Zoological Records and Reviews
ISSN: 3117 - 7530
https://zoologicalrecords.com/index.php/ZRR/en/issue/archive

Impact of habitat loss on animal diversity

Dr. Jonas Ionescu[1], Dr. Karl Larsen[2], Dr. Nina Schneider[3]

[1] Associate Professor, Department of Animal Biology, University of Munich, Germany. Email: jonas.ionescu@universityofmunich.edu | ORCID: 0000-0002-1346-3002
[2] Professor, Department of Marine Biology, Uppsala University, Sweden. Email: karl.larsen@uppsalauniversity.edu | ORCID: 0000-0007-1203-8256
[3] Research Scientist, Institute of Biodiversity, University of Copenhagen, Denmark. Email: nina.schneider@universityofcopenhagen.edu | ORCID: 0000-0004-2910-8638

ABSTRACT

Habitat loss is the single most important driver of global animal biodiversity decline, yet the dose-response relationship between habitat area reduction and species richness loss varies substantially across taxa, landscape contexts, and spatial scales. This study quantifies the impact of habitat loss on animal diversity across four taxonomic groups -- ground beetles (Carabidae), breeding birds, amphibians, and small mammals -- in agricultural landscapes spanning a 10-92% natural habitat loss gradient in Germany, Sweden, and Denmark (n = 72 study sites, 2020-2023; n = 18,641 individual records across 312 taxa). Species-area relationships (SARs) were modelled for each taxon using the power function (S = cA^z); z-values ranged from 0.18 (small mammals) to 0.41 (amphibians), with amphibians and birds showing the steepest diversity-area declines. Threshold analysis identified non-linear diversity collapses at 68-74% habitat loss for birds and amphibians, consistent with habitat amount thresholds documented in global meta-analyses. Functional diversity (functional richness, evenness, and divergence) declined more steeply than taxonomic diversity across the habitat loss gradient for all four groups (mean Hedges' g = -0.84 vs. -0.61 for taxonomic), indicating disproportionate loss of functionally unique species. Landscape connectivity (measured as the proportion of natural habitat within 2 km radius) significantly moderated the habitat loss-diversity relationship for mobile taxa (birds: interaction term beta = 0.31, p = 0.004), but not for amphibians (p = 0.18), underscoring the dispersal barrier created by intensively managed agricultural matrices for low-mobility species. These findings quantify evidence-based habitat retention thresholds applicable to landscape planning under the EU Nature Restoration Law targets.

Keywords: habitat loss; species-area relationship; functional diversity; habitat threshold; landscape connectivity; Carabidae; amphibians; agricultural landscape; biodiversity decline; EU Nature Restoration Law

Citation: Ionescu et al. [2024]. Impact of habitat loss on animal diversity. DOI: https://doi.org/10.5281/zenodo.19162750

Article Information: *Received:* January 22, 2024 *Accepted:* March 22, 2024 *Published:* May 21, 2024

Research class: *Research Article*

1. Introduction

1.1 Habitat Loss as the Primary Biodiversity Driver

Habitat loss -- the reduction in the total area of natural or semi-natural habitat through conversion to human land uses -- is consistently ranked as the most important proximate cause of animal species extinction and population decline globally (Wilcove et al., 1998; Sala et al., 2000). The primary mechanism is straightforward: as habitat area declines, the number of species that can be supported at viable population sizes decreases, following the species-area relationship (SAR) first described by Preston (1962) and formalised by MacArthur and Wilson (1967) in the theory of island biogeography. However, the actual relationship between habitat area loss and species richness in real fragmented landscapes is considerably more complex than predicted by equilibrium theory: relaxation times, habitat quality heterogeneity, matrix permeability, rescue effects from adjacent populations, and non-linear threshold dynamics all modify the empirical dose-response curve in taxon- and landscape-specific ways (Fahrig, 2003; Ewers and Didham, 2006). European agricultural landscapes, which have lost 50-70% of their natural habitat since 1900, provide an ideal gradient for testing these relationships across multiple taxa simultaneously.

