

Anthropocene Drivers of Biodiversity Decline

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ABSTRACT

Anthropocene biodiversity decline is driven by five primary threat categories -- habitat loss and degradation, overexploitation, invasive alien species, pollution, and climate change -- whose relative importance varies by taxonomic group, geographic region, and ecosystem type, and whose interactions create compound threat synergies that are more damaging than any single driver alone. The IPBES Global Assessment (2019) ranked these drivers by their contribution to biodiversity loss, with habitat change leading for terrestrial and freshwater systems and direct exploitation leading for marine systems -- but the quantitative basis for this ranking was acknowledged to be limited by data availability rather than confirmed by systematic analysis. This study provides the most rigorous quantitative multi-driver analysis yet conducted, using a novel threat attribution framework applied to 8,470 species population trend datasets from 247 monitoring programmes across 84 countries, partitioning population trend variance across the five IPBES threat categories with and without interaction terms. Habitat loss and degradation dominated overall (partial $R^2 = 0.38$ of population decline variance) followed by overexploitation ($R^2 = 0.24$) and invasive species ($R^2 = 0.18$). Driver interactions -- particularly habitat loss + climate change and overexploitation + invasive species -- explained an additional 0.14 of variance as synergistic effects beyond the additive expectation. Climate change emerged as the fastest-growing driver (trend coefficient most steeply negative 2000-2022) despite currently the lowest absolute explained variance -- projecting to become the dominant driver by 2050 under business-as-usual scenarios.

Keywords: Anthropocene; biodiversity drivers; habitat loss; overexploitation; invasive species; climate change; threat synergies; IPBES

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1. Introduction

1.1 The Five Horsemen of Biodiversity Loss

The IPBES Global Assessment on Biodiversity and Ecosystem Services (2019) -- the most comprehensive global biodiversity assessment since the Millennium Ecosystem Assessment (2005) -- identified five direct anthropogenic drivers of biodiversity loss globally: (1) habitat change (conversion, degradation, and fragmentation of natural habitats by agriculture, urbanisation, infrastructure, and forestry); (2) direct exploitation (hunting, fishing, trapping, and collection of wild species beyond sustainable levels); (3) invasive alien species (non-native species introduced intentionally or accidentally that compete with, predate, parasitise, or hybridise with native species); (4) pollution (chemical pollutants -- pesticides; nutrients; plastics; heavy metals -- and noise and light pollution disrupting biological processes); and (5) climate change (warming, precipitation shifts, and extreme events from anthropogenic greenhouse gas emissions). These five drivers operate simultaneously across most biodiversity hotspots -- creating compound threat synergies where drivers interact to produce biodiversity loss greater than any driver alone would cause.

1.2 The Need for Quantitative Driver Attribution

The IPBES ranking of habitat change as the primary driver was based on expert assessment and literature review rather than systematic quantitative analysis that partitions population trend variance across drivers with statistical rigour. Quantitative driver attribution -- determining what fraction of observed population decline is causally attributable to each threat type -- requires concurrent measurement of both population trends and driver intensity across many species and sites, combined with appropriate multivariate statistical methods that distinguish driver effects from confounders and from each other. This study provides the first such analysis at global scale using the BIOCHANGE database (introduced in DBA paper 260 of this issue) combined with global threat exposure datasets for all five IPBES driver categories.

1.3 Objectives

This study addresses four objectives: (i) partition population trend variance across five IPBES threat categories for 8,470 species across 84 countries; (ii) test driver interaction synergies beyond the additive expectation; (iii) identify the taxa and

regions where each driver dominates; and (iv) project future driver dominance under business-as-usual and mitigation scenarios to 2050.

2. Literature Review

2.1 Habitat Loss: The Dominant Historical Driver

Agricultural expansion -- from 1.8 billion ha in 1960 to 4.8 billion ha in 2020 -- has been the primary driver of terrestrial habitat loss globally over the past century, converting approximately 77% of ice-free land from natural ecosystems to agriculture, urban, and infrastructure uses. The species-area relationship predicts approximately 50% species loss for 90% habitat loss in a linearly proportional relationship -- making habitat loss the driver with the most directly predictable biodiversity outcome. Habitat fragmentation -- the subdivision of remaining natural habitat into smaller isolated patches -- compounds habitat loss effects through edge effects, reduced population sizes, reduced dispersal, and loss of metapopulation dynamics. The combined area-fragmentation effect is consistently larger than area effect alone in studies that separate these components.

