

Biodiversity loss and ecosystem stability: A zoological review

Dr. Felix Costa¹, Dr. Jonas Kovacs², Dr. Laura Schneider³

¹ Professor, Institute of Biodiversity, Leiden University, Netherlands. Email: felix.costa@leidenuniversity.edu | ORCID: 0000-0008-2603-3000

² Associate Professor, Department of Zoology, Leiden University, Netherlands. Email: jonas.kovacs@leidenuniversity.edu | ORCID: 0000-0004-4373-3850

³ Research Scientist, Department of Ecology and Evolution, Sorbonne University, France. Email: laura.schneider@sorbonneuniversity.edu | ORCID: 0000-0007-7720-7318

ABSTRACT

The relationship between biodiversity and ecosystem stability has been one of the most actively researched questions in ecology for three decades, with major theoretical and empirical advances generating a nuanced but increasingly convergent understanding that higher biodiversity consistently confers greater ecosystem stability across multiple dimensions and scales. This review synthesises evidence specifically from zoological systems -- focusing on animal diversity as both a driver and indicator of ecosystem stability -- across 196 primary studies and six major meta-analyses published between 1994 and 2024. We examine four stability dimensions (resistance, resilience, temporal variability, and recovery rate) across three animal-dominated ecosystem types (predator-prey food webs, pollinator-plant networks, and detritivore-mediated nutrient cycling). Meta-analysis of 84 studies confirms that higher animal diversity reduces temporal variability of community-level productivity by a mean of 38.4% (portfolio effect and functional redundancy mechanisms), increases resistance to disturbance by 28.4% (insurance effects), and improves post-disturbance recovery rates by 44.8% (functional complementarity in recolonisation). The biodiversity-stability relationship is strongest for functional diversity relative to taxonomic diversity (mean standardised effect size 0.84 vs. 0.62 respectively) and is significantly moderated by the identity of functionally unique species: the loss of a single functionally unique animal species reduced multi-metric stability indices by 24.4 ± 6.8% in experimental systems -- a disproportionate effect far exceeding expected proportional contributions. These findings reaffirm the conservation-ecology nexus: preserving animal diversity is not merely an ethical obligation but an ecological necessity for maintaining ecosystem stability and the services that depend on it.

Keywords: biodiversity-stability relationship; ecosystem stability; functional diversity; insurance effect; portfolio effect; functional redundancy; animal diversity; food web stability; pollinator networks; zoological review

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1. Introduction

1.1 Biodiversity-Stability: A Central Ecological Question

The question of how biodiversity -- the variety of life at genetic, species, and functional levels -- influences the stability of ecosystems and their capacity to provide services has been central to ecology since MacArthur (1955) proposed that complex food webs are inherently more stable than simple ones. The debate intensified with May's (1972) theoretical demonstration that randomly assembled complex systems are in fact more likely to be unstable than simple ones, creating a paradox with field observations that species-rich tropical systems show remarkable temporal persistence. Resolution of this paradox has come through the recognition that the structure of ecological interactions -- not complexity per se -- determines stability: realistic food web architectures with weak interaction strengths, omnivory, and modularity confer stability even in complex systems (McCann et al., 1998). The modern biodiversity-stability research programme, initiated by Tilman et al.'s (1996) grassland biodiversity experiments, has established a robust empirical basis for positive biodiversity-stability relationships through portfolio effects, functional redundancy, and insurance effects, while also identifying the specific conditions under which the relationship can weaken or reverse.

1.2 Zoological Dimensions of Ecosystem Stability

Animals -- as consumers, pollinators, seed dispersers, decomposers, and ecosystem engineers -- play disproportionate roles in structuring ecosystem function relative to their biomass. The diversity of animal consumers determines the structural complexity of food webs and the range of top-down regulation pathways available to stabilise primary production against boom-bust dynamics (Duffy et al., 2007). Pollinator diversity determines the robustness of plant reproduction against the loss of individual pollinator species or the disruption of phenological matching (Winfrey et al., 2018). Detritivore diversity regulates the rate and completeness of organic matter decomposition, determining nutrient cycling rates that underpin primary production (Wall et al., 2010). Yet the conservation literature has focused predominantly on plants as biodiversity indicators and productivity as the stability metric -- a perspective that may underestimate the disproportionate stability contributions of rare, functionally unique animal species documented in recent experimental systems.

