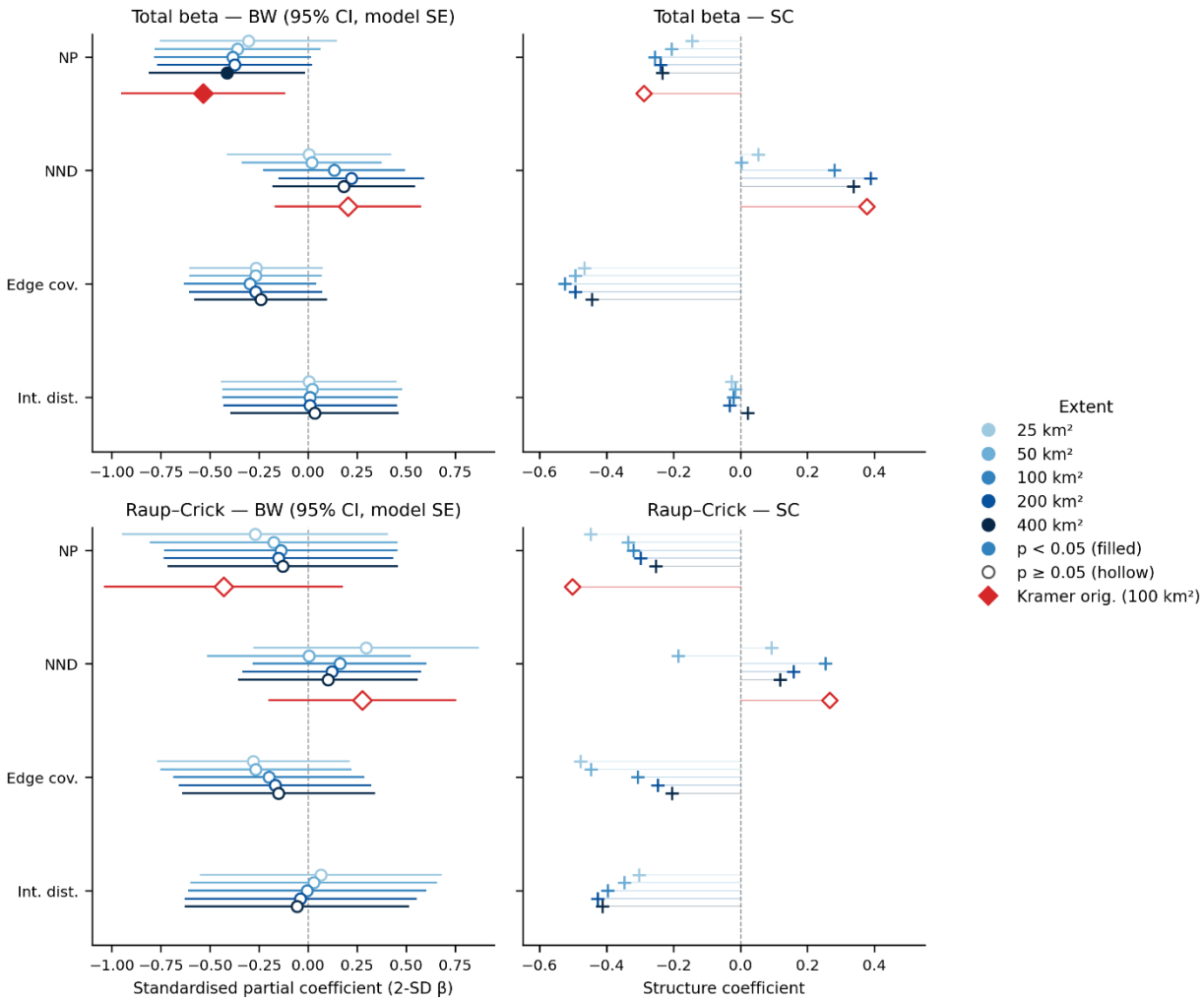

Figure 1. Mechanism triangulation for fragmentation-based inference from beta diversity in the Kramer et al. (2026) Atlantic Forest dataset. Panels compare structure coefficients (SC) and unique conditional support for patch number, nearest-neighbour distance, edge coverage, and interior distance across five operational extents (25–400 km²), for total beta diversity and Raup-Crick dissimilarity. SC is the descriptive correlation between each standardised predictor and the model's fitted linear predictor; it indexes fitted-gradient alignment, not a hypothesis test or mechanism ranking. Filled symbols indicate $p < 0.05$ and open symbols indicate $p \geq 0.05$ in the coefficient panels. Red diamonds show Kramer et al.'s original deposited predictors refit at 100 km².