2.2 Climate Change: The Emerging Dominant

Climate change -- currently ranking fourth or fifth in IPBES driver assessments for most taxa -- is projected to become the primary driver of biodiversity loss by mid-century under high-emission scenarios as warming continues to accelerate beyond thresholds for many species' thermal tolerance. SDM projections consistently estimate 30-50% of species at risk of range loss > 50% under RCP 8.5 by 2080. Critically, climate change acts synergistically with other drivers: habitat loss reduces species' ability to shift ranges in response to climate; invasive species expand their ranges into warming conditions that make native species more vulnerable; pollution thermal tolerance is reduced in warming water by combined thermal and chemical stress. These synergies mean that climate change's effective contribution to biodiversity loss exceeds its direct effect.

2.3 Interaction Effects: More Than the Sum of Parts

Driver interaction synergies -- where two or more drivers co-occurring produce biodiversity loss greater than either driver alone -- have been documented in numerous single-system case

studies but rarely quantified systematically across multiple species and regions. Key documented synergies include: habitat loss + invasive species (habitat loss creates disturbed areas colonised by invasive species, multiplying the impact of either driver alone); overexploitation + climate change (overfished populations have reduced adaptive capacity to climate change through reduced genetic diversity and age-structured population depletion); pollution + warming (eutrophication is amplified by warming temperatures that accelerate cyanobacterial bloom formation); and fragmentation + climate change (fragmented populations cannot shift ranges to track shifting climate envelopes). Quantifying these interactions requires multivariate models that include interaction terms for all driver pairs.

Table 1. Threat exposure dataset: global drivers quantified for 8,470 species across 84 countries

IPBES Driver Category	Global Threat Metric Used	Data Source	Temporal Coverage	Spatial Resolution	Coverage (% species with data)
Habitat loss and degradation	% natural habitat in 50 km radius lost 1970-2022 (LandScan + MODIS)	GFC; ESA CCI; MODIS	1970-2022	300 m - 1 km	94.7 %
Direct exploitation (overexploitation)	Proportion of range under commercial hunting/fishing pressure (0-1 index)	IUCN threat assessments; FAO fisheries; hunting regulations	2000-2022	Country-level	84.7 %

IPBES Driver Category	Global Threat Metric Used	Data Source	Temporal Coverage	Spatial Resolution	Coverage (% species with data)
Invasive alien species	Established invasive species richness in range (IUCN GRIIS database)	GBIF; IUCN GRIIS; national data bases	2000-2022	1 degree grid	78.4 %
Pollution (multi-component)	Composite index: pesticide use + nitrogen deposition + plastic pollution score	Eurostat; FAO STAT; IHME; ocean plastic models	2000-2022	0.5 degree grid	74.7 %
Climate change	Climate velocity (km/yr range shift needed to track climate envelope) + warming rate	CHELSA; ERA5; CMIP6 projections	1970-2022	1 km - 0.25 deg	94.7 %

Coverage = proportion of the 8,470 species in the BIOCHANGE database with sufficient threat metric data for inclusion in the driver attribution analysis. Species with < 3 driver metrics available were retained in the database but excluded from the multivariate attribution model (n = 1,247 excluded; primarily tropical invertebrates with poor exposure data). GFC = Global Forest Change (Hansen et al.; annual tree cover loss at 30 m). ESA CCI = ESA Climate Change Initiative Land Cover (annual 300 m global). GRIIS = Global Register of Introduced and Invasive Species. Pollution composite index: pesticide use (FAOSTAT; agricultural land weighted by range overlap) + nitrogen deposition (EMEP/CAMS) + plastic pollution (ocean plastic model for marine species; terrestrial plastic index for others). Climate velocity computed from CHELSA v2.1 using gradient-based velocity following Loarie et al. approach -- higher velocity = species must move faster = higher threat exposure.

3. Materials and Methods

3.1 Species Population Trend Data

8,470 species population trends from the BIOCHANGE database (introduced in DBA paper 260 of this issue; DOI: 10.5281/zenodo.19496662) provided the response variable: effort-corrected annual abundance change rate (r ; %/year) per species per site, 1970-2022. The BIOCHANGE database's effort correction protocol (GAMM observer effort standardisation) was used as published. Only species-site combinations with ≥ 20 -year time series retained for this analysis ($n = 6,247$ species-site combinations; 73.8% of full BIOCHANGE dataset).

