Habitat amount control is necessary but not sufficient to resolve the fragmentation debate

Juan Andrés Martínez-Lanfranco

Department of Biological Sciences, University of Alberta, Canada. Correspondence:
jacoloml@gmail.com / juanandr@ualberta.ca

Abstract

Opposing conclusions from the same global multi-taxa dataset have intensified debate over whether fragmentation effects can be inferred independently of habitat amount in observational landscape studies. Gonçalves-Souza et al. (2025) reported lower local- and landscape-scale diversity in fragmented landscapes, whereas Fahrig et al. (2026) reanalysed the same dataset with continuous, scale-matched predictors and concluded that no independent evidence for fragmentation remains once habitat amount is controlled. I argue that this stronger adjudicatory inference is not established by the reanalysis. Controlling for habitat amount is necessary, but it is not sufficient when the realised predictor structure may still fail to provide the contrast required for separately estimated coefficients to be interpreted as independent ecological effects. Supplementary design-based analyses show that the continuous predictor redesign remains embedded in the original directional landscape contrast, that same-amount contrasts are scarce, and that benign linear collinearity diagnostics do not exhaust dependence in the raw predictor pair. The point is not that the opposite ecological conclusion has been demonstrated, but that a near-zero additive coefficient under these conditions is not self-interpreting. More broadly, the comment argues that landscape-scale studies using additive habitat-amount control cannot treat coefficient separation as proof that independent ecological effects have been identified unless predictor separability is demonstrated empirically in the realised design.

Keywords: additive amount control; biodiversity conservation; configuration metrics; fragmentation per se; habitat amount hypothesis; independent effects; landscape ecology; predictor separability; spatial subdivision

Article impact statement: Additive habitat-amount control does not establish independent fragmentation effects unless predictor separability is demonstrated.

Whether habitat fragmentation affects biodiversity independently of habitat amount remains one of the most contested and consequential questions in landscape ecology and conservation science (Miller-Rushing et al. 2019). High-profile syntheses have reached opposite conclusions (Haddad et al. 2015; Fahrig 2017), and the disagreement has repeatedly implicated spatial scale, study design, and the statistical treatment of habitat amount as the main proximate sources of divergence (Fahrig et al. 2019; Fletcher et al. 2018; Hadley and Betts 2016). Most recently, two analyses of the same global multi-taxa dataset reached opposite conclusions (Fahrig et al. 2026; Gonçalves-Souza et al. 2025), mirroring rather than resolving the dichotomous state of the debate (Valente et al. 2023).

Gonçalves-Souza et al. (2025; hereafter GS25) reported lower local (α) and landscape-scale (γ) diversity in fragmented landscapes using a categorical design contrast (continuous vs. fragmented), concluding that compositional turnover (β diversity) did not compensate for diversity losses at the landscape scale. Fahrig et al. (2026; hereafter F26) reanalysed the same dataset using forest amount and number of patches as continuous, scale-matched predictors, obtaining near-zero fragmentation coefficients across all diversity components, and concluded that the GS25 signal arose from inadequate habitat amount control and that, once properly controlled, no evidence for fragmentation per se remains.

When identical data produce opposing ecological conclusions under alternative predictor representations, the discrepancy itself becomes analytically informative: it cannot be attributed to differences in study systems or geographic scope, and it exposes the inferential conditions under which fragmentation effects can and cannot be distinguished from habitat-amount effects. The argument developed below is that, although F26's redesign corrects a genuine problem, it does not establish the stronger inferential claim they draw from it, because the realised design may still fail to provide the contrast required for separately estimated coefficients to be interpreted as independent ecological effects.

That limitation follows from a condition F26 themselves state and then fail to evaluate. F26 explicitly define fragmentation-per-se inference as requiring landscapes spanning gradients in forest amount and fragmentation that are "sufficiently independent to allow estimation of their separate effects" (F26, their own emphasis). Whether the additive reanalysis satisfies that separability condition is an empirical question, not one answered by formal model inclusion. F26 state the condition but do not verify it.

