Supplementary Materials for

Extinction filters mediate the global effects of habitat fragmentation on animals

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Supplementary Materials and Methods

BIOFRAG

We used the BIOFRAG database (*18*) and software (*13*) to estimate fragmentation sensitivity of species populations (Fig. S4). While the BIOFRAG data and methodology have already been documented extensively (*13*, *18*), here we present a brief overview of the parts that are relevant to our analysis. Running the BIOFRAG software requires making certain decisions (e.g., choice of percentage cover layer, standard deviation of smoothing kernel). The choices that we made for our analysis are also described in this section.

We compiled existing primary biodiversity datasets containing abundance measurements at the plot level acquired in 109 datasets from 6 continents (the BIOFRAG database; (*18*)). As in Pfeifer et al. (*13*), each dataset contains a set of sample points within fragmented forest regions where the abundances of one or more species (generally true species, rather than morphospecies) were estimated. All regions encompassed anthropogenic forest edges and a mosaic of natural forests and other land uses. We only used datasets for which geographic coordinates of plots were provided by the authors of each dataset at high spatial accuracy. This is because the location of each plot in relation to the forest edges was important. All datasets in our analysis were from community-level surveys of a focal taxonomic group (rather than sampling for a target list of species).

Since abundances are typically quantified at the level of species, we will refer to these taxonomic groups as 'species' throughout. The species in the database used in our analysis include vertebrates and invertebrates spanning four groups: arthropods, birds, herptiles, and mammals. Unless otherwise noted, we refer to the species within datasets as simply "species," since these were treated as observations in our analysis. Thus, a single species that appears in two datasets would be treated as two species for purposes of our statistical analysis. We included species identity as a random effect to deal with this potential source of dependence (except for herptiles; see *Statistical modeling* section). We also conducted a version of our analysis where species duplicates were randomly dropped and found that results did not differ substantively (Figs. S7 & S9).

The BIOFRAG software is a suite of tools that can be used to assess biodiversity responses to habitat fragmentation. In addition to a BIOFRAG dataset, a continuous (0-100) percent cover layer is required and a non-habitat mask layer may be used as well. For the percent cover layer, we used a global 30-m resolution remotely sensed tree cover map corresponding to the year 2000 (*35*). To construct the non-habitat mask, we used the mapped land surface layer provided by Hansen et al. (*35*), which shows pixels where tree cover was mapped. For each dataset, we cropped the percent cover and mask layers to include only regions within 5 km of the minimum convex polygon associated with the dataset's sample points. The layers were extracted and cropped using Google Earth Engine (*36*). To minimize distortion, for each dataset, we then re-projected the sample points and percent cover and mask layers into an azimuthal equidistant (AEQD) projection at 30-m resolution with origin equal to the latitude/longitude centroid of the dataset's sample points.

We used these layers and the BIOFRAG software to derive edge influence maps, which quantify the local variation in percent cover. The edge influence (*EI*) of each point has magnitude equal to the maximum of the 'landscape-scale' standard deviation of the percent cover layer, and the difference between the point-scale percent cover (30-m pixel) and the landscape-scale average. We computed averages and standard deviations using a Gaussian smoothing filter with a 'landscape' radius standard deviation. We used 1 km for the primary landscape radius (termed 'depth of edge influence' in the BIOFRAG software) to maintain consistency across species and datasets, and because animal abundances have been shown to be sensitive to habitat within this distance (*13*, *37*). However, to improve classifier performance, we made dataset-specific adjustments to the depth of edge influence as described in the next section. In contrast to a circular smoothing filter, the Gaussian filter puts reduced weight on points that are further away. This reflects our expectation that edge effects amplify with increasing proximity to a focal point. The sign of the edge influence at each point is equal to the sign of the difference between that point's habitat cover value and the landscape average.

Thus, *EI* in a grid cell *i* can be expressed as:

$$EI_i = \max(\sigma_C, |\bar{C} - C_i|) \times sign(\bar{C} - C_i)$$

Where $\bar{C}$ is the landscape average of habitat cover, C_i is the point value of habitat cover (also called "point cover"; in our analysis, this is the percentage tree cover within a given 30-m pixel), and σ_C is the standard deviation of habitat cover at the landscape scale.

After calculating EI maps for each region, we then calculated Edge influence sensitivity, S – a population-specific measure of fragmentation sensitivity that ranges from 0 (least sensitive) to 1 (most sensitive) – for each species using the percent cover layer, the edge influence map, and the species abundance data using the formula:

$$Edge\ Influence\ Sensitivity = 1 - \frac{\sum abundance\ interpolated\ with\ PC\ and\ EI}{\sum abundance\ interpolated\ with\ PC}$$

If, for example, edge influence was not predictive of abundance after accounting for percent cover, then the two interpolated sums would be similar, their ratio would be near 1, and edge sensitivity would be near 0. Note that a high S does not imply negative impacts associated with edges since species that strongly prefer high edge influence regions would also have high edge influence sensitivity. Finally, for each dataset, a rating was computed that quantifies the extent to which sample points span low and high values of percent cover and edge influence and are at least partially found far (> 500 m) from habitat edges. These ratings range from 0 to 1, with higher values indicating datasets where edge influence sensitivity estimation is likely the most reliable.

While edge influence sensitivity is sufficient to learn about where species are most fragmentation sensitive, it does not distinguish between species that prefer forest habitat and those that prefer matrix habitat. Additionally, it does not distinguish between species that strongly prefer edges and those that strongly avoid them. However, BIOFRAG also attempts to classify species according to habitat specialist type (Forest, Matrix, or Generalist) and edge influence preference

(Edge, Core, or No preference) (*13*). This is done by treating abundance as a function of cover and edge influence. On the cover – edge influence graph, different patterns of abundances are matched with different classifications using a Naïve Bayes classifier-based approach where training datasets were constructed by simulating abundances as functions of point cover and edge influence for species in each category (*13*). Generally, species with estimated maximum abundance at low cover are classified as Matrix and those with estimated maximum abundance at high cover as Forest (others are classified as Generalist). Species with maximum abundance in low (near zero) edge influence regions tend to be classified as Core habitat users, in high (positive and/or negative) edge influence regions as Edge habitat users, and with uniform abundance across edge influence as having no preference. Because this classification approach distinguishes between edge-sensitive species that respond positively to edges and those that respond negatively to edges, we used it as our primary metric when modeling fragmentation sensitivity for forest species, treating Core species as those that are most (negatively) impacted by fragmentation (see <u>Statistical modeling</u> section). It is important to note that as with any statistical classifier, classification emerges solely from the datasets associated with the study, and some misclassifications undoubtedly occur due to Type I error, small sample size, and other sampling issues. Nevertheless, such misclassifications would result in error rather than bias with respect to testing our study hypotheses. It should also be noted that edge influence sensitivity (*S*) is not directly involved in the BIOFRAG classification of species. Rather, both *S* and the classification are developed using the edge influence maps (and abundance data, etc.), so they are only indirectly linked in the sense that they share common input.

<u>Depth of edge influence selection</u>

For some datasets, the 1-km main depth of edge influence that we initially selected resulted in sample points that did not fully span the point cover and edge influence plane. This can lead to the Naïve Bayes classifier exhibiting bias toward certain categories. To mitigate this bias, for each dataset, we first simulated 100 artificial species abundances (at the actual sample point locations) – that is, species abundances were randomized across the existing spatial sampling structure. For sample points with at least 60% point cover (i.e., forest-associated species), we let abundances be uniformly distributed between 0 and 1, and for points with less than 60% point cover, we set abundances to zero. Under this null model, since simulated species are forest-associated and their abundances are not dependent on edge influence, they should be categorized as "Forest No Preference." However, in 39/94 datasets, simulated species were biased toward "Forest Core" or "Forest Edge." For those datasets, we dealt with the bias using a two-step procedure: (1) test whether the bias could be remedied by using a different finer (200 m) or broader DEI (2 km), (2) if adjusting DEI did not remedy the bias we removed the dataset entirely Of the 94 BIOFRAG datasets containing our focal taxa (mammals, birds, herptiles, and arthropods), we retained 73 datasets (55 at 1-km depth of edge influence, 17 at 200-m depth of edge influence, and 1 at 2-km depth of edge influence).

The 73 datasets remaining span 35 regions and range in latitude from -42.6° to 51.8°.The Naïve Bayes classifier approach used by BIOFRAG can also classify species as "Absent," "Nonabundant", or "Unknown." We omitted species with these classifications, focusing on those classified as Forest/Matrix/Generalist and Core/Edge/noPref. This yielded a total of 8 categories rather than 9, because there were no Generalist Core species. Our final dataset contained 3,275

unique species and 4,747 combinations of datasets and species. Additional relevant sample sizes are provided in Tables S1 and S2.

<u>Predictor variables</u>

We used a number of spatial variables to predict whether or not Forest species were classified as "core" – an indicator of fragmentation sensitivity – and the likelihood of species being classified as Forest, Matrix, or Generalist. We used the approach described in Betts et al. (*3*), which we briefly outline here, to map long-term, anthropogenic historical forest loss, which we considered as a predictor of fragmentation sensitivity. Specifically, we assumed current tree cover within intact forest landscapes (IFLs) to be representative of historical tree cover there (*38*). We used a random forest model to link current tree cover to forest biome type and bioclimatic predictors (temperature, precipitation, etc.) within IFLs and then used this model to predict historical tree cover across all forest biome regions. We then computed historical forest loss, which we defined as the percentage of historical tree cover lost relative to tree cover in 2000, treating regions where year 2000 cover exceeded estimated historical cover as having 0% historical forest loss. The values range from 0% (no historical forest loss) to 100% (complete loss of historical forest). We treated regions outside of forest biomes as having 0% historical forest loss. To estimate (percent) historical forest loss for each BIOFRAG dataset, we first applied a 1-km buffer to each of the sample points (in AEQD projection). We then averaged historical forest loss (5-km resolution) across each of the resulting polygons to obtain one value per sample point. Finally, we averaged across sample points to obtain one historical forest loss estimate per dataset. Historical forest loss included any deforestation detected prior to 2000 that had not subsequently been afforested by 2000, but our results were robust to the redefinition of this variable to include only deforestation prior to 1960. This latter definition allows for the possibility that extinction debt (*39*) could result in an underestimation of the effect of forest loss on the proportion of forest core species. We acknowledge that it is not possible to quantify the complex process of forest loss and gain at evolutionary timescales. However, quantification of anthropogenic forest loss – albeit imperfect – is essential for testing extinction filter effects.

