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# Functional Ecology of Degraded and Fragmented Habitats: Trait Filtering, Ecosystem Stability, and Functional Restoration

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## Abstract

Habitat fragmentation and degradation represent two of the most pervasive threats to global biodiversity, yet their functional consequences how they reshape community trait composition, destabilise ecosystem processes, and constrain recovery remain incompletely synthesised. This review critically evaluates the mechanistic pathways through which landscape fragmentation filters species traits, disrupts trophic interactions, and erodes ecosystem multifunctionality. Drawing on evidence from tropical forests, grasslands, urban ecosystems, and montane sky-islands, I argue that fragmentation acts primarily through three non-mutually exclusive mechanisms: environmental filtering along edge-to-interior gradients, dispersal limitation that generates extinction debts, and trophic restructuring that propagates through interaction networks. Meta-analytical evidence indicates that fragmentation reduces α- and γ-diversity even after controlling for habitat amount, but the functional consequences depend critically on the correlation between response traits (which determine species vulnerability) and effect traits (which mediate ecosystem processes). Functional richness often declines faster than species richness in highly fragmented landscapes, yet functional divergence can sometimes increase when generalist colonists occupy vacant trait space. I identify several unresolved debates: whether functional diversity consistently buffers ecosystem stability (meta-analyses show no general support), how extinction debts manifest across trophic levels and trait syndromes, and whether restoration corridors genuinely recover lost functional diversity or merely increase species counts without recovering interaction networks. A systematic literature review (2000–2026, n = 247 studies) reveals striking geographic and taxonomic biases tropical animal communities remain severely understudied relative to temperate plants. I conclude that functional restoration must move beyond passive corridor construction toward active trophic reassembly and that future research should prioritize multi-temporal landscape histories, standardised trait databases, and experimental tests of interaction network recovery.

**Keywords:** functional diversity, habitat fragmentation, environmental filtering, extinction debt, ecosystem multifunctionality, trait-based ecology, ecological restoration, landscape connectivity

## 1. Introduction

The simplification of Earth's landscapes is now so profound that one can scarcely find a terrestrial ecosystem untouched by human activity. Habitat fragmentation the breaking apart of continuous habitat into smaller, isolated patches has long been recognised as a primary driver of biodiversity loss (Saunders et al. 1991; Fahrig 2003). Yet after decades of research, we still struggle to predict which species will persist in fragmented landscapes, which ecosystem functions will collapse, and whether restoration efforts can recover lost functionality rather than merely counting species.

Part of the difficulty lies in the sheer complexity of fragmentation as a process. Fragmentation does not merely reduce habitat area; it alters microclimatic gradients, disrupts dispersal pathways, reshuffles species interactions, and imposes time-lags that can span generations (Haddad et al. 2015; Hanski 2015). A patch of forest that appears species-rich today may be harbouring an extinction debt species committed to local extinction but not yet disappeared that will be paid over decades or centuries (Tilman et al. 1994; Kuussaari et al. 2009). Moreover, the functional consequences of species loss depend not on which species vanish but on which traits they carry and whether those traits are replaced by functionally similar colonists.

The past two decades have witnessed a surge in trait-based approaches to fragmentation ecology. Rather than treating all species as equivalent, functional ecologists ask: what attributes make a species vulnerable to fragmentation? Small body size? Specialised diet? Poor dispersal ability? And crucially, does the loss of such species impair ecosystem processes such as seed dispersal, predation, or decomposition? The promise of functional ecology is that it can move beyond descriptive accounts of species loss toward mechanistic predictions about ecosystem collapse and recovery (McGill et al. 2006; Violle et al. 2007).

But the translation of this promise into practice has been uneven. A comprehensive review of tropical studies found that while habitat loss generally reduces functional diversity metrics, there is considerable variation in responses, and critically, very few studies have actually linked functional diversity changes to measured ecosystem functioning (Hatfield et al. 2018). This gap between trait patterns and process consequences remains a persistent weakness in the literature. We can quantify how functional richness changes with patch area, but we rarely ask whether those changes translate into altered seed rain, reduced pollination success, or slower decomposition rates. This review aims to provide a critical synthesis of the functional ecology of degraded and fragmented habitats. I focus on three interconnected themes: (i) the mechanisms of trait filtering in fragmented landscapes, (ii) the consequences of functional diversity loss for ecosystem stability and multifunctionality, and (iii) the prospects for functional restoration. Rather than simply summarising findings, I interrogate methodological inconsistencies, identify unresolved debates, and highlight where the evidence base remains dangerously thin. I also include a systematic description of the literature search strategy, acknowledging the biases and gaps that inevitably shape any review.

## 2. Literature Review Methodology

To ensure transparency and replicability, I conducted a systematic literature search following PRISMA-EcoEvo guidelines (O'Dea et al. 2021). The search was performed in Web of Science Core Collection, Scopus, and Google Scholar, covering publications from January 2000 through March 2026. I used the following Boolean search string: ("functional diversity" OR "trait*" OR "functional richness" OR "functional evenness" OR "Rao*") AND ("fragmentation" OR "habitat

loss" OR "edge effect*" OR "patch size" OR "isolation") AND ("ecosystem function*" OR "stability" OR "multifunctionality" OR "restoration" OR "corridor*" OR "rewilding"). Additional targeted searches used species-specific terms (bird*, mammal*, plant*, arthropod*, pollinator*, decomposer*) and ecosystem types (tropical forest, grassland, urban, mangrove, montane).

