Reframing the habitat fragmentation debate around the inferential targets predicted by ecological theory

Juan Andrés Martínez-Lanfranco* and Erin M. Bayne

Department of Biological Sciences, University of Alberta, Canada.

*Correspondence: juanandr@ualberta.ca

Abstract

The habitat fragmentation debate has persisted for more than three decades because dominant empirical practice has often estimated a narrower quantity than the competing ecological theories jointly require. These frameworks differ not simply in whether fragmentation matters, but in how their predicted effects change along the habitat-amount gradient. The habitat amount hypothesis (HAH) predicts no independent configuration effect once habitat amount is controlled. Threshold dynamics predict increasingly harmful fragmentation effects after structural or demographic breakpoints are crossed at low habitat amount. Colonization–competition coexistence (C–C) tradeoff predicts a sign reversal, with fragmentation neutral or beneficial at high habitat amount where subdivision weakens competitive dominance and harmful where isolation dominates at lower amount. Extinction filtering predicts strongest effects where sensitive taxa remain at high habitat amount, fading as those taxa are lost. In a linear modeling framework, the fragmentation × habitat amount interaction is the minimum linear statistical structure needed to represent this ecological conditionality. The interaction yields β1, the fragmentation effect at mean habitat amount, and β3, how that effect changes along the gradient. HAH predicts $\beta1 \approx 0$ and $\beta3 \approx 0$. Threshold and C–C predict $\beta3 > 0$ but differ in the expected sign of β1 and beta-diversity structure. Extinction filtering predicts $\beta3 < 0$. The dominant additive model estimates only the fragmentation effect at mean habitat amount and cannot distinguish these alternatives. A null β1 is consistent with true configuration invariance, coexistence crossover, or sampling outside the response-specific recoverability window, the gradient region where effects are both biologically expressed and empirically detectable. Gradient position, beta-diversity decomposition, and metric–mechanism correspondence provide the discriminating signals. Once the target is the conditional response surface, the competing frameworks make distinguishable predictions. The debate can then move from repeated demonstration toward theory investigation.

Keywords. beta-diversity, biodiversity response surface, coexistence dynamics, extinction filter, extinction threshold, fragmentation-per-se, fragmentation threshold, habitat amount hypothesis, landscape metrics

1. The debate and its structure

Research on habitat fragmentation has produced one of the most persistent disagreements in landscape ecology and conservation biology (Miller-Rushing et al. 2019). Some studies report negative effects of spatial subdivision independent of habitat loss. Others find weak, neutral, or positive associations (Fletcher et al. 2018; Fahrig et al. 2019). Disagreement has been attributed to differences in spatial scale and study design, habitat definition, fragmentation metrics, and the difficulty of separating configuration from amount statistically in empirical landscapes (Ewers and Didham 2006; Didham et al. 2012; Hadley and Betts 2016; Fletcher et al. 2023). These concerns explain why empirical studies disagree but have not supplied a common inferential target for resolving the disagreement. The debate has therefore remained caught in a demonstration–counter-demonstration cycle for more than three decades (Andrén 1994; Valente et al. 2023a). The same global multi-taxa dataset has recently supported opposed conclusions under different implementations of amount-controlled fragmentation inference (Gonçalves-Souza et al. 2025; Fahrig et al. 2026).

These methodological diagnoses share a deeper foundation. They were formulated within a fragmentation-per-se paradigm (Fahrig 2003; Fahrig et al. 2019) that clarified the target of inference but also directed empirical practice toward amount-controlled contrasts among present-day landscapes. Fragmentation as a process is the breaking apart of habitat through time, whereas fragmentation as pattern is the spatial configuration of the remaining habitat mosaic at a given time (Fahrig 2003; Fletcher et al. 2026). Fragmentation per se is the independent effect of spatial configuration on biodiversity at a given habitat amount, defined by comparisons among landscapes that differ in arrangement but not in habitat amount (Fahrig 2003, 2013, 2017; Fahrig et al. 2019). The paradigm therefore improved conceptual precision while leaving unresolved whether the amount-controlled contrast the field adopted is the right inferential target.

In empirical landscapes shaped by habitat loss, the processes that generate these patterns couple habitat amount and configuration along the same gradient, making snapshot contrasts difficult to align with an independent fragmentation effect (Didham et al. 2012; Fletcher et al. 2018). Amount-controlled contrasts address that coupling, but the additive structure they impose constrains inference to a single configuration effect evaluated at the sample mean of habitat amount. Current empirical practice therefore estimates that quantity (Smith et al. 2009; Fahrig et al. 2026), one defined narrowly relative to what competing ecological theories predict.

1.1 The ecological conditionality problem

The conditional nature of the theoretical question has been explicit since the debate's early formulation. Fragmentation effects were already shown to emerge mainly below a cover threshold of approximately 10–30%, implying that the ecological consequence of configuration depends on where a landscape sits along the habitat-amount axis (Andrén 1994). The statistical implication was stated directly when Fahrig (2003) argued that the threshold "should result in a statistical interaction effect between habitat amount and habitat fragmentation per se." Configuration effects were later predicted to be most detectable at intermediate cover (Villard and Metzger 2014). Competitive metacommunity models identified a sign-reversal mechanism in which the fragmentation effect is positive at high cover and negative at low cover (Rybicki et al. 2020; Zhang et al. 2024). Extinction filtering predicts fading fragmentation effects as cover declines and sensitive species are lost (Betts et al. 2019). These predictions converged across three decades of distinct theoretical traditions, yet their analytical implication has not been adopted as standard practice (McGarigal and Cushman 2002; Hadley and Betts 2016; Riva et al. 2024).

The HAH is the limiting exception. It predicts that the fragmentation effect is invariant once habitat amount is controlled (Fahrig 2013, 2021; Saura 2021). The other frameworks considered here predict that fragmentation sensitivity changes along the habitat-amount gradient and may reverse sign, with the form of the change differing among mechanisms. A single average fragmentation effect cannot distinguish these alternatives.

The disagreement is therefore not simply over whether configuration matters, but over which conditional response surface best characterizes a given system. When the fragmentation effect changes along the gradient, an additive estimate becomes partly a function of where the sampled landscapes happen to sit rather than of the underlying ecology alone. The same conditional surface can therefore yield different average fragmentation effects in studies positioned at different gradient regions (Smith et al. 2009; Duncan and Kefford 2021; Spake et al. 2023).

1.2 A response-surface reframing

Progress requires identifying the inferential target the debate has been trying to characterize. That target is the conditional biodiversity response surface. Recent calls for reconciliation have identified the absence of a common conceptual framework as a key impediment to moving from demonstration to investigation (Valente et al. 2023a), while earlier gradient-based work showed that habitat configuration should matter most only in particular regions of the habitat-amount gradient (Villard and Metzger 2014; Zhang et al. 2024). The missing step has been to make habitat amount not one moderator among many, but the organizing axis along which the competing frameworks make distinguishable predictions. To our knowledge, existing syntheses have not jointly organized these frameworks around a common conditional target, derived their gradient-specific predictions, and connected those predictions to the statistical structure required to distinguish them empirically. They differ in whether configuration ever becomes independently consequential along the habitat-amount gradient, and in where and how that conditionality is biologically expressed. These alternatives are ecological hypotheses before they are statistical contrasts, and their implied response surfaces must be specified before model coefficients can resolve them.

The habitat-amount gradient can be divided into response-specific regions of persistence, configuration sensitivity, and empirical recoverability. Empirical threshold syntheses showed that configuration effects often become detectable only below particular cover ranges, with the numerical position varying among systems (Andrén 1994). Spatially explicit theory showed that habitat loss can alter persistence through extinction thresholds and connectivity loss (Fahrig 2002). Percolation models provide a structural reference point because the critical percolation threshold, p_c, marks the cover value at which habitat cells first form a connected cluster under a specified landscape-generation model, although p_c is not itself a biological threshold (Gardner et al. 1987; With and Crist 1995). For any response state variable R, ET_R denotes the lower persistence boundary, and FT_R denotes the upper configuration-saturation boundary above which configuration no longer limits the response. The interval between ET_R and FT_R is the response-specific configuration-sensitive window (W_R) in which configuration effects can be biologically expressed (Fig. 1). Empirical recovery additionally requires sampled landscapes within W_R to contain sufficient configuration contrast. This sampled portion of W_R is the recoverability window. These boundaries vary with response variable, taxon, spatial scale, matrix, configuration metric, and landscape-generation process.

This notation previews the four frameworks developed in Section 2 and the limiting-case predictions (Fig. 1; Table 1). These schematic surfaces are canonical cases for comparison, not discrete categories into which real systems must fall. Real datasets may express different signatures across taxa, configuration metrics, response variables, and gradient positions within the same landscape sample. The corresponding response-surface and marginal-effect predictions are formalized in Section 3 and visualized in Fig. 2.