Along with the anthropogenic historical forest loss variable described above, we used maps of forest fire type, glaciation, and storms to derive a set of binary "disturbance" variables (Fig. 1). We reasoned that the effect of glaciers on forest landscape structure is not just to the area covered by ice (which would not necessarily generate high edge). The land near the terminal part of the glacier undergoes disturbance and succession back into forest at different rates depending on topography, moisture, soil availability dispersal etc. (*40*, *41*). This variation will therefore affect patchiness and edge effects in pre- and post-glacial landscapes. For each BIOFRAG dataset, we determined if its location was glaciated at the last glacial maximum (LGM) using Ray & Adams (*20*), if it experiences high intensity forest crown fires using Lavorel et al. (*19*), whether or not it experiences tropical storms using Met Office (*21*), and if it had experienced at least 50% historical forest loss. We created three binary disturbance variables: "any disturbance" (fires, glaciers, storms, or historical forest loss), "natural disturbance" (fires, glaciers, or storms), and "historical forest loss" (historical forest loss). This approach grouped high intensity disturbances into three categories: natural, anthropogenic (historical forest loss), and combined ("any disturbance"). As an alternative to explicitly using disturbance, we considered absolute latitude as another predictor of fragmentation sensitivity.

Of course, the binary disturbance variables used in our analyses are limited in the sense that they do not account for many differences in disturbance nature, such as spatial pattern, length of disturbance, gradients in severity, or the time scale over which the disturbance has occurred. For historical forest loss in particular, spatial scale is important to consider because some broad-scale regions (e.g., the Atlantic Forest) may have experienced substantial deforestation, whereas BIOFRAG regions in these areas might have experienced less deforestation (because regions cannot be located in areas that are currently heavily deforested since in order to be included in the study then needed to span an edge/fragmentation gradient). The focus of our analysis is on general global patterns only, and thus more subtle relationships are better suited to being assessed with detailed landscape-specific analyses.

We considered two potential predictors of fragmentation sensitivity based on species' geographic ranges: geographic range size (km^2; base 10 log transformed) and distance to edge of range (km; base 10 $log(1+x)$ transformed). For this portion of the analysis, we used International Union for Conservation of Nature (IUCN) and BirdLife range maps, considering only polygons coded as Native and either Extant or Probably Extant (*42*, *43*). We converted the polygon range maps to 1,000 m resolution rasters in longitude/latitude format. When determining range sizes, we clipped the species range map rasters using species altitude limits given in their IUCN Red List fact sheet pages. For this step, we used the U.S. Geological Survey's Global 30 Arc-Second Elevation map. Of the taxa in our analysis, the range map sets were comprehensive for mammals, amphibians, and birds.

Biodiversity hotspots

We determined which of the low- and high-disturbance BIOFRAG regions occurred in biodiversity hotspots because conservation in these regions is likely to be particularly important (*33*). To do this, we used a map of biodiversity hotspots, 'biodiversity hotspots revisited' by Mittermeier et al. (*44*, *45*), that shows regions with 1,500 or more endemic, native plant species that have lost 70% or more of their native vegetation (*33*, *44*, *45*). Of the 35 BIOFRAG regions in our study, 24 (68.6%) were located within hotspots. Moreover, the proportion within hotspots was substantially greater in low disturbance (17/21; 81.0%) than in high disturbance (7/14; 50.0%) regions.

Statistical modeling

We used mixed-effects logistic regression to test if the likelihood of forest specialist species being classified as Core varied with respect to the cumulative effect of these disturbance variables, absolute latitude, and the other predictors described in the "Predictor variables" section. As species within a dataset occurred in the same region and were therefore not independent, we included 'dataset' as a random effect. Each observation corresponds to a species within a dataset. We fit all models predicting core/non-core species using the 'glmmTMB' function in the glmmTMB R package (*46*, *47*). We used dataset rating as the weighting variable. In addition to separate models for each of the focal taxa groups (Table S3), we fit combined model for all species together, including taxonomic group (mammals, herptiles, birds, or arthropods) as a random effect. Because some species occurred in multiple datasets, we included species identity as a random effect except for herptiles, where the species-level random effect prevented convergence. Since the majority of species appear only once in the dataset (Table S1),

the within-species variance component can be difficult to estimate. While most models converged with the default settings of nlminb (the optimizer used by glmmTMB), we slightly relaxed the convergence criteria (by decreasing the relative tolerance from 10^{-10} to 10^{-7}) to be able to fit a larger set of models. As a sensitivity analysis, we also report our main results when species-level duplicates are randomly dropped (i.e., each species is removed from all but one dataset, if needed; Figs. S7 & S9). For this sensitivity analysis, we used the default optimizer settings.

We considered a number of different sets of predictor variables. Specifically, we fit models with [1] each of the three disturbance variables alone, [2] absolute latitude alone, [3] the "top" disturbance variable (based on AIC) together with absolute latitude (to test whether disturbance has an effect independent of latitude), and [4] range size and distance to edge of range together with each disturbance variable. All p-values were false discovery rate (FDR) adjusted to control the expected proportion of Type I errors (*48*). Coefficient confidence intervals and confidence bands for the mean response were derived under the assumption that the logit scale estimates are normally distributed. To compare the models within each group, we computed differences in AIC. We did not fit models in cases where a binary disturbance variable was included as a predictor and, in either low or high disturbance regions, all species in our sample were either core or non-core. In such cases (termed "complete separation" in logistic regression), the log odds of species being core cannot be estimated well for both low- and high-disturbance regions.

We used a separate modeling approach – Bayesian multinomial regression – to estimate the likelihood of species being Forest, Matrix, or Generalist as a function of latitude and (separately) as a function of "any" disturbance. These models were fit using the 'brms' R package with default non-informative priors (*49*). As before, random intercepts by dataset identity, species identity, and taxonomic group for the "All species" model were included. Additionally, we included random slopes by class for the "All species" model here. This was not done for our other models because they did not converge with random slopes. The multinomial regression parameterization was based on treating Forest as the reference level and estimating the odds of Matrix and the odds of Generalist relative to Forest. Because of their complexity, we fit the models using variational Bayes with the mean field approximation. To regularize inferences, we used weakly informative priors: Normal(0,5) for intercepts and binary predictors, Normal(0,1) for standard deviations, and Normal (0,0.01) for slope parameters. The slope parameters are associated with absolute latitude. A value of 0.1 corresponds to an increase of 10.5% in the odds of, for example, a species being classified as Matrix versus Forest per one degree increase in absolute latitude.

Phylogenetic relatedness

We were not able to account for phylogenetic dependence among study species with phylogenetic comparative methods because comprehensive or well-resolved phylogenetic trees are not available for all species in our sample. Moreover, gaps in phylogenetic data are much more extensive in some groups, especially arthropods, potentially leading to taxonomic bias (*50*). Furthermore, Amphibia and Squamata taxonomy are unstable, making phylogenetic analyses with these taxa difficult (*51–54*). Instead, we conducted a sensitivity analysis for our primary disturbance model by including taxonomic family and order as random effects (i.e., with random

intercepts). We determined taxonomic family and order for each species in our dataset using the Encyclopedia of Life (EoL), which includes taxonomic data from many references (*55*). We opted to use the EoL here because some BIOFRAG species names are recognized only by certain taxonomic authorities. Many disagreements between taxonomic sources are at the genus or species level, which would not impact our assignment of BIOFRAG species names to taxonomic families. We excluded species for which we were not able to determine taxonomic family (206 arthropods, 1 bird, 2 herptiles, and 1 mammal). For the species with known taxonomic family and order, we fit our generalized logistic regression mixed models using "any" disturbance to predict the likelihood of species being classified as core with random intercepts by taxonomic family, species identity, and dataset identity; i.e., "(1 | order) + (1 | family) + (1 | species) + (1 | study)".

Migratory status

We hypothesized that bird species in high disturbance areas are less likely to be fragmentation sensitive (classified by BIOFRAG as using core habitat) than bird species in low disturbance areas. However, it is possible that migrant bird species are both more likely to be found in high-disturbance areas and more likely to be fragmentation insensitive (not core), making migratory status a potential confounding variable in our analysis.

To assess this possibility, we refit our primary models for birds excluding migratory species (Table S5). To do this, we determined migratory status for each of the bird species in our analysis using BirdLife's Data Zone species' fact sheet pages (*56*). For "species" listed in BIOFRAG that were actually families or genera, we instead used the most common migratory status (breaking ties alphabetically) of the species within that taxon. Of the 1,260 unique species in our analysis, 21 are altitudinal migrants, 274 are full migrants, 26 are nomadic, and 939 are not migrants. We excluded only "full migrants" from this portion of our analysis.

Rarefaction curves

We used rarefaction curves to investigate whether changes in the apparent distribution of species with respect to latitude and incomplete sampling could be influencing our results. The curves show estimated diversity as a function of number of individuals observed. We determined the number of each species that was observed within each habitat type (Forest, Matrix, or Generalist) and disturbance level (Low or High) by pooling data across sample points and datasets and rounding non-integer abundance estimates. We then calculated the rarefaction curves (with 95% confidence bands) using the 'iNext' R package (*57*).

Supplementary Text

Species' responses to landscape-scale fragmentation

Our analysis is conducted from the perspective of sample points and surrounding 1-km buffers within regions. To illustrate the connection between our measure of fragmentation – edge sensitivity (S) – and landscape-scale fragmentation per se as a landscape-scale process (sensu *6*), we conducted a simulation exercise. We repeatedly simulated landscapes of size 100 x 100 using

the two-dimensional fractional Brownian motion neutral landscape model (*58*). We varied the fractional dimension in the model, which controls the level of fragmentation for each level of habitat amount. For each simulated landscape, we used a constant threshold to divide the landscape into habitat and non-habitat pixels with a given habitat amount. Thus, these simulated landscapes represent various degrees of fragmentation and habitat amount. We varied habitat amount from 0% to 100% in increments of 5% and let the fractal dimension (inversely related to fragmentation) take values of 0.05, 0.5, 1, and 1.5. For each combination, we generated 10 separate landscapes. We then classified each habitat pixel in each landscape as either core or edge depending on whether at least one of the eight neighboring pixels occurred in the matrix (i.e., non-habitat).

Using these simulated landscapes, we plotted the proportion of core habitat in each landscape versus the landscape-scale habitat amount (either core or edge). When fragmentation is very low (i.e., fractal dimension is high), there are few edge pixels and core habitat amount and total habitat amount (core or edge) are roughly equal. When fragmentation is high, the amount of core habitat declines rapidly with decreasing total habitat amount due to the rapid increase in edge habitat. This demonstrates that edge-sensitive (core) species exhibit non-linear responses to fragmentation occurring at the landscape scale. Therefore, 'forest core' species in our analysis, all other things being equal, will be sensitive to fragmentation per se at the landscape scale.