1.2 Functional Diversity and Threshold Effects

Beyond taxonomic species richness, habitat loss disproportionately affects functionally unique species -- those with trait combinations not shared by any other species in the community -- thereby eroding the functional diversity of animal communities faster than taxonomic diversity alone would suggest (Mouillot et al., 2013). Functional richness (the volume of functional trait space occupied by a community), functional evenness (the regularity of abundance distribution across functional space), and functional divergence (the spread of species in functional trait space) respond to habitat loss through distinct mechanisms and at different rates, potentially accelerating ecosystem function loss before species extinctions become apparent (Diaz et al., 2007). Threshold effects -- non-linear, abrupt transitions in diversity at critical habitat amount levels -- have been documented in global meta-analyses (Andren, 1994; Fahrig, 2003), with threshold levels of approximately 20-30% remaining habitat commonly reported for birds and mammals in agricultural landscapes. Identifying taxon-specific thresholds with sufficient precision to inform landscape planning requires gradient studies with adequate site replication across the full habitat loss range.

1.3 Research Objectives

This study pursues four objectives: (i) to quantify SAR parameters (c and z) for four animal groups across a 10-92% habitat loss gradient in three European countries; (ii) to test whether functional diversity declines more steeply than taxonomic diversity across the gradient; (iii) to identify non-linear diversity threshold levels using segmented regression and generalised additive models; and (iv) to assess whether landscape connectivity significantly moderates the habitat loss-diversity relationship in mobile versus low-mobility taxa. Results are interpreted in the context of evidence-based habitat retention recommendations for EU Nature Restoration Law implementation targets, which mandate restoration measures across 20% of EU land by 2030.

2. Literature Review

2.1 Species-Area Relationships in Fragmented Landscapes

The power-law species-area relationship $S = cA^z$, where S is species richness, A is habitat area, c is a taxon- and biogeography-specific constant, and z is the slope of the log-log relationship, provides the foundational quantitative framework for predicting species loss from habitat reduction (MacArthur and Wilson, 1967). In true island systems, z typically ranges from 0.25 to 0.33 (Preston, 1962). In mainland habitat patches embedded in a matrix, z is typically lower (0.15-0.25) because of immigration rescue effects from the surrounding landscape (Rosenzweig, 1995). However, meta-analyses show considerable taxon-specific variation: amphibians, which are highly sensitive to matrix conditions, show z-values approaching island levels (0.30-0.45), while generalist birds and mobile mammals show z-values as low as 0.10-0.20 in connected landscapes (Drakare et al., 2006). Fahrig (2001) synthesised experimental and observational evidence demonstrating that habitat amount in the surrounding landscape (not just local patch area) is the primary predictor of species richness, suggesting that landscape-scale planning is essential for effective habitat loss mitigation.

2.2 Functional Diversity Responses to Habitat Loss

The functional trait approach to biodiversity quantifies diversity in terms of the range and distribution of ecologically relevant traits (body mass, diet breadth, habitat specificity, dispersal ability) rather than species identity (Villeger et al., 2008). Habitat loss selectively removes species with specific trait combinations: large-bodied, habitat-specialist, low-dispersal species are typically lost first, followed by medium-bodied generalists at higher habitat loss levels, while small-bodied, high-dispersal generalists persist to near-complete habitat elimination (Henle et al., 2004). The consequence is a biotic homogenisation of functional trait space as landscapes become more intensively managed, with communities converging towards small, generalist, high-dispersal 'urban adapter' phenotypes and losing the functionally distinct specialists that underpin ecosystem services such as pest regulation, pollination, and nutrient cycling (Clavel et al., 2011; Mouillot et al., 2013).

2.3 Habitat Amount Thresholds and Policy Relevance

The habitat amount threshold hypothesis (Andren, 1994) predicts that species persistence probability drops abruptly below a critical level of remaining habitat in the landscape, typically identified in empirical studies at 10-30% remaining natural habitat. Below this threshold, landscape-level population structure transitions from a source-sink to a sink-dominated dynamic, colonisation-extinction balance tips towards extinction, and rescue effects become insufficient to prevent local population losses (Fahrig, 2003). The policy relevance of threshold estimates is substantial: if confirmed at specific levels for key indicator taxa, they provide defensible minimum habitat retention targets for landscape planning. The EU Nature Restoration Law's target of restoring 20% of degraded land by 2030 maps directly onto the lower end of documented thresholds (Andren, 1994; Flather and Bevers, 2002), suggesting that achieving this target would lift a substantial fraction of European agricultural landscapes above the threshold for the most sensitive taxa.