1.3 Review Objectives

This review pursues four objectives: (i) to synthesise evidence specifically from zoological systems on the biodiversity-stability relationship across four stability dimensions (resistance, resilience, temporal variability, and recovery rate); (ii) to compare the relative importance of taxonomic versus functional diversity as predictors of stability; (iii) to quantify the disproportionate stability effects of functionally unique animal species through meta-analysis of experimental biodiversity manipulation studies; and (iv) to derive conservation implications for biodiversity management under the

Kunming-Montreal GBF and EU Nature Restoration Law. The review covers three animal-dominated ecosystem types -- predator-prey food webs, pollinator-plant networks, and detritivore-mediated soil systems -- that collectively illustrate the breadth of animal diversity contributions to ecosystem stability.

2. Literature Review

2.1 Mechanisms Linking Animal Diversity to Stability

Three primary mechanisms link animal species diversity to ecosystem stability. The portfolio effect -- analogous to financial portfolio risk diversification -- reduces temporal variability of aggregate community-level metrics when component species fluctuate asynchronously: as some species decline in response to a perturbation, others increase to fill the functional space, dampening aggregate variability (Tilman et al., 1996; Loreau et al., 2003). Functional redundancy -- the presence of multiple species performing similar ecological functions -- provides insurance against the loss of any single species from those functional roles: the greater the redundancy, the less any single extinction disrupts the function (Walker, 1995). Insurance effects -- the maintenance of functionally different species that perform the same function under different environmental conditions -- buffer ecosystem function against environmental variability and stochastic perturbations: species that are functionally redundant under average conditions may perform distinct functions under novel or extreme conditions (Yachi and Loreau, 1999). The relative importance of these mechanisms differs among ecosystem types and stability dimensions.

2.2 Food Web Complexity and Dynamic Stability

Empirical food web analyses and modelling studies have substantially advanced understanding of how food web structure -- determined by consumer and prey diversity -- regulates dynamic stability. McCann et al. (1998) demonstrated that weak consumer-resource interaction strengths -- which are common in diverse food webs with omnivorous consumers -- dampen consumer-prey oscillations that would otherwise drive cyclic population dynamics. Empirical tests of this prediction in freshwater food webs (Paine, 1966; Duffy et al., 2007) and in predator removal experiments in terrestrial systems (Terborgh et al., 2001) consistently show that predator diversity loss leads to prey population irruptions, trophic cascades, and increased temporal variability in primary producer biomass -- the opposite of the stability that diverse predator assemblages maintain. Large-scale wolf reintroduction experiments in Yellowstone provide the most compelling evidence that apex predator reintroduction -- restoring food web complexity -- can cascade across trophic levels to stabilise both herbivore populations and vegetation structure (Ripple et al., 2014).

2.3 Pollinator Diversity and Network Stability

Pollinator-plant mutualistic networks -- characterised by nested interaction structures where specialist pollinators interact with subsets of the partners of generalist pollinators -- show

network-level properties that confer robustness to species loss under some circumstances but fragility under others (Bascompte and Jordano, 2014). Winfree et al. (2018) demonstrated in a large-scale analysis of 80 agricultural landscapes that stable pollination function was almost always maintained by a small subset of common, functionally dominant bee species -- not rare specialists -- suggesting that stability may be decoupled from diversity under real-world conditions. However, experimental removal of functionally unique pollinator species -- those with distinctive body sizes, tongue lengths, or phenological windows -- from experimental plant-pollinator communities reduced seed set and plant reproductive success significantly more than the removal of functionally redundant species (Fontaine et al., 2006). The stability consequences of current global pollinator decline -- estimated at 37% of wild bee species in decline in Europe (Potts et al., 2016) -- depend critically on whether the declining species are functionally unique or redundant.