Distinguishing the effects of habitat amount from fragmentation

BIOFRAG automatically classifies species as Forest/Matrix/Generalist and Core/Edge/noPref using information about both tree cover and edge influence. Because forest usually needs to be lost to create edge, it can be argued that the Core/Edge/noPref designation may be partly driven by habitat (forest cover) amount, rather than purely associated with edge/fragmentation effects. This leads to the possibility that edge sensitivity, and in particular determination of species designated as 'forest core', could be explained as a forest cover amount effect (*59*); 'forest core' species could simply be species that are sensitive to landscape-scale forest loss (i.e., habitat amount).

To explore this possibility, we compared the BIOFRAG classifications to an alternative Core/Edge/noPref classification derived from using forest amount (as represented by forest cover) alone. If the two classification methods produce similar results, it would suggest that forest amount is heavily involved in BIOFRAG's determination of Core/Edge/noPref status, so we could not claim our findings about the proportion of forest species that require core habitat are solely related to fragmentation per se.

For our alternative classification, we first computed the mean forest cover within 100 m and within the associated BIOFRAG depth of edge influence (generally 1 km) of each sample point, which we termed Cover_100 and Cover_landscape, respectively. We then modeled abundance for each species using multiple linear regression with Cover_100 and Cover_landscape as explanatory variables. The reasoning for using these predictors is that Cover_100 statistically accounts for the degree to which a species is associated with forest at fine scales. A positive relationship between Cover_landscape and abundance supports the hypothesis that species are sensitive to forest loss at broader scales [via influences to dispersal/mass effects etc. (*60*)].

We fit one model per species within each BIOFRAG dataset. We standardized the response and predictors to have mean 0 and standard deviation 1 to make coefficients comparable across species and datasets. Because our "probability of being core" models are for Forest species only, we restricted our attention to Forest species as determined by BIOFRAG.

To obtain discrete categories, we classified species using the coefficient of Cover_landscape. Low (negative) values indicate forest species that tend to prefer low forest amounts (since abundance is negatively related to cover at 1 km after controlling for cover at 100 m), values near zero indicate species with no forest amount preference, and high values indicate high forest amount species. So, we classified species as High Forest Amount (the equivalent of Core), Low Forest Amount (the equivalent of Edge), or noPref if the coefficient was < -x, > x, or between –x and +x respectively. We chose the threshold x, which turned out to be 0.0494, so that the number of Forest noPref species in our classification system was equal to that reported in our BIOFRAG analysis.

As a further and more stringent test, we asked whether species designated as "Forest Amount" sensitive in our new analysis would produce patterns similar to those described in the main text of our manuscript. In other words, (1) Does the proportion of Forest Amount species decline strongly with increasing latitude, and (2) Does historical disturbance (natural and anthropogenic) predict the proportion of Forest Amount species? To assess this, we refit the latitude and disturbance models using, as the response variable, whether or not species were classified as "High forest amount" (analogous to Forest Core in BIOFRAG).