F26's own paper reveals a decisive limitation of their interpretive claim. On page 4, F26 acknowledge that their central causal interpretation — that the GS25 signal arose from forest amount differences at the larger scale of the continuous and fragmented landscapes — could not be directly tested: "We could not directly test this because Gonçalves-Souza et al. did not measure forest amount or fragmentation at the larger scale of the continuous and fragmented landscapes." Their main conclusion therefore rests on a surmise they explicitly concede is untestable with the available data. This is not an external critique, but F26's own statement about the limits of their reanalysis.

GS25's own published results further undercut F26's interpretation. GS25's multipredictor model-averaging analysis, which included both landscape type and habitat amount simultaneously as predictors and explicitly avoided standard AIC-based comparison because of predictor correlation, showed that landscape type retained greater scaled importance than habitat amount across all diversity components (GS25 Extended Data Fig. 7; GS25 Supplementary Tables 1–6) — a result GS25 themselves report in their main text as persisting after accounting for habitat amount, and robust across their three independent analytical approaches. A signal that persists under GS25's own analysis that explicitly accounts for habitat amount cannot be dismissed as a single-model artefact that a continuous-predictor redesign at a different scale can trivially explain away.

GS25 state in their statistical methods that no single statistical approach could overcome the inherent multicollinearity of habitat amount and configuration effects in observational landscape studies, which is why they relied on different approaches rather than treating any one analytical specification as dispositive. F26 therefore do not replace a naive GS25 analysis with a resolving one; on this evidence alone, they substitute one observational specification for a problem GS25 had already stated could not be settled by any single specification alone. Together, F26's untested surmise and GS25's own multipredictor result are sufficient to show that F26's conclusion outruns what their reanalysis demonstrates.

F26 are right that number of patches is a widely used fragmentation metric. The issue here, however, is not whether patch number is a legitimate configuration measure in general, but whether its coefficient is independently interpretable in this dataset unless separability from habitat amount is demonstrated empirically. In fixed-extent sampling units, total habitat area, mean patch size, and patch number are not free to vary independently (Fletcher et al. 2023a), meaning that configuration metrics based on patch subdivision are partly structurally constrained by habitat amount before any landscape is sampled. Patch-number metrics depend strongly and often nonlinearly on habitat amount across real landscape gradients (Neel et al. 2004; Wang et al. 2014) — a pattern also visible across GS25's own habitat-amount classes (GS25 Extended Data Fig. 5).

This nonlinear dependence matters because standard collinearity diagnostics — Pearson correlations, variance inflation factors — detect only linear dependence and cannot identify nonlinear dependence that remains after the linear association is partialled out (Dormann et al. 2013). A nonlinear diagnostic applied to the F26 predictor pair shows this directly: the GAM R^2 exceeds the linear R^2 in both directions, with the nonlinear component 7.7 times larger in one direction than the other, consistent with the asymmetric nonlinear dependence expected from the habitat-loss process (Supplementary Material S1, Table S4). F26's residual diagnostics therefore support model specification, but they do not establish predictor separability or independent coefficient interpretation, because model fit and predictor separability are different inferential targets.

The directional structure of this specific dataset also points toward violated separability without any model fitting. In 31 of 37 study pairs (84%; Supplementary Material S1, Table S1), the fragmented landscape simultaneously had more patches and lower habitat amount than the paired continuous landscape. The continuous-predictor redesign therefore does not escape the original process-coupled directional contrast; it re-expresses the same amount-dominated landscape gradient in additive continuous form. GS25 acknowledged that it was not feasible to select pairwise comparisons with precisely the same habitat amount within studies, because too few studies contained a sufficient number of same-amount fragments in both landscape types (GS25 Supplementary Text 4). The structural size asymmetry underlying this constraint is documented in Supplementary Material S1, Table S2. This constraint persists even within the highest habitat-amount classes (77–100%), where fragmentation variables are no longer significantly different between landscape types (GS25 Extended Data Fig. 5). The equal-amount, different-configuration contrast F26's redesign requires is not directly recoverable from the empirical design they reparameterised (Supplementary Material S1, Figure S1 and Table S1).