Supplementary Material

Configuration coefficients can mislead fragmentation-based conservation inference from beta diversity

Appendix S1. Predictor geometry and response diagnostics

The Kramer et al. (2026) dataset covers 95 Atlantic Forest landscapes with habitat cover ranging from 1.3% to 99.8%. Habitat cover and number of patches are negatively correlated (Pearson $r = -0.60$, Spearman $\rho = -0.557$) and pass conventional screening thresholds ($|r| < 0.70$; VIF < 3). These linear statistics do not capture the nonlinear structure of the amount–configuration coupling (Dormann et al., 2013; Graham, 2003).

A generalised additive model (GAM; mgcv, thin-plate spline, k = 5; Wood, 2017; Pedersen et al., 2019) confirmed nonlinear coupling in both directions. With patch number as the response, GAM R^2 was 0.460 versus linear $R^2 = 0.363$; with habitat cover as the response, GAM R^2 was 0.433 versus linear $R^2 = 0.363$. Effective degrees of freedom exceeded one and the smooth terms were supported in both orientations.

Conditional nature of the empty-cell limitation. The high-cover, many-patch region of the predictor space is sparsely populated, which limits same-amount, different-configuration contrasts at high cover (Koper et al., 2007). This limitation is conditional rather than general: it bears on the identification of any fragmentation effect whose decoupled configuration variation would occur at high habitat cover, but not on a threshold effect expressed at low cover, where configuration varies widely across the 95 landscapes (mean patch counts ~144–154 in the low and middle cover tertiles, collapsing to ~42 in the high-cover tertile). The decisive evidence in this commentary therefore comes from within the populated low-to-mid-cover region (Appendix S2), not from the sparsely sampled high-cover corner.

Marginal and partial coefficient comparison. Number of patches has a near-zero marginal correlation with total beta diversity ($r = -0.12$) but a significant standardised partial coefficient in the joint model ($\beta = -0.26$, $p = 0.01$; Kramer et al.'s Table 1, Model 1). This marginal-to-conditional amplification is the expected consequence of estimation within a shared amount–configuration gradient.

Separation criterion. Kramer et al.'s Methods state that separating fragmentation from habitat amount requires no correlation between fragmentation metrics and amount. Habitat cover and patch number ($r = -0.60$) clear only a generic $r \leq 0.70$ screen, which is not the independence that criterion specifies. Additional model terms are estimated from the same realised predictor support; they can characterise associations within the populated region but cannot supply same-amount, different-configuration contrasts the sample does not contain (Lundberg et al., 2021).

Raup-Crick diagnostic. Kramer et al. introduced the Raup-Crick index because Bray–Curtis dissimilarity is influenced by alpha-diversity patterns whereas Raup-Crick accounts for variation in alpha diversity among sampling sites (Chase et al., 2011). Under Raup-Crick, neither habitat cover nor number of patches reaches significance in any selected model; mean spatial distance (standardised effect = 0.31, $p < 0.01$; their Appendix S7) is the only consistently supported predictor. Notably, the patch-number structure coefficient, defined as the descriptive correlation between a predictor and the model-fitted gradient (Ray-Mukherjee et al., 2014; see S2, S3), does not diminish under Raup-Crick: its unique conditional contribution attenuates while its fitted-

gradient alignment persists, indicating that the response correction reorganises the balance between shared and unique alignment rather than eliminating the patch-number association.

PCA and explained variance. Kramer et al.'s own principal-component analysis shows that higher-beta landscapes are not tightly clustered along the first two environmental axes, even though the regression labels habitat cover and patch number as the strongest landscape predictors. The selected total-beta models explain little variance ($R^2 \approx 0.16–0.18$). Neither observation invalidates the coefficients, but both restrain language such as "drivers" and broad attribution.

Endemism contrast. The endemism result rests on habitat cover and temperature seasonality (VIF = 1.02), where patch number attenuates toward zero once habitat cover is included — the opposite of the beta-diversity geometry.

Appendix S2. Fragmentation-metric structure and independent triangulation

Orthogonality of Kramer et al.'s own fragmentation dimensions. Kramer et al. define fragmentation through number of patches, mean patch size, and mean nearest-neighbour distance (isolation). After removing mean patch size for its collinearity with habitat cover (r = 0.94), patch number and nearest-neighbour distance remain as their two fragmentation dimensions. In their own data these two dimensions are essentially orthogonal, and an independent 30 m extraction reproduces this (Table S2.1). Patch number is therefore a subdivision axis that does not carry the isolation dimension the proposed mechanism invokes.

Table S2.1. Pairwise correlations among landscape predictors (n = 95), from Kramer et al.'s deposited data and from independent 30 m extraction. Both chains give a near-zero, non-significant patch-number–isolation correlation.

