The cost of tree cover loss: quantifying global extinction rates per million hectares

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Research highlights

► Tree cover loss increased the odds of vertebrates being threatened by 1.4%

► Threatened vertebrates rose across all taxa, with reptiles increasing 3.9-fold.

► Tropical and subtropical forests lost 92 Mha despite gains elsewhere.

► Wildfire emerged as the most consistent threat across vertebrate groups.

► Shifting cultivation and infrastructure ranked among top biodiversity drivers.

Abstract

Aim:

To quantify the relationship between annual tree cover loss and changes in extinction risk across terrestrial vertebrates, expressing responses as both absolute numbers of species associated with each IUCN threat category per million hectares of tree cover loss and relative odds of assignment to higher-risk categories.

Location: Global.

Time period: Contemporary period.

Major taxa: Mammals, birds, reptiles, and amphibians.

Methods:

An ensemble of machine learning and statistical models was used to estimate associations between annual tree cover loss and IUCN threat categories—Critically Endangered (CR), Endangered (EN), and Vulnerable (VU). Responses were quantified as absolute estimates per million hectares of annual tree cover loss and as relative associations using odds ratios (ORs). Analyses further examined variation among biomes and major drivers of tree cover loss, including agricultural expansion, settlement expansion, timber extraction, and wildfire.

Key results:

Marked differences emerged among vertebrate groups. For each million hectares of annual tree cover loss, reptiles showed the highest estimated absolute numbers of species across threat categories, with 19.9 CR, 34.7 EN, and 20.6 VU species, followed by amphibians (15.3 CR, 26.3 EN, and 7.3 VU). Estimates were lower for mammals (2.4 CR, 5.4 EN, and 4.2 VU) and birds (2.8 CR, 5.1 EN, and 6.2 VU). Relative associations showed a contrasting pattern: mammals had the strongest increase in the odds of assignment to a higher-risk IUCN category (OR = 6.86), followed by birds (OR = 2.83), whereas reptiles showed little evidence of an overall association (OR ≈ 1). Amphibians showed a stronger positive association in subtropical biomes (OR = 3.08), while associations were below 1 in other biome contexts. Associations also differed among major drivers: mammalian threat status was most strongly associated with settlement expansion and shifting agriculture; reptile and amphibian responses were more strongly associated with wildfire; and bird responses were strongest in relation to logging and agricultural expansion.

Main conclusions:

The relationship between tree cover loss and extinction risk varies substantially among vertebrate groups in both magnitude and associated drivers. Absolute estimates indicate a greater burden among reptiles and amphibians, whereas mammals show the strongest relative association with higher-risk IUCN categories. Expressing biodiversity responses per unit of tree cover loss provides a common metric for comparing vulnerability among taxa and can support taxon- and context-specific prioritization of conservation interventions.

Key words: biodiversity crisis, defaunation, land use change, machine learning models, threatened vertebrates, tree cover loss.

1. Introduction

The decline and extinction of plants and animals are attributed to a variety of threatening factors, including anthropogenic activities and natural biological processes (Lande, 1998). One of the main drivers directly related to biodiversity loss is the continuous reduction of forest cover, which may result from various causes, including agricultural expansion, urbanization, resource extraction, shifting cultivation, forest fires, and other natural disturbances (Curtis et al., 2018; Sims et al., 2025).

The effects of forest cover loss extend far beyond the mere reduction in hectares of forests and woodlands. They include habitat loss and fragmentation, declines in biodiversity, overpopulation, resource extraction, the spread of invasive species, and a deterioration in the vitality of terrestrial ecosystems—all of which impair the optimal functioning of ecosystem services. This decline is driven by a complex interplay of factors. For instance, defaunation weakens species interactions, eroding ecosystem resilience (Dirzo et al., 2014; Green et al., 2020). Habitat loss disrupts food webs and reduces biodiversity, while invasive species compete with and often displace native organisms, further destabilizing ecosystems (Hoffmeister et al., 2005; Wainright et al., 2021).

The degradation of ecosystem health has undeniable consequences, posing a significant threat to many animal species and accelerating population declines or pushing them toward extinction. In the context of the International Union for Conservation of Nature (IUCN) Red List, a species classified as "threatened" (i.e., Vulnerable, Endangered, or Critically Endangered) meets quantitative criteria that estimate the probability of extinction over a given time frame, based on ecological, demographic, and biological traits, as well as observed or projected population trends (IUCN Standards and Petitions Committee, 2022). These criteria provide a standardized framework for assessing extinction risk and are essential for interpreting temporal changes in conservation status.

In this study, increases in the number of threatened species are interpreted as direct indicators of shifts in extinction risk probabilities resulting from habitat loss and other anthropogenic pressures. Approximately one million animal and plant species are currently endangered, largely due to anthropogenic pressures (Bongaarts, 2019). Numerous taxonomic groups have experienced substantial declines, including terrestrial vertebrates, which are estimated to have lost at least 322 species since 1500 (Dirzo et al., 2014).

Despite several studies examining the effects of vegetation loss on major vertebrate taxonomic groups (e.g., Brooks et al., 1999; Sánchez-Cordero et al., 2005; Becker, 2016; Tracewski et al., 2016; Gomes et al., 2019), forest loss and fragmentation have continued to accelerate in recent decades, becoming one of the most significant threats to biodiversity conservation (De la Torre and Payaguaje, 2012; Hewson et al., 2019; Lenzen, 2009). Consequently, increasingly severe negative impacts are expected, such as population declines and potential extinctions in species already classified as at risk (Silvano and Segalla, 2005).

In this context, tree cover loss—defined by Hansen et al. (2013) as the complete removal of tree vegetation—is driven by multiple anthropogenic factors. Curtis et al. (2018) identified five primary drivers: commodity-driven deforestation, shifting agriculture, forestry, wildfire, and urbanization. Building on this framework, Sims et al. (2025) proposed a more detailed classification, dividing agricultural activity into seasonal and permanent agriculture and replacing the broad category of urbanization with "settlements and infrastructure," which includes road expansion, settlement growth, urban sprawl, and built infrastructure development.

Quantifying the relationship between tree cover loss and changes in the number of threatened species is fundamental for understanding broad-scale ecological patterns and informing effective conservation strategies. Yet, the magnitude of this impact—and its consistency across taxonomic groups (birds, mammals, reptiles, amphibians) and IUCN threat categories (Vulnerable, Endangered, Critically Endangered)—remains insufficiently quantified.