A formal design-level reconstruction quantifies this point: F26's two continuous predictors explain 45.2% of the marginal variance in the original categorical landscape classification (Supplementary Material S1, Analysis S1 and Table S5), with forest amount and patches each contributing materially (53.1% and 46.9% respectively; Cohen's d: forest amount −1.43, patches +0.92), confirming that the continuous redesign reconstructs the original directional contrast rather than recovering a design in which their coefficients can be interpreted as independent ecological effects. The logical implication is direct: if the original categorical contrast encoded an amount-dominated gradient, and the continuous predictors re-encode the same gradient, then additive variance partitioning between those predictors cannot be treated as separating independent ecological effects. Together, F26's own statements, GS25's published design, and the realised predictor structure documented in Supplementary Material S1 are sufficient to show that F26's reparameterisation does not by itself recover the equal-amount, different-configuration contrast that fragmentation-per-se inference requires.

The concern raised here applies generally to landscape-scale studies that estimate fragmentation effects using additive habitat-amount control and treat coefficient separation as evidence of independent ecological effects by model construction. In that analytical family, separability cannot be taken as secured by specification alone; it must be demonstrated empirically in the realised predictor space. Precision around a constrained null is not evidence that the null is ecologically diagnostic. A near-zero additive coefficient is not self-interpreting; without demonstrated predictor separability it cannot distinguish between ecological independence and a non-diagnostic null generated by the shared predictor structure of the dataset. This argument does not establish the opposite ecological conclusion. It shows only that F26's null additive coefficients are inferentially non-diagnostic under unresolved predictor separability, and that broader review-level claims about "most empirical evidence" requires case-by-case empirical verification that separability conditions are met in each study's realised predictor structure, rather than transfer by assertion (Fahrig et al. 2019). Furthermore, the F26 reanalysis operates at a single fixed spatial grain; the inferential scope of any null finding is bounded by that grain and cannot be taken to exclude scale-dependent fragmentation effects in multi-taxa assemblages. The Smith et al. (2009) framework justifies additive control under the predictor relations in which it was established, not as an automatic guarantee of independent interpretability in any realised dataset.

The appropriate path forward is not to abandon habitat amount control, which remains necessary, but to require empirical demonstration that predictor separability has been achieved rather than assuming it from model specification alone. Experimental fragmentation designs that explicitly manipulate configuration at constant habitat amount (e.g., Fletcher et al. 2023b) are closer to the inferential standard F26 themselves state for valid fragmentation-per-se inference (Riva et al. 2024). The broader lesson is therefore methodological rather than adversarial: habitat amount should be controlled, but additive control cannot by itself be treated as proof that independent ecological effects have been identified.

The implication for the conservation recommendation is direct. F26 conclude that biodiversity protection should proceed irrespective of patch sizes, on the basis that fragmentation per se has no independent effect. Any downstream claim that patch size is ecologically irrelevant inherits the same inferential limitation as the coefficient on which it rests, particularly given the conservation consequences of patch-size criteria and the undervaluation of small patches (Riva and Fahrig 2023). This does not imply the opposite conservation recommendation; it shows only that the evidence reported by F26 cannot adjudicate the ecological question they use it to settle.

F26 title their reanalysis around resolving the fragmentation debate. But resolution requires more than a redesigned additive specification alone. Resolution demands that study design and data match the spatial scale and contrast of the ecological question, that model structure corresponds to the ecological hypothesis under test, and that the assumptions needed for reliable inference are demonstrated in the realised dataset rather than assumed from model specification — a fit-for-purpose principle: data, scale, model, and inferential target must be explicitly matched to the question at hand (Guillera-Arroita et al. 2015).

In sum, additive habitat amount control is necessary to advance the fragmentation debate, but it is not sufficient.