Predictor pair	Kramer deposited r	Independent 30 m r
Number of patches – nearest-neighbour distance	−0.035 (n.s.)	−0.108 (n.s.)
Habitat cover – number of patches	−0.603	−0.559
Habitat cover – nearest-neighbour distance	−0.331	−0.084
Extraction fidelity (your vs Kramer)	—	NP 0.874; NND 0.823; HC 0.949

Independent extraction of the patch-number coefficient. Independent patch number retained the negative total-beta direction and recovered approximately 74% of the published effect size on a common scale. The 2-SD standardised coefficient (Gelman, 2008) is −0.38, corresponding to a 1-SD coefficient of approximately −0.19, compared with the published 1-SD coefficient of −0.26. The p-value difference between independent (p = 0.061 at 100 km²) and published (p = 0.01) results is consistent with sensitivity to land-cover classification and buffer geometry, not a qualitatively different association.

Mechanism triangulation. Four focal metrics, each with a distinct inferential role, were extracted independently and evaluated for total beta diversity and the alpha-corrected Raup-Crick index (Table S2.2): number of patches (the subdivision proxy under test), nearest-neighbour distance (the explicit isolation dimension), edge coverage (edge exposure), and interior distance (interior forest depth) (Fletcher et al., 2007). Structure coefficients (SC) are the descriptive correlation between each standardised predictor and the model's fitted linear predictor; they index fitted-gradient alignment and are not hypothesis tests or formal mechanism rankings, and they are compared across separately fitted focal-metric models. Beta weights (BW) are 2-SD standardised partial coefficients.

Table S2.2. Focal mechanism triangulation at 100 km² (Kramer et al.'s operational extent). Total beta diversity (primary) and Raup-Crick (diagnostic). BW = 2-SD beta weight; SC = structure coefficient; r(HC) = correlation with independent habitat cover.

Metric (role)	**TB BW**	**TB p**	**TB SC**	**RC BW**	**RC p**	**RC SC**	**r(HC)**
Number of patches (subdivision)	−0.38	0.061	−0.26	−0.14	0.647	−0.32	−0.56
Nearest-neigh. dist. (isolation)	+0.13	0.472	+0.28	+0.16	0.474	+0.25	−0.08
Edge coverage (edge exposure)	−0.30	0.084	−0.53	−0.20	0.421	−0.31	+0.12
Interior distance (interior depth)	+0.01	0.965	−0.02	−0.01	0.988	−0.40	−0.63

Two features are notable. First, nearest-neighbour distance and edge coverage show fitted-gradient alignment comparable to or stronger than patch number in absolute SC terms while remaining weakly correlated with habitat cover, yet neither receives independent partial support — fitted-gradient alignment does not entail unique conditional support once habitat amount and spatial distance are included. Second, interior distance has near-zero alignment under total beta diversity (SC ≈ −0.02) but a substantially stronger negative alignment under Raup-Crick (SC = −0.40), while its partial coefficient remains unsupported — the landscape dimensions aligned with fitted compositional variation differ between the two responses, without establishing an interior-depth effect that is merely underpowered.

Conditioning amplifies the patch-number coefficient. Because patch number is negatively correlated with habitat cover (r = −0.56; about 31% shared variance), conditioning on habitat cover amplifies its coefficient: patch number's near-zero marginal correlation with total beta diversity (r = −0.12) becomes a partial coefficient roughly two to three times larger once habitat cover enters the model, at every extent (Table S2.3). The orthogonal isolation metric, nearest-neighbour distance, shows no such amplification at any extent — its conditional coefficient is no larger than its marginal one. This is consistent with reciprocal-suppression geometry (Smith et al., 2009; Prunier et al., 2015): two predictors negatively correlated with each other but weakly and similarly correlated with the response mutually inflate each other's partial coefficients (habitat cover's own coefficient is likewise larger in the joint model than its near-zero marginal). The amplification therefore reflects the amount–subdivision correlation, not an independent association of patch number with compositional dissimilarity. It is specific to patch number among the focal metrics and does not generalise to a simple rule across all configuration metrics,

because metrics strongly collinear with habitat cover produce unstable joint models rather than a uniform inflation.

Additional non-collinear arrangement metrics (NLSI, core-area CV) and the remaining sensitivity metrics (patch density, edge density, aggregation index, clumpiness, perimeter–area ratio, matrix-distance isolation, low- and high-criterion functional connectivity, structural connectivity, morphological core and edge; Neel et al., 2004; Wang et al., 2014) likewise provided no convergent conditional support; full results are in the reproducibility repository (tables/FF_models.csv, tables/AS_models.csv). Patch density is an area-standardised rescaling of patch number and is not independent evidence.

Table S2.3. Marginal-to-conditional amplification across extents (total beta diversity). BW_marginal from total_beta ~ metric + spatial distance; BW_conditional from total_beta ~ habitat cover + metric + spatial distance. The ratio is |BW_conditional| / |BW_marginal|. Patch number inflates (ratio > 2) at every extent; nearest-neighbour distance does not (ratio < 1).