The disturbance effect estimates were substantially smaller when modeling whether or not species were categorized as 'High Forest Amount' compared to when using BIOFRAG Forest Core status as the response (Table S3 versus S8). This indicates that forest amount cannot explain, on its own, the effects of either latitude or disturbance on the proportion of forest core species, as defined using the BIOFRAG approach.
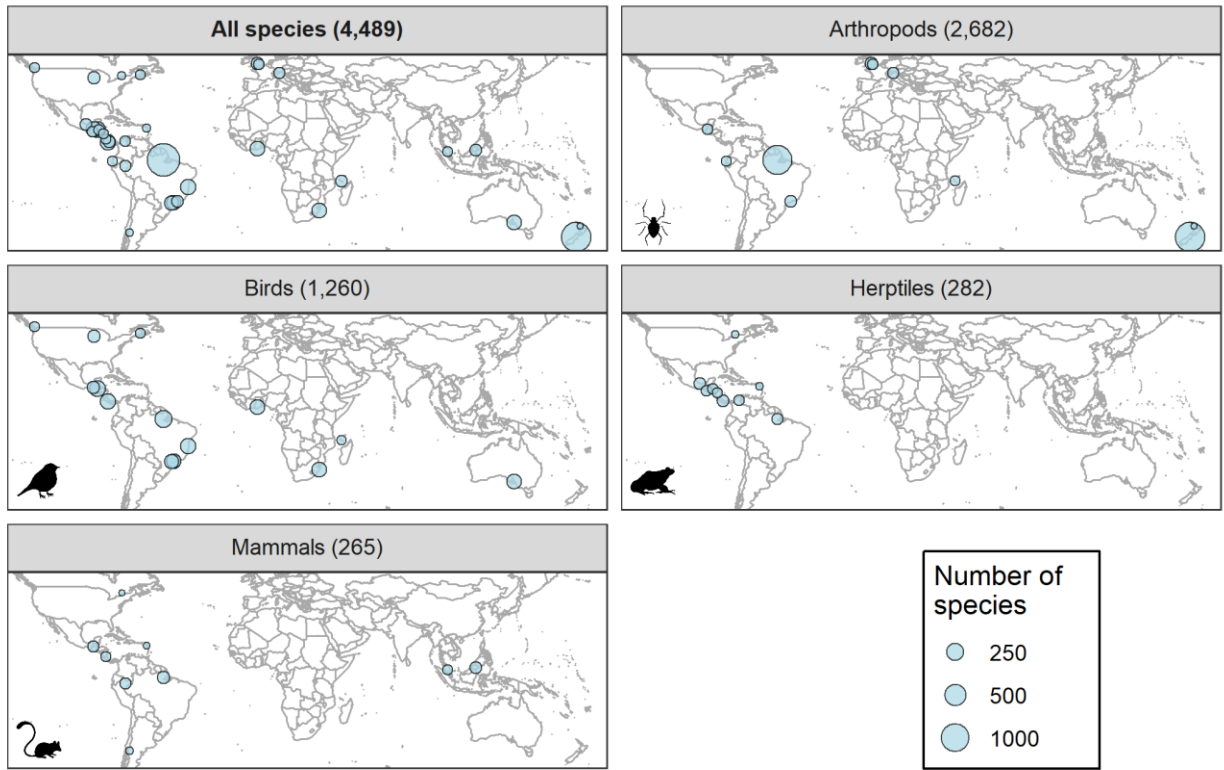
Fig. S1. BIOFRAG dataset locations for the species groups in our analysis. Sizes of circles indicate numbers of species in each region that were used in our analysis and numbers in panel titles indicate totals across all relevant regions.
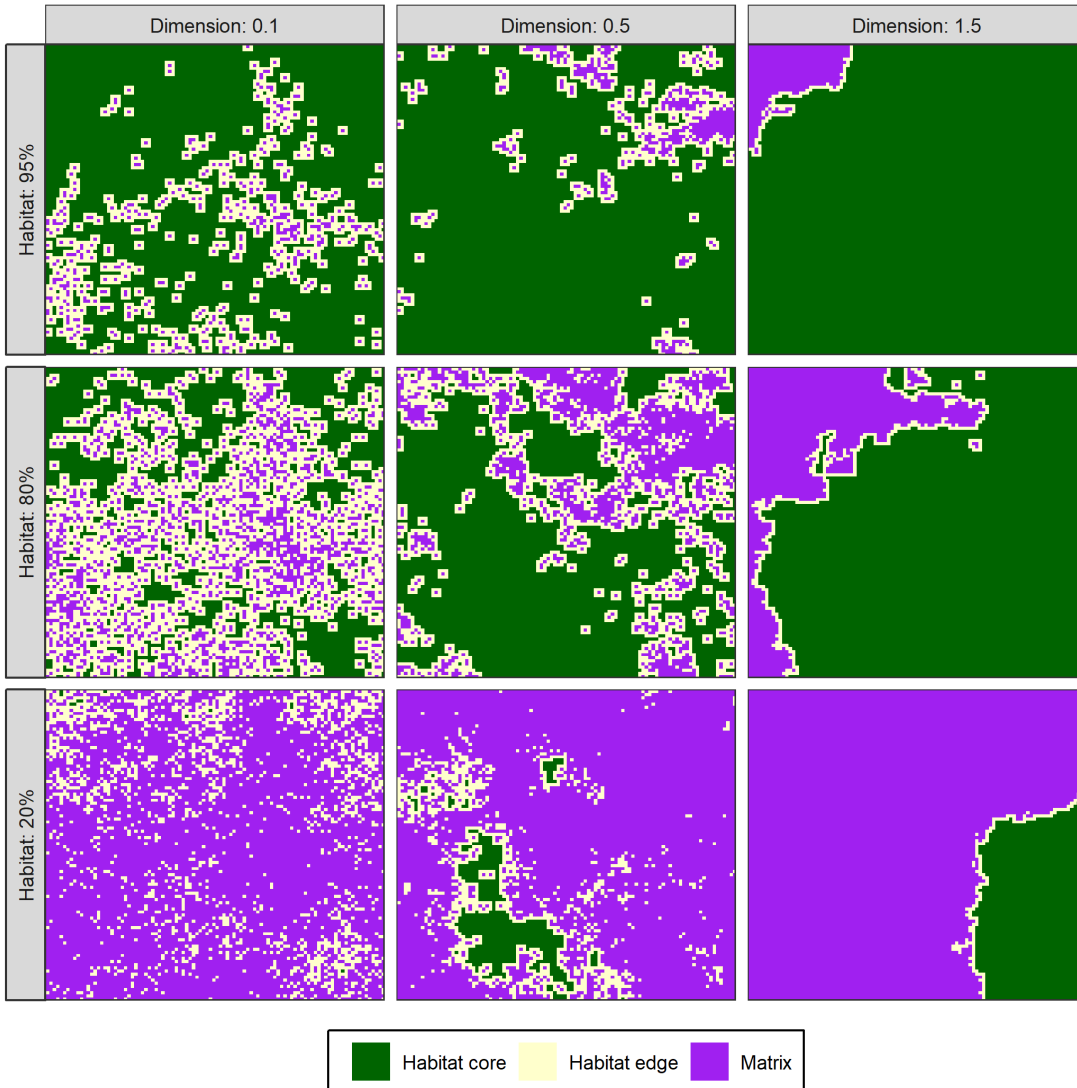
Fig. S2. Examples of simulated landscapes with different levels of habitat amount (either core or edge) and fragmentation (inversely related to fractal dimension). Edge-avoiding species show highly non-linear abundance declines as habitat is lost at high levels of fragmentation (left column) due to the rapid increase in edge pixels (Fig. S3). In contrast, when fragmentation is low (right column), the change in number of edge pixels is small, so the decline in core species abundances (or proportion of core habitat) is roughly linear. This demonstrates that edge sensitivity scales up to induce landscape-scale fragmentation effects for core species.
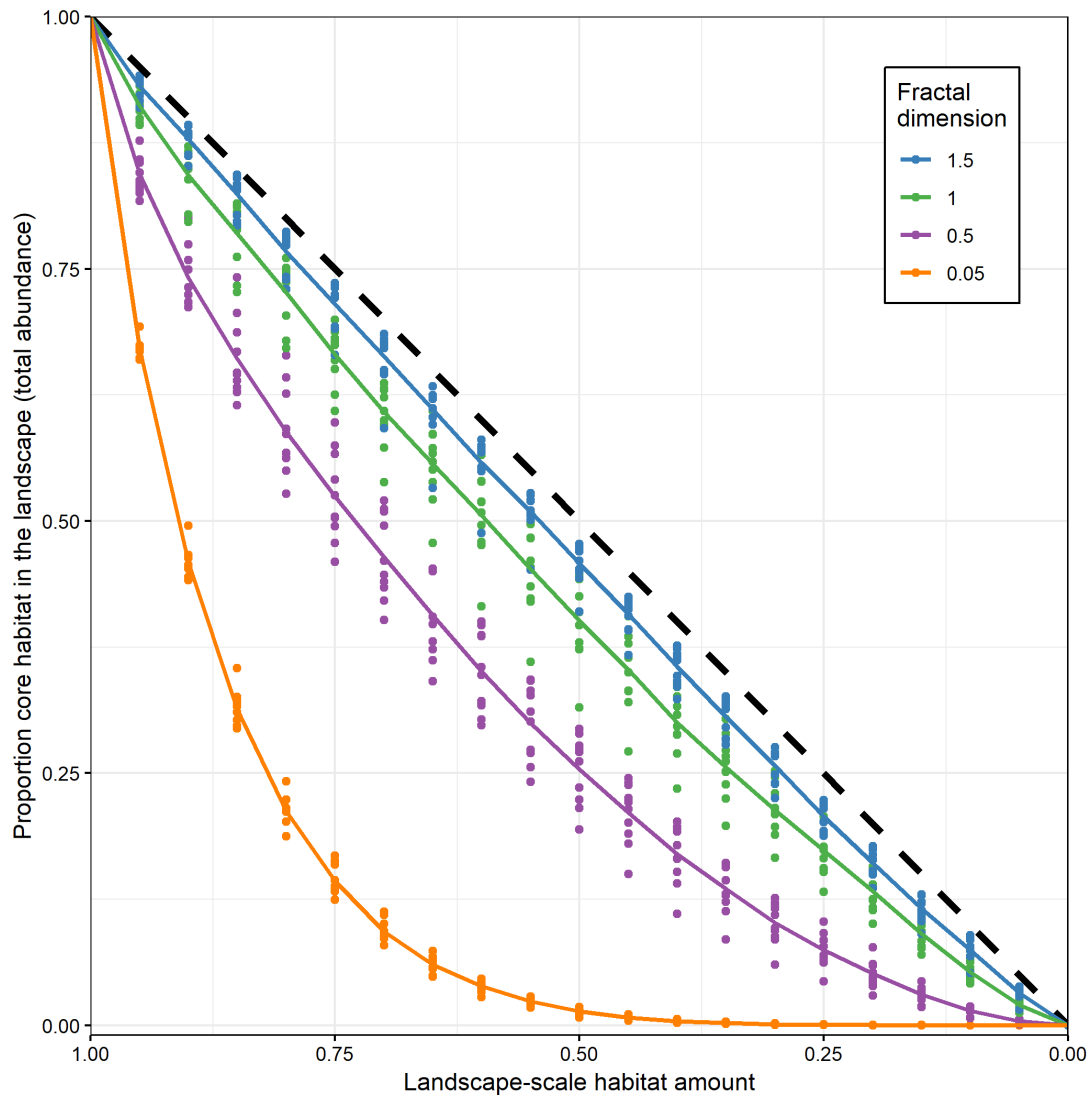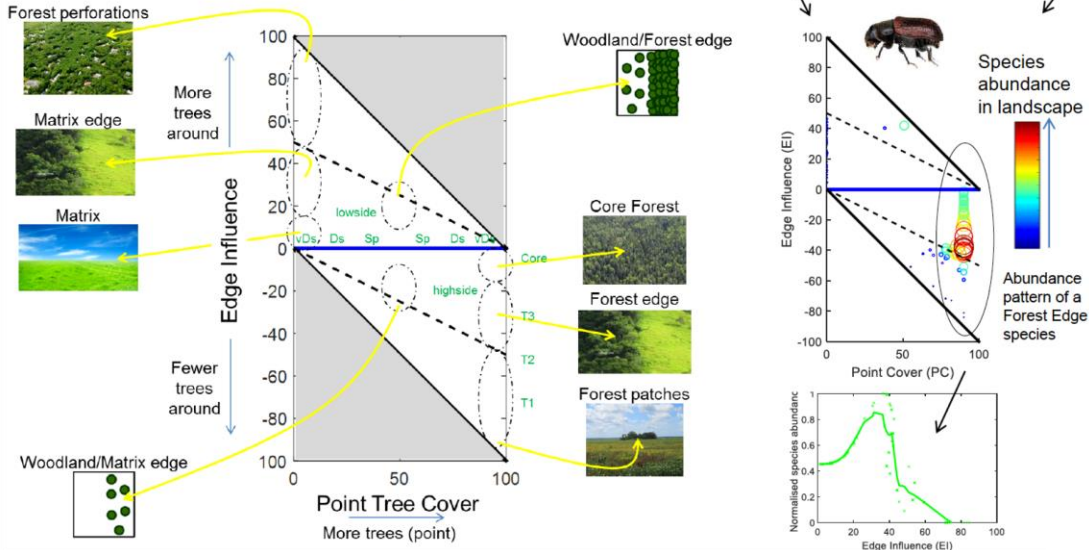
Fig. S3. Change in population size (assuming constant species density in remaining habitat) as a function of habitat loss for four habitat fragmentation scenarios (measured as 'fractal dimension' with low values of fractal dimension reflecting high fragmentation. When fragmentation is high, the drop in