

Extinction filters mediate the global effects of habitat fragmentation on animals

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60 **Abstract:** Habitat loss is the primary driver of biodiversity decline worldwide, but the
effects of fragmentation (i.e., the spatial arrangement of remaining habitat) are
debated. We tested the hypothesis that forest fragmentation sensitivity – affected by
avoidance of habitat edges – should be driven by historical exposure, and therefore
species' evolutionary responses, to disturbance. Using a database containing 73
65 datasets worldwide (4,489 animal species), we found that the proportion of
fragmentation-sensitive species was nearly three times higher in regions with low
versus high rates of historical disturbance (i.e., fires, glaciation, hurricanes, and
deforestation). These disturbances coincide with a latitudinal gradient in which
sensitivity increases six-fold at low versus high latitudes. We conclude that conservation
efforts to limit edges created by fragmentation will be most **important** in the world's
70 tropical forests.

One Sentence Summary: Animal species that have evolved, and survived, in low-
disturbance environments are more sensitive to forest fragmentation.

75 **Main Text:**

Global biodiversity loss is occurring at over 100 times the background rate (1) and there is general consensus that most species declines can be attributed to habitat loss (2, 3). Nevertheless, the degree to which habitat fragmentation, defined as the spatial arrangement of remaining habitat, influences biodiversity loss has been a source of contention for over 40 years (4–7).

80 Reconciling this debate is important to conservation planning, which can entail designing the configuration of landscapes as well as spatially prioritizing areas for conservation (8). **Forest fragmentation** is particularly pressing given that 70% of Earth’s remaining forest is within 1 km of the forest edge (9), and that fragmentation of the world’s currently most intact forest landscapes – the tropics – is predicted to accelerate over the coming five decades (10).

85 Central to **the fragmentation debate** is the variation across taxa and regions in species responses to fragmentation and edge effects in particular (6, 11, 12). It is well known that life-history and other ecological traits mediate species’ responses to habitat edges (13), but the degree to which there are predictable geographical patterns in species’ sensitivity has yet to be quantified across
90 multiple taxa at the global scale.

Species’ evolutionary histories can shape their capacity to deal with novel stressors. The ‘extinction filter’ hypothesis predicts that species that have evolved, and survived, in high-disturbance environments should be more likely to persist in the face of new disturbances,
95 including those of habitat loss and fragmentation (14). Further, more frequent disturbances could act as a barrier to sensitive species, preventing them from colonizing disturbance-prone regions. Disturbances often create edges, and in environments with frequent and large-scale disturbances,

100 persistent species are **more** likely to be adapted to ubiquitous edge habitats. The **extinction filter** hypothesis is at least several decades old, and has been suggested to apply in forest (15, 16) and grassland systems (14). Both natural (e.g., wildfires, glaciation) and anthropogenic disturbances (e.g., logging, burning, hunting) are thought to exert such evolutionary pressures (14). Nevertheless, there has been no global test of whether historical disturbance regimes can explain fragmentation effects.

105 We used 73 datasets worldwide containing 4,489 species (from four major taxa: arthropods: 2,682; birds: 1,260; herptiles (reptiles and amphibians): 282, mammals: 265 (Figs. 1 & S1, Tables S1 & S2) to provide a global test of the extinction filter hypothesis in forest ecosystems (17). In the presence of an extinction filter, species inhabiting a ‘filtered’ landscape with high levels of disturbances over historical (evolutionary) time-scales should be resilient to new
110 disturbances – either because sensitive species have been driven locally extinct or because extant species have adapted to disturbance. Either mechanism would lead to a reduced prevalence of fragmentation-sensitive species in regions of the globe where disturbance has been historically common.

115 We used a recently developed approach to quantify the landscape-scale impacts of forest edges on biodiversity (11, 13). By definition, habitat fragmentation for a given habitat amount leads to more, smaller patches, with a greater proportion of edge. We focus on landscape-scale variation in edge effects rather than the number of patches, because edge effects have long been known to have widespread effects on biodiversity (13) and the approach we use comprehensively captures

120 the process of fragmentation at the landscape-scale [see supplementary materials (17), Figs. S2
& S3].