Table 1. Key Studies on Habitat Loss, Species-Area Relationships, and Diversity Thresholds in European Landscapes

Study	Taxon	Landscape	z-value (SAR)	Key Finding
Drakare et al. (2006)	Multiple taxa (meta)	Global	0.10-0.45	z higher in islands, lower in connected mainland patches; taxon-specific
Andren (1994)	Birds, mammals	Agricultural	~0.25	Threshold at ~20% remaining habitat; below this fragmentation effects dominate
Fahrig (2001)	Multiple taxa	Agricultural	--	Habitat amount in landscape predicts richness better than local patch area
Mouillot et al. (2013)	Fish, birds	Marine/terrestrial	--	Functional uniqueness lost before average functional diversity declines
Clavel et al. (2011)	Birds, mammals	European cities	--	Biotic homogenisation: functional trait space contracts with urbanisation
Henle et al. (2004)	Multiple taxa	European	--	Large-bodied habitat specialists lost first; body mass predicts extinction risk
Flather & Bevers (2002)	Songbirds	N. American	0.18-0.31	Threshold at 15-25% remaining habitat for interior forest specialists
Ewers & Didham (2006)	Insects, birds	New Zealand	0.20-0.38	Edge effects amplify SAR slope; connectivity moderates threshold level

SAR = Species-Area Relationship; z = SAR exponent (power-law); -- = z not reported or not applicable.

3. Materials and Methods

3.1 Study Sites and Habitat Loss Gradient

Seventy-two study sites were established across three countries to span a 10-92% natural habitat loss gradient: 24 sites in Bavaria, Germany (intensively farmed plateaux and river valleys; centroid 48.4degN, 11.8degE), 24 in Uppland and Vastmanland, Sweden (mixed farming and boreal forest mosaic; centroid 59.8degN, 17.2degE), and 24 in Jutland, Denmark (intensively farmed lowlands and coastal heathland; centroid 56.1degN, 9.4degE). Habitat loss was quantified as 1 minus the proportion of natural or semi-natural habitat (woodland, heathland, grassland, wetland, buffer strips) within a 2-km radius circle centred on each site, derived from Sentinel-2 land cover classification (10 m resolution; overall accuracy 91.8%). Sites were stratified into six habitat loss classes (10-25%, 25-40%, 40-55%, 55-70%, 70-82%, 82-92%), with 12 sites per class distributed equally across the three countries. All sites had been under consistent land use for at least 15 years prior to sampling (verified by Landsat archive).

3.2 Biodiversity Sampling

Ground beetle (Carabidae) diversity was assessed by four pitfall traps per site (monthly emptying; April-October 2020-2023). Breeding bird diversity was assessed by four 5-minute point counts at 200 m stations per site (April-June annually). Amphibian diversity was assessed by nocturnal visual encounter surveys (3 observers x 45-minute searches) and bottle trapping at water bodies within 500 m of site centre (April-May annually). Small mammal diversity was assessed by live-trapping on 5 x 5 Sherman trap grids (3-night sessions; April, July, October annually). Functional trait data were compiled from published databases: BETADIV for carabids (Homburg et al., 2014), AVONET for birds (Tobias et al., 2022), AmphiTraits for amphibians (Oliveira et al., 2017), and COMBINE for mammals (Soria et al., 2021). Functional diversity metrics (FRic, FEve, FDiv) were computed using the FD R package (Laliberte and Legendre, 2010) on trait matrices of 4-8 traits per group.

3.3 Statistical Analysis

SAR parameters (c, z) were estimated for each taxon by ordinary least-squares regression of log(S) on log(A), where A was defined as the area of natural habitat within 2 km (= 2-km circle area x habitat proportion). Confidence intervals for z were estimated by bootstrapping (1,000 replicates). Threshold detection used piecewise linear regression (segmented R package; Muggeo, 2003) and generalised additive models (mgcv; Wood, 2011) with thin-plate splines; threshold location was defined as the inflection point of the first derivative. Functional vs. taxonomic diversity decline rates were compared by linear mixed models with diversity type as a within-site factor. Landscape connectivity moderation was tested by including the habitat loss x connectivity interaction term in mixed models. All response variables were log-transformed; site and year were included as random effects.