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

Data and code availability: Reproducibility code, computed tables, and figures are available at https://github.com/jacoloml/Reply2_F26. Analyses use the publicly archived dataset of Gonçalves-Souza and Vancine (2025; Zenodo: https://doi.org/10.5281/zenodo.14885581).

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Supplementary Material S1

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Juan Andrés Martínez-Lanfranco

Department of Biological Sciences, University of Alberta, Canada. Correspondence:
jacoloml@gmail.com / juanandr@ualberta.ca

Contents

Note: forest amount and patch-number values in Figure S1, Tables S1 and S3, and Analysis S1 are the 2-km predictor values used by F26, derived from GS25’s published dataset. They should not be confused with the study-level counts of sampling sites in GS25 Supplementary Table 7, which record the number of fragments or plots sampled per landscape rather than the landscape-configuration metric analysed by F26.

Section A. Design contrast in the GS25–F26 dataset

Figure S1 and Tables S1–S2 document the realised directional contrast, same-amount scarcity, and structural size asymmetry in the F26 predictor space.

Text S1. From GS25's paired landscape contrast to F26's additive redesign

Gonçalves-Souza et al. (2025; GS25) analysed 37 independent study pairs defined as continuous versus fragmented landscapes, reporting lower local (α) and landscape-scale (γ) diversity in fragmented landscapes. F26 reparameterised this design by replacing the categorical landscape-type contrast with two continuous predictors — forest amount (% cover within a 2-km buffer) and fragmentation (number of patches within a 2-km buffer) — allowing separate additive estimation of each predictor's effect. GS25's Extended Data Figs. 3–5 and Supplementary Text 4 provide the original descriptive basis for the inferential limitation argued in the main text; Figure S1 and Tables S1–S5 translate those source materials into the specific 2-km predictor definitions used by F26, allowing direct evaluation of the realised F26 predictor space. GS25's Extended Data Figs. 3–4 document the directional differentiation of habitat amount and patch number across buffer sizes, while Extended Data Fig. 5 shows that several fragmentation-related metrics vary nonlinearly across habitat-amount classes; both use GS25's original predictor scale rather than F26's 2-km grain. That argument does not require estimation of biodiversity responses. It requires only transparent documentation of the realised predictor structure underlying the GS25–F26 comparison. This supplement addresses three descriptive questions: whether GS25's paired landscapes remain directionally differentiated in F26's 2-km predictors (Figure S1, Tables S1–S2); how much same-amount contrast is actually available in those predictors (Table S1); and to what extent F26's continuous predictors reconstruct the original categorical contrast while remaining mutually dependent (Table S3–S4, Figure S2, Analysis S1, Table S5).