This reframing changes the object of the debate. Except under the HAH, fragmentation is not predicted to have one gradient-invariant effect once habitat amount is controlled. It is predicted to have effects that appear, reverse, or fade depending on where taxa and landscapes sit along the habitat-amount gradient, and on which configuration metrics and response variables are analyzed. The task is therefore not to assess whether fragmentation effects are positive, negative, or null, but to identify which conditional surface a system expresses and where that surface can be recovered.

2. Ecological mechanisms generating conditional fragmentation effects

The conditional framework applies to any ecological response variable Y for which a fragmentation metric F and a cover measure A can be jointly estimated at a biologically meaningful spatial scale. "Cover" denotes the landscape-level measurement used to quantify A; "habitat" refers to its species-specific ecological sense, because a cover type constitutes habitat only for species whose requirements it meets (Fahrig 2013).

Four main theoretical frameworks have organized much of the fragmentation debate and define the limiting cases considered here (Table 1; Fig. 1). Each proposes a distinct ecological mechanism and a distinct prediction about how fragmentation effects change along the habitat-amount gradient. All predict conditional fragmentation effects except the HAH, which predicts invariance once habitat amount is controlled. The frameworks disagree about the direction, shape, and gradient position of that conditionality.

2.1 Habitat amount hypothesis and configuration invariance

Fahrig (2013, 2015) proposed that biodiversity at a sample site responds primarily to the total amount of habitat within the local landscape surrounding that site, with spatial configuration exerting little independent influence once amount is controlled. The local landscape is defined empirically as the radius at which habitat amount most strongly predicts the response, and this scale must be estimated rather than assumed a priori. The mechanism applies at any level of organization because local habitat amount determines the species pool available regardless of spatial arrangement. Under HAH, the fragmentation effect is zero, or near zero, everywhere along the gradient. HAH is the amount-only limiting case in Fig. 1. An extinction threshold may arise from habitat loss, but no fragmentation threshold is expected. Saura (2021) formalized the HAH in a way that corresponds here to the joint restriction $\beta1 = 0$ and $\beta3 = 0$ in the interaction framework. This makes the HAH a specific falsifiable case rather than a default assumption. Evidence bearing on this broader invariance claim is mixed. A vote-counting review of 381 effects across 118 studies found no subset of conditions with predominantly negative responses

(Fahrig 2017), and a model-based synthesis of 35 species-density studies found non-significant interactions between habitat amount and patch size, isolation, or fragmentation (Watling et al. 2020; De Camargo et al. 2018). Controlled experiments, by contrast, found steeper species–area relationships in isolated than in connected treatments at fixed habitat amount, with the divergence widening over 15 years (Haddad et al. 2017a). These results address different aspects of the HAH prediction set and are not automatically commensurable as tests of a single estimand. Because the HAH is defined relative to the local landscape, its predictions are scale dependent and most directly tested when A is measured at the empirically determined scale of effect for the focal taxon (Jackson and Fahrig 2015).

2.2 Threshold and scarcity models below cover thresholds

Andrén (1994) synthesized bird and mammal studies across a cover gradient and proposed that fragmentation effects intensify specifically when landscape cover falls below approximately 10–30%. Above the threshold, habitats remain structurally connected and subdivision imposes little additional cost. Below it, patches become small, isolated, and edge-dominated, and spatial configuration amplifies extinction risk beyond what habitat loss alone would predict. The connectivity threshold has a formal theoretical basis in spatially explicit metapopulation dynamics, where patch isolation drives disproportionate extinction at low habitat amounts (Hanski 2015; Fahrig 2002). The threshold prediction was later translated into observational study design (Fahrig 1998; Villard and Metzger 2014). The 10–30% range is not fixed. Percolation theory predicts structural disconnection at approximately 59% cover under random habitat loss, but empirically observed thresholds are lower because land clearing is non-random, producing more spatially aggregated loss patterns than random models assume (Gardner et al. 1987; With and Crist 1995).

Threshold-like fragmentation responses arise through multiple pathways, including connectivity breakdown, edge proliferation, interior habitat collapse, and local patch-viability failure. Their relative importance depends on species traits and the habitat-amount range studied (Villard and Metzger 2014). Threshold dynamics should therefore be read as a family of structural and demographic breakpoints rather than a single universal low-cover rule. Fragmentation per se can raise ET_R by reducing colonization rates or increasing edge-mediated matrix mortality (Fahrig 2002, 2003), and p_c provides a structural reference point that can help determine FT_R but is not equivalent to it. Fahrig (2003) made the statistical implication explicit. If threshold dynamics operate, the effect of fragmentation per se should depend on habitat amount, producing a habitat amount × fragmentation interaction. Smith et al. (2011) report this directional signature on fragmentation-sensitive bird richness across five landscape radii, with the fragmentation effect intensifying at low cover as threshold dynamics predict. This places threshold/scarcity dynamics in the lower portion of the configuration-sensitive window, where configuration effects are expected before persistence failure truncates the response (Fig. 1).

2.3 Metacommunity coexistence and sign reversal across the gradient

A mechanistic explanation for positive fragmentation effects was formalized by Rybicki et al. (2020). At high habitat amounts, fragmentation can promote coexistence by breaking competitive dominance. Large patches support strong competitors, small patches support superior colonizers, and the landscape mosaic maintains both. The mechanism is a colonization–competition coexistence (C–C) tradeoff. As habitat amount declines, isolation overwhelms the coexistence-promoting effect and fragmentation becomes detrimental. Zhang et al. (2024) identified slope reversals consistent with this prediction across 71 systems and five taxonomic groups (Riva and Fahrig 2022, 2023). These reversals do not require positive and negative effects to have symmetric magnitudes. The crossover should shift with species traits, dispersal, mortality, competition strength, and the sampled habitat-amount domain (Rybicki et al. 2020; Zhang et al. 2024). Whether these reversals reflect C–C or another mechanism generating similar richness patterns depends on beta-diversity decomposition and assemblage composition history. The fragmentation effect is positive or neutral at high cover and negative at low cover. This sign-changing response occurs within the configuration-sensitive domain (Fig. 1). Because the mechanism operates through compositional differentiation among patches, the C–C tradeoff also predicts higher turnover in fragmented landscapes at intermediate-to-high cover, declining at low cover as competitive dominants are lost.

2.4 Extinction filtering and fading configuration effects

In landscapes with long histories of habitat loss, fragmentation-sensitive species may already have been progressively removed from assemblages by prior extinction, leaving communities dominated by matrix-tolerant taxa that do not respond strongly to configuration regardless of cover level (Betts et al. 2019). Extinction filtering is the community-level consequence of sensitive taxa progressively crossing species-specific ET_R values as habitat amount declines. Fragmentation per se can raise individual ET_R values and accelerate the process, but the trajectory is driven primarily by habitat loss (Fahrig 2002; Villard and Metzger 2014). The taxa remaining after filtering often have broad habitat associations and high dispersal capacity, conferring resilience to fragmentation effects (Henle et al. 2004; Weeks et al. 2023; Püttker et al. 2020). Extinction filtering is therefore a historical corollary describing how prior compositional pruning alters the detectability of configuration effects in the present (Balmford 1996). This interpretation assumes that habitat associations remain stable enough for lost taxa to be identified as fragmentation-sensitive from traits or history, and extinction debt can attenuate filtering signals where sensitive species have not yet disappeared (Kuussaari et al. 2009). The conditional relationship is one in which fragmentation effects are most negative at high cover, where sensitive species remain, and weaken toward zero as those species are progressively lost. Null results from heavily deforested systems should not be interpreted as ecological invariance without first characterizing assemblage filtering history. The beta-diversity signature is nestedness, meaning ordered species loss, rather than turnover. This places extinction filtering toward the higher-cover portion of the recoverable domain, where sensitive taxa remain, with the signal fading as species-specific extinction thresholds are crossed (Fig. 1).

In the statistical framework of Section 3, filtering corresponds to a negative fragmentation × habitat amount interaction when biodiversity is the response and higher F values denote greater fragmentation per se. The fragmentation effect should be most negative where habitat amount remains high enough for sensitive taxa to persist, and should weaken toward zero as habitat loss progressively filters those taxa from the assemblage. Across 19,432 vertebrate species, the risk consequences of recent forest loss were disproportionately strong in landscapes retaining high initial forest cover (Betts et al. 2017). Historical anthropogenic deforestation further attenuates impacts of current land-use change, with longer deforestation histories associated with trait profiles shifted toward greater deforestation tolerance (Hua et al. 2024).