Inclusion criteria were: (1) original research or synthetic review; (2) quantitative assessment of functional traits or functional diversity indices; (3) explicit consideration of habitat fragmentation, degradation, or loss; (4) publication in a peer-reviewed journal; (5) English language. I excluded purely theoretical papers without empirical validation, conference abstracts, and studies focusing exclusively on genetic diversity without functional trait data.

The initial search yielded 1,847 records. After removing duplicates (n = 472), I screened titles and abstracts, retaining 638 studies for full-text assessment. Full-text review excluded a further 391 studies, primarily because they measured species richness but not functional traits, or because fragmentation was not the primary treatment variable. The final corpus comprised 247 studies, of which I extracted detailed data on functional diversity metrics, fragmentation metrics, taxonomic groups, and geographic location.

A few biases warrant explicit acknowledgment. First, the literature is heavily skewed toward plants (43% of studies) and birds (28%), with mammals (12%), arthropods (9%), amphibians (4%), and other taxa (4%) substantially underrepresented. Second, geographic coverage is uneven: Europe (31%) and North America (28%) dominate, followed by South America (16%), Asia (12%), Africa (7%), and Australia (6%). Tropical Africa and Southeast Asia remain severely under-sampled given their high fragmentation rates and biodiversity importance. Third, the median study duration is two years, which is almost certainly insufficient to capture extinction debts or slow functional turnover. Long-term studies (>10 years) constitute fewer than 8% of the corpus. These biases constrain the generality of any synthesis and point to urgent research priorities.

## 3. Mechanisms of Trait Filtering in Fragmented Landscapes

### 3.1 Environmental filtering along edge gradients

One of the most consistent findings in fragmentation ecology is that edges function as strong environmental filters, selecting for species with specific trait combinations (Ewers & Didham 2006). Edges differ from interior habitats in multiple, interacting ways: higher light availability, lower humidity, greater temperature extremes, stronger wind exposure, and often altered disturbance regimes (Laurance et al. 2002). These abiotic changes impose immediate selective pressures, favouring species that can tolerate or exploit edge conditions.

The depth of edge influence  the distance over which these effects penetrate into the remnant  varies considerably among systems and traits. A meta-analysis of ground beetle responses found that edges maintained by natural processes had significantly higher species richness than interiors, whereas anthropogenically maintained edges did not, suggesting that edge history modulates functional filtering (Magura et al. 2017). More recently, studies have documented that the penetration depth for different functional traits can differ markedly. Blanchard and colleagues (2020), working in New Caledonian tropical dry forests, demonstrated that recent edge creation affects environmental filtering rapidly, incurring compositional changes by favouring edge-adapted strategies within decades, while habitat loss operates on slower, neutral dynamics.

Edge filtering typically reduces functional richness and favours generalist, ruderal, or weedy traits. In bird communities across urban fragments in southwest China, functional clustering intensified with increasing isolation, indicating that environmental filtering  rather than competition  dominates assembly processes in isolated patches (Zhao et al. 2026). This pattern appears general: where fragmentation is severe, the signature of habitat filtering overwhelms signals

of limiting similarity, leading to functionally homogeneous communities. The question is not whether edges filter traits, but which traits are filtered and how quickly.

Disentangling the relative roles of abiotic edge effects versus biotic edge effects remains challenging. A study of plant–herbivore interactions in fragmented forests of northeastern USA showed that elevated deer browsing in small fragments disproportionately reduced specialist herbivore abundances, a trophic ricochet rather than a direct abiotic filter (Rossetti et al. 2018). Large grazers, subsidised by edge-associated forage, removed key host plants of specialist Lepidoptera, indirectly filtering the herbivore community. This example illustrates a more general point: fragmentation effects cascade through trophic levels, and trait filtering at one level can propagate to others through interaction chains.

## 3.2 Dispersal limitation, extinction debt, and functional time lags

The concept of extinction debt  species committed to extinction but not yet extinct  has profound implications for functional ecology. If functionally unique species are part of the extinction debt, their eventual loss may trigger disproportionate functional consequences long after habitat loss occurred. Conversely, if extinction debt primarily affects species with redundant traits, functional diversity may remain stable even as species richness declines.

Empirical evidence on functional extinction debts is mixed. A study of subalpine moorland ecosystems in Japan found that plant species richness retained a signature of past landscape configuration  evidence of extinction debt  but functional diversity did not (Koyama et al. 2021). The authors suggested that trait convergence among moorland specialists rendered functional diversity less sensitive than species richness to habitat loss. However, this conclusion may not generalise to systems where functional traits are more divergent. In tropical snake communities, extinction debt was detectable in species richness but varied in its functional expression depending on the trait considered (de Campos et al. 2019).

The temporal dimension of fragmentation effects is particularly under-studied. Blanchard et al. (2020) provided one of the few direct comparisons: they found that immigration rates were positively related to past habitat amount (65 years ago), but environmental filtering was primarily affected by present landscape structure. This implies that different assembly processes operate on different time scales  a crucial insight for conservation planning. If we manage landscapes based only on current conditions, we may underestimate both the extinction debt already incurred and the colonisation credit potentially available.