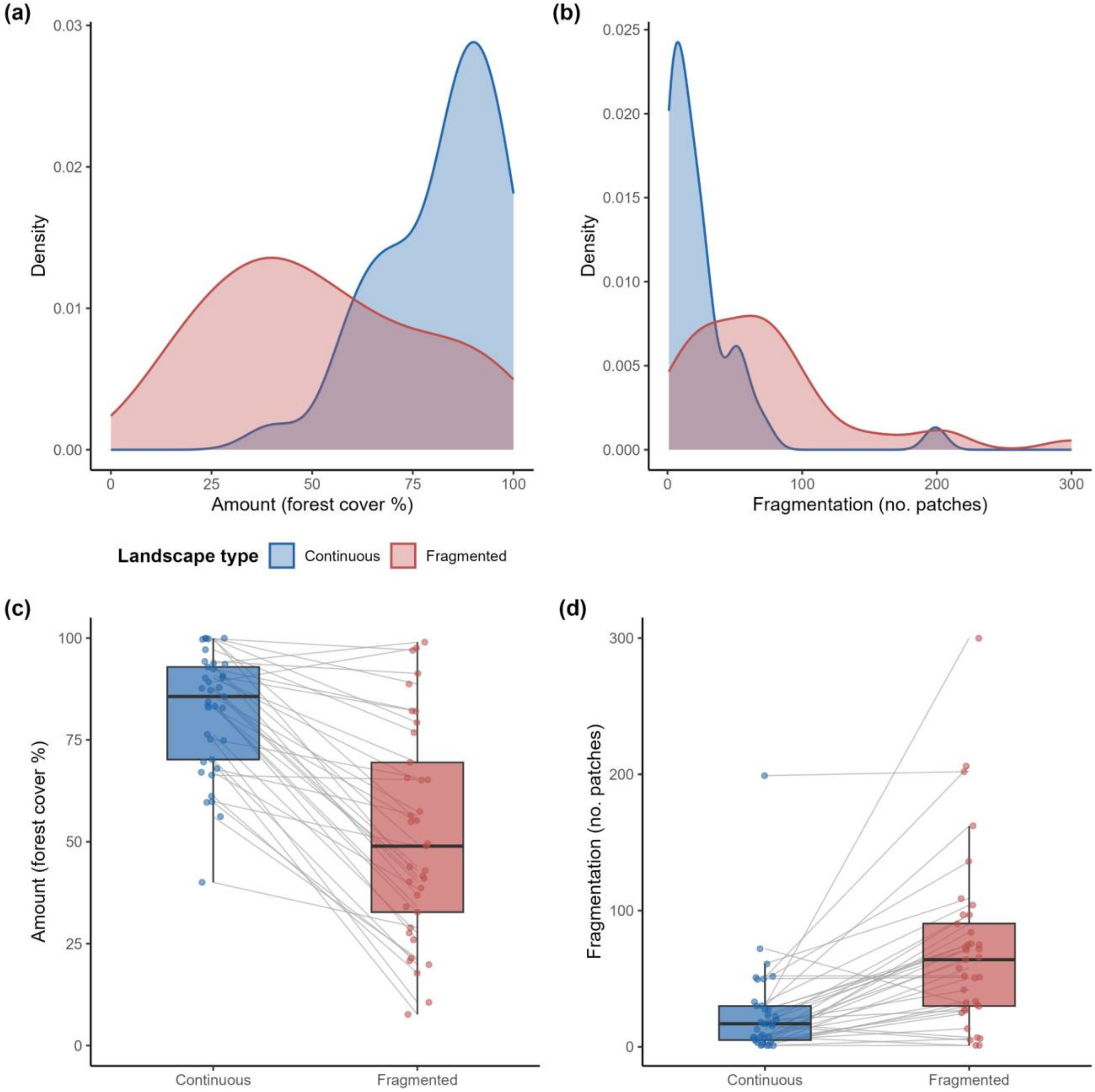

Figure S1. Realised 2-km predictor space underlying the GS25–F26 comparison. Panels (a) and (b): density distributions of the two continuous predictors by landscape type (blue = continuous; red = fragmented). Panel (a): amount (forest cover %); panel (b): fragmentation (no. patches). Panels (c) and (d): paired boxplots showing within-study contrasts for each predictor; grey lines connect paired continuous and fragmented landscapes within each study. Together, the four panels show that F26's additive redesign remains embedded in a strongly directional contrast: fragmented landscapes have lower amount (forest cover) and higher fragmentation (no. patches) than their continuous counterparts in 31 of 37 study pairs. Predictor values are F26's 2-km grain values derived from the publicly available GS25 dataset.