2.5 Shared conceptual structure and mixed regimes

Despite their ecological differences, all four frameworks can be characterized by asking how the configuration effect behaves along the habitat-amount gradient. Under the HAH, it stays near zero across the entire gradient. Under threshold/scarcity dynamics, it becomes harmful within W_R after cover falls below FT_R but before ET_R truncates the response. Under C–C coexistence, it switches sign within the coexistence portion of W_R. Under extinction filtering, it is strongest where sensitive taxa remain and fades as species-specific ET_R crossings accumulate. The fragmentation debate can therefore be reframed as a question about how the configuration effect varies with habitat amount. Each hypothesis yields a different response-surface geometry relating ecological context to the biodiversity consequences of spatial subdivision (Fig. 2).

These regimes are not necessarily mutually exclusive in real landscapes. A system with a long history of fragmentation may show extinction-filtering signatures at mid-to-high cover while threshold dynamics operate at low cover among the remaining habitat-sensitive taxa. Table 1 should therefore be read as a set of limiting cases rather than discrete categories. Mixed regimes are expected when mechanisms operate in different portions of the cover gradient or on different response components. Threshold dynamics may persist among remaining sensitive taxa while extinction filtering simultaneously weakens the aggregate signal. The C–C tradeoff may generate turnover and positive richness effects where competitive structure remains intact, while filtering progressively removes the taxa carrying that signal at lower cover. Identifying the dominant process requires explicit evaluation of the response variable, the beta-diversity decomposition, assemblage history, and the spatial scale at which taxa perceive habitat.

Response variables differ in what they can diagnose. Population-level responses can show whether configuration affects persistence, colonization, extinction, or demography, but they cannot by themselves separate mechanisms that depend on community responses such as the C–C tradeoff or extinction filtering. Community-level responses such as species richness, occupancy, or aggregate diversity indices can reveal mechanism signatures, but only when decomposed. Total richness can be invariant while specialist composition or beta-diversity components are not. The richness response combines turnover and nestedness contributions that the four frameworks separate (Anderson et al. 2011; Baselga 2010; Socolar et al. 2016). Tests of these frameworks at the community level should report richness alongside the decomposed beta-diversity components, and conclusions should be reported as response-specific, scale-specific, and metric-specific rather than as global statements about fragmentation effects on biodiversity. For single-species responses, C–C has no direct analogue as formulated, although positive edge effects, competitive release, resource complementation, connectivity and source–sink dynamics, or response truncation can generate similar response-surface geometries at the population level (Fahrig et al. 2019).

3. From ecological mechanism to statistical identifiability

The competing frameworks imply different response-surface geometries. The statistical question is whether those geometries can be distinguished in data. Ecological theory specifies the form of the conditional relationship; statistical models determine whether that relationship can be evaluated empirically. A coefficient can be statistically valid while still failing to represent the ecological effect the analysis intends to measure. Defining the target quantity is what connects statistical evidence to theory (Lundberg et al. 2021). When theory predicts that the fragmentation effect depends on habitat amount, empirical tests require models that allow the slope of fragmentation to vary along the gradient. Models that constrain this variation impose the invariance component of the HAH without evaluating it against the alternatives. The interaction between fragmentation and habitat amount is therefore the minimum linear statistical structure required to distinguish among the competing predictions (Fahrig 2003; Saura 2021; Spake et al. 2023).

3.1 Model structures

Let Y be any ecological response variable, such as species richness, diversity index, occupancy, or abundance, F a fragmentation metric, A habitat amount, and ε error. In what follows, A is expressed as deviation from its sample mean, so that $A = 0$ denotes typical habitat amount in the sampled region.

Here, F refers to fragmentation per se, that is, the effect of habitat configuration considered independently of habitat amount (Fahrig 2003; Riva et al. 2024). Higher values of F indicate greater fragmentation per se. Analysis using aggregation-based metrics where higher values indicate less fragmentation should invert the metric before fitting for full alignment with Table 1 and Fig. 2. Without inversion, the predicted signs of $\beta 1$ and $\beta 3$ are reversed relative to those displays, and the qualitative descriptions in Table 1 and the curve directions in Fig. 2 apply to the low end of the metric rather than the high end.

The inferential target is not a single fragmentation coefficient but the slope of biodiversity with respect to fragmentation, evaluated as a function of habitat amount. In response-surface notation, this is $\partial Y/\partial F = f(A)$. The HAH is the limiting case in which this function is approximately zero, once habitat amount is controlled. Other frameworks predict non-zero functions whose sign or magnitude changes along the gradient.

The terms “marginal” and “conditional” are used here in an estimand sense. The marginal effect is the local slope $\partial Y/\partial F$ evaluated at a value of A, and the effect is conditional because that slope is evaluated along the habitat-amount gradient, f(A). This usage is distinct from the marginal–conditional distinction in mixed-model prediction, where the contrast concerns whether predictions are averaged over or conditioned on random effects.

The dominant empirical model is the additive specification.

Model 1 (additive). $Y = \beta 0 + \beta 1 \cdot F + \beta 2 \cdot A + \varepsilon$

The minimum linear conditional model adds the fragmentation × habitat amount interaction.

Model 2 (interaction). $Y = \beta 0 + \beta 1 \cdot F + \beta 2 \cdot A + \beta 3 \cdot (F \times A) + \varepsilon$

These coefficients correspond, respectively, to the fragmentation effect ($\beta 1$), the habitat amount effect ($\beta 2$), and the fragmentation × habitat amount interaction ($\beta 3$). We retain the numerical notation used throughout the debate literature (Fahrig 2003; Smith et al. 2009; Koper et al. 2007). The habitat amount effect $\beta 2$ is included to statistically partial out habitat amount from the fragmentation coefficient and is not interpreted further. $\beta 1$ denotes the estimated fragmentation effect at mean habitat amount, the reference point used throughout Table 1 and Fig. 2.

In Model 1, the fragmentation effect is $\partial Y/\partial F = \beta 1$, constant and independent of A. In Model 2, it is $\partial Y/\partial F = \beta 1 + \beta 3 \cdot A$, a function of habitat amount. Model 2 is therefore the linear implementation of the general statement $\partial Y/\partial F = f(A)$, with $f(A) = \beta 1 + \beta 3 \cdot A$. On the linear predictor scale, β3 estimates the linear rate at which the fragmentation slope changes with habitat amount, formally the cross-partial derivative $\partial^2 Y/\partial F \partial A$. If the true f(A) is nonlinear, threshold-shaped, or varies among taxa or systems, β3 is a first-order summary of conditionality rather than a complete description of the response surface.

β1 and β3 have direct ecological readings. β1 is the fragmentation effect at mean habitat amount in the sampled dataset. β3 describes how that effect changes as cover increases or decreases from that baseline. A positive β3 means the fragmentation effect becomes more positive as cover increases, or more negative as cover declines. This direction is consistent with threshold/scarcity when fragmentation is harmful at low cover and with C–C tradeoff when the effect crosses from negative at low cover to neutral or positive at higher cover. A negative β3 means the fragmentation effect becomes more negative as cover increases, as predicted when sensitive taxa remain in higher-cover landscapes and the signal fades after filtering at lower cover. β3 equal to zero means the fragmentation effect is constant across the habitat-amount gradient. This is the invariance component of the HAH; the HAH further predicts that this constant effect is zero, or near zero, once habitat amount is controlled.

These two quantities are most directly communicated through the paired visualization in Fig. 2. Predicted biodiversity at representative cover levels on the response scale provides the ecological entry point, showing whether fragmentation is harmful, neutral, or beneficial at low, intermediate, and high cover. The marginal fragmentation effect plotted against habitat amount on the model scale makes β1 + β3A the primary visual object rather than an inference from comparing slopes across panels (Duncan and Kefford 2021). Given the recoverability conditions in Fig. 1, the four canonical frameworks generate distinct limiting-case curves. The HAH predicts a horizontal line at zero. Threshold dynamics predict a curve that is most negative at low cover and weakens toward zero as cover increases. C–C tradeoff predicts a curve that crosses zero at the coexistence crossover and becomes increasingly positive at higher cover. Extinction filtering predicts a curve that intensifies toward more negative values as cover increases. Treating habitat amount as the moderator of the fragmentation effect reflects the causal structure of landscape change, because habitat loss generates configuration. The fragmentation effect conditional on habitat amount is therefore the ecologically interpretable quantity (Ruffell et al. 2016; Spake et al. 2023). In models with non-identity links the two panels are not numerically equivalent. The predicted-biodiversity panel shows response-scale values, and the marginal-effect panel remains on the model scale where β1 + β3A is defined. For empirical applications using generalized models, back-transformed predictions are appropriate for the conditional plot while the marginal effect stays on the link scale (Spake et al. 2023; Duncan and Kefford 2021).