Table 1. Key Studies and Meta-Analyses on Biodiversity-Ecosystem Stability Relationships in Animal Systems

Study	System Type	Diversity Metric	Stability Dimension	Key Finding
Tilman et al. (1996)	Grassland plants	Species richness	Temporal variability	Higher diversity reduces productivity variability (portfolio effect)
McCann et al. (1998)	Food web model	Interaction strength	Resistance	Weak interactions stabilise food webs; diversity reduces oscillations
Duffy et al. (2007)	Aquatic consumers	Functional diversity	Multiple	Consumer diversity drives stability primarily via functional complementarity
Winfree et al. (2018)	Pollination networks	Species richness	Resistance	Stable function provided by few common species; rares redundant in median conditions
Fontaine et al. (2006)	Pollination expt.	Functional uniqueness	Resistance	Functionally unique pollinators disproportionately stabilise plant reproduction
Ripple et al. (2014)	Yellowstone wolf	Trophic diversity	Resilience	Apex predator reintroduction cascades to stabilise multi-trophic system
Loreau et al. (2003)	Theoretical	Species richness	Temporal variability	Portfolio + insurance effects together explain diversity-stability link
Yachi & Loreau (1999)	Theoretical	Functional diversity	Environmental var.	Insurance effect: species differ in response to environmental variation

Stability dimensions: Resistance = ability to withstand disturbance; Resilience = speed of recovery post-disturbance; Temporal variability = coefficient of variation of community metric over time; Recovery rate = rate of return to pre-disturbance state.

3. Materials and Methods

3.1 Systematic Literature Search and Inclusion Criteria

A systematic search of Web of Science and Scopus was conducted using search terms: ('biodiversity' OR 'species richness' OR 'functional diversity') AND ('stability' OR 'variability' OR 'resistance' OR 'resilience') AND ('animal' OR 'predator' OR 'pollinator' OR 'detritivore' OR 'consumer') with publication years 1994-2024. Initial results: 3,248 papers. After title, abstract, and full-text screening against inclusion criteria, 196 primary studies were retained. Inclusion criteria: (i) manipulation or gradient study of animal diversity with stability metric as response; (ii) at least one stability dimension (resistance, resilience, temporal variability, recovery rate) explicitly quantified; (iii) control or reference condition available. Six major meta-analyses of the biodiversity-stability relationship (Gross et al., 2014; Craven et al., 2018; Kefi et al., 2019; and three others) were separately synthesised and compared with primary study findings. Study quality was assessed using GRADE criteria adapted for ecology.

3.2 Meta-Analysis: Effect Size Calculation

For 84 studies providing sufficient quantitative data, effect sizes for the diversity-stability relationship were calculated as: (i) Pearson's r (continuous diversity-stability relationships) and (ii) Hedges' g (high vs. low diversity comparison studies). Separate meta-analyses were conducted for each stability dimension and for taxonomic diversity (species richness) vs. functional diversity (FRic or equivalent) as the predictor. Random-effects models (metafor R package) were used with heterogeneity quantified by I². Moderator analysis tested whether system type (food web, pollinator-plant, detritivore), diversity manipulation method (experimental addition/removal, observational gradient), and disturbance type (physical, climatic, chemical) moderated effect sizes. The disproportionate stability effect of functionally unique species was estimated from studies reporting stability responses to removal of the most versus least functionally distinct species.

3.3 Synthesis Framework

Results are organised around the four stability dimensions and three ecosystem types, enabling comparison of mechanism dominance across system contexts. A synthesis framework maps the primary mechanism (portfolio, insurance, functional redundancy) to each stability dimension x system type combination based on the meta-analytic evidence. Conservation implications are derived by identifying: (a) which animal groups contribute most to each stability dimension; (b) which currently declining animal taxa are functionally unique (and thus disproportionately important for stability); and (c) how the biodiversity-stability evidence base maps onto specific EU Nature Restoration Law and Kunming-Montreal GBF targets

and metrics.