core habitat is most extreme because of the rapid rise in edge pixels (Fig. S2). At lower levels of fragmentation, fewer edge pixels are present for a given amount of habitat, so the decline is closer to linear. The dashed isometric black line indicates the rate at which an edge insensitive species would decline with habitat loss.
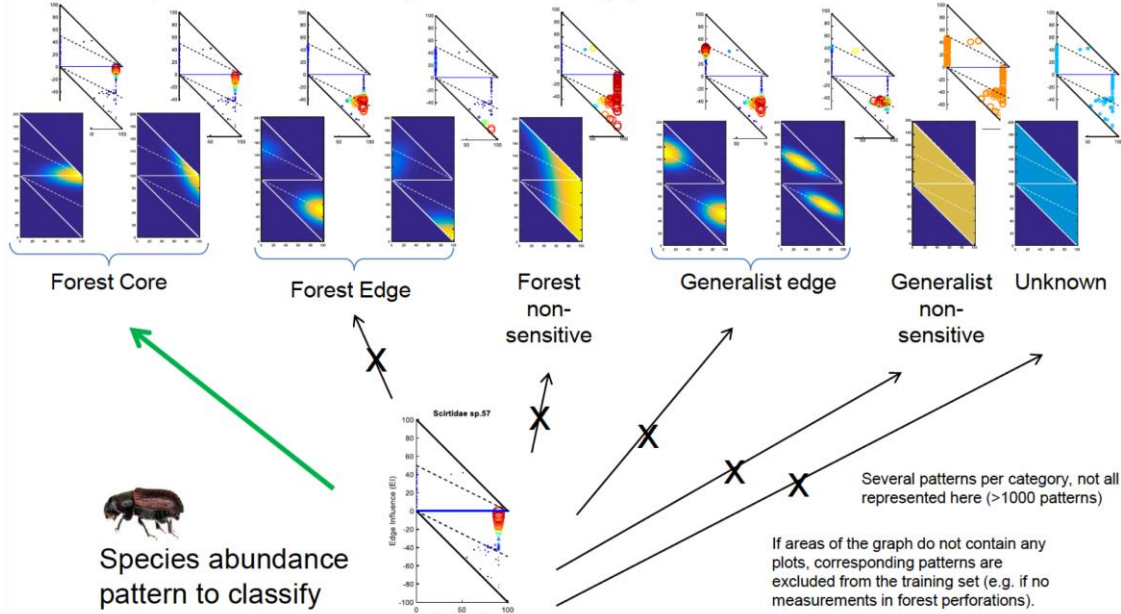
Fig. S4. Conceptual diagrams with examples of how Edge Influence (EI) and species' sensitivity to edge (S) are calculated using the Biofrag method. For details, see user manual at: https://github.com/VeroL/BioFrag/blob/master/Edge_response_software_user_manual_20160827.pdf
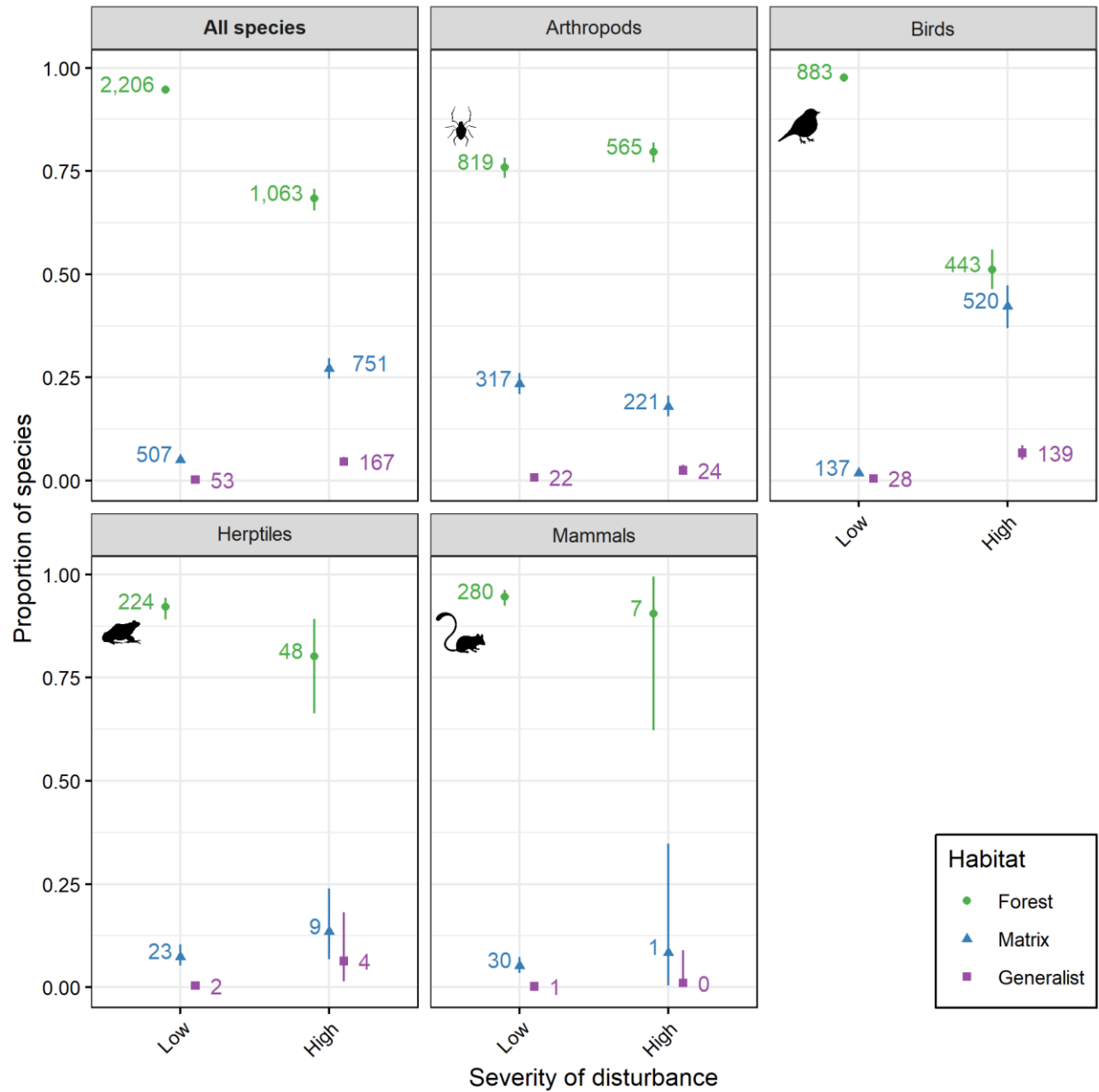
Fig. S5. Distributions of species across habitat types (Forest, Matrix, and Generalist) at low and high disturbance locations. Estimates with 95% credible intervals were derived using a hierarchical Bayesian multinomial regression model that accounts for variability associated with datasets (and taxonomic group for the "All species" model). The odds of species being classified as Matrix or Generalist (relative to Forest) tend to be greater in high disturbance areas than in low disturbance areas, although this is not true in all cases (Table S4).
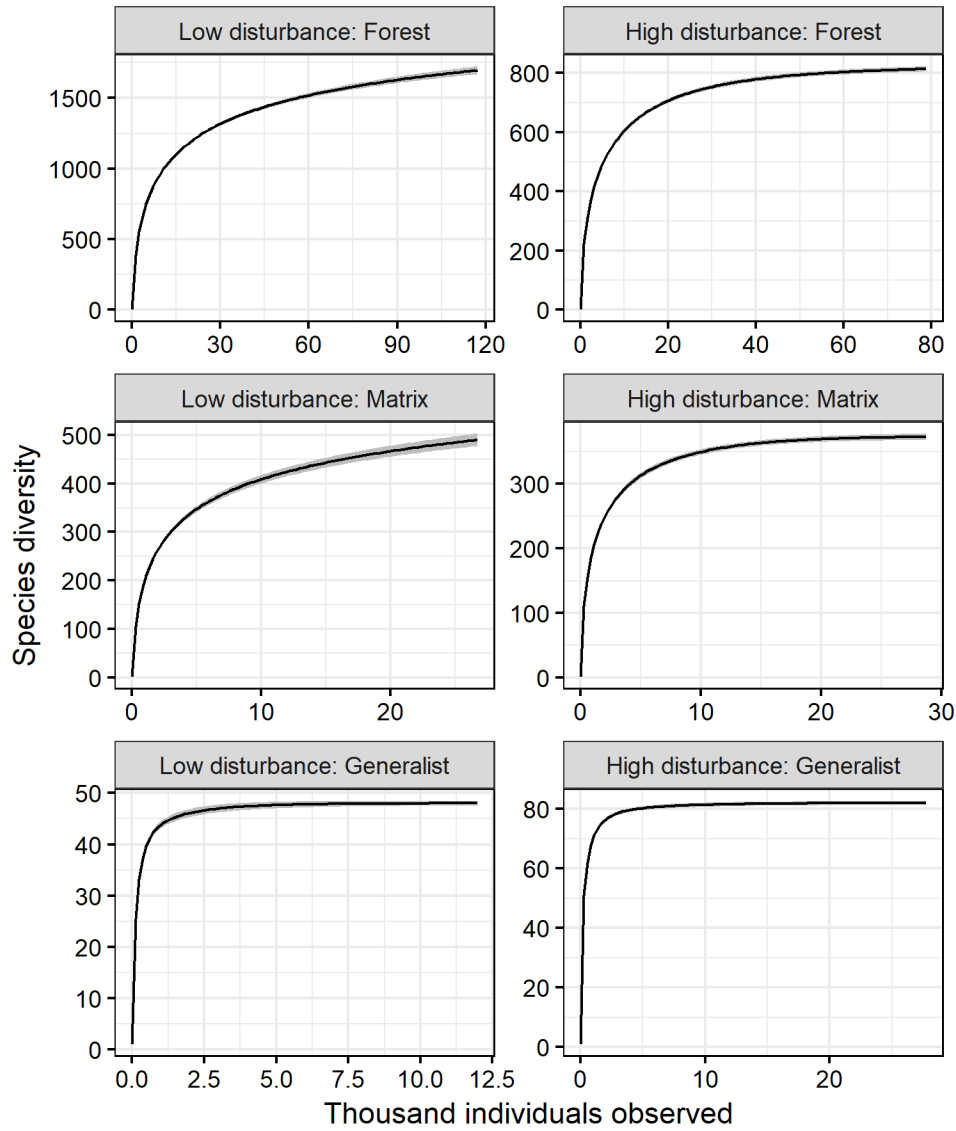
Fig. S6. Rarefaction curves (with 95% confidence bands) for low and high intensity disturbance regions. Each region type includes multiple BIOFRAG datasets, which in turn contain multiple sample points where abundances were measured. Species diversity is plotted as a function of the sample size in terms of number of individuals observed (rather than number of sample points). These curves indicate that species accumulation nearly saturates in high disturbance areas and for generalist species.