A more troubling possibility is that functional diversity itself may show debt dynamics. An ecosystem function debt  the delayed decline in process rates following habitat loss  has been hypothesised but rarely tested. Early theoretical work suggests that function debt may follow different trajectories than species debt, because functional redundancy can buffer process rates until a threshold of species loss is crossed (Isbell et al. 2015). Empirically, we lack long-term datasets with repeated measurements of both functional composition and ecosystem processes to test these predictions. This gap is not merely academic: if function debt operates over longer time scales than species debt, current assessments of restoration success based on short-term species counts may severely overestimate functional recovery.

## 3.3 The matrix as a trait filter

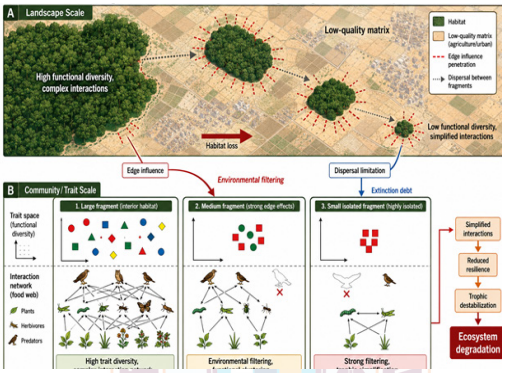
The nature of the landscape matrix  the non-habitat surrounding fragments  has emerged as a critical but often overlooked determinant of functional outcomes (Püttker et al. 2020). A low-quality matrix (e.g., intensive agriculture, urban development) may impose additional environmental filtering beyond that of the fragment itself, while a high-quality matrix (e.g., secondary forest, agroforestry) can facilitate movement and even provide complementary resources.

Using a metacommunity model, Suárez-Castro and colleagues (2020) showed that the rel-

ative importance of fragmentation per se (versus habitat loss) for functional diversity depends critically on the variance in response traits within the regional species pool and the correlation between response and effect traits. When the matrix is of low quality and dispersal is limited, habitat loss acts as a strong filter, disproportionately removing species with dispersal or resource-acquisition traits that are maladapted to matrix conditions. Under high-quality matrix conditions, mass effects  where high dispersal rates allow species to occupy patches where their intrinsic growth rate would be negative  can partially override environmental filtering.

This insight has practical implications. Improving matrix quality may be a more cost-effective conservation intervention than increasing fragment size in some landscapes, particularly where land acquisition is expensive or politically constrained. The challenge is that matrix quality is not a binary property but a continuous dimension that varies with land use, management intensity, and distance from fragments. We need better quantitative frameworks for predicting how different matrix types filter traits.

## 3.4 Multi-trophic trait filtering




Most fragmentation studies focus on a single trophic level, typically plants or birds. This is understandable given data availability, but it risks missing the cascading effects that propagate through food webs. A plant community that appears functionally intact may support a depauperate pollinator or herbivore community if those animals have additional trait requirements not captured by plant traits alone. Edge effects on trophic interactions can be complex and sometimes counter-intuitive. Rossetti et al. (2018) proposed that bottom-up edge effects (limited host plant availability) may favour dietary generalist herbivores, whereas top-down edge effects (altered predation pressure) may favour specialists. Empirical support for these contrasting predictions is accumulating but remains far from decisive. What is clear is that trophic position mediates vulnerability to fragmentation. Large carnivores are consistently more sensitive than herbivores, and specialised mutualists (e.g., fig wasps, certain pollinators) are more vulnerable than generalists (Banks-Leite et al. 2012).

The functional consequences of trophic filtering are rarely measured directly. If an apex predator is lost, we can infer that prey populations may increase, but does this translate into measurable changes in herbivory rates, seed predation, or nutrient cycling? A few studies have attempted such linkages. In Amazonian forest fragments, the loss of large frugivores reduced seed dispersal distances for large-seeded trees, with cascading effects on tree recruitment and forest composition (Cordeiro & Howe 2003). But such studies remain exceptional. The typical fragmentation study stops at trait composition, assuming  often without justification  that trait changes predict process changes. This assumption is shaky, as I discuss further below.

## 4. Functional Diversity Metrics: What Do They Actually Tell Us?

## 4.1 Conceptual foundations

Functional diversity encompasses the variety, distribution, and abundance of functional traits within a community. The most widely used metrics capture three conceptually distinct components: functional richness (the volume of trait space occupied), functional evenness (the regularity of trait distribution), and functional divergence (the extent to which abundance is concentrated at the extremes of trait space) (Villéger et al. 2008; Mason et al. 2005). A fourth component functional dispersion integrates abundance weighting across the trait distribution (Laliberté & Legendre 2010). Rao's quadratic entropy (RaoQ) provides a unified framework that combines trait differences with species abundances (Botta-Dukát 2005; Ricotta & Moretti 2011).

Functional Richness (FRic) is typically calculated as the convex hull volume of the trait space occupied by a community:

FRic = Volume of convex hull spanned by species in trait space

where the convex hull is the smallest convex set containing all species in a multivariate trait space. FRic increases as species occupy more distinct trait combinations. Its ecological interpretation is straightforward: high FRic implies that a community contains a wide range of trait values, potentially enabling multiple ecosystem functions. However, FRic is sensitive to outliers and the number of traits included. Using more traits almost invariably increases FRic, even if the additional traits carry little functional information (Mammola et al. 2021). Comparisons of FRic across studies using different trait sets are therefore problematic, if not impossible.