This study tests the hypothesis that annual tree cover loss increases the extinction risk of terrestrial vertebrates, as reflected by a rise in the number of species classified as threatened by the IUCN. To evaluate this hypothesis, we: (1) assess the relationship between annual tree cover loss and the number of threatened species across risk levels; (2) identify the primary drivers of tree cover loss that most strongly influence each taxonomic group and threat level; and (3) quantify the average change in threatened species numbers associated with rising annual tree cover loss, using global-scale data from IUCN historical records (2009–2024) and the Global Forest Watch platform.

2. Materials and methods

2.1. Obtaining data and variable definition

This study uses annual tree cover loss data (available up to 2024) from the Global Forest Watch (GFW) platform (www.globalforestwatch.org), developed by the World Resources Institute. GFW is an open-source tool that monitors and quantifies global tree cover loss using satellite-based methods, as outlined in Hansen et al. (2010) and Hansen et al. (2013). The analysis focuses exclusively on tree cover loss and does not account for gains from reforestation, natural regrowth, or other sources.

Regarding extinction risk data, the International Union for Conservation of Nature (IUCN) is the most authoritative source (Lamoreux et al., 2003; Mace et al., 2008). The IUCN monitors and compiles data on the conservation status of various animal, plant, and fungal species according to specific standards, guidelines, and criteria (Rodrigues et al., 2006; Butchart et al., 2007). This technical framework has enabled the standardized assessment and monitoring of the conservation status of terrestrial organisms (Rodríguez et al., 2015).

For this study, annual records of threatened species, mammals, birds, reptiles, and amphibians, were analyzed using data from the IUCN platform (www.iucnredlist.org), version 2025-1. Although the IUCN has compiled records of threatened species annually since 1996 (with the first publication in 1998), the process became more consistent starting in 2009 (IUCN, 2024). From that point onward, at least a second, corrected version of each year's records was published, except for the year 2023 (see Table A.1). Therefore, this study focuses on global records reported by the IUCN from 2009 to 2024, with descriptive statistics shown in Table 1.

Table 1.- Descriptive statistics of the taxonomic groups studied according to IUCN Red List version 2024-1.

	Mammals	Birds	Reptiles	Amphibians
Estimated number of described species by 2024	6701.00	11195.00	12162.00	8744.00
Number of species evaluated by 2024	5983.00	11195.00	10309.00	8011.00
% of described species evaluated by 2024 (Ver. 2024-1)	89.29	100.00	84.76	91.62
Annual average of endangered species for the period 2009-2024	1227.06	1373.94	1201.56	2202.31
Standard deviation of threatened species for the period 2009-2024	83.10	92.34	466.96	339.84
Annual % threatened species (2009-2024)	21.59	12.75	19.96	32.32
Asymmetry coefficient of the number of threatened species (2009-2024)	0.43	-0.22	0.19	1.08

2.2. *Impact of global loss of annual tree cover*

The first research question was whether global annual tree cover loss significantly affects the number of threatened vertebrate species. To test this, we employed a three-tiered modeling approach to evaluate the null hypothesis that tree cover loss (measured in million hectares, Mha) has no effect on species threat status. The three approaches were as follows:

(1) Generalized linear mixed models (GLMMs): A negative binomial model was employed to account for overdispersion in the count data. Models were fitted both with and without an interaction between tree cover loss and species threat status (threatened vs. non-threatened). Random intercepts for the year and taxonomic group were included to account for temporal and group-level variability. The model without the interaction term was prioritized to avoid dilution of the covariate's effect, which may result from pooling divergent group responses. The GLMMs were implemented using the glmmTMB package (Brooks et al., 2017) and the lmer function from the lme4 package v1.1-35.5 (Bates et al., 2015) in R.

(2) Proportional analysis: The proportion of threatened species (i.e., threatened_count / total species per group-year) was modeled using beta regression via the glmmTMB package. The beta distribution was chosen to accommodate the bounded, continuous nature of

proportional data. Random intercepts for year were included to control for temporal variability. The absence of boundary values (0 or 1) was confirmed, and residuals were checked to ensure model adequacy.

(3) First-order autoregressive models (AR(1)): These models were implemented using the gls function from the nlme package (Pinheiro et al., 2024), with maximum likelihood estimation applied. The AR(1) structure was used to account for temporal autocorrelation in the data. The same fixed effects as in the primary models were included, and the "year" variable defined the temporal structure to address correlation in residuals.

In addition to the formal analyses, a complementary analysis was conducted to assess the relationship between average tree cover loss percentages per ecozone (Global Forest Watch, 2009-2024) and the number of threatened species listed for each ecozone (IUCN Red List version 2025-1). Based on this analysis, a Threat Displacement Index (TDI) was proposed, calculated as the ratio between the percentage of tree cover loss per ecozone and the percentage of threatened species in that ecozone. Additionally, a marginal impact value per million hectares lost (Mha/Sp) was estimated for each ecozone by dividing a unit loss (1 Mha) by the average loss per threatened species. Ecozones were classified according to GFW's system as boreal, temperate, tropical and subtropical, with tropical and subtropical categories combined to align with IUCN classifications.

2.3. Main causes of tree cover loss

The second question addressed in this study was: Which of the six primary drivers of tree cover loss—hard commodities, logging, permanent agriculture, settlements & infrastructure, shifting cultivation, and wildfire (excluding natural disturbances, as defined by GFW, 2025)—has the strongest impact on each taxonomic group and associated risk level? To address this, three machine learning methods were employed: random forest regression, k-nearest neighbors (k-NN) regression, and support vector machine (SVM) regression. These methods were chosen because no a priori assumptions are required, and complex, non-linear relationships can be effectively modeled.

Prior to analysis, all predictor variables were standardized (mean-centered and scaled by their standard deviation) to ensure comparability across features. Using the three algorithms, the total annual number of species within each taxonomic group was modeled as a function of the six standardized drivers, irrespective of risk level. Subsequently, a second analysis was conducted in which the number of species at each IUCN risk level (CR, EN, and VU) within each taxonomic group was modeled using the same predictors.