Model 1 is Model 2 under the restriction β3 = 0, but it does not test whether this restriction holds. It imposes the restriction structurally. Fitting Model 1 assumes fragmentation effects are invariant across the cover gradient. This is the specific invariance prediction that the HAH makes and that all other frameworks reject. It is not equivalent to adopting the HAH in full. The HAH also predicts β1 = 0, whereas an additive model with significant β1 imposes invariance while reporting a non-zero average effect whose value depends on where the sample sits on the gradient. Testing whether β3 = 0 requires fitting Model 2 and comparing it to Model 1 via likelihood ratio test or information criterion.

Models 1 and 2 are written here in their simplest form to clarify the inferential target. In empirical applications, this structure may be implemented within generalized, hierarchical, multivariate community, spatial, or temporal models as required by the response variable's distribution and the study's sampling design (Pedersen et al. 2019; Tredennick et al. 2021; Ovaskainen and Soininen 2011; Popovic et al. 2024). The conditional fragmentation effect of interest remains $\partial Y/\partial F = f(A)$. The interaction term is its minimal linear parameterization. In all such implementations, the testable prediction is whether the fragmentation slope varies systematically along the habitat-amount gradient.

3.2 Conditions for β3 interpretability

The interaction coefficient β3 is interpretable as a test of the competing theoretical predictions only when several prior conditions are satisfied, operating at different inferential stages. These conditions are empirical and dataset-specific. Their violation cannot be corrected post hoc by model specification alone. Where geometry conditions are not met, the interaction term parameterizes variation along a shared habitat-loss gradient rather than isolating a configuration effect, and may therefore reproduce the same inferential limitations as the additive model in a more complex form.

Design conditions are established before data collection. First, the habitat layer underlying both F and A must be ecologically appropriate to the focal taxon or assemblage. A cover type constitutes habitat only for taxa whose biological requirements it meets, and using generic land-cover classifications as proxies introduces systematic error into both predictors before any model is estimated (Betts et al. 2014; Halstead et al. 2019; Almeida-Gomes et al. 2016; Dennis et al. 2026). For forest-interior taxa, breaking apart of forest at constant forest cover reduces interior habitat amount, while for forest-edge taxa the same configuration change increases edge habitat amount, so fragmentation manipulations holding generic land cover constant do not hold species-specific habitat amount constant (Fahrig 1999). Second, F, A, and Y must be measured at the scale at which the taxon is sensitive to configuration; the scale of effect is frequently outside the range researchers evaluate, producing null results attributable to scale mismatch rather than ecological invariance (Jackson and Fahrig 2015). Third, the fragmentation metric must track the ecological property relevant to the mechanism under investigation, namely aggregation or isolation of correctly defined habitat (Neel et al. 2004; Fletcher et al. 2023).

Metric–mechanism correspondence. Species- and population-level fragmentation effects commonly operate through edge-mediated changes in local conditions or movement-mediated changes in colonization or immigration, which are captured by different metrics and may activate at different positions along the habitat-amount gradient (Fletcher et al. 2016). A connectivity metric can show near-zero F effects where the binding constraint is local habitat sufficiency rather than inter-patch movement, even when the canonical conditional surface predicts strong negative effects at low cover (Villard and Metzger 2014; Fletcher et al. 2016). Connectivity metrics that embed patch area in their formulation (Hanski-type indices) compound this problem because they suppress connectivity values at low A independently of movement biology, partially confounding the metric with the habitat-amount predictor (Fahrig et al. 2021). At the community level, no single fragmentation metric is likely to capture all operative mechanisms simultaneously, so trait-informed or mechanism-specific complementary metrics may improve inference (Fahrig et al. 2011).

Geometry conditions are evaluable once the dataset is assembled. Habitat amount and configuration must be sufficiently separable in the realized predictor space for the interaction coefficient to identify a conditional configuration effect rather than a position along a shared habitat-loss gradient. When F and A are co-generated along a directed, asymmetric landscape gradient before any landscape is sampled (Didham et al. 2012), additive regression yields statistically valid partial coefficients for the quantities it defines, but those quantities need not correspond to the intended ecological contrasts (Koper et al. 2007; Smith et al. 2009). Low pairwise correlations or acceptable variance-inflation factors do not by themselves establish separability when habitat amount and configuration are generated nonlinearly along the same landscape gradient (Dormann et al. 2013; Martínez-Lanfranco 2026). Additive models recover direct effects rather than total effects. Where habitat loss operates partly through configuration as an indirect pathway, the partial configuration coefficient underestimates the total ecological effect of fragmentation (Ruffell et al. 2016; Püttker et al. 2020).

Configuration variance must also exist across the sampled gradient. Fragmentation metrics exhibit constrained variability near the gradient extremes, where few configurations are geometrically possible. Percolation theory makes this mechanism explicit because the set of possible configurations changes nonlinearly with habitat amount (Gardner et al. 1987; With and Crist 1995; Neel et al. 2004; Fletcher et al. 2023). These geometry constraints correspond to the response-specific recoverability window summarized in Fig. 1. Metric choice must also be evaluated against the ecological process tested, because interventions that increase functional connectivity can be scored by simple configuration metrics as increased fragmentation even when they improve habitat reachability (Villard and Metzger 2014).

The specification condition operates at the level of model form. The linear interaction model is interpretable as a first-order summary only when curvature in the amount response, the fragmentation response, and the bivariate A–F surface has been evaluated. If either main-effect relationship is nonlinear, residual curvature can be absorbed by $\beta 3$, biasing the interaction estimate independently of genuine fragmentation conditionality (Pedersen et al. 2019; Tredennick et al. 2021). Diagnostic flexible models, including univariate smooths of Y against A and F and a bivariate smooth of Y across the A–F plane, can identify whether the linear interaction adequately summarizes the conditional surface before $\beta 3$ is interpreted mechanistically (Pedersen et al. 2019; Duncan and Kefford 2021).

3.3 The additive default as rational origin and present insufficiency

Each study that fits an additive fragmentation model is effectively estimating the fragmentation effect only around the part of the gradient it happens to sample. If the fragmentation effect varies with habitat amount, as all frameworks except the HAH predict, that local estimate depends on where on the gradient the study's landscapes are located. Studies positioned at different points on the gradient will therefore measure different tangent slopes and report different fragmentation effects, even when the underlying surface is the same.

When the fragmentation effect varies with habitat amount ($\beta 3 \neq 0$), the additive estimate of $\beta 1$ approximates the average of $\beta 1 + \beta 3 \cdot A$ over the sample's habitat-amount distribution. This quantity is a property of where the study's landscapes sit on the gradient, not a property of the ecology alone. A study sampling primarily low-cover landscapes will estimate a more negative average $\beta 1$ than an otherwise identical study sampling high-cover landscapes, even if the underlying surface is identical. Neither result is incorrect given its model. Both are uninformative about the shape of the surface.

This sampling artefact generates a testable prediction. If β3 ≠ 0, studies sampling different regions of the gradient should produce directionally different average fragmentation effects even when the underlying ecology is identical. The interaction model tests that prediction rather than assuming it. The debate's pattern of unresolved directional disagreement is consistent with this prediction. Better controls and larger samples within the additive framework have not resolved it. Recent theory and reanalysis show explicitly that the parameter space of fragmentation is constrained by total habitat amount, such that empirical scenarios often span only restricted portions of the attainable joint space and therefore recover local slopes rather than the full response surface (Zhang et al. 2024).

The additive specification was not adopted carelessly. It arose from legitimate concerns about collinearity. Fragmentation metrics and habitat amount covary in most landscape datasets, and separating their effects has been a central methodological preoccupation of the field (McGarigal and Cushman 2002; Ewers and Didham 2006; Smith et al. 2009). That preoccupation, however, addresses a different question from the one theory poses. Disentangling the independent effects of F and A is a problem of partial regression. Testing whether the effect of F changes as A changes is a problem of moderation. The field solved for the former and left the latter unaddressed. Adding an interaction between two correlated predictors amplifies collinearity and reduces precision, and for single-study datasets with limited cover range the interaction model may be underpowered (Dormann et al. 2013). These were real constraints that justified the additive default in an earlier data environment, and additive attempts to separate the effects of correlated predictors can also assign shared variance differently across parameterizations, causing their apparent importance to reverse (Koper et al. 2007; Smith et al. 2009).