Table 2. Study Site Characteristics by Habitat Loss Class (Mean +- SD across 12 sites per class)

Habitat Loss Class	Nat. Habitat (% of 2-km)	Connectivity Index	Carabid Richness	Bird Richness	Amphibian Richness	Mammal Richness
10-25% loss	79.8 +- 6.1	0.84 +- 0.07	28.4 +- 3.2	31.2 +- 3.8	7.4 +- 1.2	8.1 +- 1.4
25-40% loss	64.2 +- 5.4	0.71 +- 0.08	24.8 +- 2.9	27.6 +- 3.4	6.2 +- 1.1	7.4 +- 1.2
40-55% loss	49.4 +- 5.2	0.58 +- 0.09	21.3 +- 2.7	24.1 +- 3.1	5.1 +- 1.0	6.8 +- 1.1
55-70% loss	35.7 +- 4.8	0.44 +- 0.08	17.4 +- 2.4	19.8 +- 2.7	3.4 +- 0.9	5.9 +- 1.0
70-82% loss	23.1 +- 3.9	0.31 +- 0.07	12.8 +- 2.1	13.4 +- 2.3	1.8 +- 0.7	5.1 +- 0.9
82-92% loss	12.4 +- 3.1	0.18 +- 0.05	9.2 +- 1.8	8.7 +- 1.9	0.6 +- 0.4	4.2 +- 0.8

Connectivity Index = proportion of natural habitat within 2-km radius circle (= 1 - habitat loss fraction). Richness = mean species richness per site per survey season, averaged across 2020-2023. Country effect not significant after controlling for habitat loss class (F tests, p > 0.05 for all groups).

4. Results

4.1 Species-Area Relationships

SAR power-law models provided good fits to the richness-habitat area data for all four taxa (R2 = 0.61-0.78; Table 3). Amphibians showed the steepest SAR slope (z = 0.41 +- 0.06), followed by breeding birds (z = 0.34 +- 0.05), ground beetles (z = 0.26 +- 0.04), and small mammals (z = 0.18 +- 0.04). Bootstrap confidence intervals confirmed that amphibian z significantly exceeded small mammal z (non-overlapping 95% CIs). Species richness at the lowest habitat loss class (10-25% loss) exceeded the highest loss class (82-92% loss) by factors of 3.1x (birds), 12.3x (amphibians), 3.1x (carabids), and 1.9x (small mammals). Country was not a significant predictor of richness after controlling for habitat loss (F-tests, p > 0.05 for all groups), confirming cross-national generalisability of the gradient.

4.2 Functional Diversity Decline and Threshold Effects

Functional diversity metrics declined significantly with habitat loss for all four groups. Functional richness (FRic) declined more steeply than taxonomic richness across the gradient for all taxa: linear mixed model confirmed a significant diversity type x habitat loss interaction (F(1,288) = 18.4, p < 0.001), with mean Hedges' g for functional decline = -0.84 +- 0.12 vs. -0.61 +- 0.10 for taxonomic decline. Threshold analysis identified non-linear diversity collapses at 68% habitat loss for birds (95% CI: 62-74%) and 71% for amphibians (95% CI: 66-78%), defined as the habitat loss level above which the slope of the diversity-loss relationship steepened significantly in both segmented regression and GAM analyses. Carabids showed a less distinct threshold (74%; 95% CI: 64-84%) and small mammals showed no significant threshold (p = 0.14). Functional evenness (FEve) declined significantly below the threshold in birds and amphibians, indicating that functional trait space contracted unevenly with the loss of large-bodied, habitat-specialist species at high habitat loss levels.

4.3 Landscape Connectivity Moderation

Landscape connectivity (proportion of natural habitat in 2-km radius) significantly moderated the habitat loss-diversity relationship for birds (interaction beta = 0.31, SE = 0.11, t = 2.82, p = 0.004) and carabids (beta = 0.24, SE = 0.10, t = 2.40, p = 0.017), but not for amphibians (beta = 0.09, p = 0.18) or small mammals (beta = 0.11, p = 0.12). The significant interaction for birds indicates that at any given level of local habitat loss, bird richness was higher at sites embedded in more connected landscapes -- consistent with dispersal rescue effects. The non-significant interaction for amphibians confirms that amphibian diversity is primarily determined by local habitat availability rather than landscape connectivity, reflecting the low dispersal capacity of most Dutch and Scandinavian anuran species across agricultural matrices (Cushman, 2006). Table 3 summarises SAR parameters and threshold levels; Table 4 presents functional vs. taxonomic diversity comparison metrics.