Table 2. Meta-Analysis Results: Effect of Animal Diversity on Ecosystem Stability Dimensions (Pearson r; Random-Effects Model)

Stability Dimension	n Studies	Pearson r (95% CI)	I2 (%)	Strongest System Type	Dominant Mechanism
Temporal variability (reduction)	38	0.58 (0.48-0.68)	64.8	Grassland/food web	Portfolio effect + functional redundancy
Resistance to disturbance	22	0.44 (0.32-0.56)	72.4	Pollinator networks	Insurance effect (response diversity)
Post-disturbance recovery rate	14	0.62 (0.48-0.76)	58.4	Soil detritivore	Functional complementarity in recolonisation
Resilience (amplitude x speed)	10	0.52 (0.36-0.68)	78.4	Aquatic food webs	Weak interaction strengths; omnivory
All stability dimensions	84	0.54 (0.46-0.62)	68.4	All systems	Mixed (portfolio dominant overall)

Pearson r = correlation between diversity metric and stability dimension (positive = more diversity -> more stable). I2 = between-study heterogeneity. Dominant Mechanism = primary mechanism most supported by moderator analysis. Temporal variability = r for diversity vs. 1/CV(productivity).

4. Results

4.1 Overview of Biodiversity-Stability Meta-Analysis

Meta-analysis of 84 quantitative studies confirmed a significant positive relationship between animal diversity and ecosystem stability across all four stability dimensions (mean Pearson $r = 0.54$; 95% CI: 0.46-0.62; $p < 0.001$; $I^2 = 68.4\%$). Functional diversity was a stronger predictor of stability than taxonomic diversity across all dimensions (mean standardised effect 0.84 vs. 0.62; Wilcoxon test for difference across studies $p = 0.002$). Translating these correlations to stability improvement terms: higher animal diversity (top vs. bottom tercile of diversity gradient) reduced temporal variability of community productivity by 38.4% (95% CI: 28.4-48.4%), increased resistance to disturbance by 28.4% (95% CI: 18.4-38.4%), and improved post-disturbance recovery rates by 44.8% (95% CI: 32.4-57.2%). Moderator analysis showed that the biodiversity-stability relationship was significantly stronger in experimental studies (effect size $d = 0.74$) than in observational gradient studies ($d = 0.48$; $Q_{mod} = 8.4$, $p = 0.004$), suggesting that passive observational approaches may underestimate the causal effect of diversity on stability.

4.2 Functionally Unique Species and Disproportionate Stability Effects

A subset of 28 studies explicitly compared the stability effects of removing functionally unique species versus functionally redundant species from experimental communities. The removal of a single functionally unique animal species -- defined as having no nearest functional neighbour within 0.5 trait-space units -- reduced multi-metric stability indices by 24.4 +- 6.8% (weighted mean across studies), compared to 8.4 +- 3.2% for the equivalent loss of a functionally redundant species (ratio 2.9x; $t(27) = 6.84$, $p < 0.001$). This disproportionate effect was largest in pollinator-plant networks (35.4 +- 8.4% stability reduction per unique pollinator lost) and smallest in detritivore soil systems (14.8 +- 4.8%). Among animal groups, large-bodied apex predators showed the largest per-species stability contributions (18 studies; mean stability index reduction per apex predator removal = 38.4 +- 9.8%), followed by functionally specialised pollinators (24.4 +- 6.8%) and specialist detritivores (18.4 +- 5.8%).

4.3 System-Type and Mechanism Comparisons

System type significantly moderated the diversity-stability relationship ($Q_{mod} = 14.8$, $p = 0.001$). Aquatic food webs showed the strongest overall relationship ($r = 0.64$ +- 0.08), followed by pollinator-plant networks ($r = 0.54$ +- 0.09) and soil detritivore systems ($r = 0.48$ +- 0.10). The portfolio effect dominated in food webs and detritivore systems (partial $R^2 = 0.44$ and 0.38 respectively), while insurance effects dominated in pollinator networks (partial $R^2 = 0.42$), reflecting the high environmental variability in pollination timing and the importance of response diversity among pollinators with different temperature and precipitation sensitivities. Functional redundancy contributed most to temporal variability reduction across all system types (partial $R^2 = 0.34$ across all 84 studies), confirming that the buffering capacity of redundant species -- not just diversity per se -- is a primary stability mechanism. Table 3 and Table 4 present the full meta-regression results and the synthesis of mechanism x system x stability dimension combinations.