Table S1. Summary diagnostics of the realised GS25–F26 design contrast

Diagnostic	N (of 37)	Value / %
A. Directional differentiation in F26's predictors (2-km grain)		
Fragmented landscape has lower amount (forest cover)	35	94.6%
Fragmented landscape has higher fragmentation (no. patches)	31	83.8%
Fragmented landscape has lower amount and higher fragmentation (both conditions)	**31**	**83.8%**
B. Effect size of paired predictor contrasts		
Median Δ amount (continuous − fragmented)	—	28.4 pp
Median Δ fragmentation (fragmented − continuous)	—	44.5 patches
C. Same-amount contrast availability		
Pairs with |Δ forest amount| ≤ 5%	3	8.1%
Pairs with |Δ forest amount| ≤ 10%	7	18.9%
Both landscapes in 77–100% HA class	8	21.6%
Both in 77–100% class AND |Δ HA| ≤ 5%	2	5.4%

Note: Predictor values are F26's 2-km grain values. Same-amount scarcity is evident directly in rows C1–C4: only 3/37 pairs (8.1%) have |Δ forest amount| ≤ 5%, and only 2/37 (5.4%) are simultaneously in the 77–100% class with |Δ HA| ≤ 5%. Computed from the publicly available GS25 dataset (Gonçalves-Souza et al. 2025; Zenodo: https://doi.org/10.5281/zenodo.14885581).

Table S2. Structural size asymmetry across GS25 study pairs

Statistic	Value
Studies with numeric area for both landscape types	28 of 37 (76%)
Studies with continuous landscape designated as "continuous" (no numeric area)	9 of 37 (24%)
Median size ratio (largest forest / smallest fragment)	1,672×
Range of size ratios	10× – 125,000×

Statistic	**Value**
Studies with ratio > 100×	26 of 28 (93%)
Studies with ratio > 1,000×	15 of 28 (54%)
Fragmented landscape has more sampling sites than continuous	33 of 37 (89%)

Note: Size ratio = area of largest continuous forest member / area of smallest fragment in each study pair, extracted from GS25 Supplementary Table 7. The large size asymmetries explain why same-amount, different-configuration contrasts are structurally scarce in this dataset. Study-level values are provided in the GitHub repository (https://github.com/jacoloml/Reply2_F26).

Section B. Linear and nonlinear dependence in the F26 predictor pair

The issue here is not whether F26's additive model is statistically legitimate — it is. The question is whether benign model diagnostics are sufficient to establish that the corresponding coefficients are independently interpretable in the realised predictor space. Tables S3–S4 and Figure S2 show they are not ('nonlinear coupling' here refers to residual nonlinear dependence between the two predictors, as quantified in Table S4).

Table S3. Standard linear diagnostics for the F26 predictor pair

Diagnostic	**Value**	**Conventional threshold**	**Status**
Pearson correlation (r)	−0.674	$\lvert r \rvert < 0.7$	Below threshold
Variance inflation factor (VIF)	1.847	VIF < 5	Below threshold
Tolerance ($1 - R^2$)	0.541	> 0.2	Above threshold

Note: Predictors are amount (forest cover %) and fragmentation (no. patches) at the 2-km landscape grain used by F26. Pearson correlation and VIF computed on the 74-observation predictor matrix (37 continuous + 37 fragmented landscapes). Tolerance = $1 - R^2$*. Standard thresholds are met, but linear metrics cannot detect nonlinear coupling that remains after the linear association is partialled out (Dormann et al. 2013); see Table S4.*

Table S4. Nonlinear coupling diagnostics for the F26 predictor pair

Direction	Linear R^2	GAM R^2	Nonlinear component
NP ~ s(HA): fragmentation (no. patches) as response, amount (forest cover %) as predictor	0.454	0.486	0.032
HA ~ s(NP): amount (forest cover %) as response, fragmentation (no. patches) as predictor	0.454	0.702	0.248

Note: GAMs fitted with mgcv::gam(), thin-plate spline smoother (default k; Wood 2017). Linear R^2 = Pearson r^2 (symmetric, both directions). Nonlinear component = GAM R^2 minus linear R^2. Asymmetry ratio (larger / smaller nonlinear component): 7.7×.