That practical difficulty does not justify omitting the interaction test across all studies. The appropriate response is to accumulate multi-landscape datasets with adequate gradient coverage and to interpret null interaction results in relation to power and gradient breadth rather than as evidence of invariance by default. The historical rationale for the additive default does not extend to the current data environment, where multi-taxa, multi-landscape compilations spanning the full cover gradient are available (e.g., Zhang et al. 2024).

4. Translating mechanism into testable predictions

The four frameworks generate distinguishable predictions for the sign and shape of β3, the beta-diversity structure of communities, and the gradient position at which effects are expressed and recoverable. Together, these three signals provide the strongest basis for mechanism identification. β3 sign alone does not distinguish threshold from C–C, both of which predict β3 > 0, but it does distinguish extinction filtering, which uniquely predicts β3 < 0. Mechanism identification requires evaluating all three signals together. Even then, the results are diagnostic rather than determinative. Cases should remain ambiguous when multiple mechanisms generate overlapping signatures or when gradient coverage is limited. These limiting-case signatures are summarized in Table 1 and visualized as marginal-effect geometries in Fig. 2.

4.1 β3 sign and gradient shape as primary discriminators

The sign of β3 is the primary empirical clue, but it is not sufficient on its own (Table 1). The HAH uniquely predicts β3 = 0 (together with β1 = 0 at mean cover; Section 2.1). Extinction filtering uniquely predicts β3 < 0, and the fragmentation effect therefore intensifies as cover increases, reaching its maximum negative value where sensitive species remain. Threshold and C–C both predict β3 > 0 and are distinguished from each other not by β3 sign but by the sign of β1 at mean A, the beta-diversity component signatures, and the gradient position of recoverable effects. The HAH is compatible with an extinction threshold generated by habitat loss, but not with a fragmentation threshold generated by configuration, because HAH requires the fragmentation effect to remain near zero across the habitat-amount gradient.

Where the sample mean sits within the coexistence window, β1 is positive or near zero, the only case among the four frameworks in which fragmentation is ecologically beneficial or neutral at mean cover. Because β1 represents the fragmentation effect at the sample mean of A rather than at a fixed ecological reference point, its interpretation depends on where that mean lies relative to the coexistence window. Cross-study comparisons therefore require explicit reporting of gradient position or re-centering to comparable ecological reference points. β1 is a property of the sample as much as of the system.

This creates a specific inferential collapse under the dominant additive specification. Where a C–C system is sampled with its mean cover near the coexistence crossover, the fitted additive coefficient β_1 approaches zero, which is the same signature HAH produces by prediction. The two frameworks therefore become statistically indistinguishable under the additive model alone, even though they imply different ecological responses away from the sample mean. Null results for β1 at mean cover therefore do not discriminate HAH from C–C without further evidence, including explicit estimation of β3, beta-diversity decomposition, or evaluation of the fragmentation effect away from the sample mean.

Threshold and extinction filtering both yield negative β1 at mean cover but differ in β3 sign. Threshold predicts β3 > 0 (effects intensify as cover declines, concentrated below the connectivity threshold), whereas extinction filtering predicts β3 < 0 (effects intensify as cover increases, because sensitive species are still present in high-cover landscapes and vulnerable to isolation). Among the four limiting cases considered here, extinction filtering is the only framework predicting that fragmentation effects grow stronger as habitat becomes more abundant. Neither signal is accessible under the additive model.

At the species level, the extinction-filtering pattern (β3 < 0) has been documented in dynamic occupancy models of a threatened forest songbird (Hart and Bayne 2025). The C–C tradeoff pattern (β3 > 0 with sign reversal above approximately 20% habitat cover) has been documented in habitat selection of a farmland passerine across ten spatial scales (Bosco et al. 2021). Multi-taxon implementations recover several Table 1 signatures jointly. A Swedish forest analysis fitted 163 forest-associated plant taxa using an aggregation index. Ninety-five taxa showed no significant configuration effect or interaction, 33 showed gradient-invariant negative fragmentation effects, and 4 showed gradient-invariant positive effects. Among 31 taxa with a significant forest area × configuration interaction, 19 recovered β3 > 0 consistent with the threshold signature, 8 recovered a β3 > 0 pattern consistent with C–C sign reversal, and 4 showed a positive high-cover effect only (Lehtilä et al. 2020). Species richness recovered the threshold pattern, while extinction filtering was not over-represented. Forest amount fitted jointly with two configuration metrics across 70 eastern Ontario landscapes yielded metric-specific surfaces. Patch-number fragmentation showed little interaction with forest amount, whereas wooded-corridor connectivity showed a sign-reversing interaction, increasing biodiversity at low forest amount and decreasing it above approximately 30–40% (Daly et al. 2025). β3 therefore expresses different conditional surfaces along both the taxon axis within a community and the metric axis within a pooled response.

The empirical literature on the cover × fragmentation interaction is therefore not convergent on a single result. Studies recovering negative-and-fading β3 (Hart and Bayne 2025; Betts et al. 2017; Hua et al. 2024), positive-and-sign-reversing β3 (Bosco et al. 2021; Zhang et al. 2024), threshold-consistent β3 (Smith et al. 2011), and joint-signature heterogeneity within single datasets (Lehtilä et al. 2020; Daly et al. 2025) document conditional response surfaces. Studies reporting null β3 (Trzcinski et al. 1999; Watling et al. 2020) document either HAH-consistent invariance, recoverability-window failure under the response–scale–metric–taxon combination tested, or partial-identification artefacts (Sections 3.2 and 3.3). The empirical task the framework specifies is the joint distribution of β3 sign, gradient shape, β1 at mean cover, gradient coverage, beta-diversity decomposition, and assemblage filtering history, reported across response variables and configuration axes within each system and aggregated across systems.

A parallel heterogeneity–diversity literature makes a related point from the opposite direction. Increasing heterogeneity can promote richness through niche diversification, but subdivision can reduce richness when effective area per condition becomes limiting (Allouche et al. 2012; Ben-Hur and Kadmon 2020; Laanisto et al. 2013). The geometric convergence is adjacent rather than mechanistic. The same conditional logic appears in both traditions, with subdivision effects depending on where the system sits along an amount and persistence axis.

Beyond the sign of β3, the shape of the conditional surface provides additional discrimination. Threshold theory predicts a near-flat surface at high cover that bends sharply negative below the threshold, a nonlinear, step-structured change that the linear interaction term approximates poorly and that generalized additive or hierarchical threshold models are better positioned to detect. The C–C framework predicts a more gradual sign reversal across the gradient. Extinction filtering predicts a surface that declines monotonically but with a slope that weakens as cover decreases. For threshold detection specifically, flexible response-surface models, including generalized additive or hierarchical threshold models, are better suited than a single linear interaction term (Pedersen et al. 2019).

4.2 Beta-diversity as a secondary discriminator

Because beta diversity is an emergent property of assembled multi-species communities, decomposition into turnover and nestedness components is available as a secondary discriminator wherever community-level data are present (Baselga 2010; Legendre 2014; Rybicki et al. 2020; Betts et al. 2019). Under the C–C tradeoff, landscape-scale diversity benefits arise from compositional differentiation among patches, expressed as turnover. Large patches support competitive dominants, small patches support strong colonizers, and the landscape mosaic maintains both. Turnover should therefore be elevated in fragmented landscapes at intermediate-to-high cover, where the coexistence window is open, and should decline at low cover as competitive dominants are globally lost. Nestedness, reflecting species loss rather than replacement, should increase at low cover as extinction progresses.

Under extinction filtering, turnover among patches should be weak across all cover levels, because the community is dominated by matrix-tolerant generalists whose occurrence patterns reflect dispersal capacity rather than competitive hierarchy (Betts et al. 2019). Nestedness should increase at mid-to-high cover, where filtering is underway but not complete. The sign of β3 for the turnover component provides corroborative contrast between C–C (positive β3 for turnover) and extinction filtering (near-zero or negative β3 for turnover), although the strength of this contrast depends on gradient coverage, sampling completeness, richness gradients, and the decomposition used. These components are not independent of richness gradients, so beta-diversity signatures should be interpreted alongside richness, sampling completeness, and gradient coverage (Baselga 2010; Legendre 2014; Anderson et al. 2011). These signatures should be reported alongside the corresponding richness response, because a turnover increase from coexistence, a nestedness increase from filtering, and a dissimilarity increase driven by local richness loss are not equivalent conservation signals even when each increases some measure of beta diversity (Anderson et al. 2011; Socolar et al. 2016).

For extinction filtering specifically, Baselga's nestedness-resultant component operationalizes the mechanism's prediction more precisely than richness-difference formulations (Baselga 2010; Legendre 2014). Nestedness-resultant quantifies the degree to which compositional differences arise from one community being a proper subset of another, whereas richness-difference formulations detect any count asymmetry between communities without requiring that subset structure.