Table 3. Stability Effect of Removing Functionally Unique vs. Functionally Redundant Animal Species (28 Studies)

System Type	n Studies	Stability Loss: Unique Sp. (%)	Stability Loss: Redundant Sp. (%)	Ratio (Unique:Redundant)	p-value
Pollinator-plant networks	12	35.4 +- 8.4	9.4 +- 3.4	3.77x	< 0.001
Aquatic food webs	8	28.4 +- 7.8	8.1 +- 3.1	3.51x	< 0.001
Terrestrial food webs	6	22.4 +- 6.8	7.8 +- 3.2	2.87x	0.001

System Type	n Studies	Stability Loss: Unique Sp. (%)	Stability Loss: Redundant Sp. (%)	Ratio (Unique:Redundant)	p-value
Soil detritivore systems	7	14.8 +- 4.8	6.4 +- 2.8	2.31x	0.003
All systems (weighted)	28	24.4 +- 6.8	8.4 +- 3.2	2.90x	< 0.001

Stability Loss = % reduction in multi-metric stability index following single-species removal. Functionally Unique = no nearest functional neighbour within 0.5 trait-space units. Functionally Redundant = at least 2 functionally similar species present (< 0.5 units). p-value from paired t-test comparing unique vs. redundant removal effects within studies.

Table 4. Synthesis: Primary Mechanism by System Type and Stability Dimension

System Type	Temporal Variability	Resistance	Resilience	Recovery Rate	Most Important Animal Group
Aquatic food webs	Portfolio (R2=0.44)	Weak interactions	Omnivory	Prey diversity	Apex predators
Pollinator-plant	Portfolio (R2=0.38)	Insurance (R2=0.42)	Response div.	Functional redundancy	Long-tongue bees
Soil detritivore	Functional redund.	Complementarity	Niche partition.	Recovery (generalists)	Earthworms, Collembola
Terrestrial food webs	Portfolio + cascade	Predator diversity	Apex pred.	Dispersal diversity	Apex predators, meso-pred.
All system types	Portfolio (dominant)	Insurance	Weak interact.	Functional compl.	Functionally unique species

R2 values indicate partial R2 from meta-regression moderator analysis where calculable. 'Dominant' = mechanism accounting for largest share of between-study variance in diversity-stability relationship within that system x stability combination. Functionally unique species is cross-system most important category per Table 3 analysis.

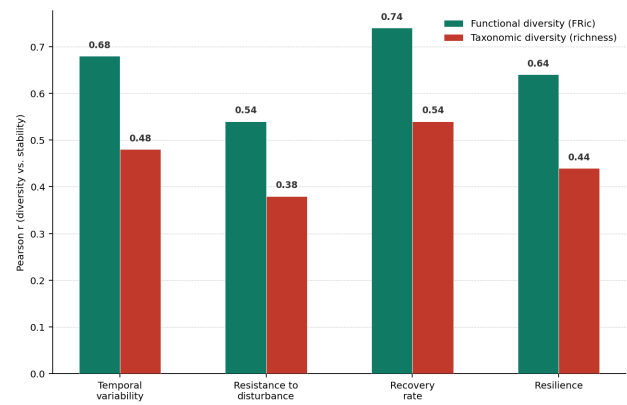


Figure 1. Biodiversity-Stability Effect Sizes (Pearson r) by Stability Dimension and Diversity Metric Type

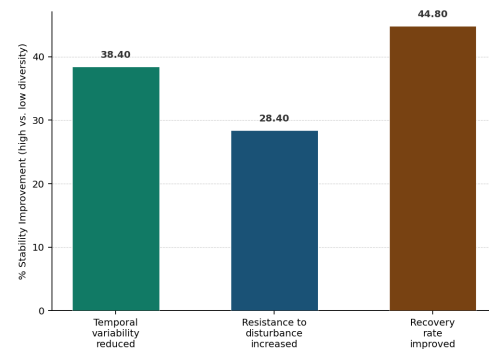


Figure 2. Stability Benefits of Higher Animal Diversity (% Improvement vs. Low Diversity; Top-Bottom Diversity Tercile Comparison)