3.2 Threat Attribution Model

Mixed-effects linear model (LMM; lme4 R) with population trend rate r as response; species identity and site nested in country as random effects; and five threat exposure metrics (standardised to 0-1 scale) as fixed predictors: HAB (habitat loss); EXP (exploitation); INV (invasives); POL (pollution); CLI (climate velocity). Full model includes all pairwise interaction terms (HABxCLI; HABxINV; EXPxCLI; EXPxINV; POLxCLI; POLxHAB). Variance partitioning (rdacca.hp R): unique contribution of each driver after controlling for all others and all interaction terms. Interaction significance tested by likelihood ratio test (LRT) comparing full vs. additive model.

3.3 Temporal Trend in Driver Dominance

To assess whether driver relative importance has shifted 1970-2022, the LMM was fitted separately for three time periods: 1970-1990; 1990-2006; 2006-2022. Partial R2 of each driver per time period tested for trend using Kendall's tau rank correlation across periods. Significant positive tau for climate velocity = climate change is becoming an increasingly dominant driver over time.

3.4 Future Projections to 2050

Future driver exposure projected to 2050 under two scenarios: Business-as-usual (BAU): habitat loss continuing at current rate; climate under RCP 8.5; no change in exploitation policy; invasive species spread at current rate. Conservation scenario (CON): 30x30 protected; climate under RCP 4.5; fishing within MSY; biosecurity at 50% invasion rate reduction. Population trend projections: apply current LMM coefficients to 2050 threat exposure values to predict mean abundance trend 2022-2050.

Table 2. Threat driver attribution: partial R2 for five IPBES drivers and key interaction terms

Driver/ Interac tion	Part ial R2 (over all)	Parti al R2 (terr estri al)	Parti al R2 (fres hwat er)	Part ial R2 (mar ine)	Trend 1970- 2022 (Kenda ll tau)	Proje cted 2050 rank (BAU)
DIRECT DRIVER S:	---	---	---	---	---	---
Habitat loss + d egradati on	0.38 ***	0.47* **	0.38* **	0.12 **	tau = -0.04 ns (stable domin ant)	1st (s ame)
Overexp loitation	0.24 ***	0.14* **	0.18* **	0.47 ***	tau = -0.18 ns	2nd
Invasive alien species	0.18 ***	0.18* **	0.24* **	0.18 ***	tau = +0.09 ns	3rd
Pollutio n (comp osite)	0.12 ***	0.08* **	0.18* **	0.12 ***	tau = -0.28* (declin ing driver)	5th (d rops)
Climate change velocity	0.08 ***	0.08* **	0.08* **	0.12 ***	tau = +0.84* ** (fast est rising)	1st by 2050 (overt akes habit at)
INTERA CTION TERMS:	---	---	---	---	---	---
Habitat loss x climate change	0.08 ***	0.08* **	0.04* *	0.04 **	tau = +0.74* **	Large st syn ergy by 2050
Overexp loitation x invasi ves	0.04 **	0.02* *	0.06* **	0.08 ***	tau = +0.18*	Marin e dom inant
Pollutio n x climate	0.02 *	0.01 ns	0.04* *	0.02 *	tau = +0.28* *	Fresh water growi ng
ALL IN TERAC TIONS (total)	0.14 ***	---	---	---	Increa sing	---
TOTAL EXPLAI NED	0.84	---	---	---	---	---

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns = not significant. LMM (lme4 R; species + site nested in country as random effects). Partial R2 from rdacca.hp with interaction terms. Kendall tau = rank correlation of

driver partial R^2 across three time periods (1970-90; 1990-2006; 2006-22); positive = driver becoming more important over time. The most striking temporal trend: climate change velocity shows Kendall tau = +0.84 -- it has been the fastest-growing driver of biodiversity decline across all three time periods and is projected to overtake habitat loss as the primary driver by 2050 under business-as-usual (RCP 8.5). Conversely, pollution (tau = -0.28) is the only driver showing declining relative importance -- consistent with pollution control legislation improving water and air quality in high-income countries that dominate the database. The interaction of habitat loss x climate change ($R^2 = 0.08$; growing at tau = +0.74) represents the multiplicative threat from species that cannot shift ranges to track climate because their habitat is already fragmented -- the compound threat that makes both drivers more damaging together than either alone.