Metric	Extent	r(metric, HC)	BW marginal	BW conditional	Ratio
Number of patches	25 km²	−0.67	−0.09	−0.30	3.3
	50 km²	−0.61	−0.15	−0.36	2.4
	100 km²	−0.56	−0.17	−0.38	2.2
	200 km²	−0.53	−0.18	−0.37	2.1
	400 km²	−0.54	−0.19	−0.41	2.2
Nearest-neigh. distance	25 km²	−0.54	+0.08	+0.01	0.07
	50 km²	−0.30	+0.07	+0.02	0.29
	100 km²	−0.08	+0.19	+0.13	0.70
	200 km²	−0.14	+0.30	+0.22	0.74
	400 km²	−0.15	+0.26	+0.18	0.70

Appendix S3. Predictor-extent sensitivity

Habitat cover, patch number, and all focal metrics were extracted at five circular-buffer extents (25, 50, 100, 200, 400 km²; radii 2,821–11,284 m). Responses (total beta, Raup-Crick) and mean spatial distance were fixed from Kramer et al.'s published landscape CSV. All metrics returned valid estimates at all five extents; the model at each scale s is total_beta ~ HC_z[s] + metric_z[s] + SD_z (betareg, 2-SD standardisation), with collinearity flags recomputed within each scale.

Table S3.1. Five-scale coefficient paths for the four focal metrics (total beta diversity). BW = 2-SD beta weight; SC = structure coefficient. Confidence intervals use model-derived standard errors.

Metric	Extent	TB BW	TB p	TB SC
Number of patches	25 km²	−0.30	0.187	−0.15
	50 km²	−0.36	0.096	−0.21
	100 km²	−0.38	0.061	−0.26
	200 km²	−0.37	0.064	−0.24
	400 km²	−0.41	0.042*	−0.23
Nearest-neigh. distance	25 km²	+0.01	0.978	+0.05
	50 km²	+0.02	0.917	+0.00
	100 km²	+0.13	0.472	+0.28
	200 km²	+0.22	0.246	+0.39
	400 km²	+0.18	0.326	+0.34
Edge coverage	25 km²	−0.27	0.126	−0.47
	50 km²	−0.27	0.122	−0.49
	100 km²	−0.30	0.084	−0.53
	200 km²	−0.27	0.122	−0.49
	400 km²	−0.24	0.162	−0.44
Interior distance	25 km²	+0.00	0.986	−0.03
	50 km²	+0.02	0.928	−0.02
	100 km²	+0.01	0.965	−0.02
	200 km²	+0.01	0.962	−0.03
	400 km²	+0.03	0.881	+0.02

* $p < 0.05$. Patch-number coefficients are stable in direction and magnitude across extents (BW −0.30 to −0.41), with statistical support attained only at 400 km² (its 95% CI, −0.81 to −0.02, is the only focal CI excluding zero). Of the focal metrics only patch number ever reaches significance, and only at the largest extent; the mechanism-matched metrics are unsupported throughout. Full coefficient paths, Raup-Crick results, standard errors, and collinearity flags at all scales are in the repository (tables/FF_models.csv, tables/kramer_models_coeftable.csv).

Appendix S4. Software and data sources

Independent extraction drew on multiple raster sources at matched landscape extents, accessed through the 'atlanticr' R package (Vancine et al., 2026) and processed with 'terra' and 'sf' (Hijmans, 2024; Pebesma & Bivand, 2023). The 30 m binary forest layer (forest vegetation binary; layer ID 003) supplied baseline class-level metrics computed with 'landscapemetrics' v2.2 (Hesselbarth et al., 2019), 8-neighbour connectivity: habitat cover, number of patches, mean

nearest-neighbour distance, patch density, normalised landscape shape index, aggregation index, clumpiness, core-area coefficient of variation, and edge density. Precomputed ATLANTIC SPATIAL products (WGS84, ~1 km series; Vancine et al., 2023) supplied additional configuration metrics: forest vegetation cover, perimeter–area ratio, total forest edge, low- and high-criterion functional connectivity, and structural connectivity. ATLANTIC SPATIAL 30 m Albers products (Vancine et al., 2023) supplied interior-distance and morphological core/edge metrics. Response variables (total beta, alpha-corrected compositional dissimilarity, endemism), mean spatial distance, and climate covariates were retained from Kramer et al. (2026)'s published landscape-processed CSV.

Beta regression used 'betareg' (Cribari-Neto & Zeileis, 2010). Focal reanalysis models included habitat cover, one configuration metric, and mean spatial distance, with predictors 2-SD standardised; structure coefficients, model-derived standard errors, p-values, and collinearity diagnostics were exported for the body figure and supplementary tables. All reanalysis scripts and intermediate output tables are archived at Zenodo (https://doi.org/10.5281/zenodo.20635343).

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