Fig. S7. Sensitivity of our results to the method used to account for taxonomic/phylogenetic dependence. The plots show the estimated proportions (mean ± 95% CI) of forest species associated with core habitat at low and high disturbance sites according to mixed-effects logistic regression models where study identity is included as a random effect. The binary 'disturbance' variable indicates whether or not each of the 73 BIOFRAG datasets comes from a location that has had high severity disturbances of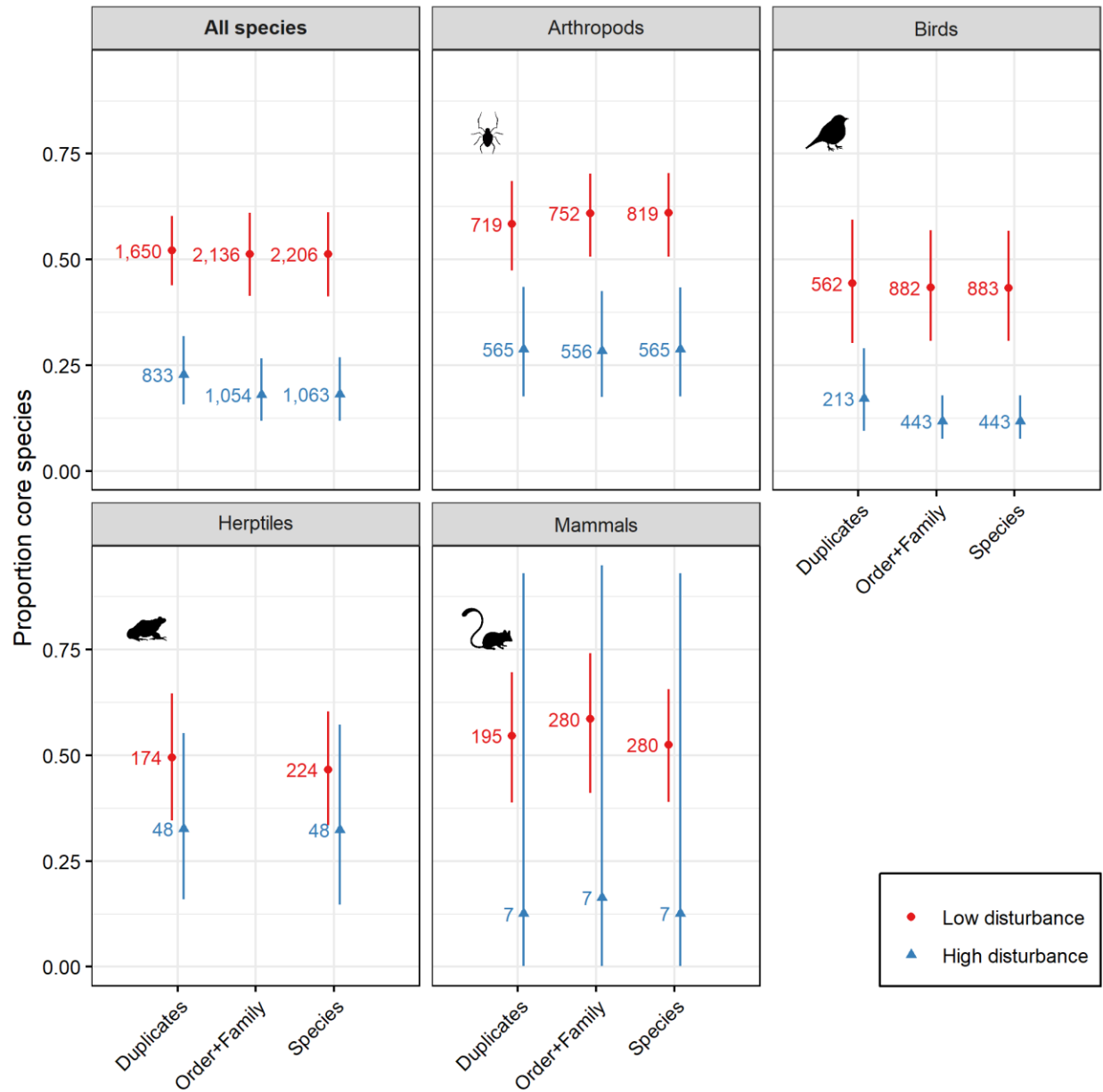 any type (glaciation, tropical storms, crown fires, or greater than 50% historical forest loss). In the "Duplicates" method, when a species occurs in multiple datasets, it is randomly dropped from all but one of the datasets, in the "Order+Family" method, random intercepts by taxonomic order and family were included. This approach accounts for potential statistical non-independence resulting from similar responses by species within the same family or order. Lastly, in the "Species" method (see also Table S3), all data are used and only random intercepts by species and study were included. Note the "Order+Family" herptiles model results are omitted because this model did not converge.
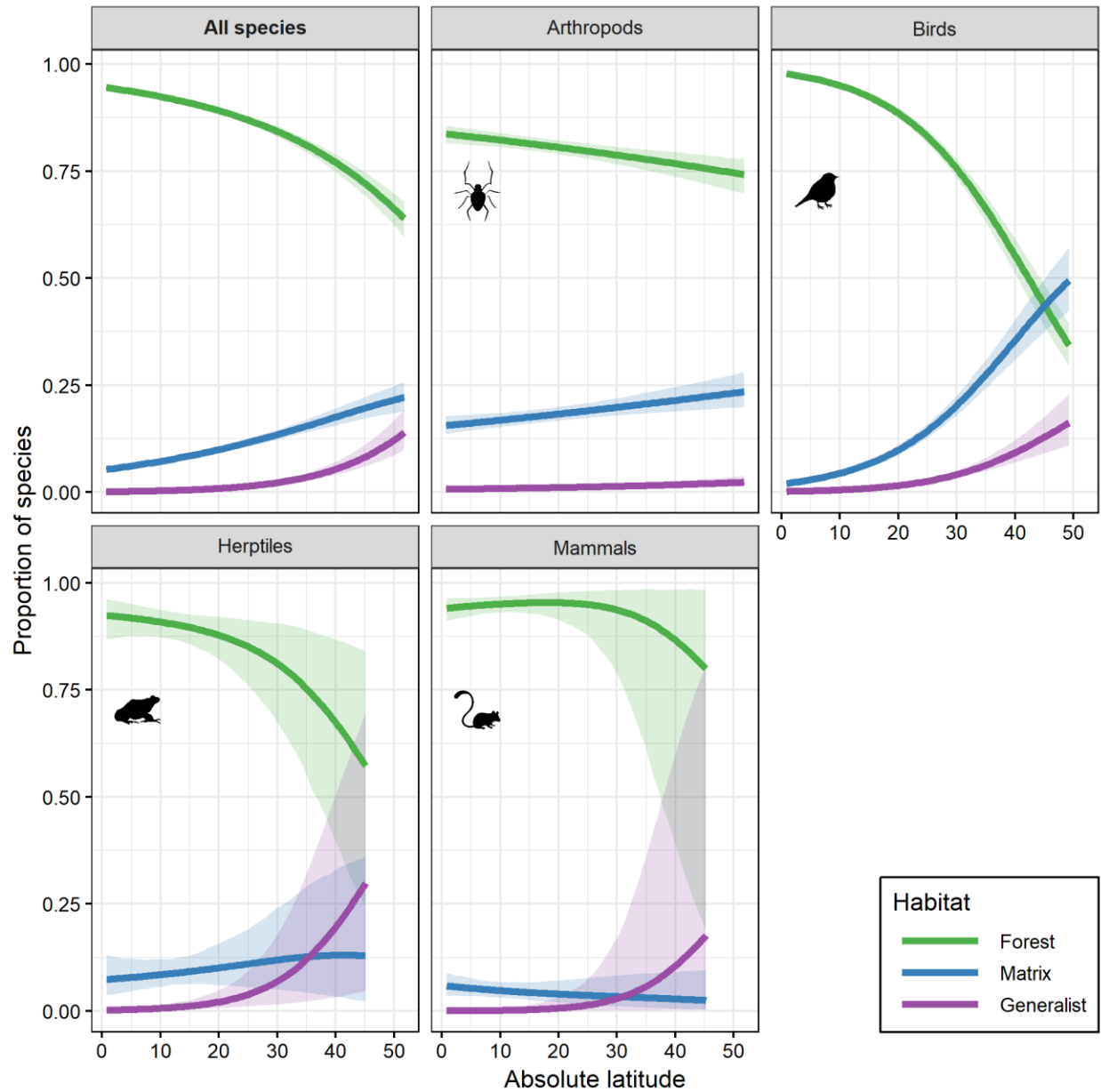
Fig. S8. Distributions of species across Forest, Matrix, and Generalist habitat types as functions of absolute latitude. Lines show mixed multinomial regression model fitted probabilities with random intercepts by dataset and random slopes by class for "All species." In general, the likelihood of species being categorized as Forest decreases as latitude increase. This result could be expected under the hypothesis that low latitude-tropical regions have had reduced historical disturbance, thereby reducing the prevalence of species evolved for disturbed habitats. Conversely, high latitudes have a relatively high proportion of species adapted to 'matrix' (disturbed areas). Note that this result is not an artifact of incomplete sampling of forest or matrix species at high or low latitudes; rarefaction curves indicate that matrix species were well sampled across latitudes (see Fig. S6). 95% credible bands are shown around the fitted lines.
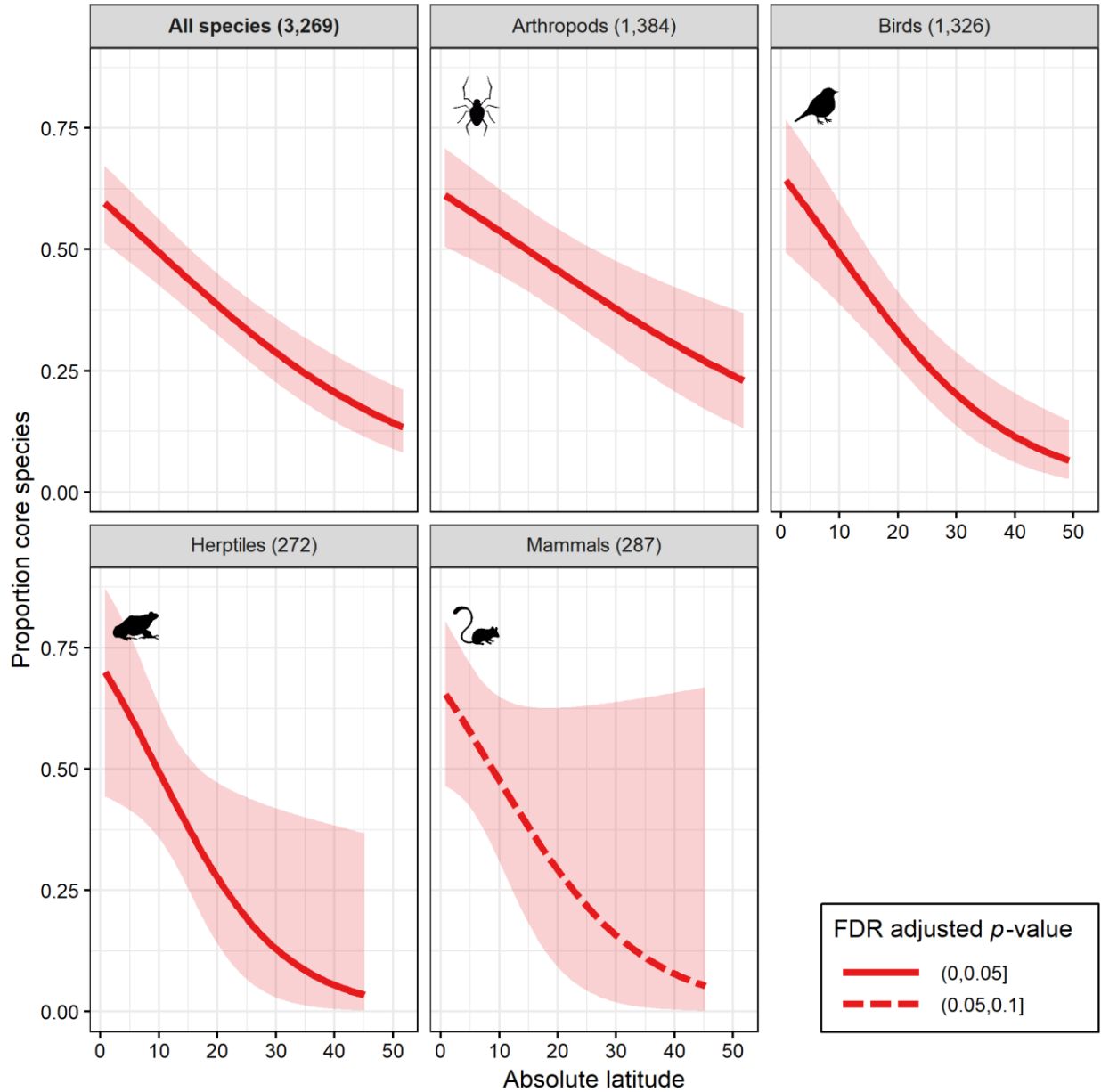
Fig. S9. Logistic regression models used to estimate the proportion of core species as a function of absolute latitude when "duplicate" species are randomly dropped from the dataset as a form of sensitivity analysis (SI Methods; compare with Fig. 3). The response variable is whether or not a species was classified as preferring core habitat (e.g., forest core). Overall, the general pattern observed (decreasing relationship with latitude for forest species) is what one would predict if high-latitude species have evolved to cope with disturbance. Numbers of observations are shown next to each of the fitted lines. All *p*-values were false discovery rate (FDR) adjusted to control the expected proportion of Type I errors.