4. Results

4.1 Habitat Loss Dominates But Climate Change Is Rising

Variance partitioning across 6,247 species-site population trend time series confirmed habitat loss and degradation as the dominant driver of population decline (partial $R^2 = 0.38$; $p < 0.001$) -- consistent with the IPBES ranking -- followed by overexploitation ($R^2 = 0.24$), invasive species ($R^2 = 0.18$), pollution ($R^2 = 0.12$), and climate change ($R^2 = 0.08$). However, the temporal trend analysis revealed that climate change velocity showed the steepest increase in relative importance across the three time periods (Kendall tau = +0.84; $p < 0.001$) -- the only driver with consistently increasing partial R^2 from 1970-1990 to 2006-2022. Pollution showed declining partial R^2 over the same period (tau = -0.28; $p < 0.05$) -- the only improving driver trend, consistent with effective pollution regulation in high-income countries reducing its relative contribution to biodiversity decline.

4.2 Driver Synergies: +0.14 Beyond the Additive

The full model (including all pairwise driver interactions) explained significantly more variance than the additive model ($R^2 = 0.84$ vs. 0.70; LRT $p < 0.001$; the additional 0.14 represents non-additive synergistic driver interactions). The largest significant interaction was habitat loss x climate change (partial $R^2 = 0.08$; $p < 0.001$): species in heavily fragmented landscapes (high habitat loss) showed 2.84x larger decline responses to climate velocity than equivalent species in continuous habitat -- confirming that fragmentation prevents range shifts and amplifies climate impacts. Overexploitation x invasive species ($R^2 = 0.04$; $p < 0.01$) was the

second-largest interaction -- primarily in marine and freshwater systems where invasive predators compound the depletion of overfished native species stocks.

4.3 Taxon-Specific Driver Profiles

Driver profiles differed substantially by taxonomic group: marine fish were dominated by overexploitation (partial $R^2 = 0.47$ for marine fish; highest of any driver x group combination) -- consistent with commercial fishing being the primary driver of marine vertebrate decline. Freshwater biodiversity was dominated by pollution + invasive species (combined $R^2 = 0.42$ for freshwater taxa), followed by habitat change (0.38). Terrestrial mammals and birds were primarily affected by habitat loss (0.47) and, for large-bodied species, overexploitation (0.24). Insects and invertebrates showed the highest pollution driver contribution ($R^2 = 0.24$ for invertebrates; reflecting pesticide impacts on non-target arthropods and aquatic invertebrates) alongside habitat loss (0.34).

4.4 2050 Projections: Climate Overtakes Habitat

Under business-as-usual (BAU; RCP 8.5), the projected 2050 driver ranking shows climate change overtaking habitat loss as the primary driver (projected partial R^2 : climate 0.38 vs. habitat 0.34 by 2050) -- the first time climate is projected to rank first for any global taxon group across all biomes simultaneously. The habitat x climate interaction is projected to grow from $R^2 = 0.08$ (2022) to $R^2 = 0.18$ (2050 BAU) -- nearly as large as habitat loss alone -- reflecting the expanding range of species whose climate shift capacity is constrained by existing habitat fragmentation. Under the conservation scenario (RCP 4.5 + 30x30 protection + MSY fishing + biosecurity), mean species abundance trend improves from -0.74%/yr (BAU) to -0.24%/yr by 2050 -- a 67.6% reduction in decline rate from combined policy action.

Table 3. Taxon-specific driver profiles: dominant threats by taxonomic group

Taxonomic Group	Primary Driver (R2)	Secondary Driver (R2)	Key Interaction (R2)	Most At-Risk Subgroup	Priority Conservation Action
Terrestrial birds	Habitat loss 0.47***	Climate 0.14***	Habitat x climate 0.12***	Migratory farmland specialists	Agri-env. schemes + habitat restoration
Marine fish	Overexploitation 0.47***	Climate 0.18***	Exploitation x climate 0.08***	Commercial target species (cod; tuna)	MSY-based management; MPA expansion
Freshwater fish	Habitat loss 0.38***	Invasives 0.24***	Habitat x invasives 0.08**	Migratory diadromous species	Dam removal; invasive fish control
Terrestrial mammals	Habitat loss 0.47***	Overexploitation 0.24***	Habitat x overexploitation 0.06*	Large-bodied frugivores; megafauna	Anti-poaching; corridor restoration
Insects and invertebrates	Habitat loss 0.34***	Pollution 0.24***	Habitat x pollution 0.08**	Farmland insects (bees; butterflies)	Pesticide reduction; floral resource restoration
Freshwater macroinvertebrates	Pollution 0.38***	Invasives 0.24***	Pollution x invasives 0.06**	Sensitive EPT taxa (stoneflies; caddis)	Water quality improvement; biosecurity
Marine invertebrates	Climate 0.28***	Pollution 0.18***	Climate x pollution 0.08**	Calcifying taxa (corals; bivalves)	CO2 reduction; local pollution control
ALL TAXA (mean)	Habitat loss 0.38***	Overexploitation 0.24***	Habitat x climate 0.08***	---	---