4.3 The recoverability window

Conditional fragmentation effects are empirically recoverable only where the focal response remains biologically sensitive to configuration and the sampled landscapes provide enough configuration contrast to estimate that sensitivity. These conditions are response-specific and may shift with taxon, spatial scale, matrix permeability, fragmentation metric, and landscape-generation process. Continental analyses confirm that maximally fragmented configurations are structurally achievable only in low-cover landscapes, because high-cover landscapes retain most habitat in a single dominant patch regardless of sampling design (Rueda et al. 2013). For threshold dynamics, the configuration-sensitive window W_R spans the gradient between ET_R and FT_R. Above FT_R configuration effects are weak because habitat remains functionally connected. Below ET_R sensitive taxa may no longer persist. Within W_R, β3 is most likely to be recoverable, but configuration variability peaks at intermediate habitat amounts and collapses at very low cover (Andrén 1994; Hanski 2015). The C–C sign reversal requires observations spanning both high and low cover to detect the full slope transition (Rybicki et al. 2020; Zhang et al. 2024). Extinction filtering effects are detectable at mid-to-high cover, before filtering is complete, and collapse at low cover where the signal species have been lost (Betts et al. 2019).

Scale dependency of the recoverability window itself is a source of null results. The interaction is recoverable only where F and A are measured at the scale at which the taxon responds to configuration; 44% of species in a global review had their scale of effect at the extreme of the range evaluated, indicating the true scale was not measured (Jackson and Fahrig 2015). The interaction has been detected at territory and home-range scales but becomes non-significant at broader landscape scales in both boreal songbirds and farmland passerines (Hart and Bayne 2025; Bosco et al. 2021). It can also reverse sign across scales, with negative effects at landscape scale and positive effects at local scale in a marbled murrelet occupancy analysis (Valente et al.

2023b). Matrix quality also modulates the recoverability window. Low-quality matrices intensify habitat-loss filtering, while higher-quality matrices relax filtering through mass effects and resource supplementation (de Souza Leite et al. 2022).

For movement-mediated mechanisms specifically, the recoverability window may peak at intermediate rather than lowest habitat amounts, where patches exceed local viability thresholds, but isolation still limits colonization. At very low cover, local habitat sufficiency can become the binding constraint, and the marginal effect of connectivity can collapse regardless of isolation (Villard and Metzger 2014).

A study restricted to a narrow gradient range may produce a null or weakly significant β3 not because the interaction is absent, but because the sample does not span the gradient region where it operates. Characterizing the cover distribution of the sample is therefore necessary context for interpreting any null interaction. This includes the range, mean, and representation across the low-cover gradient where threshold and filtering mechanisms operate. A non-significant β3 from a study spanning the full gradient, combined with $\beta1 \approx 0$ at mean cover, narrow confidence intervals, and adequate power, constitutes genuine support for the HAH. A non-significant β3 from a study restricted to high-cover landscapes is uninformative about threshold predictions and cannot be presented as resolving the debate. Cover-restricted analyses can still test local mechanism-specific predictions, but they cannot estimate the full conditional response surface or resolve the debate-level question (Villard and Metzger 2014; Betts et al. 2019). Apparent null fragmentation coefficients can arise from configuration invariance under the HAH, reachability saturation above FT_R, response collapse below ET_R, or cancellation, insufficient configuration contrast, or a flat local surface inside W_R.

Existing syntheses and experiments test different inferential targets. Species-density interaction tests aggregated across studies (Watling et al. 2020) estimate an average interaction coefficient at the alpha-diversity scale, independent of gradient-position effects and of beta-diversity decomposition (Section 4.2). Sign-counting reviews (Fahrig 2017) aggregate across response variables, mechanisms, and gradient positions without estimating any specific β3. Controlled fragmentation experiments with temporal resolution (Haddad et al. 2017a) estimate configuration effects on species–area relationships at specific amount-configuration contrasts and reveal the temporal dynamics of extinction filtering as it unfolds (Section 2.4), a signal that cross-sectional designs cannot directly observe. The full conditional response surface locates each of these inferential targets and clarifies what β3 captures. Their apparent disagreements reflect partial characterization by each design rather than irreconcilable findings about whether configuration matters.

5. Four informative outcomes

The four outcomes below define inferential conditions rather than analytical prescriptions. They identify the minimum evidential standard for contributing to the debate and the circumstances under which the predictions can be distinguished in data.

Outcome 1. $\beta3$ significantly $\neq 0$ with adequate gradient coverage and power. The data support a conditional fragmentation effect, and the response surface is therefore not flat along the fragmentation axis. Evaluate direction and functional form against Table 1, using β1 at mean A and the beta-diversity signatures to identify which framework is most consistent with the data. Where $\beta3 > 0$ and β1 is negative, threshold dynamics are consistent. Extinction filtering is not supported as the dominant mechanism, although mixed filtering-plus-threshold systems remain possible and should be evaluated using beta-diversity signatures and assemblage history. Where β3 < 0 and β1 is negative, extinction filtering is consistent. Confirmation requires nestedness at mid-to-high cover and absence of turnover elevation. Where β3 > 0 and β1 is positive or near zero, C–C tradeoff is consistent, subject to gradient position and turnover signatures. The result is diagnostic rather than causal proof. It identifies patterns consistent with mechanisms but does not assign exclusive causation where multiple processes generate overlapping signatures.

Outcome 2. β1 ≈ 0 at mean cover and β3 ≈ 0 with narrow confidence intervals, adequate gradient coverage, and sufficient power. This constitutes genuine empirical support for the HAH at the spatial scale and taxonomic group analyzed. Because the interaction framework nests all competing hypotheses within the same statistical model, evidentiary standards must be applied symmetrically. Strong support for any framework requires gradient coverage spanning the recoverability windows of all competing frameworks, sufficient statistical power to detect biologically plausible interaction effects, and consistency of the β3 signature across richness and beta-diversity components. For HAH specifically, this means β1 ≈ 0 at mean cover and β3 ≈ 0 at the richness level with narrow confidence intervals under these conditions. Where community composition data are available, the same absence of configuration-driven conditionality should also hold for turnover and nestedness components, distinguishing genuine ecological invariance from a failure to detect conditionality.

A boundary case distinct from Outcome 2 arises when β3 ≈ 0 with narrow confidence intervals but β1 is detectably non-zero. HAH is rejected because it requires both restrictions simultaneously. None of the three conditional frameworks applies, since threshold, C–C tradeoff, and extinction filtering all predict β3 ≠ 0. The result identifies configuration as consequential but gradient-invariant within the sampled range. It should be reported as such and not conflated with Outcome 2. The 33 plant taxa in Lehtilä et al. (2020) with significant negative fragmentation main effects and no significant interaction exemplify this outcome.

Outcome 3. β3 ≈ 0 with wide confidence intervals, restricted gradient coverage, or insufficient power. β3 carries information only when reported with uncertainty and interpreted in relation to gradient coverage and sensitivity to biologically plausible conditional effects. This outcome is inconclusive. The fragmentation effect may be genuinely invariant across the gradient. Opposing conditional effects may cancel at the sample mean, leaving β1 near zero even when β3 is large. The gradient may also be sampled too narrowly to detect an interaction operating elsewhere. These are fundamentally different ecological conclusions, and an additive model cannot distinguish between them. The result is interpretable only in the context of gradient characterization and sensitivity assessment, and should not be presented as resolution of the debate. A fourth possibility arises when the sample mean lies near the zero-crossing of the conditional fragmentation effect, the C–C coexistence-to-isolation transition. In that case, β1 will be near zero even when β3 is large and ecologically meaningful. This is the sampling artefact of §3.3 at a specific gradient position. Beta-diversity decomposition provides the diagnostic, with turnover revealing the C–C signal even when richness cancels near the mean.

Outcome 4. β3 inconclusive with a significantly negative β1. A detectably negative mean fragmentation effect exists at the sample mean of habitat amount, but the dataset cannot resolve whether that effect intensifies, reverses, or fades along the cover gradient. Where design, scale, and predictor-geometry conditions are adequate for interpreting β1, this outcome rejects the

HAH, which requires both β1 ≈ 0 and β3 ≈ 0. It should not be reported as inconclusive in the sense of uninformative. The interaction model has revealed that fragmentation is harmful on average under the realized gradient conditions, while leaving the shape of that effect unresolved. The appropriate conclusion is that conditionality remains unresolved rather than absent, and that the correct remedies are wider gradient coverage, larger sample size, or beta-diversity decomposition rather than abandonment of the conditional framework. Treating this outcome as equivalent to Outcome 3 collapses a distinction the framework is specifically designed to preserve. All four outcomes advance the debate. Only omission of the interaction test, or conflation of Outcome 3 with the β1-negative subcase, preserves stasis.