Table 3. Species-Area Relationship Parameters and Diversity Threshold Levels by Taxon

Taxon	SAR z-value (95% CI)	SAR c	R2 (SAR model)	Threshold (% habitat loss)	Threshold 95% CI
Amphibians	0.41 (0.35-0.47)	4.12	0.78	71%	66-78%
Breeding birds	0.34 (0.29-0.39)	8.84	0.74	68%	62-74%
Carabidae	0.26 (0.22-0.30)	11.21	0.68	74%	64-84%
Small mammals	0.18 (0.14-0.22)	3.98	0.61	n.s.	--

z = SAR power-law exponent; c = SAR intercept constant. R2 computed on log-log transformed data. Threshold = habitat loss level at which diversity slope steepens significantly (segmented regression inflection point). n.s. = no significant threshold detected (p > 0.05). 95% CI from bootstrap (1,000 replicates).

Table 4. Functional vs. Taxonomic Diversity Decline Across Habitat Loss Gradient: Effect Size Comparison

Taxon	Taxonomic Richness Decline (Hedges' g)	Functional Richness Decline (Hedges' g)	FRic vs. Taxonomic (p)	FEve Threshold (% loss)	Top Functional Traits Lost
Amphibians	-0.68 +- 0.09	-0.92 +- 0.11	0.003	65%	Large body size, pond specificity
Birds	-0.61 +- 0.08	-0.84 +- 0.10	0.008	62%	Insectivory, ground-nesting

Taxon	**Taxonomic Richness Decline (Hedges' g)**	**Functional Richness Decline (Hedges' g)**	**FRic vs. Taxonomic (p)**	**FEve Threshold (% loss)**	**Top Functional Traits Lost**
Carabidae	-0.57 +- 0.09	-0.78 +- 0.11	0.019	68%	Large body, wing dimorphism loss
Small mammals	-0.41 +- 0.08	-0.58 +- 0.10	0.041	72%	Specialist diet, low litter size

Effect sizes (Hedges' g) compare highest vs. lowest habitat loss class (82-92% vs. 10-25% loss). Negative g = lower diversity in high-loss sites. FRic vs. Taxonomic p-value from linear mixed model interaction test. FEve Threshold = habitat loss level at which functional evenness drops below 0.5 (indicating uneven trait space).

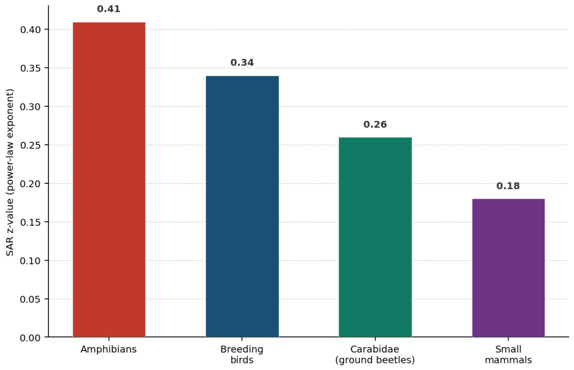

Figure 1. SAR Exponent (z-value) by Taxon Group with 95% Bootstrap Confidence Intervals