The random forest algorithm was implemented using the *randomForest* package (RColorBrewer, 2002) in R (R Core Team, 2023, Ver. 4.1.2), with 500 trees per forest. Variable importance was calculated via permutation importance, measured by the percentage increase in mean squared error (%IncMSE) when each predictor was randomly shuffled. Due to the limited sample size, bootstrap resampling (1,000 iterations) was used to estimate robust importance metrics and confidence intervals at the 95% level.

The k-nearest neighbors (k-NN) algorithm was implemented using the *train* function from the *caret* package (version 6.0-94; Kuhn, 2024) in R. The model was trained with 50-fold cross-validation to ensure robust performance estimation. Predictor importance was quantified using the built-in *varImp* function in *caret*, which calculates variable importance based on the magnitude of model coefficients (for regression).

The support vector machine (SVM) algorithm was implemented using the *e1071* package (Meyer et al., 2024) for model fitting and the *caret* package (Kuhn et al., 2024) for cross-validation. A radial basis function (RBF) kernel was selected due to its flexibility in capturing nonlinear relationships. To evaluate the significance of each predictor, the mean squared error (MSE) was permuted using the *FeatureImp* function from the *iml* R package (Fisher et al., 2019).

Variable importance scores (mean ± 95% CI) were derived from 1,000 bootstrap iterations, quantified as the relative increase in mean squared error (MSE) when each predictor was permuted using the *iml package* (Casalicchio et al., 2025). Predictors are ranked by their mean importance across iterations, with error bars indicating the 2.5–97.5 percentile range. Results were visualized to highlight each variable's contribution to model accuracy. All analyses were conducted in R (R Core Team, 2023, Ver. 4.1.2).

2.4. The response of threatened species to the increase in tree cover loss.

The third research question sought to determine the average increase in the number of species for each taxonomic group and risk level corresponding to a unit increase in the total global deforested area. To address this, an analysis of covariance (ANCOVA) was executed.

The ANCOVA model included the number of vertebrate species as the dependent variable, the annual global tree removal area as a covariate, and the taxonomic groups and/or risk levels as categorical variables to assess their effects.

Prior to running the ANCOVA, Pearson's correlation coefficient was employed to identify taxonomic groups that exhibited a significant linear correlation with the total global deforested area, with a significance level set at $p < 0.05$. The ANCOVA was executed using the "*lm" and "aov*" functions in R 3.6.1 (R Core Team, 2019), and two specific hypotheses were verified:

(1) The interaction between the covariate (tree cover loss) and vertebrate groups (mammals, birds, reptiles, and amphibians) is null, which implies that there is a similar response pattern in all vertebrate groups to an increase in tree cover loss.

(2) The interaction between the covariate and the risk categories (critically endangered, endangered, and vulnerable) is null, indicating that the variable of interest responds similarly across the three threatened categories to an increase in tree cover loss.

2.5. Evaluation of results and goodness-of-fit indicators

To evaluate the results, the following aspects were considered:

(1) The p-value in each model was evaluated with a reference value of 0.05. However, it is important to recognize that this reference value should not be seen as a strict cutoff for making binary decisions. Lower p-values indicate stronger evidence against the null hypothesis (Antúnez et al., 2021).

(2) The models were assessed using the Akaike Information Criterion (AIC), the Bayesian Information Criterion (BIC), and the Root Mean Square Error (RMSE). Smaller values of these indicators suggest a better model fit.

(3) Both the numerical and graphical behavior of residuals were considered to assess the robustness and validity of the models.

(4) Given that the focus in the first two stages of the analysis was solely on whether the contribution was significant or not, the percentage of variability explained by a covariate became particularly valuable for evaluating linear regression models in the third stage.

3. Results

3.1. Does the loss of total tree cover have significant effects on the species in risk categories?

The mixed-effects model indicated that tree cover loss affects threatened and non-threatened species equally ($p = 0.957$) (Table 2). However, a combined estimate from the final model—accounting for taxonomic group and year-specific variability—showed that threatened species were disproportionately affected, with baseline counts 74.1% lower than those of non-threatened species ($p < 2e-16$).

Notably, each 1 Mha increase in tree cover loss was associated with a 2.8% multiplicative increase in species counts ($\exp(0.0276) \approx 1.028$) ($p = 8.21e-05$).

The beta regression suggested that habitat loss disproportionately favors threatened species: a + 0.014 unit increase in log-odds per 1 Mha loss. That is, each 1 Mha increase raised the log-odds of a species being classified as threatened by 0.014 ($p = 0.0003$), equivalent to approximately a 1.4% increase in odds ($OR \approx 1.014$).

Table 2. Model coefficients from, negative binomial generalized linear mixed models (NB-GLMM) analyzing species counts, beta regression (Beta-GLMM) modeling threat proportions, and generalized least squares with AR(1) correlation (GLS AR(1)) for temporal autocorrelation control. All models assess effects of annual tree cover loss on vertebrate species, with estimates presented on their original scales (log-count, log-odds, and raw counts).

Type of model	Term	Estimate (log)	Std. Error	Effect size	P-value
NB_GLMM (interaction)	Intercept	8.138	0.228	—	< 2e-16
	Tree cover loss (Mha)	0.027	0.009	+2.7 % counts	0.00334
	Threat status (threatened)	-1.366	0.315	74% ↓ counts	1.47E-05
	Interaction	0.001	0.013	No difference (NS)	0.95748
NB_GLMM (no interaction)	Tree cover loss (Mha)	0.0276	0.007	+2.8% counts	8.21E-05

	Threat status (threatened)	-1.35	0.053	74.1% ↓ counts	< 2e-16
Beta_GLMM	Tree cover loss (Mha)	0.014 (log-odds)	0.004	+1.4% (log-odds change per 1 Mha)	0.000316
GLS AR(1) Non-threatened	Intercept	2543.2048	1.967987	—	0.0535
	Tree cover loss (Mha)	148.7266	2.76741	+148.7 counts/Mha	0.0074
GLS AR(1) Threatened	Intercept	588.8257	1.812162	—	0.0748
	Tree cover loss (Mha)	37.9744	2.810251	+37.9 counts/Mha	0.0066

By independently modeling each subset (threatened and non-threatened) using an autoregressive GLS model, tree cover loss was found to significantly affect both groups (Table 2). Although the effect was statistically significant for both subsets, the magnitude of the effect was approximately four times greater in non-threatened species. Specifically, for every 1 Mha of tree cover loss, the expected increase in species counts was +148.7 for non-threatened species and +37.9 for threatened species. In both models, the intercepts were marginally significant.