6. Implications for fragmentation research

Long-term fragmentation datasets contain the raw material for the first test. Re-analyses that estimate β3 with explicit characterization of gradient coverage would establish, without new data, how many published null results are uninformative rather than ecologically invariant. New designs should prioritize landscapes spanning the recoverability window each framework predicts (Section 4.3) rather than those optimized for predictor decorrelation alone. Decorrelating predictors across too narrow a cover range estimates β3 on a sample that cannot distinguish the framework-specific predictions. Community-level analyses should report β3 sign and gradient shape and, where community composition data allow, beta-diversity decomposition. These quantities allow framework-specific signatures to be recovered jointly rather than conflated under an aggregate effect (Section 4.2).

These design and reporting reforms address a problem that has been institutionalized in empirical practice. Recent design-level critique reaches the same conclusion in the specific context of amount-controlled fragmentation inference, showing that habitat amount control is necessary, but not sufficient, unless predictor separability is demonstrated in the realized dataset (Martínez-Lanfranco 2026). Independent audits across more than two decades confirm that the proportion of fragmentation studies separately testing configuration and amount has remained low, with stricter separability criteria rarely met in earlier reviews and the weaker “control for habitat amount” criterion satisfied by approximately one in five studies in more recent ones (McGarigal and Cushman 2002; Hadley and Betts 2016; Riva et al. 2024). The reanalysis programme above is therefore a remediation of accumulated practice as much as a prospective agenda.

The reframing extends the existing call for theory investigation (Valente et al. 2023a) by identifying the conditional quantity along which the competing theoretical predictions are defined, treating it not as one source of variance among contextual moderators but as the organizing axis of the inferential target. Whether subdivision of remaining habitat is expected to harm, benefit, or leave unaffected a focal assemblage depends on where that landscape sits along the habitat-amount gradient and which response-surface geometry its community reflects. Minimum-patch-size thresholds and connectivity priorities for reserve design and restoration may therefore differ not only across taxa but across positions on the gradient. Additive models cannot recover this dependence, whereas the interaction framework makes it directly estimable (Riva and Fahrig 2022, 2023; Fahrig et al. 2021). To our knowledge, no published multi-taxon implementation has yet demonstrated the full discriminatory potential of this approach by jointly estimating β3 signatures, beta-diversity components, gradient-position diagnostics, and metric–mechanism contrasts across multiple taxa and landscapes. Such a test is the most direct route from conceptual reframing to empirical resolution.

7. Conclusions

The fragmentation debate is about the shape of the biodiversity response surface, not the sign of a single coefficient. Competing theories make predictions about how fragmentation effects vary across the habitat-amount gradient, not only about whether one average configuration effect exists. Analyses that sample different parts of the gradient or constrain the fragmentation effect to be invariant across it need not converge on the same answer even when the underlying ecology converges.

The field has had the necessary analytical components for decades. The threshold logic was established early on (Andrén 1994). The interaction implication was stated directly soon after (Fahrig 2003). Configuration sensitivity was later placed along the habitat-amount gradient, and recent work has shown habitat-amount-constrained fragmentation domains and slope reversals (Villard and Metzger 2014; Zhang et al. 2024). The persistence of the debate reflects a translation failure. Theoretical predictions were repeatedly formalized, but statistical practice repeatedly omitted their operationalization (Haddad et al. 2017b; Valente et al. 2023a; Didham et al. 2012). In its most compressed form, the problem is that dominant empirical practice has estimated $\beta 1$, the fragmentation effect at the sample mean of cover, where theory predicts conditionality. In the linear model, $\beta 3$ summarizes that conditionality as the rate at which the fragmentation effect changes along the habitat gradient.

Null results require a higher evidential standard. A non-significant main effect of fragmentation in an additive model is not evidence that fragmentation has no effect on biodiversity. It is evidence that the average slope of the response surface at mean cover in that sample is not distinguishable from zero, a local and gradient-dependent quantity. Whether this reflects genuine ecological invariance (flat surface), a mispositioned sample on the gradient (non-flat surface sampled away from the active region), extinction filtering (signal species lost), or predictor geometry cannot be determined without estimating $\beta 3$, characterizing the cover gradient, and assessing assemblage composition. To our knowledge, this is the first synthesis to organize the habitat amount hypothesis, threshold/scarcity dynamics, colonization–competition coexistence, and extinction filtering around a common conditional inferential target. In the linear interaction model, β_3 formalizes that target as the rate at which the fragmentation effect changes along the habitat-amount gradient. This synthesis derives the distinguishable gradient predictions each framework makes and specifies the statistical structure needed to distinguish them empirically. That connection between theoretical prediction and empirical practice is what has been missing from the debate.

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Table 1. Limiting-case predictions of four fragmentation frameworks for the conditional fragmentation effect along the habitat-amount gradient. β1 is the fragmentation effect at the sample mean of habitat amount. Its interpretation depends on where that mean lies relative to the response-specific threshold, coexistence crossover, or filtering window. β3 is the fragmentation × habitat amount interaction and describes how the fragmentation effect changes as habitat amount increases. A positive β3 means the effect becomes less negative, or reverses to positive, as cover increases. A negative β3 means the fragmentation effect becomes increasingly negative as cover increases. Recoverability windows indicate where each mechanism is both biologically expressed and empirically recoverable. ET_R, FT_R, and W_R denote the response-specific extinction threshold, fragmentation threshold, and configuration-sensitive window, respectively. In systems where multiple mechanisms co-occur, the observed β3 sign depends on which gradient region dominates sample variance, and ambiguity in mechanism identification should be reported. C–C denotes colonization–competition coexistence. F is coded so that higher values indicate greater fragmentation per se. Analysts using aggregation-based metrics should invert them before fitting or read predicted β signs and curve directions as reversed. Beta-diversity predictions apply to community-level implementations. Population-level applications should interpret the corresponding mechanisms through occupancy, abundance, or demographic responses.

Framework	**β1 (F at mean A)**	**β3 (F × A interaction)**	**Recoverability window**	**Beta-diversity prediction**
Habitat amount hypothesis (HAH)	= 0 no effect at mean cover	= 0 invariant across gradient	Full sampled gradient. Support requires β1 ≈ 0 and β3 ≈ 0 with adequate power, gradient coverage, and configuration contrast across the relevant response-specific range	No configuration-driven turnover or nestedness shift once habitat amount is controlled.
Threshold / scarcity	< 0 negative effect at mean cover	> 0 effect weakens as cover increases	Between ET_R and FT_R. Often low-to-intermediate cover, but position depends on landscape-generation process, matrix permeability, species traits, spatial scale, and response variable	Nestedness may increase within the lower portion of WR as persistence becomes limited. Turnover is not expected to be elevated at high cover.

Metacommunity C–C tradeoff sign reversal	> 0 or ≈ 0 neutral to positive at mean cover	> 0 effect becomes more positive as cover increases, producing sign reversal	Requires sampling across the response-specific coexistence crossover within W_R. The positive high-cover limb occurs inside the configuration-sensitive domain, not above FT_R	Turnover elevated at intermediate-to-high cover when the coexistence window is open. C–C is identified jointly by $\beta1 \approx 0$ and elevated turnover at high cover
Extinction filtering	< 0 negative effect at mean cover	< 0 effect intensifies as cover increases, reaching its most negative at high cover	Mid-to-high cover or any region where sensitive taxa remain. The signal fades after species-specific ET_R crossings accumulate and filtering is complete	Nestedness increases at mid-to-high cover, while turnover remains weak or absent. $\beta3 < 0$ is the unique signature distinguishing extinction filtering from threshold and C–C, both of which predict $\beta3 > 0$