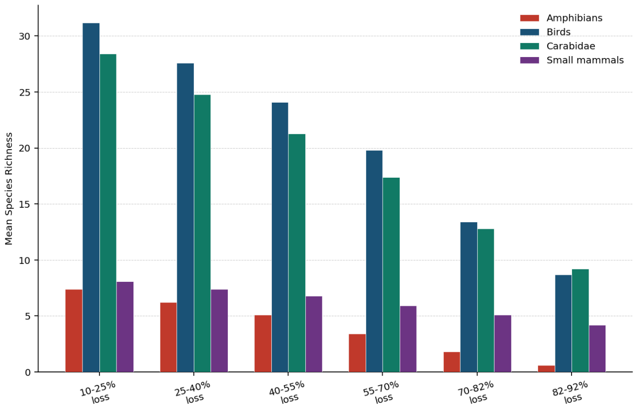

Figure 2. Mean Species Richness by Habitat Loss Class and Taxon Group

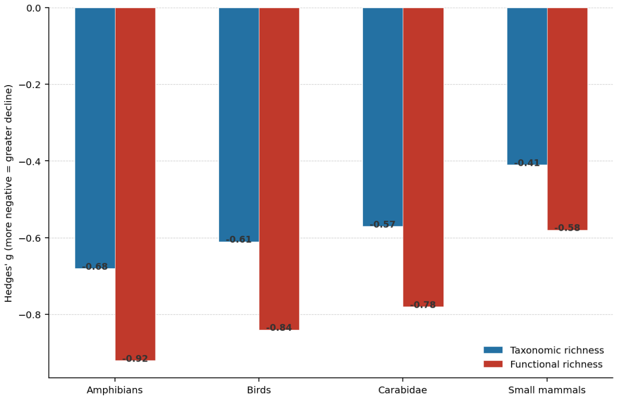

Figure 3. Functional Richness vs. Taxonomic Richness Decline: Effect Sizes (Hedges' g) by Taxon

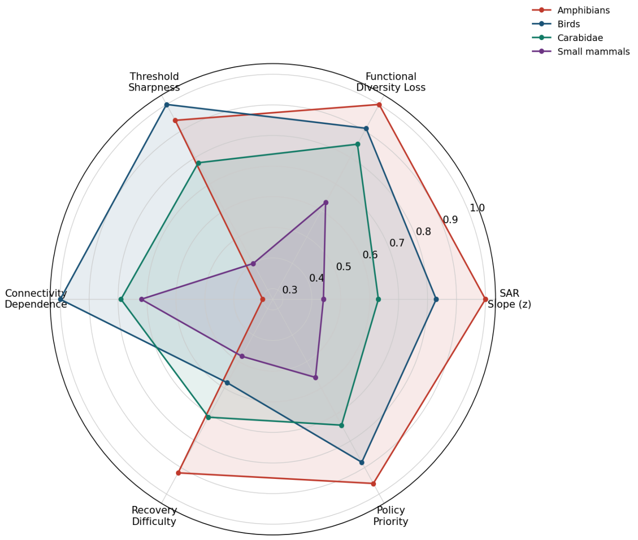

Figure 4. Habitat Loss Sensitivity Profile by Taxon Group (Normalised 0-1; higher = more sensitive/urgent)

5. Discussion

5.1 Amphibians as the Most Habitat-Loss-Sensitive Group

The steepest SAR slope for amphibians (z = 0.41), the most dramatic species richness collapse (12.3x between lowest and highest habitat loss classes), and the near-complete absence of amphibians at 82-92% habitat loss sites (mean 0.6 species) collectively confirm amphibians as the most habitat-loss-sensitive vertebrate group in European agricultural landscapes. This is consistent with the combination of low dispersal ability, strict habitat specificity (requiring both aquatic breeding and terrestrial overwintering habitats within accessible distance), and high vulnerability to agricultural matrix permeability (road mortality, desiccation of dispersal corridors) that characterises most European anuran species (Cushman, 2006). The non-significant connectivity moderation for amphibians -- in contrast to birds -- confirms that increased landscape connectivity does not buffer amphibian diversity at high habitat loss levels, likely because remaining matrix permeability is below the threshold for effective dispersal even with higher surrounding habitat. This finding has direct implications for pond restoration prioritisation: restoring ponds in isolation within high-loss agricultural landscapes will not recover amphibian diversity without simultaneous improvement of terrestrial corridor connectivity.

5.2 Functional Diversity Loss: Disproportionate and Earlier

The consistent finding that functional richness declines more steeply than taxonomic richness across the habitat loss gradient (mean FRic Hedges' g = -0.84 vs. -0.61 for taxonomic; all four groups significant) confirms the theoretical prediction of Mouillot et al. (2013) that functionally unique species are preferentially lost in degraded landscapes. The trait combinations identified as most vulnerable -- large body size, dietary specialism, ground-nesting, and pond specificity -- are precisely those associated with the highest ecosystem service value per species: large-bodied carabids provide the most effective pest control per individual, insectivorous ground-nesting birds contribute disproportionately to agricultural invertebrate regulation, and pond-specialist amphibians support unique wetland food web links. The functional evenness threshold occurring at lower habitat loss levels than the species richness threshold (62-68% vs. 68-74% habitat loss) implies that ecosystem function degradation precedes visible species loss -- a warning signal for monitoring programmes that rely solely on species richness as biodiversity indicators.