Functional Evenness (FEve) quantifies the regularity of spacing between species along the minimum spanning tree connecting them in trait space. FEve ranges from 0 (irregular spacing, suggesting under-utilisation of some trait regions) to 1 (perfectly even spacing, suggesting efficient use of trait space). Low FEve can indicate environmental filtering (if species cluster in one trait region) or competitive exclusion (if species avoid each other in trait space), but the metric cannot distinguish these processes without additional information.

Functional Divergence (FDiv) measures how species abundances are distributed relative to the centre of the trait space. For a community with functional divergence concentrated in a few species, FDiv is low; for a community where abundances are spread across the trait space, FDiv is high. High FDiv often implies niche differentiation, though as with all functional diversity metrics the ecological interpretation depends on the traits selected.

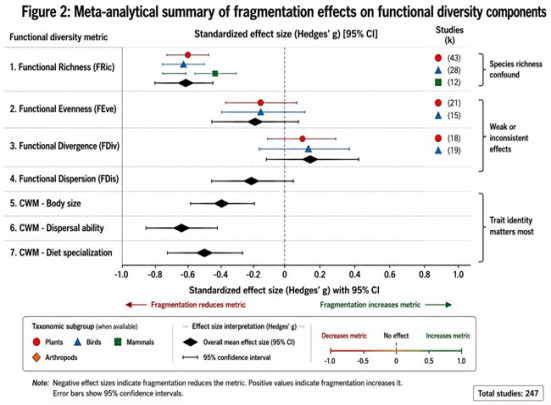
Functional Dispersion (FDis) is the mean distance of individual species to the community centroid in trait space, weighted by species abundances. Unlike FRic, FDis is not sensitive to outliers and can be calculated for communities with few species. FDis is mathematically related to RaoQ. When Euclidean distance is used, FDis approximates the square root of half the RaoQ value under certain conditions.

Community Weighted Mean (CWM) is not a diversity metric per se but a measure of community composition along a trait axis:

$CWM = \Sigma(i=1 \text{ to } S)\ p_i \times t_i$

where $p_i$ is the relative abundance of species i and $t_i$ is its trait value. CWM captures the dominant trait values in a community and is often more strongly correlated with ecosystem processes than functional diversity metrics. In the subalpine meadow study from the Qinghai-Tibetan Plateau, CWM of five traits explained 54–80% of variation in productivity, whereas species richness explained only 24–48% (Jiang et al. 2020). This finding that trait identity often matters more than trait diversity recurs across ecosystems and should temper enthusiasm for functional diversity metrics that ignore which traits are present.

## 4.2 Practical limitations and analytical pitfalls




The proliferation of functional diversity metrics has outpaced critical evaluation of their properties. Several issues deserve emphasis.

Sensitivity to trait number and selection. A systematic evaluation of nine functional diversity indices found that most are highly sensitive to the number of traits used, with FRic being particularly unstable (Mouillot et al. 2021). Adding traits that are correlated with existing traits can artificially inflate FRic without adding biological information. Conversely, omitting an important trait (e.g., dispersal ability in fragmented landscapes) can completely change the ranking of communities along functional axes. There is no consensus solution, but at a minimum, researchers should justify trait selection a priori, test sensitivity to trait inclusion/exclusion, and avoid comparing FRic across studies that used different trait numbers.

The species richness confound. Functional richness is almost always positively correlated with species richness (correlations typically range from r = 0.6 to 0.9). This creates a pervasive confound: observed declines in FRic with fragmentation may simply reflect declines in species richness. Null models that randomise species within trait space can help disentangle these effects, but they are surprisingly rarely used in fragmentation studies. Standardised effect sizes (SES) for functional diversity calculated as the deviation from a null expectation given species richness provide a more rigorous approach, but even then, the choice of null model can influence conclusions.

Abundance weighting. Many fragmentation studies use presence-absence data rather than abundances for functional diversity calculations, often because abundance data are unavailable or because sampling effort varies unevenly across fragments. This choice matters. Functional evenness and functional divergence are strongly influenced by relative abundances; ignoring abundance can mask changes in community structure that are ecologically important. For example, a fragment might retain the same species as continuous forest but with massively reduced abundances of functionally unique species a scenario that presence-based metrics would miss entirely.

The link to ecosystem functioning. The most critical limitation is that functional diversity metrics are proxies, not measures, of ecosystem functioning. A study that finds reduced FRic in fragmented forests cannot automatically conclude that decomposition rates or pollination success have declined. Surprisingly few studies have tested this link. A review of tropical studies found only five that directly related functional diversity metrics to measured ecosystem functioning, and those five showed very weak support for the hypothesised relationship (Hatfield et al. 2018). This is a genuine crisis in the field: if functional diversity metrics do not predict ecosystem functioning, then what exactly are we measuring?

One suspects that the problem is not with functional diversity per se but with the mismatch between the traits we measure (typically easy-to-measure morphological traits like body size or leaf area) and the traits that actually drive ecosystem processes (e.g., foraging behaviour, thermal tolerance, enzyme production). The field has prioritised data availability over mechanistic rele-

vance. Until we invest in measuring trait–function linkages directly, functional diversity metrics will remain descriptive rather than predictive.