It was observed that 92.9% of the threatened species were concentrated in the tropical/subtropical ecozone, where the total tree cover loss during the study period was 14.218 million hectares (Mha). However, this ecozone exhibited the lowest tree cover loss per threatened species, with a value of approximately 0.00187 Mha per species (Table 3).

The temperate ecozone followed, with a moderate loss of tree cover (2.63 Mha) and a smaller number of threatened species, resulting in a per-species loss of 0.00471 Mha (Table 3). In contrast, the boreal ecozone showed an exceptionally high loss per threatened species (0.3806 Mha), despite accounting for only 0.2% of the total number of threatened species analyzed. This value is roughly 200 times greater than in the tropics (Table 3).

These results may suggest that vertebrate species in boreal regions are either more resilient to tree cover loss or that the detection and assessment of threatened species in this ecozone are underestimated (Table 3). Nevertheless, the marginal conservation impact is highest in the tropical/subtropical ecozone: for each Mha of forest conserved, approximately 535 species could benefit (1 / 0.00187 ≈ 535), compared to 212 species in the temperate ecozone and only 2.6 in the boreal (Table 3). Consequently, conserving tropical forests protects more than 500 times as many species per unit area as conserving boreal forests.

Table 3. Average tree cover loss (2000–2024) and proportion of threatened species by ecozone, based on the IUCN Red List (2025-1). TDR: Threat displacement rate. Marginal impact: estimated number of species potentially protected per million hectares (Mha) conserved.

Ecozone	Total threatened species (%)	Tree cover loss (Mha/24yr)	Tree cover loss per threatened species (Mha/Sp)	% of total loss	% of threatened species	TDR	Marginal impact (species per Mha)
Tropical/Subtropical	7,608 (92.9%)	14.218	0.00187	59.98%	92.90%	0.65	≈ 535 especies/Mha
Temperate	559 (6.8%)	2.63	0.00471	11.09%	6.80%	1.63	≈ 212 especies/Mha
Boreal	18 (0.2%)	6.851	0.3806	28.91%	0.20%	144.6	≈ 2.63 especies/Mha
Total	8,185 (100%)	23.699		100%	100%		

3.2. Which of the factors associated with tree cover loss have the greatest impact on threatened species?

The relative importance of drivers varied slightly across machine learning algorithms, though the top-ranked factors remained consistent when comparing standardized scores (Figures A.1, A.2 and A.3). Among threatened mammals, settlements & infrastructure, wildfire, and shifting cultivation were most influential (Figure 1). For reptiles, the primary drivers were wildfire and shifting cultivation, followed by equally significant contributions from settlements & infrastructure and hard commodities. Amphibians showed strongest responses to wildfire and settlements & infrastructure, with hard commodities as a secondary factor. Birds were predominantly affected by shifting cultivation, logging, and wildfire. Across all vertebrate groups, wildfire, shifting cultivation, and settlements & infrastructure emerged as the dominant threats (Figure 1).

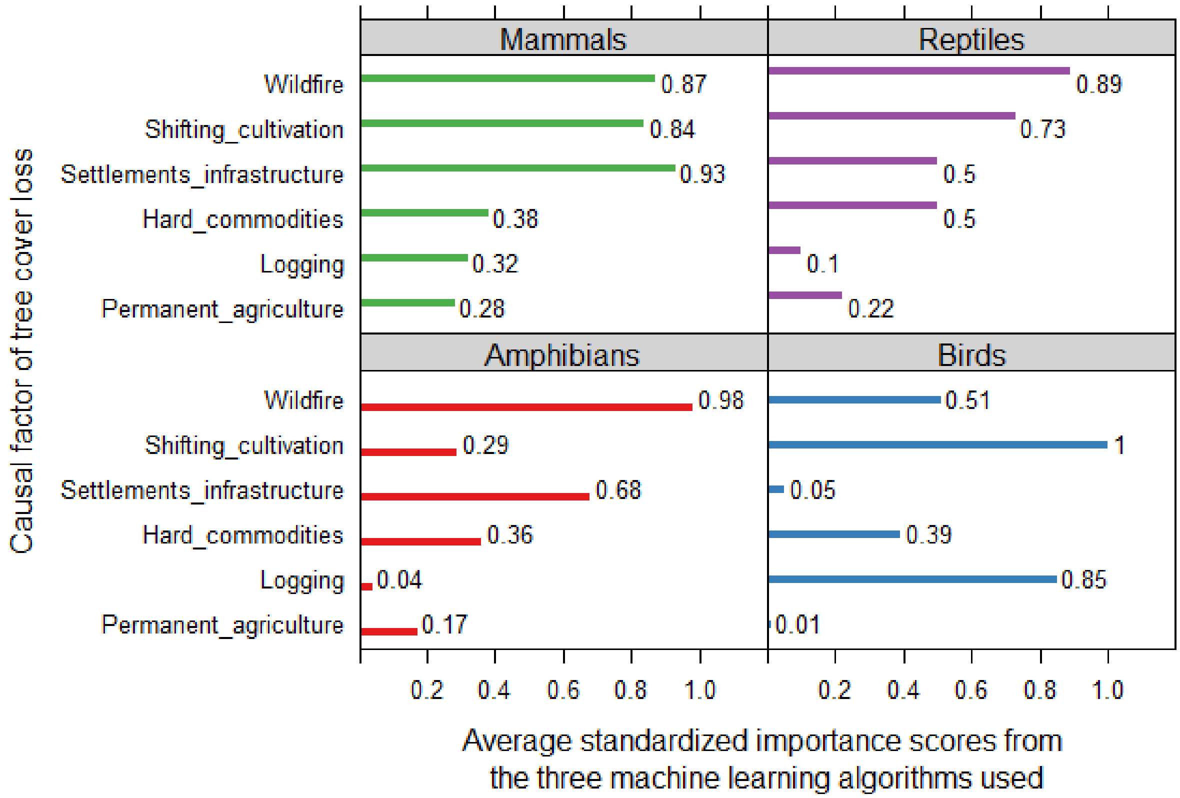

Figure 1. Mean of standardized importance index of drivers influencing the four vertebrate groups, as determined by three learning algorithms. Values near 1 indicate a strong impact, while values near 0 suggest a weak impact.