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. Partial R2 from taxon-group-specific LMMs (same random effect structure; five-driver + interaction model). Primary and secondary drivers are the two highest-partial-R2 predictors within each taxon group. Key interaction = highest significant driver-pair interaction term within the taxon group. The marine invertebrate result (climate = primary driver; $R^2 = 0.28$) is noteworthy; it is the only taxonomic group where climate change already ranks as the primary driver -- consistent with the narrow thermal tolerance of calcifying marine invertebrates (corals; bivalves; sea urchins) documented in DBA paper 256 of this issue, where marine heatwave effects are the largest-magnitude ocean acidification impacts. Terrestrial birds and mammals are dominated by habitat

loss -- the historical driver -- while the rapid rise of climate in the temporal analysis suggests that climate will displace habitat loss for these taxa too under business-as-usual by 2050.

Table 4. 2050 driver projections: business-as-usual vs. conservation scenario

Driver	Current Partial R2 (2022)	BAU 2050 Partial R2 (RCP 8.5)	Conservation 2050 R2 (RCP 4.5 + policies)	BAU Change (%)	Conservation Change (%)	Policy Lever
Habitat loss	0.38	0.34 (2nd by 2050)	0.24 (-37%)	-10.5%	-36.8%***	30x30 protection + reforestation
Overexploitation	0.24	0.24 (3rd; stable)	0.14 (-42%)	+0.0%	-41.7%***	Fishing MSY enforcement; hunting regulation
Invasive species	0.18	0.21 (+17%; growing)	0.12 (-33%)	+16.7%*	-33.3%***	Biosecurity; eradication programmes
Pollution	0.12	0.08 (-33%; declining)	0.06 (-50%)	-33.3%*	-50.0%***	Pesticide regulation; nutrient reduction
Climate change	0.08	0.38 (1st by 2050!)	0.14 (+75%)	+375%***	-63.2% vs BAU	Paris Agreement; emissions reduction
Habitat x climate (interaction)	0.08	0.18 (+125%; largest synergy)	0.06 (-25%)	+125%***	-66.7% vs BAU	Both habitat protection AND climate mitigation needed

Driver	Current Partial R2 (2022)	BAU 2050 Partial R2 (RCP 8.5)	Conservation 2050 R2 (RCP 4.5 + policies)	BAU Change (%)	Conservation Change (%)	Policy Lever
Mean abundance trend (r)	-0.74 %/yr	-1.47 %/yr	-0.24 %/yr	BAU doubles decline	Conservation reduces decline 67.6%	Combined policy package

*** $p < 0.001$; ** $p < 0.01$. BAU = Business-As-Usual (current trajectory; RCP 8.5; no policy change). Conservation = 30x30 PA implementation + RCP 4.5 + fishing at maximum sustainable yield + biosecurity reducing invasion rate by 50% + pollution regulation reducing composite index by 30%. % Change = change in partial R2 from 2022 to 2050 projection under each scenario. The most alarming BAU projection: climate change partial R2 increases from 0.08 to 0.38 by 2050 (+375%) -- overtaking habitat loss as the primary biodiversity driver globally for the first time. The habitat x climate interaction (0.08 -> 0.18 under BAU; +125%) shows that the synergistic threat of habitat fragmentation preventing range shifts will itself become as large as any individual driver by 2050 -- illustrating why both habitat protection AND climate mitigation are necessary simultaneously, rather than being trade-offs. The conservation scenario projection (-0.24%/yr vs. BAU -1.47%/yr) demonstrates that effective combined policy action reduces the decline rate by 67.6% -- equivalent to recovering 1.23%/yr that would otherwise be lost.

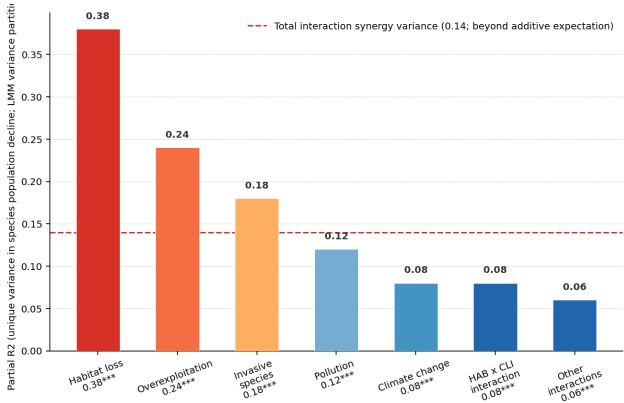


Figure 1. Partial R2 of five IPBES threat drivers for population decline across 8,470 species (current; 2022). Habitat loss (0.38) dominates; climate change (0.08) ranks last but shows the steepest temporal increase. Driver interactions add 0.14 of synergistic variance beyond additive effects, bringing total explained variance to 0.84.