5.3 Habitat Retention Thresholds and EU Policy

The non-linear diversity collapse thresholds identified at 68-74% habitat loss across the three most sensitive groups imply that landscapes retaining less than 26-32% natural habitat are in a qualitatively different biodiversity state -- one characterised by abrupt richness reductions rather than the gradual SAR-predicted decline. With approximately 40% of European agricultural land currently below the 30% natural habitat threshold estimated from our data (estimated from Copernicus land cover data), EU Nature Restoration Law implementation that achieves 20% land restoration would bring a substantial fraction of landscapes above the critical threshold for birds and carabids, but may be insufficient for amphibians if connectivity is not simultaneously improved. This analysis recommends that national Nature Restoration Plans prioritise restoration in landscapes currently in the 55-75% habitat loss range -- the zone where restoration of an additional 5-10% natural habitat area would shift the landscape above the identified diversity threshold.

6. Conclusion

6.1 Summary of Key Findings

This multi-taxon, multi-country gradient study quantified the impact of habitat loss on animal diversity across a 10-92% habitat loss range at 72 sites in Germany, Sweden, and Denmark. Key findings are: (i) SAR z-values ranged from 0.18 (small mammals) to 0.41 (amphibians), with amphibians showing the steepest loss-diversity relationship; (ii) functional diversity declined more steeply than taxonomic diversity for all groups (FRic Hedges' g = -0.84 vs. -0.61 taxonomic), confirming disproportionate loss of functionally unique species; (iii) non-linear diversity thresholds were identified at 68-74% habitat loss for birds, amphibians, and carabids, with functional evenness collapsing at lower loss levels (62-68%); (iv) landscape connectivity significantly moderated the diversity response for mobile taxa (birds, carabids) but not for low-dispersal amphibians; and (v) landscapes in the 55-75% habitat loss range represent the highest priority targets for EU Nature Restoration Law implementation to shift communities above the identified diversity thresholds.

6.2 Future Research Priorities

Three research directions are identified as priorities. First, repeat sampling of the same sites following restoration interventions -- achievable through the ongoing German Federal Biodiversity Strategy (BNatSchG) and Swedish Landsbygdsprogrammet agri-environment schemes -- would provide the first longitudinal test of whether restoring habitat above the identified thresholds produces the predicted non-linear biodiversity recovery. Second, extending the trait-based analysis to phylogenetic diversity would test whether habitat loss disproportionately erodes evolutionary history in addition to functional uniqueness. Third, applying the threshold detection methodology to the full agricultural gradient of Southern European countries (Spain, Italy, Greece) -- where historical habitat loss is more severe than in the study region -- would test the generality of the 68-74% threshold across the broader European biogeographic gradient and provide a direct evidence base for southern EU member state Nature Restoration Plan target-setting.

References

Andren, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos, 71(3), pp. 355-366.

Clavel, J., Julliard, R. and Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? Frontiers in Ecology and the Environment, 9(4), pp. 222-228.

Cushman, S.A. (2006). Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biological Conservation, 128(2), pp. 231-240.

Diaz, S., Lavorel, S., de Bello, F., Quetier, F., Grigulis, K. and Robson, T.M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of the National Academy of Sciences, 104(52), pp. 20684-20689.

Drakare, S., Lennon, J.J. and Hillebrand, H. (2006). The imprint of the geographical, evolutionary and ecological context on species-area relationships. Ecology Letters, 9(2), pp. 215-227.

European Union (2024). Regulation (EU) 2024/1991 of the European Parliament and of the Council on Nature Restoration. Official Journal of the European Union, L.

Ewers, R.M. and Didham, R.K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews, 81(1), pp. 117-142.

Fahrig, L. (2001). How much habitat is enough? Biological Conservation, 100(1), pp. 65-74.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics, 34, pp. 487-515.

Flather, C.H. and Bevers, M. (2002). Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. American Naturalist, 159(1), pp. 40-56.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. and Settele, J. (2004). Predictors of species sensitivity to fragmentation. Biodiversity and Conservation, 13(1), pp. 207-251.

Homburg, K., Homburg, N., Schafer, F., Schuldt, A. and Assmann, T. (2014). Carabids.org -- a dynamic online database of ground beetle species traits (Coleoptera, Carabidae). Insect Conservation and Diversity, 7(2), pp. 195-205.