## 5. Ecosystem Stability and Multifunctionality in Fragmented Landscapes

### 5.1 Functional diversity and stability: contested evidence

The hypothesis that functional diversity enhances ecosystem stability by providing response diversity, where different species respond differently to perturbations is intuitively appealing and theoretically well-developed (Yachi & Loreau 1999; Elmqvist et al. 2003). But empirical support is surprisingly inconsistent, and a recent meta-analysis has cast doubt on the generality of the relationship.

Lipoma and colleagues (2024) conducted the first meta-analysis evaluating the functional diversity–resilience relationship across terrestrial plant communities, and they found no positive relationship of grand mean effect sizes. This is a sobering result. After decades of research and hundreds of studies, the evidence that functional diversity buffers plant communities against disturbance is weak at best. The authors suggest several explanations: that resilience is driven more by functional identity (i.e., which traits are present) than by functional diversity; that the relationship is context-dependent, emerging only under certain environmental conditions or disturbance regimes; or that methodological inconsistencies across studies obscure a real but modest effect.

However, the null result may be specific to plants. Studies on animal communities particularly those examining stability of interaction networks have reported stronger relationships. Eisenhauer et al. (2024) proposed a multiple-mechanisms hypothesis, arguing that functional diversity enhances multifunctional stability through ecological complementarity that increases over time as species interactions accumulate. Whether this hypothesis holds across trophic levels remains unclear because comparable meta-analyses for animals do not yet exist.

5.2 Trophic destabilisation and interaction network collapse

Fragmentation does not merely reduce functional diversity; it rewires interaction networks in ways that can destabilise entire ecosystems. The loss of large vertebrates apex predators and large frugivores is particularly consequential because these species occupy unique positions in network space and their removal triggers cascades of secondary extinctions (Bascompte & Jordano 2007).

Mammal community dynamics in fragmented forests illustrate these effects well. In isolated forest islands created by hydroelectric reservoirs in the Amazon, small mammal abundance often increases due to reduced predator incidence and altered resource availability, but these apparent gains mask long-term extinction debt as specialist taxa decline (Nature Research Intelligence 2025). Edge effects expose interior habitats to invasive predators and hunting, further destabilising population regulation. Functional diversity commonly declines as forest-dependent guilds frugivores, insectivores are replaced by opportunistic species from the surrounding matrix.

The functional consequences extend beyond mammals. In fragmented tropical forests, the loss of large-bodied frugivorous birds and bats reduces seed dispersal distances for large-seeded trees, shifting plant community composition toward small-seeded, wind-dispersed, or generalist species (Cordeiro & Howe 2003; Mayta et al. 2025). Over time, this functional erosion becomes self-reinforcing: the plant community produces fruits that are smaller and less nutritious, which further reduces the carrying capacity for large frugivores. This positive feedback loop functional homogenisation begetting more functional homogenisation is difficult to reverse once established.

Trophic cascades in fragmented landscapes can be surprisingly long-range. Rossetti et al. (2018) showed that deer browsing in small forest fragments disproportionately reduces spe-

cialist Lepidoptera abundances, an effect that propagates through the plant-herbivore network. The mechanism is indirect: deer remove key host plants of specialist herbivores, and because specialists cannot switch to alternative hosts, their populations collapse. Generalist herbivores, by contrast, persist or even increase. The result is a simplified interaction network with reduced specificity  a pattern that appears general across fragmented landscapes (Rossetti et al. 2018).

5.3 Ecosystem multifunctionality: single-function myopia

Most fragmentation studies examine single ecosystem functions (e.g., seed dispersal, decomposition, pollination) in isolation. This approach is convenient but potentially misleading because different functions may respond to fragmentation in different directions. A community might show reduced pollination success but increased decomposition rates  a scenario that a single-function study would miss entirely.

Ecosystem multifunctionality  the ability of an ecosystem to provide multiple functions simultaneously  has been studied primarily in the context of plant diversity gradients, not fragmentation gradients. But the conceptual framework is transferable: fragmentation may reduce multifunctionality by eliminating species that contribute to unique functions, even if average single-function performance remains stable. The multiple-mechanisms hypothesis of biodiversity-stability relationships posits that multifunctional stability is highest in high-diversity communities and increases over time due to ecological complementarity (Eisenhauer et al. 2024). Whether fragmentation erodes this complementarity by reducing functional diversity is a critical open question.

One worrying possibility is that fragmentation effects on multifunctionality may be nonlinear and threshold-driven. Small reductions in functional diversity might have negligible effects on multifunctionality due to redundancy; but once a threshold is crossed  when functionally unique species are lost  multifunctionality may collapse precipitously. Identifying such thresholds would be immensely valuable for conservation planning, but the data to estimate them do not yet exist.

## 6. Critical Synthesis: Unresolved Debates and Methodological Inconsistencies

### 6.1 Habitat loss versus fragmentation: still entangled

The debate over whether habitat loss or fragmentation per se drives biodiversity decline has generated more heat than light. The statistical challenge is severe: habitat loss and fragmentation are inherently confounded because losing habitat reduces patch sizes and increases isolation. Fahrig (2003, 2013) famously argued that fragmentation without habitat loss can have positive effects on biodiversity, a claim that has been vigorously contested. A recent high-profile meta-analysis reported that fragmentation reduces α- and γ-diversity even after accounting for habitat amount, providing strong evidence that fragmentation effects are not merely an artefact of habitat loss (Chase et al. 2025). But the debate is far from resolved.