Interpretation: Both directions are evaluated using response-model notation (y ~ s(x)): in one direction fragmentation (no. patches) is the response and amount (forest cover %) is the predictor (NP ~ s(HA)); in the other, amount is the response and fragmentation is the predictor (HA ~ s(NP)). The nonlinear component (GAM R^2 minus linear R^2) quantifies residual nonlinear dependence not captured by standard linear diagnostics. The nonlinear component is 7.7× larger in one direction (HA ~ s(NP): 0.248) than the other (NP ~ s(HA): 0.032), indicating strongly asymmetric nonlinear dependence not detectable by the standard linear checks in Table S3. Together, Tables S3 and S4 document benign linear collinearity alongside substantial residual nonlinear dependence — the specific condition that standard pre-regression checks do not flag and that the main text argues prevents reliable additive attribution.

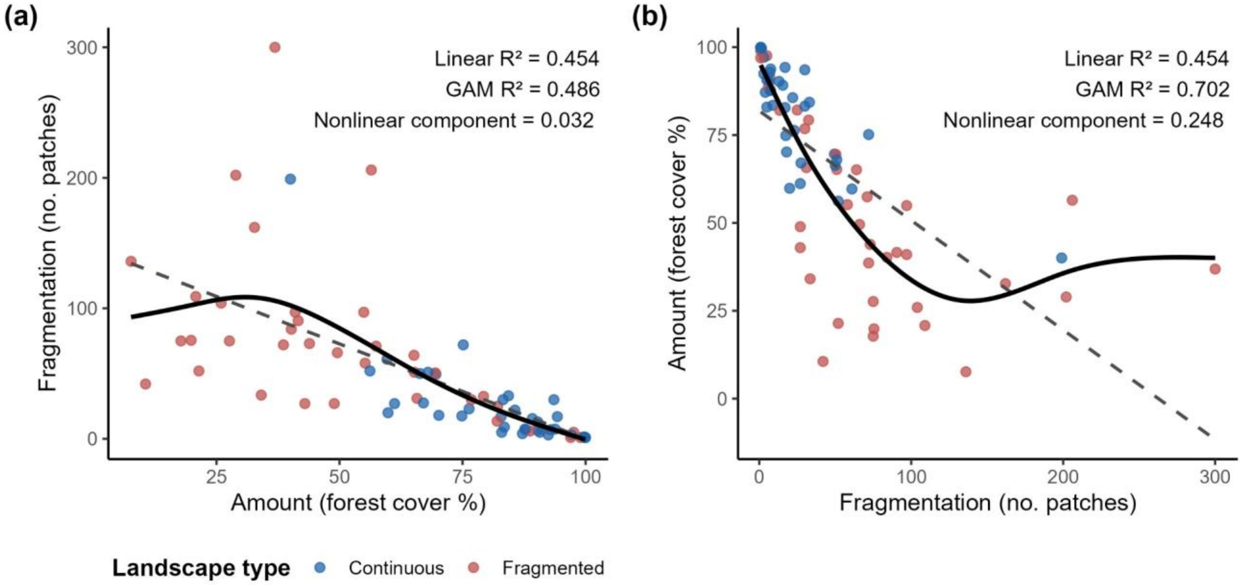

Figure S2. Bidirectional linear and nonlinear fits for the F26 predictor pair at the 2-km grain (n = 74; 37 continuous + 37 fragmented landscapes). Panel (a): fragmentation (no. patches) as response, amount (forest cover %) as predictor [NP ~ s(HA)]; panel (b): amount (forest cover %) as response, fragmentation (no. patches) as predictor [HA ~ s(NP)]. In each panel, points are colour-coded by landscape type (blue = continuous; red = fragmented); dashed line = linear fit; solid line = GAM fit. R^2 annotations summarise the values in Table S4.

Section C. Formal reconstruction of GS25 landscape type

Analysis S1 and Table S5 quantify the extent to which F26's continuous redesign reconstructs the original GS25 categorical contrast.

Analysis S1. Formal reconstruction of GS25 landscape type from F26's continuous predictors

Purpose

To quantify the extent to which F26's two continuous predictors reconstruct the original GS25 categorical landscape contrast (continuous vs. fragmented). A strong reconstruction indicates that the continuous redesign remains embedded in the original directional contrast rather than recovering a design in which the two predictors span independent ecological gradients.