From the perspective of risk category levels, it was determined that within the critically endangered category, wildfire emerged as the most relevant factor for mammals and amphibians, with agriculture following closely (Figures 2). For reptiles, mammals, and amphibians, wildfire ranked highest in importance, followed by shifting cultivation for reptiles and settlement infrastructure for mammals and amphibians (Figure 2).

In the endangered category, wildfire was the leading factor for reptiles and amphibians, while settlement infrastructure was most important for mammals. For birds, shifting cultivation and logging were the primary drivers.

In the Vulnerable category, wildfire was the foremost factor for reptiles, mammals, and amphibians. For birds, logging was the most critical factor, followed by shifting cultivation (Figure 2).

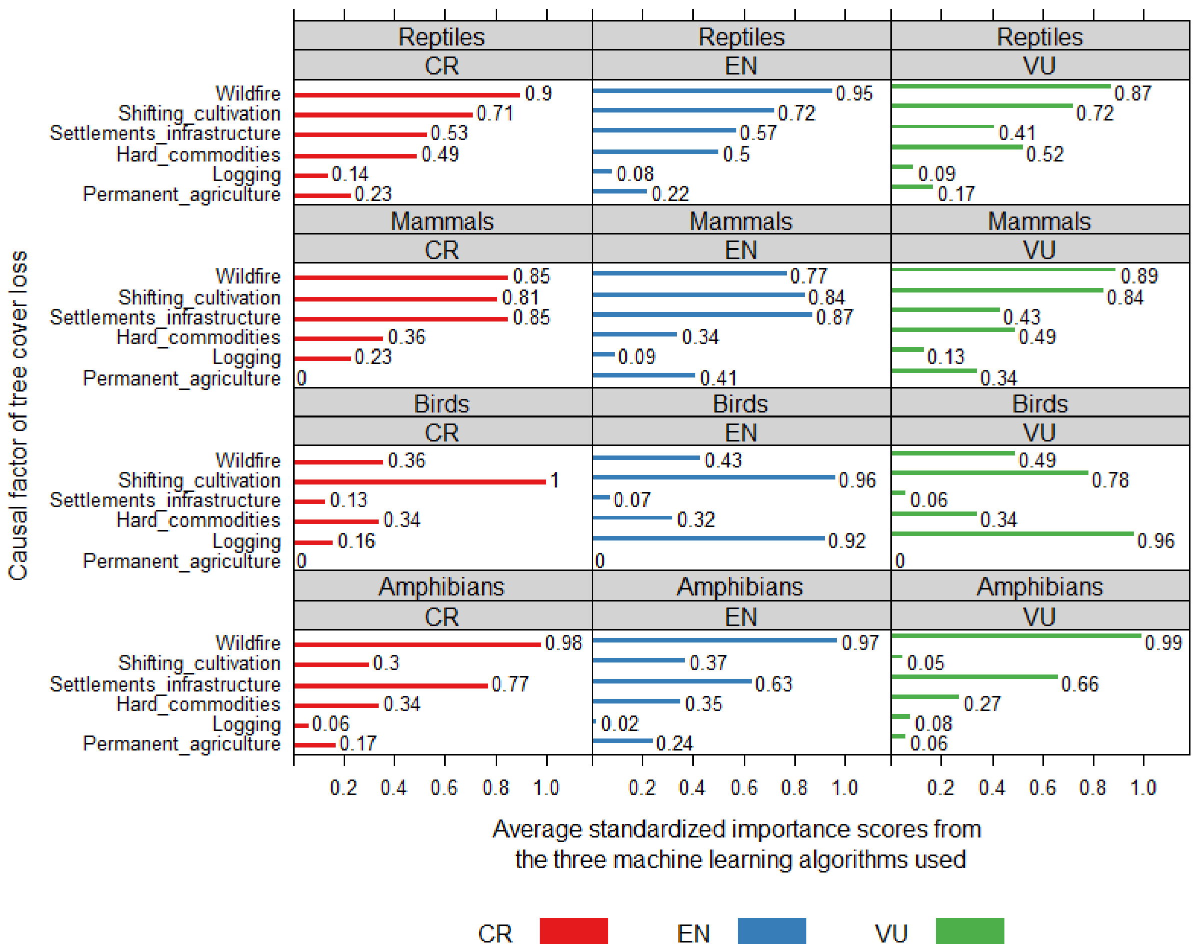

Figure 2. Mean standardized importance of drivers influencing the four vertebrate groups at each IUCN risk level (CR: critically endangered, EN: endangered, and VU: vulnerable), based on results from the three machine learning algorithms. Values close to 1 indicate a strong influence, while values near 0 indicate a weak influence.

3.3. How is the relationship between tree cover loss and vertebrate species in threatened?

Pearson's coefficients revealed a positive and significant association (p<0.05) between annual forest cover loss and the four taxonomic groups studied, with reptiles exhibiting the highest coefficients (Table A.2).

In the ANCOVA, both the factor and the covariate were statistically significant ($p < 0.05$) in all cases (Table 4). When evaluating the assumption of no interaction between the covariate and the factor (threat levels), there was insufficient evidence to reject the null hypothesis for any of the taxonomic groups: mammals ($p = 0.4118$), reptiles ($p = 0.3104$), birds ($p = 0.3942$), and amphibians ($p = 0.1158$) (Table 4).

Table 4. Analysis of the covariance table: Covariate is global annual tree cover loss; group denote taxonomic groups; response variable is absolute counts of threatened species.