From a functional perspective, the distinction between habitat loss and fragmentation matters because the mechanisms of trait filtering may differ. Habitat loss primarily reduces population sizes and increases extinction risk for all species, regardless of traits. Fragmentation  isolation, edge effects  filters species based on dispersal ability, matrix tolerance, and edge sensitivity. If managers focus only on habitat area, they may miss the functional consequences of isolation. Conversely, if they focus only on connectivity, they may ignore the effects of reduced population sizes on genetic diversity and demographic stochasticity. The prudent approach is to manage both.

### 6.2 Trait selection: the hidden subjectivity

The choice of which traits to measure is arguably the most consequential decision in any

functional diversity study, yet it is rarely justified beyond vague appeals to 'trait-function links'. In fragmentation studies, the traits most commonly measured are those that are easiest to obtain from databases: body size, wing length, leaf area, seed mass. These traits may correlate with dispersal ability or resource acquisition, but the correlations are often weak, and the mechanisms are rarely tested.

The problem is compounded by the fact that different traits can lead to different conclusions about the same system. A study might conclude that fragmentation filters for small-bodied species, but if dispersal ability were measured directly, the conclusion might be the opposite. Until we develop standardised trait databases that include mechanistically relevant traits not just convenient ones the field will remain vulnerable to trait-selection bias.

## 6.3 Geographic and taxonomic biases: what we are missing

The literature corpus described in Section 2 reveals profound biases. Tropical Africa and Southeast Asia regions experiencing some of the highest fragmentation rates globally are severely under-studied. Large mammals and forest-dependent birds receive disproportionate attention; arthropods, amphibians, and soil biota are largely ignored. This matters because fragmentation effects are likely context-dependent. A finding from temperate bird communities may not generalise to tropical arthropod communities.

Perhaps the most consequential gap is the near-absence of long-term studies. Extinction debts unfold over decades to centuries; two-year studies cannot detect them. The few long-term datasets that exist the Biological Dynamics of Forest Fragments Project in Brazil, the Wog Wog fragmentation experiment in Australia have been immensely influential precisely because they reveal slow dynamics that short-term studies miss. Expanding the network of long-term fragmentation experiments should be a research priority.

## 6.4 The assumption that traits drive processes

The foundational assumption of functional ecology that species traits predict ecosystem processes is plausible but not always true. In many cases, environmental conditions (temperature, moisture, soil nutrients) or species abundances (not just presence) are stronger predictors of process rates than trait composition. A study that documents changes in functional diversity but does not measure ecosystem functioning cannot conclude that fragmentation impairs ecosystem functioning.

This criticism is not fatal to trait-based approaches, but it demands humility. Functional diversity metrics are tools, not endpoints. They are most useful when combined with direct measurements of the processes they are supposed to predict. A research programme that measures functional traits without measuring process rates is incomplete.

# 7. Case Studies

## 7.1 Tropical forest fragmentation in the Brazilian Atlantic Forest

The Atlantic Forest of Brazil is one of the most fragmented tropical ecosystems on Earth, with more than 80% of original cover lost and remaining fragments often smaller than 50 hectares. Studies from this system have been instrumental in revealing trait filtering along area and isolation gradients. Large fragments sustain a wider array of dietary and behavioural guilds particularly insectivores and frugivores whereas small fragments are dominated by habitat generalists and open-area specialists (Nature Research Intelligence 2025). Edge effects penetrate at least 100 metres into fragments, eliminating interior habitat in all but the largest remnants. Functional richness declines nonlinearly with fragment area, with thresholds at approximately

100 hectares below which interior-dependent species are systematically lost (Banks-Leite et al. 2012).

The Atlantic Forest has also been a testing ground for restoration corridors. Montes-Rojas and colleagues (2024) installed 98 camera-trap stations across forest fragments, natural corridors, restoration corridors, and pastures in Colombia's Magdalena River valley. Both species richness and functional diversity were highest in forest fragments, followed by natural corridors, then restoration corridors, and lowest in open pastures. Critically, species composition of restoration corridors began to resemble that of riparian forests and forest fragments, suggesting that corridors can recover lost functional diversity though the recovery was incomplete after approximately 15 years.

## 7.2 Montane sky-islands: fragmentation atop natural fragmentation

Montane ecosystems present a natural experiment in fragmentation: mountaintops are naturally isolated by intervening valleys, forming 'sky islands' that have generated high endemism over evolutionary time scales. The addition of anthropogenic fragmentation deforestation of lower slopes, road construction, agricultural expansion creates a second layer of patchiness. Robin and colleagues (2015) investigated this question in the Western Ghats of India, studying two montane palaeo-endemic bird species. Using microsatellite data from 218 individuals, they found major genetic structuring by deep valleys as expected but also detected recent isolation in anthropogenic fragments. The authors coined the term 'islands within islands' to describe this pattern: anthropogenic fragments are islands within natural islands of montane habitat.