Methods

Predictors were centred and scaled prior to fitting (divided by two standard deviations; Gelman 2008). The model was fitted as a logistic mixed-effects model with landscape type (fragmented = 1) as the binary response, forest amount and number of patches as fixed effects, and study identity as a random intercept (lme4::glmer, Bates et al. 2015). Marginal R^2 was computed with performance::r2_nakagawa (Lüdecke et al. 2021). Hierarchical partitioning of the marginal R^2 used glmm.hp (Lai et al. 2022). Cohen's d values for each predictor were computed as the standardised mean difference between landscape types (Nakagawa & Cuthill 2007).

Table S5. Formal reconstruction results

Quantity	**Value**
Marginal R^2 (fixed effects only)	0.452
Forest amount contribution (glmm.hp)	53.1%
Fragmentation contribution (glmm.hp)	46.9%
Cohen's d, forest amount	−1.428
Cohen's d, fragmentation (no. patches)	+0.916

Note: Marginal R^2 = proportion of variance in landscape type (continuous/fragmented) explained by the two fixed-effect predictors. glmm.hp contributions (53.1% / 46.9%) represent each predictor's unique variance plus its proportionally shared contribution; they are not purely independent fractions. A large shared component indicates the two predictors co-explain the same landscape gradient.

Interpretation: Strong reconstruction of GS25 landscape type indicates that F26's continuous redesign remains substantially embedded in the same realised contrast as the categorical paired design. The two predictors together explain 45.2% of marginal variance in landscape type, with hierarchical partitioning indicating that both predictors contribute materially to that reconstruction. It does not create the design argument; that argument is already visible descriptively in Figure S1 and Table S1. Nor does a strong reconstruction imply that the categorical design and the continuous redesign are analytically equivalent; it shows only that the realised continuous predictors preserve a large portion of the original directional landscape contrast. This result does not establish any biodiversity response, nor does it prove the opposite ecological conclusion. Cohen's d values are reported only as descriptive measures of directional separation between landscape classes.

Section D. Scope and reproducibility

Text S2. What this supplement can and cannot show

The materials in this supplement document the realised predictor structure underlying the GS25–F26 comparison. They show that the realised F26 predictor space does not meet the separability condition F26 themselves state as necessary for valid fragmentation-per-se inference.

These materials do not estimate biodiversity responses and do not establish that fragmentation per se has a negative effect. The comment therefore stands even without Analysis S1; that analysis is included only as a formal quantitative summary of the same design reconstruction. For reference, the main-text claims supported by this supplement are: 31/37 directional co-occurrence (Table S1, row A3); same-amount scarcity (Table S1, rows C1–C4); structural size asymmetry (Table S2); benign standard linear diagnostics (Table S3); nonlinear coupling in the raw F26 predictor pair (Table S4 and Figure S2); realised 2-km predictor-space directional structure (Figure S1); and formal reconstruction of the original categorical contrast from F26's two predictors (Analysis S1 and Table S5).

Code S1. R code and session information

The R Markdown script (Reply2_F26_SupplS1_reproducibility.Rmd) that reproduces all figures and tables is provided in the GitHub repository:

(https://github.com/jacoloml/Reply2_F26). All outputs are generated from Data/diversity_of_2.csv (Gonçalves-Souza et al. 2025; Zenodo: 10.5281/zenodo.14885581) with no manual data entry.

R 4.4.0 (Windows 11 x64). Packages: lme4 v1.1-36 (Bates et al. 2015); glmm.hp v0.1-8 (Lai et al. 2022); performance v0.13.0 (Lüdecke et al. 2021); car v3.1-3 (Fox & Weisberg 2019); mgcv v1.9-1 (Wood 2017); patchwork v1.3.0 (Pedersen 2024); knitr v1.50 (Xie 2015); kableExtra v1.4.0 (Zhu 2024); tidyverse v2.0.0 (Wickham et al. 2019).

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