Taxonomic group	Sources of variation	degrees of freedom	sum of squares	Mean squares	F-value	P-value
Mammals	Covariable	1.00	12697.00	12697.00	19.77	0.0001
	group	2.00	964889.00	482445.00	751.38	<0.0001
	Covariable:group	2.00	1164.00	582.00	0.91	0.4118
	Residuals	42.00	26967.00	642.00		
Reptiles	Covariable	1.00	500520.00	500520.00	32.63	<0.0001
	group	2.00	480634.00	240317.00	15.67	<0.0001
	Covariable:group	2.00	36910.00	18455.00	1.20	0.3104
	Residuals	42.00	644306.00	15341.00		
Birds	Covariable	1.00	17368.00	17368.00	20.87	0.0000
	group	2.00	2257658.00	1128829.00	1356.66	<0.0001
	Covariable:group	2.00	1584.00	792.00	0.95	0.3942
	Residuals	42.00	34947.00	832.00		
Amphibians	Covariable	1.00	212578.00	212578.00	20.06	0.0001
	group	2.00	959152.00	479576.00	45.26	<0.0001
	Covariable:group	2.00	48122.00	24061.00	2.27	0.1158
	Residuals	42.00	445057.00	10597.00		

Figure 2 shows that the relationship between vertebrate counts at threat status (CR+EN+VU) and annual tree cover loss (Mha) varies among taxonomic groups. The regression lines for birds, mammals, and amphibians have similar slopes, indicating similar rates of change in response to tree cover loss. In contrast, the reptile regression line crosses the bird and mammal lines, indicating a distinct interaction, where the reptile response is more pronounced. Reptiles show the highest rate of change (75.2), followed by amphibians (49.03), birds (14.01), and mammals (11.9). The amphibian regression line is positioned above the others, highlighting a notably different response, but with a lower rate of change than reptiles (Figure 2).

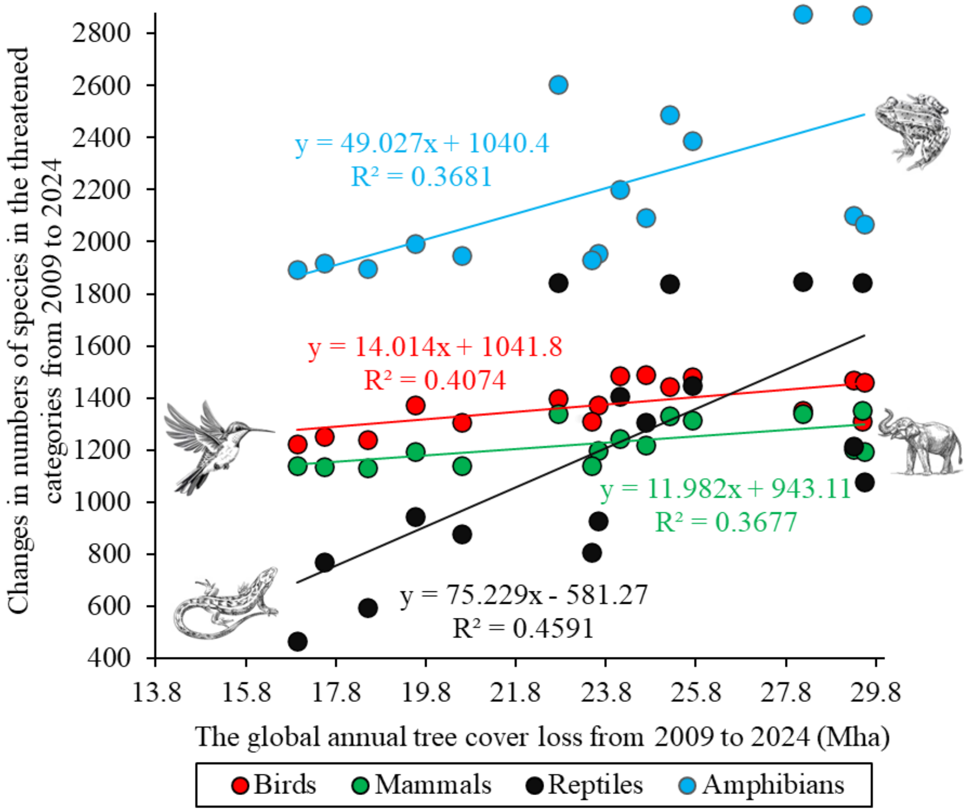

Figure 2. Scatter plot of the number of threatened species against the tree cover loss increases, superimposing linear regression line.

The coefficients of determination indicate that, under a linear model, the annual global loss of tree cover explains between 45% and 47% of the variability in the number of threatened species within the reptiles' taxonomic group, 32% to 57% in birds, 30% to 37% in amphibians, and 29% to 47% in mammals (Table 5).

Table 5 summarizes the average response of threatened vertebrate species to annual global forest cover loss. For every additional 1 million hectares of tree cover lost per year, the following average increases in species at risk are observed: mammals—2.4 additional species in the critically endangered (CR) category, 5.4 in the endangered (EN) category, and 4.2 in the vulnerable (VU) category; reptiles—19.9 in CR, 34.7 in EN, and 20.6 in VU; birds—2.8 in CR, 5.1 in EN, and 6.2 in VU; amphibians—15.3 in CR, 26.3 in EN, and 7.3 in VU.

These rates of change represent average responses under a linear relationship assumption. However, the significant quadratic terms in the polynomial models indicate nonlinearity. The strongest concavity occurs in reptiles (quadratic coefficient = -7.9), suggesting a decelerating response to tree cover loss at higher loss levels. Birds show moderate curvature (-2.5), while amphibians exhibit the weakest nonlinear effect (-0.9) (Figure 3).

Table 5. Average rates of increase in the number of threatened species per 1 million that the area of the global annual tree cover loss increases. AIC is the Akaike information criterion; BIC is the Bayesian information criterion; r^2 is the coefficient of determination; MSRE is the mean square root of error; CR is critically endangered; EN is endangered; VU is vulnerable; and TH is threatened (CR+EN+VU).