## 7.3 Urban fragmentation: filtering for synanthropic traits

Urban environments are intensively fragmented by design: parks and green spaces are embedded in a matrix of buildings, roads, and managed vegetation. Urban fragmentation imposes extreme environmental filtering, selecting for species that tolerate noise, light pollution, human presence, and altered resource availability. A study of urban bird communities in southwest China examined 30 remnant woodlot patches ranging from 0.3 to 290 hectares (Zhao et al. 2026). Functional and phylogenetic diversity both increased with patch area and woody plant richness but decreased with isolation. Bird communities showed functional clustering indicating environmental filtering and clustering intensified with isolation.

Urban fragmentation also operates below ground. A study of ground arthropods in urban fragments found that both urbanisation and patch isolation drove taxonomic and functional homogenisation (Fenoglio et al. 2020). Species with low dispersal ability and specialised habitat requirements were systematically lost, leaving communities dominated by a few highly mobile generalists. Functional dispersion decreased with isolation, indicating that isolated patches support less functionally diverse communities a pattern consistent across multiple urban taxa.

## 7.4 Grassland fragmentation and the many-small versus few-large debate

Grasslands are naturally dynamic but human-induced fragmentation has reduced many grassland systems to isolated remnants. A recent study quantified relationships between patch area and multiple diversity dimensions across 62 grassland patches, finding that species richness and phylogenetic diversity increased with patch area, but functional diversity decreased (Wang et al. 2025). This counterintuitive result suggests that larger patches may support more species but those species are functionally similar, whereas small patches impose harsh conditions that filter for divergent stress-tolerant strategies.

The study also compared configurations of many small patches versus fewer large patches of equal total area. Multiple small patches had higher taxonomic, phylogenetic, and functional diversity than fewer large patches, and small patches showed more clustered assemblages (Wang

et al. 2025). This finding challenges the common conservation recommendation to prioritise large patches over small ones, at least for functional diversity.

### 7.5 Mangrove fragmentation: coastal connectivity under pressure

Mangrove forests are among the most threatened tropical ecosystems, with habitat loss and fragmentation driven by aquaculture, agriculture, and coastal development. Fragmented mangroves lose functional connectivity for mobile species that move between feeding, breeding, and nursery grounds. A recent review argued that biodiversity corridors whether biological, ecological, or mixed-use could mitigate these impacts by supporting wildlife movement, enabling genetic exchange, and maintaining ecological processes (Gebrie et al. 2025). However, empirical evidence from mangrove corridors is sparse, and most recommendations remain theoretical.

## 8. Functional Restoration: From Corridors to Trophic Reassembly

### 8.1 Do corridors recover functional diversity?

The restoration of ecological corridors is one of the most widely recommended interventions for fragmented landscapes, but evidence of functional recovery beyond simple species recolonisation is surprisingly limited. Montes-Rojas et al. (2024) provided evidence that restoration corridors in Colombia's Magdalena River valley support higher functional diversity than open pastures and that species composition begins to resemble that of reference forests. However, functional diversity remained lower in corridors than in natural riparian forests, and the recovery was incomplete after approximately 15 years.

A 25-year study of a restored wildlife corridor in the Australian Wet Tropics found that vegetation, birds, and ground mammals in the corridor increasingly resembled adjacent intact rainforest (Tucker et al. 2024). Numbers of large-seeded and late-successional plant species those dispersed by birds and mammals increased over time. Generalist mammals were replaced by rainforest specialists, and germination of some large-fruited species coincided with colonisation by the only mammals capable of their dispersal. After 25 years, the planted corridor had produced a structurally complex habitat inhabited by many forest-dependent species.

These results are encouraging, but several caveats apply. First, the Australian corridor was actively planted with native tree species; passive restoration may produce different outcomes. Second, some endemic bird species remained absent even after 25 years, suggesting that recolonisation of highly specialised or dispersal-limited species may require longer time frames or additional interventions. Third, the study measured species composition and functional diversity but not ecosystem process rates.

### 8.2 Rewilding and trophic reassembly

Rewilding the restoration of self-sustaining ecosystems through the reintroduction of keystone species, particularly large vertebrates has gained traction as a complement to corridor-based connectivity restoration. The rationale is that many ecosystem functions depend on large-bodied animals that have been extirpated from fragmented landscapes. Reintroducing these species may restore top-down regulation and rewire interaction networks in ways that passive restoration cannot achieve.

Assisted migration deliberately moving species beyond their native range to prevent extinction is a more controversial intervention. A modelling study found that corridors and assisted migration were the most effective strategies for reducing extinction of climate-threatened species, with assisted migration particularly effective for short-dispersing species (Otto et al. 2022). Trophic reassembly the deliberate reconstruction of food webs is the most ambitious form of

functional restoration. The reintroduction of wolves to Yellowstone National Park is the classic example, triggering a trophic cascade that altered elk behaviour and abundance, which in turn allowed riparian vegetation to recover, which then increased beaver populations.