Table S1. Numbers of populations and species in the BIOFRAG database and in our analysis. Species' populations are specific to individual BIOFRAG datasets. Since the same species may appear in multiple datasets, the numbers of unique species (termed 'Unique only') are typically less than the corresponding numbers of populations. In some cases, a 'species' can represent a broader taxonomic unit (e.g., Family). For simplicity, we refer to populations as species in the text. For our statistical analysis, we further omitted species that could not be classified as Forest, Matrix, or Generalist and Core, Edge, or No Preference.

	Our focal taxa		Our statistical analysis	
	Populations	Unique only	Populations	Unique only
Arthropods	2,955	2,682	1,968	1,803
Birds	3,145	1,260	2,150	997
Herptiles	354	282	310	249
Mammals	394	265	319	226
Plants	0	0	0	0
Other	0	0	0	0
All species	6,848	4,489	4,747	3,275

Table S2. Numbers of species in each habitat and type of edge preference category ("noPref" indicates no edge preference) that were included in our statistical analysis. We omitted species that could not be placed into this categorization system due to, for example, having extremely low abundances across all sample points (Supporting Methods). The final three columns show the proportions of species associated with each type of edge preference.

Group	Habitat	Number of species				Proportion of species		
		Core	Edge	noPref	Sum	Core	Edge	noPref
All species	Any habitat	1615	2504	628	4747	0.340	0.527	0.132
	Forest	1404	1383	482	3269	0.429	0.423	0.147
	Generalist	2	186	32	220	0.009	0.845	0.145
	Matrix	209	935	114	1258	0.166	0.743	0.091
Arthropods	Any habitat	742	1054	172	1968	0.377	0.536	0.087
	Forest	686	526	172	1384	0.496	0.380	0.124
	Generalist	0	46	0	46	0.000	1.000	0.000
	Matrix	56	482	0	538	0.104	0.896	0.000
Birds	Any habitat	609	1141	400	2150	0.283	0.531	0.186
	Forest	460	608	258	1326	0.347	0.459	0.195
	Generalist	0	137	30	167	0.000	0.820	0.180
	Matrix	149	396	112	657	0.227	0.603	0.170
Herptiles	Any habitat	125	158	27	310	0.403	0.510	0.087
	Forest	119	128	25	272	0.438	0.471	0.092
	Generalist	2	2	2	6	0.333	0.333	0.333
	Matrix	4	28	0	32	0.125	0.875	0.000
Mammals	Any habitat	139	151	29	319	0.436	0.473	0.091
	Forest	139	121	27	287	0.484	0.422	0.094
	Generalist	0	1	0	1	0.000	1.000	0.000
	Matrix	0	29	2	31	0.000	0.935	0.065

Table S3. Table of model results for probability of Forest species being "Forest Core." BIOFRAG classifies species as core if they prefer core habitat. Different models are separated by black lines beginning at the "Variable" column. Each row shows information on the effect of historical forest loss (a measure of anthropogenic disturbance), natural disturbance (tropical storms, fires, or glaciers), or any disturbance (either historical forest loss of natural disturbance) on the odds of a species being classified as core. The "Estimate" and "Std. error" columns are on the log odds scale. The p-values have been false discovery rate adjusted (with significant relationships highlighted in green). The columns with asterisks show the percentage effect (with 95% CI) of being in a region with high disturbance or historical forest loss on the odds of species being classified as core. The estimates provide evidence that the fragmentation sensitivity of forest core tends to increase with latitude and decrease with disturbance. Δ AIC values are relative to the best fitting model in each group. Results are omitted for cases where models could not be fit due to non-convergence or separation (e.g., no core species in high disturbance regions). Parameters with p-values less than 0.05 are highlighted in green.

Group	Variable	Estimate	Std. error	p-value	Estimate*	Lower*	Upper*	Δ AIC
All species (n=3,269)	Natural disturbance	-1.709	0.265	< 0.001	-81.9%	-89.2%	-69.5%	0.000
	Any disturbance	-1.559	0.247	< 0.001	-79.0%	-87.0%	-65.9%	3.115
	Historical forest loss	-0.299	0.438	0.494	-25.8%	-68.5%	74.8%	34.62
Arthropods (n=1,384)	Any disturbance	-1.351	0.39	0.002	-74.1%	-87.9%	-44.3%	0.000
	Natural disturbance	-1.307	0.488	0.019	-72.9%	-89.6%	-29.5%	2.859
	Historical forest loss	-0.799	0.773	0.439	-55.0%	-90.1%	104.6%	7.462
Birds (n=1,326)	Natural disturbance	-1.956	0.346	< 0.001	-85.9%	-92.8%	-72.1%	0.000
	Any disturbance	-1.744	0.372	< 0.001	-82.5%	-91.6%	-63.7%	6.833
	Historical forest loss	0.595	0.726	0.442	81.3%	-56.3%	651.9%	22.579
Herptiles (n=272)	Any disturbance	-0.601	0.593	0.439	-45.2%	-82.9%	75.5%	0.000
	Natural disturbance	-0.601	0.593	0.439	-45.2%	-82.9%	75.5%	0.000
	Historical forest loss	-0.601	0.593	0.439	-45.2%	-82.9%	75.5%	0.000
Mammals (n=287)	Any disturbance	-2.032	2.318	0.439	-86.9%	-99.9%	1132.1%	0.000
	Natural disturbance	-2.032	2.318	0.439	-86.9%	-99.9%	1132.1%	0.000
	Historical forest loss	-2.032	2.318	0.439	-86.9%	-99.9%	1132.1%	0.000

Table S4. Bayesian multinomial regression model results for the effects of absolute latitude and disturbance on the likelihood of species being classified as Forest, Matrix, or Generalist. Models are separated by black lines. In each case, the reference level is Forest. That is, each row shows the effect of either going from low to high historical disturbance intensity or a one-degree increase in absolute latitude on the odds of either Matrix or Generalist habitat type versus Forest habitat type. The "Estimate" and "Std. error" columns are on the log odds scale, while the columns marked with asterisks show the estimates with 95% credible intervals on the odds scale. The generally positive estimates and many credible intervals that do not contain zero provide evidence that the odds of being classified as Matrix and the odds of being classified as Generalist generally increase as absolute latitude and disturbance intensity increase. The models are hierarchical in that they account for variability associated with BIOFRAG dataset identity (and taxonomic group for the "All species" model). Because there were no high-disturbance generalist mammals and no low-disturbance generalist herptiles in our dataset and we used weakly informative priors, these estimates tended to diverge.

Variable	Group	n	Habitat	Estimate	Std. error	Estimate*	Lower*	Upper*
Absolute latitude	All species	4,747	Matrix	0.036	0.003	3.6%	3.1%	4.2%
			Generalist	0.096	0.005	10.1%	9.0%	11.2%
	Arthropods	1,968	Matrix	0.010	0.003	1.0%	0.4%	1.7%
			Generalist	0.025	0.006	2.5%	1.2%	3.8%
	Birds	2,150	Matrix	0.087	0.004	9.1%	8.2%	10.1%
			Generalist	0.112	0.007	11.8%	10.2%	13.4%
	Herptiles	310	Matrix	0.020	0.023	2.0%	-2.5%	6.7%
			Generalist	0.121	0.025	12.8%	7.3%	18.6%
	Mammals	319	Matrix	-0.022	0.023	-2.2%	-6.5%	2.2%
			Generalist	0.132	0.040	14.1%	5.4%	23.4%
Disturbance (any)	All species	4,747	Matrix	2.006	0.090	643.5%	522.7%	787.6%
			Generalist	3.273	0.157	2539.7%	1839.7%	3492.2%
	Arthropods	1,968	Matrix	-0.317	0.106	-27.2%	-40.8%	-10.4%
			Generalist	1.129	0.295	209.1%	73.5%	451.0%
	Birds	2,150	Matrix	3.812	0.136	4422.2%	3362.7%	5805.8%
			Generalist	3.199	0.182	2351.4%	1615.1%	3403.8%
	Herptiles	310	Matrix	0.706	0.396	102.6%	-6.8%	340.4%
			Generalist	2.772	0.695	1498.6%	309.5%	6140.2%
	Mammals	319	Matrix	-0.011	1.241	-1.1%	-91.3%	1025.6%
			Generalist	-2.330	3.188	-90.3%	-100.0%	4928.2%

Table S5. Table of model results for probability of species being forest core for non-migratory birds only (compare with Table S3). Different models are separated by black lines beginning at the "Variable" column. Each row shows information on the effect of historical forest loss (a measure of anthropogenic disturbance), natural disturbance (storms, fires, or glaciers), or any disturbance (either historical forest loss of natural disturbance) on the odds of a species being classified as core. The "Estimate" and "Std. error" columns are on the log odds scale. The p-values have been false discovery rate adjusted (with significant relationships highlighted in green). The columns with asterisks show the percentage effect (with 95% confidence interval) of being in a region with high disturbance or historical forest loss on the odds of species being classified as core. Parameters with p-values less than 0.05 are highlighted in green. The removal of migratory birds from the dataset did not substantially alter our primary results (Table S3).

Group	Variable	Estimate	Std. error	p-value	Estimate*	Lower*	Upper*	Δ AIC
Non-migratory Birds (n=1,036)	Natural disturbance	-2.139	0.419	< 0.001	-88.2%	-94.8%	-73.3%	0.000
	Any disturbance	-1.839	0.432	< 0.001	-84.1%	-93.2%	-62.9%	6.543
	Historical forest loss	0.808	0.944	0.392	124.5%	-64.7%	1328.5%	20.305

Table S6. Additional model results for probability of species being classified as forest core that incorporate distance to edge of range and/or range size. Different models are separated by black lines beginning at the "Variable" column. Each row shows information on the effect of natural disturbance (storms, fires, or glaciers), any disturbance (either historical forest loss or natural disturbance), distance to edge of species' geographic range, or geographic range size on the odds of a species being classified as core. Δ AIC values are relative to the best fitting model in each group. The "Estimate" and "Std. error" columns are on the log odds scale. The p-values have been false discovery rate adjusted. The columns with asterisks show the percentage effect (with 95% confidence interval) of either a 1 unit increase (continuous variables) or going from low to high (disturbance variables). Results are omitted for cases where models could not be fit due to non-convergence or separation.