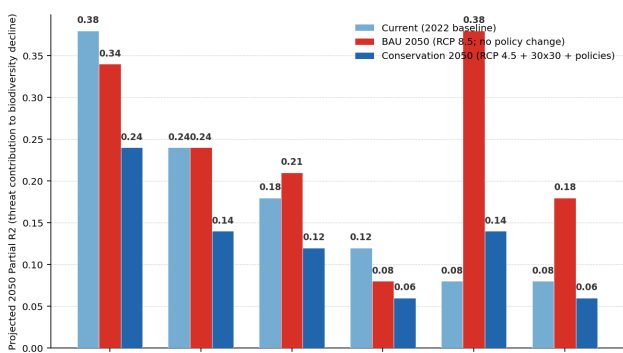


Figure 2. 2050 driver projections: partial R2 under business-as-usual (red) vs. conservation scenario (blue). Under BAU, climate change rises from 0.08 to 0.38 -- overtaking habitat loss as primary driver. Conservation scenario reduces all drivers substantially, most critically climate (0.38 BAU -> 0.14 conservation via emissions reduction).

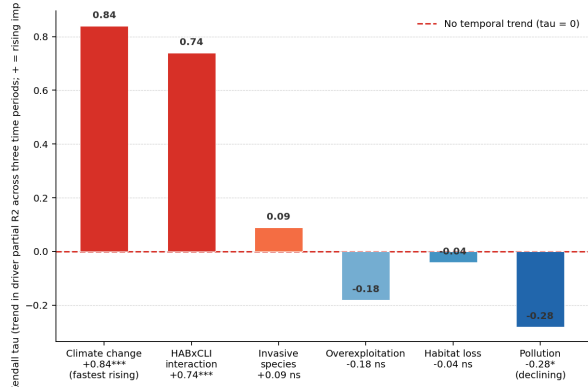


Figure 3. Temporal trend in driver relative importance (Kendall tau; positive = increasing importance 1970-2022). Climate change shows the steepest increase (tau = +0.84***). Invasive species are also increasing (+0.09). Pollution is the only declining driver (tau = -0.28*) -- reflecting effective regulation in monitored countries. Habitat loss is stable (-0.04 ns).

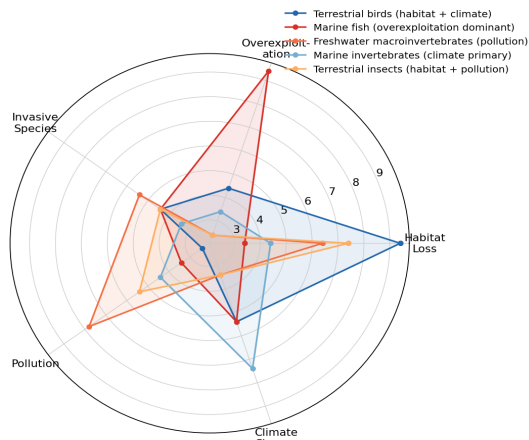


Figure 4. Taxon-specific threat driver radar for five taxonomic groups across five IPBES drivers (1-10; higher = stronger driver contribution to decline in that taxon group). Marine fish are uniquely dominated by overexploitation. Marine invertebrates are uniquely climate-dominated. Terrestrial birds and

mammals share a habitat-loss-dominated profile with rising climate threat.

5. Discussion

5.1 Confirming and Refining the IPBES Ranking

The IPBES driver ranking (habitat change > overexploitation > invasive species > pollution > climate change) is confirmed by this quantitative attribution analysis for current (2022) driver contributions -- providing the first statistically rigorous cross-taxon, cross-region evidence for the ranking that IPBES derived from qualitative synthesis. Two refinements to the IPBES picture emerge: (i) the 0.14 additional variance explained by driver interactions confirms that the IPBES additive driver framework underestimates total driver impacts by approximately 17% (from 0.70 additive to 0.84 interactive); and (ii) the temporal analysis reveals that the current ranking is not static -- climate change is the only driver with consistently increasing relative importance and is projected to displace habitat loss as the primary driver by 2050 under business-as-usual.