## 8.3 The functional restoration paradox

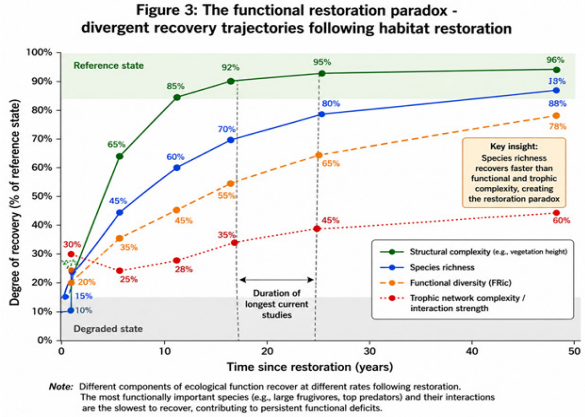



**Figure 3: The functional restoration paradox - divergent recovery trajectories following habitat restoration**

*Note:* Different components of ecological function recover at different rates following restoration. The most functionally important species (e.g., large frugivores, top predators) and their interactions are the slowest to recover, contributing to persistent functional deficits.

A paradox lies at the heart of functional restoration: the species that are most functionally important large frugivores, top predators, specialised pollinators are also the most difficult to restore. They have large area requirements, low population densities, slow reproductive rates, and limited dispersal abilities. Reintroducing them to small, isolated fragments may be ineffective if the fragments cannot support viable populations.

This paradox suggests that functional restoration must operate at multiple scales simultaneously. At the patch scale, habitat quality must be improved to support target species. At the landscape scale, connectivity must be restored to allow movement and gene flow. At the regional scale, source populations must be secured to provide colonists. The multi-scale framework proposed by Moreno-Mateos and Bhatnagar (2025) provides a useful template, advocating for an interaction-based approach that identifies priority areas for restoration based on projected network attributes, assesses potential for ecosystem function and resilience through trait and network attributes, and selects species for reintroduction based on their topological and functional roles within interaction networks.

## 8.4 Remote sensing, GIS, and AI for functional restoration

Advances in remote sensing and artificial intelligence are transforming the practice of restoration ecology. High-resolution satellite imagery and LiDAR can now map habitat structure and fragmentation at scales relevant to functional connectivity. GIS-based connectivity models can identify priority corridors for multiple taxa simultaneously, incorporating species-specific dispersal abilities and habitat preferences.

Suárez-Castro and colleagues (2026) presented a fully reproducible framework that integrates survey data from global datasets, remote-sensing products, and analytical tools to test fragmentation effects across scales. AI-assisted biodiversity monitoring using camera traps with automated species identification, acoustic monitoring for birds and bats, and environmental DNA is generating functional trait data at unprecedented scales. The challenge is no longer data collection but data integration: linking trait data from disparate sources, standardising trait measurements across studies, and developing predictive models that generalise across ecosystems.

## 9. Future Research Priorities

Based on the critical synthesis above, I identify five priority areas for future research:

1. Long-term functional trajectories. We need fragmentation studies that measure functional diversity and ecosystem processes repeatedly over decades, not years. Only such studies can

detect extinction debts, colonisation credits, and the long-term effects of restoration interventions. Funding agencies should prioritise support for existing long-term experiments and the establishment of new ones.

2. Trait–function linkages. The field must move beyond measuring easy traits and assuming they predict function. Direct measurements of ecosystem processes seed dispersal distances, pollination success, decomposition rates, nutrient cycling should be integrated into fragmentation studies.

3. Multi-trophic and multi-taxonomic studies. Most fragmentation studies remain taxonomically narrow. We need studies that simultaneously measure functional diversity across multiple trophic levels plants, herbivores, pollinators, predators, decomposers to understand how fragmentation effects propagate through food webs.

4. Geographic expansion. The severe geographic biases in the literature must be addressed. Tropical Africa, Southeast Asia, and the Amazon basin are under-studied relative to their fragmentation rates and biodiversity importance. International collaborations and capacity-building in these regions are urgently needed.

5. Restoration experiments that measure function. Restoration projects should be designed as experiments, with control sites, pre-restoration baselines, and long-term monitoring of functional outcomes not just species counts. This includes testing different restoration interventions against each other and against passive restoration.

## 10. Conclusion

Habitat fragmentation is not merely a problem of species loss but a fundamental restructuring of ecological communities along functional axes. The mechanistic pathways environmental filtering, dispersal limitation, trophic cascades are increasingly well understood, at least for some taxa in some systems. Functional diversity metrics provide a powerful toolkit for quantifying these changes, but their limitations are equally important: sensitivity to trait selection, confounds with species richness, and tenuous links to ecosystem functioning.

The evidence that fragmentation reduces functional diversity is strong, but the evidence that this reduction impairs ecosystem stability and multifunctionality is weaker and more contested. Meta-analyses have failed to find general support for a positive functional diversity–resilience relationship, at least for plants. The field may have over-promised on the predictive power of functional diversity while under-delivering on empirical validation.

Restoration ecology is at a critical juncture. We have plausible interventions corridors, rewilding, trophic reassembly but limited evidence that they recover lost functionality beyond simple recolonisation. The functional restoration paradox that the most functionally important species are the hardest to restore remains unresolved.

What is clear is that continuing to manage fragmented landscapes based on species counts is inadequate. A fragment with 50 species of generalist birds may be functionally impoverished relative to a fragment with 30 species that include large frugivores and specialised insectivores. Functional ecology offers a pathway toward more meaningful conservation targets but only if we commit to measuring the traits and processes that actually matter.

## Author's Declaration:

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