Taxonomic group	Risk category	Rate of change in %	Std.Error	T-value	P-value	AIC	BIC	r^2	RMSE
Mammals	CR	2.418	0.88	2.74	0.0161	134.60	136.92	0.35	13.46
	EN	5.356	2.24	2.39	0.0316	164.41	166.73	0.29	34.17
	VU	4.208	1.20	3.50	0.0036	144.50	146.82	0.47	18.34
	TH	11.982	4.20	2.85	0.0128	184.48	186.80	0.37	63.98
Reptiles	CR	19.922	5.80	3.44	0.0040	194.79	197.10	0.46	88.29
	EN	34.700	10.25	3.39	0.0045	213.04	215.36	0.45	156.21
	VU	20.609	5.90	3.50	0.0036	195.35	197.66	0.47	89.85
	TH	75.229	21.82	3.45	0.0039	237.22	239.54	0.46	332.52
Birds	CR	2.779	0.65	4.27	0.0008	124.79	127.11	0.57	9.91
	EN	5.070	1.76	2.88	0.0122	156.70	159.02	0.37	26.85
	VU	6.164	2.43	2.54	0.0235	166.91	169.23	0.32	36.95
	TH	14.014	4.52	3.10	0.0078	186.82	189.14	0.41	68.83
Amphibians	CR	15.290	5.37	2.85	0.0129	192.35	194.67	0.37	81.83
	EN	26.347	9.05	2.91	0.0114	209.04	211.36	0.38	137.83
	VU	7.389	3.03	2.44	0.0284	173.98	176.30	0.30	46.09
	TH	49.030	17.17	2.86	0.0127	229.54	231.86	0.37	261.56

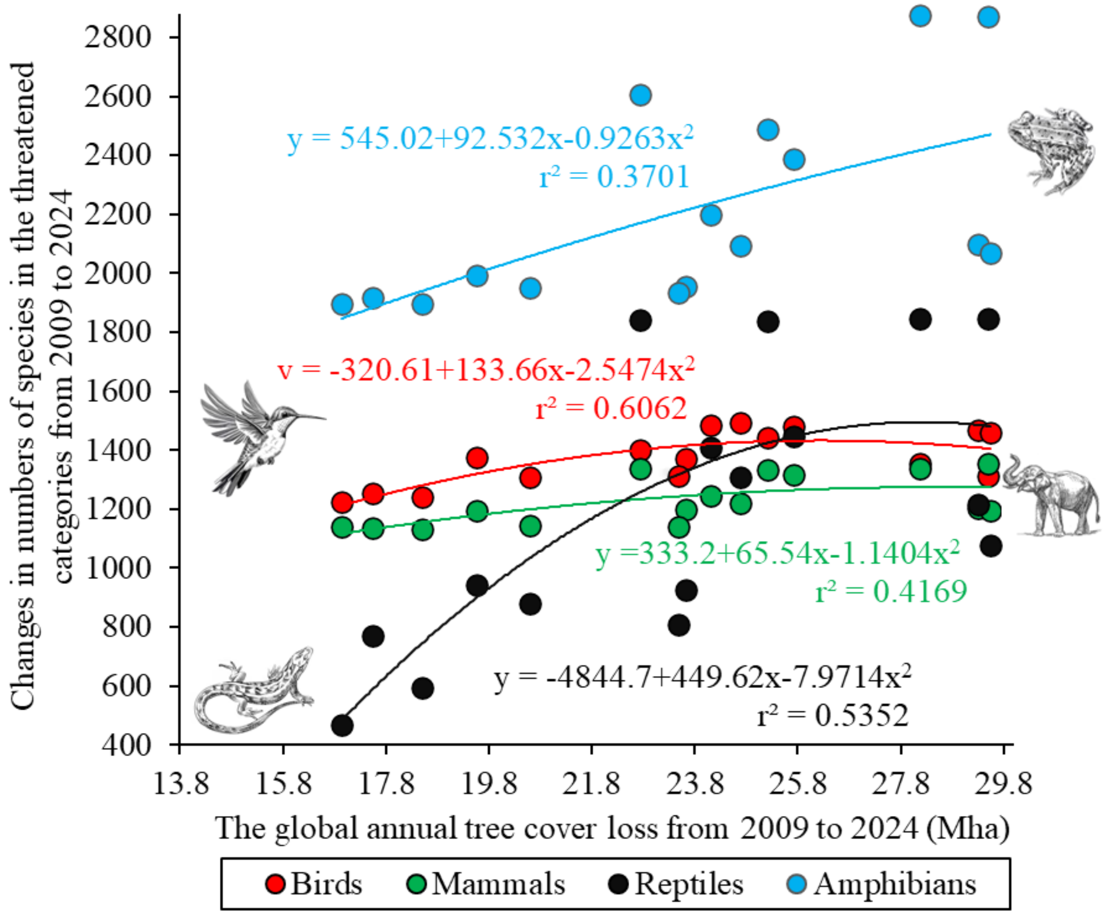

Figure 3. Scatter plot of the number of threatened species against the tree cover loss increases, superimposing linear regression line.

4. Discussion

4.1. Differential effects of tree cover loss on threatened vertebrates

Since the beginning of the 21st century, the world has lost approximately 517 million hectares (Mha) of tree cover—equivalent to 13% of the total tree cover in 2000 (GFW, 2025). Although 130.9 Mha of tree cover was gained between 2000 and 2020, net losses still reached 100.6 Mha (GFW, 2025). This decline has followed a persistent upward trend (Potapov et al. 2022; MacCarthy et al., 2024), with annual losses rising from 13.3 Mha in 2001 to 29.5 Mha in 2024 (GFW, 2025). These trends have raised significant concerns about biodiversity loss and ecosystem stability.

This study found that threatened vertebrate species were disproportionately affected by tree cover loss compared to non-threatened species, with distinct patterns across taxonomic groups (Table 2). Although threatened species showed higher baseline vulnerability (with counts 74.1% lower than non-threatened species, $p < 0.0001$), their numerical response to tree cover loss was markedly lower, indicating their inherent vulnerability (Table 3). However, tree cover loss increased non-threatened species counts 4× more (+148.7 vs. +37.9 species per 1 Mha loss), suggesting threatened species may be less responsive to recent habitat changes or suffer from detection biases (Table 3).

Tropical forests offer the highest conservation return per unit area: 92.9% of threatened species clustered in tropical/subtropical zones, where 1 Mha of conservation protects ~535 species—200× more than boreal zones (2.6 species/Mha). Despite higher absolute tree cover loss (14.218 Mha), tropics had the lowest loss per species (0.00187 Mha/species), highlighting their efficiency as conservation targets.

4.2. Drivers of tree cover loss and taxon-specific biodiversity impacts

Wildfires, shifting cultivation, and infrastructure expansion were the dominant drivers of tree cover loss, with taxon-specific impacts: mammals were most strongly affected by settlement and infrastructure expansion; reptiles by wildfires and shifting cultivation; amphibians by wildfires and infrastructure; and birds by shifting cultivation, logging, and wildfires. These findings align with studies by Kadoya et al. (2022) and Cordier et al. (2021), who likewise linked deforestation, silviculture, and urbanization to vertebrate declines.