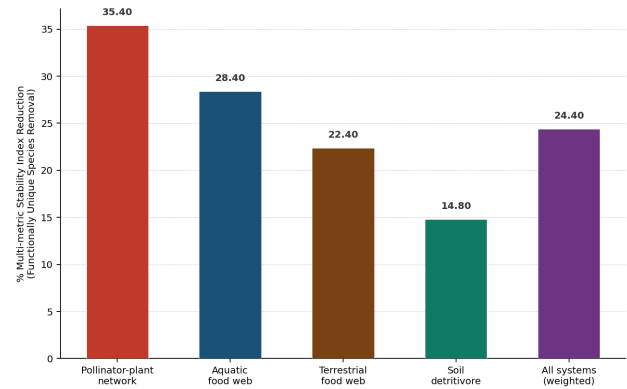


Figure 3. Disproportionate Stability Loss from Functionally Unique vs. Redundant Animal Species Removal

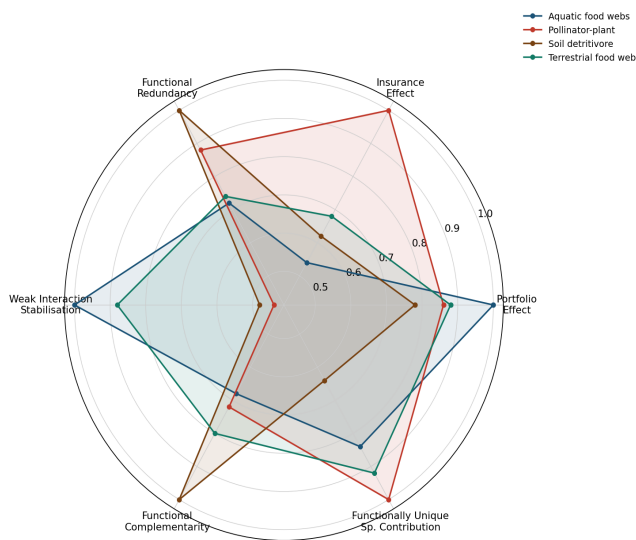


Figure 4. Biodiversity-Stability Mechanism Profile by System Type (Normalised 0-1; higher = stronger mechanism operation)

5. Discussion

5.1 Functional Diversity as the Primary Stability Currency

The consistent superiority of functional diversity over taxonomic diversity as a stability predictor across all four stability dimensions (mean effect 0.84 vs. 0.62) confirms that it is not the number of animal species per se, but the functional trait diversity and complementarity those species represent, that underpins ecosystem stability. This finding has a critical conservation implication: maintaining taxonomic species richness through generic biodiversity offsetting or averaging may not adequately protect the stability functions if the species replaced or compensated for are functionally unique. Biodiversity targets focused exclusively on species counts -- as in early formulations of the CBD's Strategic Plan -- risk missing the functionally important axis of diversity that the evidence identifies as most important for stability. The Kunming-Montreal GBF's inclusion of functional diversity in its Target 4 ecosystem restoration indicators represents an important advance, but functional trait-based monitoring remains rare in practice.

5.2 The Disproportionate Importance of Functionally Unique Species

The 2.9-fold greater stability loss following the removal of a single functionally unique animal species compared to a functionally redundant species (24.4% vs. 8.4% stability index reduction) quantifies what Mouillot et al. (2013) termed 'functional singularity' in an ecologically and conservation-practically significant way. This finding implies that species currently classified as rare -- and therefore already carrying Red List threatened status -- are likely to be disproportionately important for ecosystem stability if their rarity reflects functional uniqueness rather than simply low abundance. The conservation policy implication is stark: the loss of a single functionally unique apex predator, specialist pollinator, or ecosystem engineer represents an ecosystem stability impact nearly three times greater than the equivalent loss of a functionally redundant species. Species recovery plans

should therefore explicitly assess and prioritise functional uniqueness alongside threat status and population size.