Group	Variable	Estimate	Std. error	p-value	Estimate*	Lower*	Upper*	Δ AIC
	Natural disturbance	-1.995	0.315	< 0.001	-86.4%	-92.7%	-74.8%	0.000
	Natural disturbance	-1.887	0.322	< 0.001	-84.8%	-91.9%	-71.5%	0.368
	Range size	-0.237	0.184	0.319	-21.1%	-45.0%	13.3%	
	Natural disturbance	-1.941	0.339	< 0.001	-85.6%	-92.6%	-72.1%	1.563
All species	Distance to edge	-0.151	0.213	0.564	-14.0%	-43.4%	30.6%	
(n=1,718)	Any disturbance	-1.824	0.313	< 0.001	-83.9%	-91.3%	-70.2%	5.151
	Any disturbance	-1.713	0.327	< 0.001	-82.0%	-90.5%	-65.8%	6.012
	Range size	-0.209	0.196	0.439	-18.8%	-44.7%	19.1%	
	Any disturbance	-1.848	0.306	< 0.001	-84.2%	-91.3%	-71.3%	6.404
	Distance to edge	-0.193	0.217	0.462	-17.5%	-46.1%	26.3%	
	Natural disturbance	-1.964	0.351	< 0.001	-86.0%	-92.9%	-72.1%	0.000
	Natural disturbance	-1.918	0.333	< 0.001	-85.3%	-92.4%	-71.8%	0.098
	Distance to edge	-0.358	0.246	0.292	-30.1%	-56.9%	13.3%	
	Natural disturbance	-1.98	0.396	< 0.001	-86.2%	-93.7%	-70.0%	1.992
Birds	Range size	0.024	0.264	0.952	2.4%	-38.9%	71.7%	
(n=1,318)	Any disturbance	-1.721	0.326	< 0.001	-82.1%	-90.6%	-66.1%	6.148
	Distance to edge	-0.478	0.265	0.168	-38.0%	-63.2%	4.3%	
	Any disturbance	-1.744	0.377	< 0.001	-82.5%	-91.6%	-63.4%	6.8
	Any disturbance	-1.731	0.446	< 0.001	-82.3%	-92.6%	-57.5%	8.797
	Range size	-0.017	0.312	0.956	-1.7%	-46.6%	81.0%	
	Any disturbance	-1.083	0.63	0.18	-66.1%	-90.2%	16.4%	0.000
	Natural disturbance	-1.083	0.63	0.18	-66.1%	-90.2%	16.4%	0.000
	Any disturbance	-1.201	0.654	0.168	-69.9%	-91.6%	8.4%	0.095
	Distance to edge	0.704	0.536	0.316	102.1%	-29.3%	478.0%	
Herptiles	Natural disturbance	-1.201	0.654	0.168	-69.9%	-91.6%	8.4%	0.095
(n=167)	Distance to edge	0.704	0.536	0.316	102.1%	-29.3%	478.0%	
	Any disturbance	-0.759	0.795	0.462	-53.2%	-90.2%	122.5%	1.569
	Range size	0.26	0.396	0.568	29.7%	-40.3%	181.5%	
	Natural disturbance	-0.759	0.795	0.462	-53.2%	-90.2%	122.5%	1.569
	Range size	0.26	0.396	0.568	29.7%	-40.3%	181.5%	

	Any disturbance	-3.38	2.577	0.316	-96.6%	-100.0%	431.5%	0.000
	Range size	-0.84	0.466	0.168	-56.8%	-82.7%	7.6%	
	Natural disturbance	-3.38	2.577	0.316	-96.6%	-100.0%	431.5%	0.000
	Range size	-0.84	0.466	0.168	-56.8%	-82.7%	7.6%	
Mammals (n=233)	Any disturbance	-2.049	2.339	0.462	-87.1%	-99.9%	1162.4%	0.801
	Natural disturbance	-2.049	2.339	0.462	-87.1%	-99.9%	1162.4%	0.801
	Any disturbance	-2.146	2.344	0.462	-88.3%	-99.9%	1057.2%	2.637
	Distance to edge	-0.164	0.398	0.716	-15.1%	-61.1%	85.1%	
	Natural disturbance	-2.146	2.344	0.462	-88.3%	-99.9%	1057.2%	2.637
	Distance to edge	-0.164	0.398	0.716	-15.1%	-61.1%	85.1%	

Table S7. Classification of forest species into Core, Edge, and No Preference (noPref) in our study compared to classification using the habitat amount method [see supplementary methods (*17*)]. In the habitat amount method, we used tree cover within 100 m and 'landscape' radius (generally 1 km) to model abundances. For each species, the coefficient associated with tree cover within 1 km was used to group species into high forest amount (large positive coefficient; analogous to Core), low forest amount (large negative coefficient; analogous to Edge), and forest noPref (coefficient near zero). The two-way table shows that these methods were in agreement 53.0% of the time, which provides evidence that the original categories cannot be recovered using habitat alone, and thus provide information about sensitivity to fragmentation.

| | Habitat amount method category | | | |
	High For Amount (Core)	Low For Amount (Edge)	Forest noPref	Sum
Forest Core	808	419	177	1,404
Forest Edge	323	840	220	1,383
Forest noPref	213	184	85	482
Sum	1,344	1,443	482	3,269

(Original category)

Table S8. Table of model results for probability of species being associated with "High Forest Amount." This is the habitat amount method analogue of BIOFRAG "Core" classification [see supplementary methods (*17*)]. Different models are separated by black lines beginning at the "Variable" column. Each row shows information on the effect of historical forest loss (a measure of anthropogenic disturbance), natural disturbance (tropical storms, fires, or glaciers), or any disturbance (either historical forest loss of natural disturbance) on the odds of a species being classified as core. The "Estimate" and "Std. error" columns are on the log odds scale. The p-values have been false discovery rate adjusted (with significant relationships highlighted in green). The columns with asterisks show the percentage effect (with 95% CI) of being in a region with high disturbance or historical forest loss on the odds of species being classified as 'High Forest Amount' species. Δ AIC values are relative to the best fitting model in each group. Results are omitted for cases where models could not be fit due to non-convergence or separation (e.g., no core species in high disturbance regions). Parameters with p-values less than 0.05 are highlighted in green. The disturbance effect estimates for species categorized as 'High Forest Amount' associates tended to be substantially reduced than when using BIOFRAG Forest Core status as the response (compare with Table S3). This indicates that forest habitat amount alone cannot, by itself, explain the effects of either latitude or disturbance on the proportion of forest core species, as defined using the BIOFRAG approach.

Group	Variable	Estimate	Std. error	p-value	Estimate*	Lower*	Upper*	Δ AIC
All species (n=3,269)	Natural disturbance	-0.926	0.247	0.002	-60.4%	-75.6%	-35.7%	0.000
	Any disturbance	-0.761	0.244	0.008	-53.3%	-71.0%	-24.7%	3.688
Arthropods (n=1,384)	Historical forest loss	0.863	0.653	0.522	137.0%	-34.1%	752.9%	0.000
	Natural disturbance	-0.58	0.482	0.534	-44.0%	-78.2%	44.0%	0.306
	Any disturbance	-0.077	0.442	0.862	-7.4%	-61.1%	120.3%	1.648
Birds (n=1,326)	Any disturbance	-1.287	0.402	0.008	-72.4%	-87.4%	-39.2%	0.000
	Natural disturbance	-1.198	0.4	0.009	-69.8%	-86.2%	-34.0%	0.737
	Historical forest loss	0.693	0.681	0.617	100.1%	-47.3%	659.9%	7.487
Herptiles (n=272)	Any disturbance	-0.375	0.561	0.705	-31.3%	-77.1%	106.3%	0.000
	Natural disturbance	-0.375	0.561	0.705	-31.3%	-77.1%	106.3%	0.000
	Historical forest loss	-0.375	0.561	0.705	-31.3%	-77.1%	106.3%	0.000
Mammals (n=287)	Any disturbance	-0.402	1.662	0.862	-33.1%	-97.4%	1638.0%	0.000
	Natural disturbance	-0.402	1.662	0.862	-33.1%	-97.4%	1638.0%	0.000
	Historical forest loss	-0.402	1.662	0.862	-33.1%	-97.4%	1638.0%	0.000

Table S9. Model results showing effects of disturbance on the probability of a Forest species being "Forest Core" after statistically accounting for latitude. BIOFRAG classifies species as core if they are associated with core habitat. Different models are separated by black lines beginning at the "Variable" column. Each row shows information on the effect of absolute latitude on the odds of a species being classified as core. The "Estimate" and "Std. error" columns are on the log odds scale. The p-values have been false discovery rate adjusted (with significant relationships highlighted in green). The columns with asterisks show the percentage effect (with 95% confidence interval) of either a 1-degree increase in absolute latitude or being in a region with high disturbance (either natural or of any type) on the odds of species being classified as core. The estimates provide evidence that the fragmentation sensitivity of forest core tends to increase with latitude and decrease with disturbance. Δ AIC values are relative to the best fitting model in each group. Results are omitted for cases where models could not be fit due to non-convergence or separation. Parameters with p-values less than 0.05 are highlighted in green. The disturbance variable considered for each class is the best performing disturbance predictor (based on AIC for disturbance-only model – Table S3). Note that for herptiles and mammals, all disturbance variables were equivalent.

Group	Variable	Estimate	Std. error	p-value	Estimate*	Lower*	Upper*	Δ AIC
All species (n=3,269)	Natural disturbance	-0.819	0.307	0.023	-55.9%	-75.8%	-19.5%	0.000
	Latitude	-0.036	0.008	< 0.001	-3.5%	-5.1%	-1.9%	
	Latitude	-0.051	0.007	< 0.001	-5.0%	-6.3%	-3.7%	5.076
Arthropods (n=1,384)	Latitude	-0.035	0.008	< 0.001	-3.4%	-5.0%	-1.9%	0.000
	Any disturbance	-0.389	0.585	0.542	-32.3%	-78.5%	113.2%	1.569
	Latitude	-0.028	0.013	0.061	-2.8%	-5.3%	-0.2%	
Birds (n=1,326)	Natural disturbance	-0.929	0.509	0.093	-60.5%	-85.5%	7.1%	0.000
	Latitude	-0.048	0.019	0.033	-4.7%	-8.2%	-1.0%	
	Latitude	-0.076	0.012	< 0.001	-7.3%	-9.4%	-5.2%	1.562
Herptiles (n=272)	Latitude	-0.098	0.041	0.037	-9.4%	-16.4%	-1.7%	0.000
	Natural disturbance	0.662	0.75	0.435	93.8%	-55.4%	742.2%	1.218
	Latitude	-0.129	0.056	0.04	-12.1%	-21.2%	-1.9%	
Mammals (n=287)	Latitude	-0.081	0.042	0.083	-7.7%	-15.0%	0.2%	0.000
	Natural disturbance	-0.638	2.481	0.797	-47.1%	-99.6%	6732.6%	1.927
	Latitude	-0.077	0.044	0.096	-7.4%	-15.0%	0.8%	

References and Notes

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