Importantly, these threats tend to be concentrated in regions with high species richness and endemism (Gonçalves-Souza et al., 2020), where anthropogenic pressures are especially intense. Shifting cultivation, in particular, is widespread in tropical mountainous regions of Asia, Africa, and Latin America and is often closely tied to the cultural, ecological, and economic practices of rural communities (Karthik et al., 2009). In such areas, traditional smallholder farming systems contribute significantly to habitat fragmentation and degradation, likely amplifying the vulnerability of tropical vertebrates already at risk from land-use change (Foley et al., 2005).

The beta regression model estimated that each additional million hectares (Mha) of loss led to a 1.4% rise in the log-odds of a species being classified as threatened ($p = 0.0003$; Table 2), though this effect varied among taxonomic groups (Tables 2 and 5; Figures 2 and 3). The strongest effect was observed in amphibians, possibly due to an influx of non-threatened, generalist species colonizing disturbed areas. In contrast, the reference threat proportions were higher for reptiles and lower for birds, independent of habitat loss. Surprisingly, a 2.8% increase in threatened proportions per Mha was observed in some cases, possibly due to monitoring bias (e.g., greater survey effort in deforested areas) or the proliferation of widespread species, including invasives.

To further explore the dynamics between threatened and non-threatened species, each subset was modeled independently using autoregressive models (Table 2). The marginal significance of the intercepts suggests uncertainty in baseline species counts, potentially indicating delayed declines in threatened taxa. One possible interpretation is that threatened species may display greater resilience to habitat loss; alternatively, biased sampling in deforested areas could be influencing detection rates. The effect size observed in non-threatened species was four times greater than that in threatened species, suggesting that tree cover loss may disproportionately benefit common or generalist taxa. This pattern may contribute to ecological homogenization and poses challenges for conservation efforts, as rare species may be less responsive to area-based indicators and might require more nuanced protection strategies.

4.3. Vertebrate responses and vegetation types most affected.

The response of vertebrates to vegetation loss varies significantly depending on the context. For instance, mammals have been identified as particularly sensitive to changes in canopy cover. While an increase in canopy openness may decrease the rates of threatened species in some regions (Cudney-Valenzuela et al., 2023), in other cases, such as with large carnivores, canopy loss leads to heightened vulnerability (Mikusiński and Angelstam, 2004). These examples highlight that vertebrate responses to canopy loss are not uniform and are contingent on the specific species and their environmental context.

Another critical aspect to consider is that the effects of tree cover loss are not always direct but can be indirect. Deforestation can trigger a cascade of other issues (Harfoot et al., 2021).

For example, deforestation and land use change can intensify the decline of insect populations, which subsequently impacts birds and mammals that rely on these insects, leading to a series of ecosystem alterations (Dirzo et al., 2014; Ceballos et al., 2015).

In this regard, tropical ecosystems are particularly affected, having experienced the most significant loss of tree cover, primarily due to agricultural expansion (GFW, 2024). It is particularly concerning that in certain parts of the Americas, these forests often face additional challenges such as illegal wildlife trafficking (Antía and Gómez, 2010; Acosta, 2013) or clandestine hunting. Conversely, in boreal and temperate regions, the primary causes of tree cover loss are forestry and forest fires.

A mitigating factor in the impacts of tree cover loss is the establishment of semi-natural and planted forests, which have increased in recent years (Richter et al., 2024). However, it is uncertain whether affected fauna can adapt swiftly to these new environments (Sánchez-Cordero et al., 2005) or survive in new habitats adjacent to their original ones (Peterson and Holt, 2003).

4.4. Strengths, limitations and implications

The findings underscore the biodiversity crisis driven by tree cover loss, which extends beyond habitat destruction to disrupt ecosystem dynamics and species' life-history traits (e.g., reproductive timing, dispersal patterns). For instance, habitat fragmentation restricts the mobility of large carnivores, limiting their access to resources and breeding partners—pressures that may lead to maladaptive trade-offs (Giam, 2017; Cosset et al., 2019).

This study reveals three key insights. First, although both threatened and non-threatened species were significantly affected by tree cover loss, the results suggest that threatened species are more sensitive to habitat loss in relative terms, exhibiting lower baseline abundances and increased odds of being classified as threatened. Second, settlements and infrastructure, forest fires, and shifting cultivation emerged as the primary threats to mammals; reptiles were most affected by wildfires, shifting cultivation, and hard commodities; birds were mainly threatened by shifting cultivation, followed by logging and wildfires; and amphibians faced the greatest risks from forest fires, infrastructure expansion, and hard commodities. Third, for every million hectares of tree cover lost annually, the number of threatened species increased by approximately 75.2 for reptiles, 49.0 for amphibians, 14.0 for birds, and 12.0 for mammals (Figure 2, Table 5).

A major strength of this study lies in its use of multiple analytical methods, each tailored to specific objectives while applied to the same dataset—thereby minimizing the risk of drawing false conclusions. Three machine learning algorithms—k-Nearest Neighbors (k-NN), Random Forest, and Support Vector Machines (SVM)—were employed to identify the most significant factors for each taxonomic group and risk level, increasing the robustness of the findings. Each method offers distinct advantages: k-NN is straightforward and interpretable but sensitive to the choice of k; Random Forest is well-suited for nonlinear relationships and robust to outliers; and SVM excels in high-dimensional spaces, modeling complex patterns through kernel functions.

By identifying specific impacts across taxonomic groups and threat levels, this study provides a valuable foundation for designing more targeted conservation strategies. This is especially urgent given the context of the accelerating sixth mass extinction, largely driven by human activities (Cowie and Fontaine, 2022). Conservation planning will require judicious allocation of resources by government agencies and organizations, prioritizing the most critical drivers and the species most at risk. The results also contribute to ongoing evaluations of progress toward achieving Target 15 of the Sustainable Development Goals, which seeks to protect, restore, and promote the sustainable use of terrestrial ecosystems (Obrecht et al., 2021).

As a suggestion, future work could integrate species–area relationship (SAR) (Triantis et al., 2012) and region-specific approaches such as endemism–area relationships (Gonçalves-Souza et al., 2020), along with finer taxonomic or ecological categorizations (e.g., dietary guilds) and improved spatial resolution via remote sensing technologies.

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