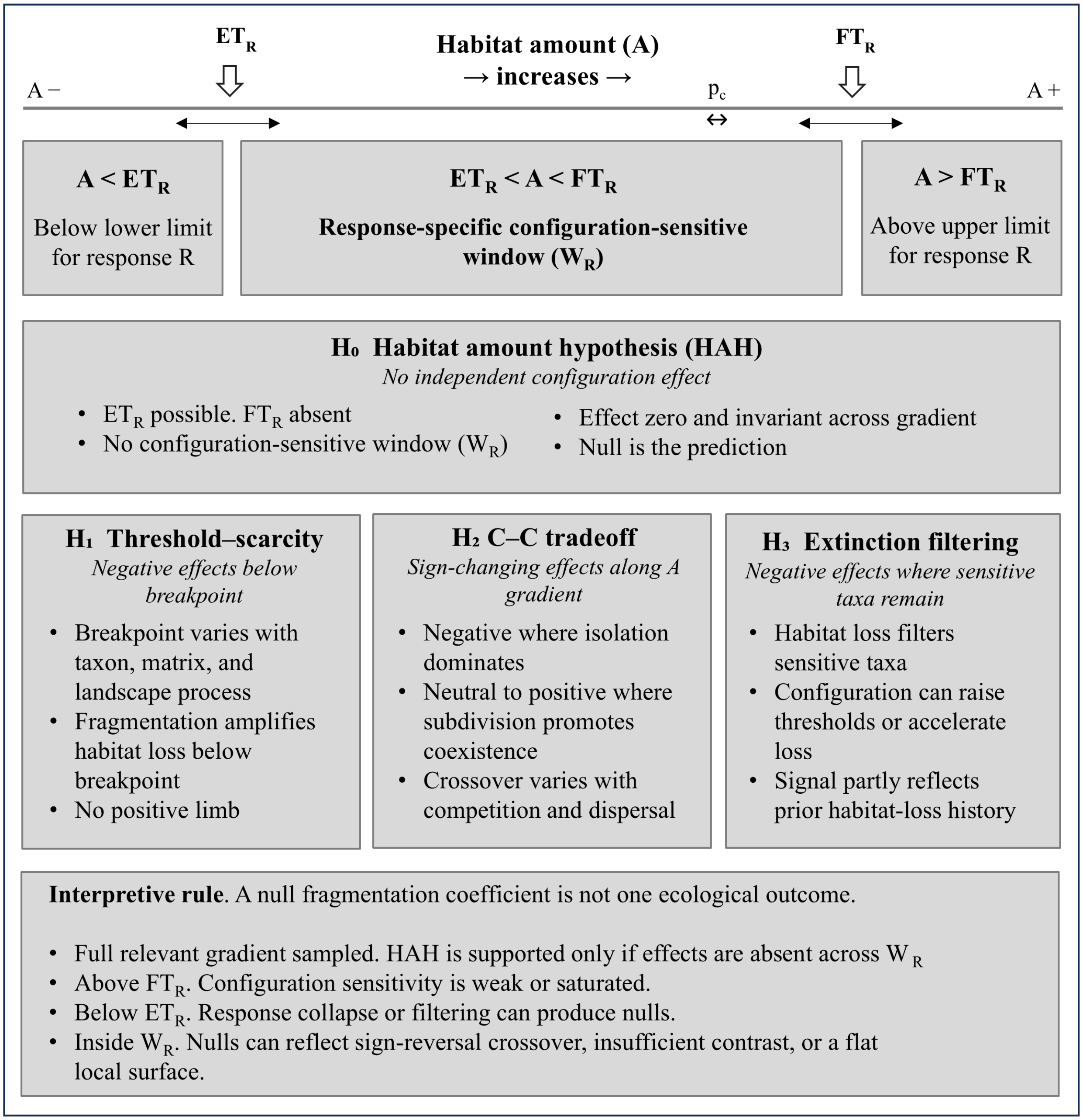

Figure 1. Conceptual response-surface framework for four competing fragmentation theories. The top panel defines regions along the habitat-amount axis. ETR is the lower persistence boundary, FTR is the upper configuration-saturation boundary, and WR is the response-specific configuration-sensitive window between them. pc marks a structural percolation threshold that can help determine FTR but is not equivalent to it. H_0 denotes the habitat amount hypothesis, H_1 threshold/scarcity, H_2 colonization–competition coexistence, and H_3 extinction filtering. H_0 predicts no configuration-sensitive window because configuration effects are invariant once habitat amount is controlled. H_1 predicts negative effects in the lower portion of WR, strongest where the response persists. H_2 predicts sign-changing effects within WR. H_3 predicts negative effects strongest where sensitive taxa remain, fading as assemblage composition simplifies. Boundaries are schematic and vary with response variable, taxon, spatial scale, matrix,

configuration metric, and landscape-generation process. The bottom panel shows when null additive fragmentation coefficients can reflect gradient position rather than ecological invariance. The statistical translation of these canonical cases appears in Fig. 2.

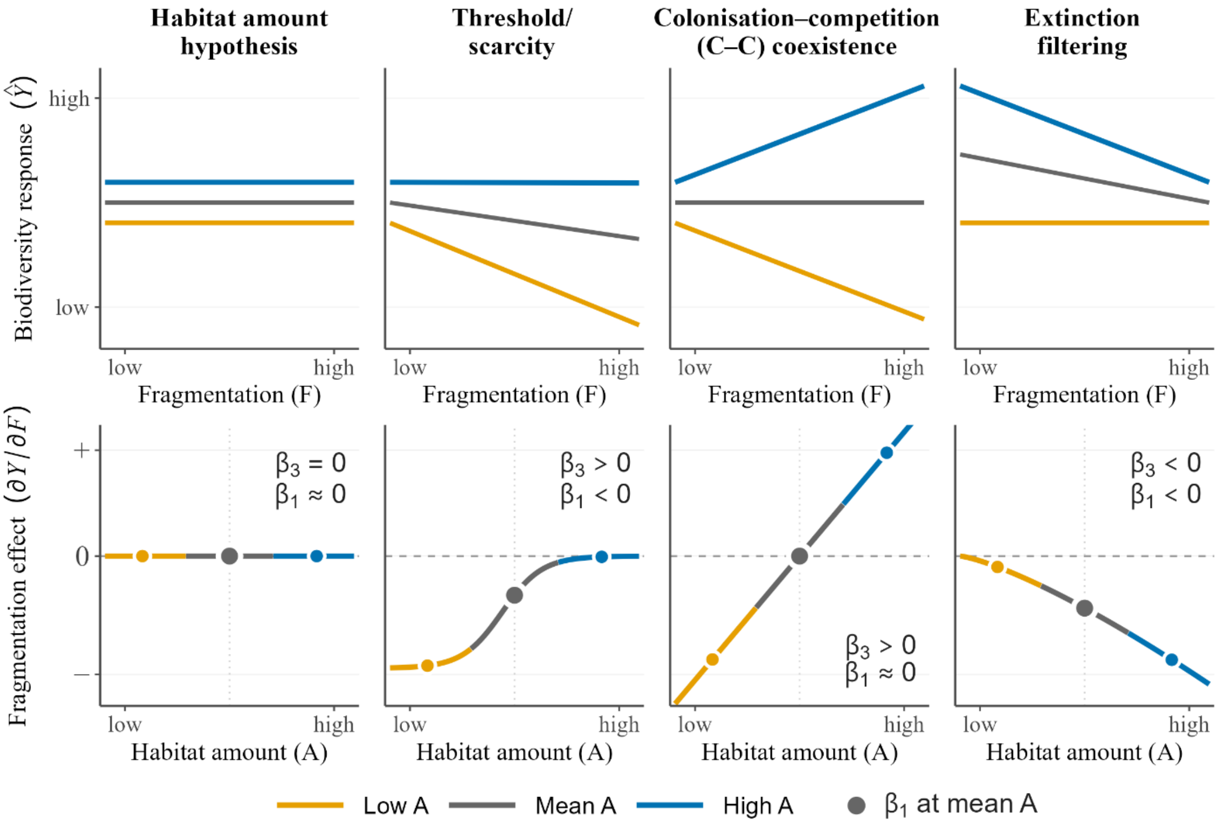

Figure 2. Statistical translation of the canonical alternatives in Fig. 1. The top row shows schematic response-scale biodiversity predictions ($\hat{Y}$) against fragmentation at low, mean, and high habitat amount. The bottom row shows the corresponding marginal fragmentation-effect functions, $\partial Y/\partial F = \beta_1 + \beta_3 A$, on the model scale. Open circles mark β_1, the fragmentation effect at mean habitat amount and the quantity estimated by additive models. Curve direction represents β_3. HAH predicts a near-zero effect across the gradient. Threshold/scarcity predicts negative effects that weaken as cover increases. C–C tradeoff predicts a sign reversal. β_1 can approach zero when mean A lies near the coexistence crossover, making C–C and the HAH indistinguishable in additive models alone unless β_3 is estimated and shown to be positive. Extinction filtering predicts stronger negative effects at higher habitat amounts, where sensitive taxa remain, and weaker effects at lower amounts as those taxa are progressively lost. Curves are schematic limiting cases, not fitted estimates. In non-identity-link models, the top row uses back-transformed predictions, whereas the bottom row remains on the link scale where $\beta_1 + \beta_3 A$ is defined. F is coded so that higher values indicate greater fragmentation per se. Analysts using aggregation-based metrics should invert before fitting or read predicted β signs and curve directions as reversed.