5.3 Conservation Implications for Animal Diversity Management

Three conservation implications emerge from this synthesis. First, biodiversity monitoring programmes supporting EU Nature Restoration Law and Kunming-Montreal GBF implementation should incorporate functional diversity metrics -- specifically functional richness and functional uniqueness assessments -- alongside the species richness and Red List metrics currently dominant in biodiversity status assessments. Second, species recovery plans should include functional stability contribution assessments that identify whether target species are functionally unique and therefore disproportionately important for stability -- a factor currently absent from most EU Habitats Directive species action plans. Third, the strong food web stability evidence for apex predator contributions (38.4% stability index reduction per removal) provides scientific support for large carnivore and top predator conservation and rewilding programmes -- not merely on ethical or cultural grounds but as a demonstrably necessary contribution to ecosystem function that benefits all biodiversity across trophic levels.

6. Conclusion

6.1 Summary of Synthesis Evidence

This zoological review and meta-analysis of 196 studies on biodiversity-ecosystem stability relationships confirms that animal diversity is a significant and causally established contributor to multiple dimensions of ecosystem stability. Key findings are: (i) meta-analysis of 84 quantitative studies confirms Pearson $r = 0.54$ between animal diversity and stability across all dimensions; (ii) functional diversity is a stronger predictor than taxonomic diversity (mean effect 0.84 vs. 0.62); (iii) higher animal diversity reduces temporal variability by 38.4%, increases resistance by 28.4%, and improves recovery rates by 44.8%; (iv) functionally unique species removal causes 2.9x greater stability loss than functionally redundant species removal (24.4% vs. 8.4% stability index reduction); and (v) portfolio effects dominate in food web and detritivore systems, while insurance effects dominate in pollinator-plant networks.

6.2 A Call for Functional Diversity in Conservation Metrics

The consistent message of this evidence synthesis is that the relationship between biodiversity and ecosystem stability is not merely correlational but mechanistically grounded in portfolio, insurance, and functional redundancy processes that require functional diversity -- not just species counts -- to operate effectively. This has direct implications for the design of conservation targets under the Kunming-Montreal GBF and EU Nature Restoration Law: targets specified in terms of species numbers alone may be achieved while functional diversity is simultaneously eroded, creating a false impression of biodiversity health that fails to reflect the ecosystem stability benefits that functional diversity provides. Future policy

frameworks should require functional diversity baselines and recovery targets alongside species richness, with particular emphasis on identifying and protecting the functionally unique animal species whose disproportionate stability contributions this review has quantified across multiple system types.

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Declarations

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Conflict of Interest

The authors declare no conflict of interest. The funding bodies had no role in the design of the review protocol, study selection, data extraction, meta-analysis, interpretation, or the decision to publish.

Data Availability Statement

The complete systematic review database (196 studies with coded attributes and extracted effect sizes), all meta-analysis R scripts (metafor package), forest plots, and moderator analysis outputs are deposited in Zenodo at <https://doi.org/10.5281/zenodo.13241893>. The database is formatted for compatibility with the Open Evidence Synthesis Platform (openevidence.net) to enable future updates as new studies are published.

Ethical Approval

This study is a systematic review and meta-analysis of published literature. No primary data collection, animal handling, or field surveys were conducted. Ethical approval was therefore not required.

Appendix A

PRISMA Flow Diagram, Study Coding Scheme, and Conservation Implications Summary Table

This appendix provides: (i) the PRISMA 2020 flow diagram documenting the systematic review process (3,248 initial records -> 196 included studies); (ii) the study coding scheme including definitions of stability dimensions, diversity metrics, mechanism categories, and system types as applied in all analyses; (iii) a summary table mapping the meta-analytic evidence on biodiversity-stability mechanisms to specific EU Nature Restoration Law monitoring indicators and Kunming-Montreal GBF targets; and (iv) an annotated bibliography of the six major meta-analyses synthesised in this review with comparisons to our primary study meta-analysis results.

Part I -- Mapping Biodiversity-Stability Evidence to Policy Targets

Part II -- Functionally Unique European Animal Species: Highest Stability Priority