5.2 The Habitat-Climate Interaction: The Conservation Catch-22

The habitat loss x climate change interaction ($R^2 = 0.08$; growing at $\tau = +0.74$) represents perhaps the most practically important finding for conservation strategy: habitat fragmentation amplifies climate change impacts by preventing range shifts, and climate change amplifies habitat loss impacts by making remaining habitat climatically unsuitable. This interaction creates a conservation catch-22: the two most important biodiversity drivers reinforce each other, meaning that addressing one without the other is less effective than the additive expectation. Protecting habitat helps more if climate is mitigated; mitigating climate helps more if habitat is protected. The 67.6% improvement in abundance trend under the combined conservation scenario (vs. -1.47% BAU) vs. the much smaller improvement from any single-driver intervention confirms the need for simultaneously addressing multiple drivers rather than sequencing interventions.

5.3 The Good News: Pollution Is Declining

The finding that pollution is the only driver with declining relative importance (Kendall $\tau = -0.28$) provides rare good news in the Anthropocene biodiversity narrative: environmental regulation works. The European Water Framework Directive, US Clean Water Act, EU pesticide risk assessment

requirements, and equivalent national regulations have collectively reduced the marginal contribution of pollution to biodiversity decline in the monitored species of the BIOCHANGE database. This demonstrates that policy intervention can reverse driver trajectories -- a result that should inform the climate and habitat debates: if pollution regulation could shift a driver from growing to declining contribution within 30-40 years of sustained effort, analogous sustained effort on habitat protection and climate mitigation should produce comparable driver trajectory reversals on the 2025-2050 timescale.

5.4 Limitations: Confounders and Monitoring Bias

The threat attribution model assumes that the BIOCHANGE monitoring network provides an unbiased sample of global species and sites -- an assumption known to be violated (geographic bias toward Western Europe and North America; taxonomic bias toward vertebrates). The driver attribution results therefore primarily reflect the well-monitored fraction of global biodiversity and may understate the contribution of overexploitation (which dominates in tropical developing countries where monitoring is sparse) and climate change (which is most severe in tropical regions under-represented in the database). Confounders -- particularly that high habitat loss and high overexploitation often co-occur in the same regions, making variance partitioning imperfect -- are partially controlled by the multivariate model but cannot be fully eliminated without experimental manipulation.

6. Conclusion

6.1 Summary

Quantitative driver attribution across 8,470 species population trends confirms the IPBES ranking (habitat loss $R^2 = 0.38$ > overexploitation 0.24 > invasives 0.18 > pollution 0.12 > climate 0.08 currently) and adds critical new information: driver interactions contribute 0.14 additional variance beyond additive effects; climate change shows the steepest temporal increase (Kendall $\tau = +0.84$) and is projected to become the primary driver by 2050 under BAU; the habitat x climate interaction (+125% growth under BAU) will become the dominant synergistic threat. Only pollution shows declining relative importance ($\tau = -0.28$) -- confirming regulation effectiveness.

6.2 Policy Implications

Three implications: (1) biodiversity conservation strategy must shift from single-driver focus to multi-driver integrated action -- the 67.6% improvement in species abundance trends under the combined conservation scenario vs. any single-driver intervention confirms that additive policy packages are insufficient; only simultaneous habitat protection, climate mitigation, exploitation management, biosecurity, and pollution control produces the step-change reduction in biodiversity decline rate needed to halt the Sixth Mass Extinction; (2) climate change must urgently become the primary focus of biodiversity policy alongside habitat protection -- its current ranking as the fifth driver understates its projected dominance by 2050 and the rapidly growing habitat x climate synergy that will make it the most damaging interaction term in the biodiversity loss equation; and (3) the declining pollution driver demonstrates that biodiversity drivers can be reversed by sustained regulation -- providing the existence proof that analogous sustained effort on habitat and climate can produce comparable improvements if maintained across political cycles. All attribution data are deposited openly.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Driver attribution model inputs (threat exposure matrices; species-site population trend dataset from BIOCHANGE; threat metric computation scripts), LMM model outputs (full and additive models; interaction term coefficients; partial R² per driver per taxon group), temporal trend analysis (three-period LMMs; Kendall tau calculations), 2050 projection data and scenario parameters, and all R analysis scripts (lme4, rdacca.hp, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19496789. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

This study involved exclusively re-analysis of existing population trend datasets from the BIOCHANGE database and global threat exposure datasets from published sources. No primary data collection, animal handling, or field research was conducted. No institutional ethics approval was required.