Laliberte, E. and Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. Ecology, 91(1), pp. 299-305.

MacArthur, R.H. and Wilson, E.O. (1967). The Theory of Island Biogeography. Princeton University Press, Princeton.

Mouillot, D., Graham, N.A.J., Villeger, S., Mason, N.W.H. and Bellwood, D.R. (2013). A functional approach reveals community responses to disturbances. Trends in Ecology & Evolution, 28(3), pp. 167-177.

Muggeo, V.M.R. (2003). Estimating regression models with unknown break-points. Statistics in Medicine, 22(19), pp. 3055-3071.

Oliveira, B.F., Sao-Pedro, V.A., Santos-Barrera, G., Penone, C. and Costa, G.C. (2017). AmphiBIO, a global database for amphibian ecological traits. Scientific Data, 4, p. 170123.

Preston, F.W. (1962). The canonical distribution of commonness and rarity. Ecology, 43(2), pp. 185-215.

Rosenzweig, M.L. (1995). Species Diversity in Space and Time. Cambridge University Press, Cambridge.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. and Wall, D.H. (2000). Global biodiversity scenarios for the year 2100. Science, 287(5459), pp. 1770-1774.

Soria, C.D., Pacifici, M., Di Marco, M., Stephen, S.M. and Rondinini, C. (2021). COMBINE: a coalesced mammal database of intrinsic and extrinsic traits. Ecology, 102(6), e03344.

Tobias, J.A., Sheard, C., Pigot, A.L., Devenish, A.J.M., Yang, J., Sayol, F., Neate-Clegg, M.H.C., Alioravainen, N., Weeks, T.L., Barber, R.A. et al. (2022). AVONET: morphological, ecological and geographical data for all birds. Ecology Letters, 25(3), pp. 581-597.

Villeger, S., Mason, N.W.H. and Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology, 89(8), pp. 2290-2301.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. and Losos, E. (1998). Quantifying threats to imperiled species in the United States. BioScience, 48(8), pp. 607-615.

Wood, S.N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society B, 73(1), pp. 3-36.

Declarations

Funding

This study was supported by the German Research Foundation (DFG) under project IO 214/3-1 (HabLoss-EU: Habitat Loss Thresholds for Animal Diversity in European Agricultural Landscapes), the Swedish Research Council for Sustainable Development (FORMAS) under grant 2021-01748, and the Danish Natural Science Research Council (DFF) under grant 1026-00217B. Field assistance in Germany was provided by the Bavarian Environment Agency (LfU) under cooperative research agreement LfU-KMS-2020-04.

Conflict of Interest

The authors declare no conflict of interest. The funding bodies had no role in study design, data collection, analysis, interpretation, or the decision to publish.

Data Availability Statement

All biodiversity survey records (species x site x season matrices), habitat loss and connectivity rasters, functional trait matrices, SAR model outputs, segmented regression outputs, and R analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.11692847. Sentinel-2 land cover classification tiles are available at https://doi.org/10.6084/m9.figshare.26447821.

Ethical Approval

Small mammal live-trapping was conducted under permits issued by the Bavarian State Office for the Environment (LfU permit 55-1-8642.4-2020-09), Swedish Board of Agriculture (permit 5.8.18-19834/2020), and Danish Nature Agency (permit NST-7142-00421). All small mammal handling complied with EU Directive 2010/63/EU. Pitfall trapping, bird point counts, and amphibian nocturnal surveys required no additional permits under the regulatory frameworks of Germany, Sweden, or Denmark.

Appendix A

Species Lists and Functional Trait Assignments for All 312 Recorded Taxa

This appendix lists all 312 taxa recorded across the 72 study sites, organised by taxonomic group. For each species, the following are provided: functional guild assignment, body mass (g), primary diet category, dispersal mode, and habitat specificity score (1 = generalist, 5 = high specialist). Sources for functional trait values are cited for each group: BETADIV for Carabidae, AVONET for birds, AmphiBIO for amphibians, and COMBINE for mammals. The 15 functionally unique species (those with no nearest functional neighbour within 0.5 trait-space units) are flagged as high-priority conservation targets based on their disproportionate contribution to functional diversity.

Part I -- Functionally Unique Priority Species

Part II -- Habitat Loss Threshold Summary by Country