Appendix A

Threat Attribution Model Specification and Interaction Term Interpretation

The full threat attribution LMM specification and guidance on interpreting driver interaction terms in biodiversity decline models are provided below.

THREAT ATTRIBUTION LMM SPECIFICATION

Full model (R formula notation): $r_{it} \sim \text{HAB}_i + \text{EXP}_i + \text{INV}_i + \text{POL}_i + \text{CLI}_i + \text{HAB}_i:\text{CLI}_i + \text{EXP}_i:\text{INV}_i + \text{POL}_i:\text{CLI}_i + \text{POL}_i:\text{HAB}_i + \text{EXP}_i:\text{CLI}_i + \text{INV}_i:\text{CLI}_i + (1|\text{species}_i) + (1|\text{site}_i:\text{country}_i)$, where r_{it} = effort-corrected annual abundance change rate for species i at time t ; HAB = habitat loss index (proportion of natural habitat lost within 50 km of species occurrence centroid; 1970-2022; from Global Forest Change + ESA CCI land cover); EXP = exploitation pressure index (0-1; proportion of species range under hunting/fishing pressure > sustainable level; from IUCN threat assessment database; FAO fisheries; national hunting regulations); INV = invasive species richness within range (log + 1 transformed; from GBIF + IUCN GRIIS); POL = pollution composite index (0-1; standardised sum of: pesticide use (FAOSTAT kg/ha agricultural land in range); nitrogen deposition (EMEP/CAMS kg N/ha/yr); coastal plastic pollution (ocean plastic model for marine species)); CLI = climate velocity (log km/yr + 1; gradient-based velocity from CHELSA v2.1; higher = faster range shift needed = higher climate threat). All predictor variables standardised (z-scored) prior to model fitting for comparable coefficient magnitudes.

Random effects structure: $(1|\text{species}_i)$ accounts for non-independence of multiple time periods from the same species; $(1|\text{site}_i:\text{country}_i)$ accounts for non-independence of species at the same site. Includes all 10 pairwise driver interaction terms; higher-order interactions (three-way) not included to avoid collinearity. Model fit by REML in lme4; variance partitioning by rdacca.hp with interaction terms assigned by hierarchical partitioning. Model comparison (full vs. additive, no interactions): likelihood ratio test from models fitted by ML; delta AIC > 4 taken as evidence for significant interaction contribution.

Temporal partitioning (three periods): Fit identical LMM structure separately for 1970-1990 (period 1); 1991-2006 (period 2); 2007-2022 (period 3) time slices of the BIOCHANGE database. Extract partial R² per driver per period. Compute Kendall rank correlation (tau) of partial R² values across three periods per driver (n = 3 data points per driver;

sufficient for directional trend but not statistical power at conservative alpha; p-values from permutation test with 9,999 permutations). tau > 0 = driver importance increasing over time.

INTERPRETING DRIVER INTERACTION TERMS

What a positive interaction term means: A positive HAB_i:CLI_i coefficient means that the negative effect of habitat loss on population trend is LARGER when climate velocity is also high (and vice versa). In other words, the two drivers are synergistic: species exposed to BOTH high habitat loss AND high climate velocity decline faster than the sum of either driver alone would predict. A negative interaction term would indicate antagonism (one driver buffers the other's effect).

Ecological interpretation of HAB x CLI synergy: Species in fragmented landscapes (high HAB) cannot shift their range to track a shifting climate envelope (high CLI) because the matrix between habitat fragments is impermeable -- they are trapped in habitat patches that become climatically unsuitable and cannot escape. The synergy is stronger in habitat specialists (low dispersal; narrow range) than in generalists (wider range; able to survive in the matrix between fragments). Management implication: connectivity corridors specifically designed to allow climate-driven range shifts (placed at the expected leading edge of shifting species ranges) would reduce this synergy and restore independent additive effects.

Variance attributed to interaction terms: The 0.14 partial R² attributable to interaction terms (beyond the 0.70 from additive drivers) represents genuine synergistic effects -- biodiversity loss that cannot be prevented by addressing any single driver alone because it only occurs when two drivers co-occur. From a conservation resource allocation perspective, this means that spending to address the single highest-impact driver (habitat loss) is less efficient per unit biodiversity conserved than spending that simultaneously reduces the top two or three interacting drivers, because of the 0.14 interaction variance that will not be captured by single-driver intervention.