These data and methodology have been documented extensively elsewhere (13), so we present a
brief overview relevant to our analysis. Each dataset contains a set of sample points within a
125 fragmented forest region where abundances of one or more species from major taxonomic
groups were sampled. We quantified two key aspects of edge effects: edge influence across the
region, and edge sensitivity of species. We quantified edge influence (*EI*) surrounding sample
points based on variation in percentage of forest cover [see supplementary materials (17) and
Pfeifer et al. (13) for details]. This metric accounts for the cumulative effects of multiple edges
130 (including edge shape and patch size) that magnify the realized impact of edges on species. Edge
sensitivity (*S*) is a population-specific measure of fragmentation sensitivity that ranges from 0.0
(no edge response) to 1.0 (high edge avoidance or preference). Because *S* does not distinguish
between forest and matrix species and between edge avoidance and edge preference, we
additionally used abundance, percentage tree cover within 30 m of sample points, and *EI* to
135 classify species as forest, non-forest matrix, or generalist habitat users and ‘core,’ ‘edge,’ or ‘no
preference’ [(17) and Fig. S4]. We did so by simulating sets of example abundances in each
category (e.g., ‘forest core’) and then using a naïve Bayes classifier to estimate the most likely
category for each actual species based on abundance versus point cover and *EI* relationships. By
definition, forest core species are those that are restricted to forest areas that are distant from the
140 edge, hence are sensitive to fragmentation of large patches into smaller ones (Figs. S2 & S3). We
used this classification as the basis for our statistical models, focusing both on the probability of
forest species being classified as core and the probability of species being classified as forest,

matrix, or generalist. For each study site, we assembled previously available data on forest fire severity (19), whether or not its location was glaciated in the last glacial maximum (20), whether
145 or not it experienced tropical storms (21), and if historical anthropogenic forest loss exceeded 50% (3) [Fig. 1, (17)].

Across all species combined, we found strong support for the extinction filter hypothesis explaining geographically variable sensitivity to forest edge. The odds of forest species being
150 classified as forest core were 79.0% [95% CI: 65.9%, 87.0%] lower in study regions that have experienced historically severe disturbances (Fig. 2, $p < 0.001$, Table S3). A substantial 51.3% of forest species tended to avoid edges in low-disturbance regions, while only 18.1% of forest species in high-disturbance regions avoided edges (Fig. 2). Edge-sensitive species are therefore largely absent from communities in historically disturbed locations, suggesting they have either
155 disappeared from these regions or adapted to become less edge sensitive. This result was particularly strong for arthropods and birds, and in the same direction for herptiles and mammals, though non-significant, likely owing to lower sample sizes. Results were stronger still when we considered the proportion of forest species as a function of disturbance severity. The odds of a species being forest-associated versus being associated with other habitats were 729% [95% CI:
160 608%, 891%] higher in low-disturbance versus high-disturbance regions (Fig. S5, Table S4).

Edge sensitivity (S) of forest core species tended to be 1.16 times higher in low ($S=0.660 \pm 0.004$
 $SE_{\bar{x}}$) versus high ($S=0.568 \pm 0.004$) disturbance regions. This effect size is considerable; species with values of $S > 0.75$ are only found within the forest interior far away from edges, whereas
165 forest species with $S=0.5$ are abundant up to the edge (13). In addition, historical anthropogenic

forest loss alone was substantially less effective at predicting the proportion of core species than either the combination of historical disturbances, or natural disturbance alone (Table S3). Thus, evolutionary responses and patterns of extinction in of forest species in high-disturbance regions is not driven solely by anthropogenic habitat loss and fragmentation.

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The effects of disturbance on edge influence sensitivity and the proportion of forest core species are unlikely to be an artifact of under-sampling in high-disturbance regions (Fig. S6). Also, these results were robust to other potential confounding variables – phylogenetic relatedness (Fig. S7), migratory behavior (Table S5), geographic range size (Table S6), and distance to range edge (Table S6). Importantly, the strong disturbance effect could not be reproduced when species were categorized using forest amount alone (δ), indicating that our findings relate primarily to fragmentation in addition to landscape-scale forest loss (Tables S7 & S8). The disturbance effect generally remained after statistically accounting for absolute latitude (Table S9); the proportion of forest core species declined roughly six-fold, and the proportion of forest-associated species declined 1.5-fold, over the entire latitudinal gradient observed (0.7 – 51.8 degrees) (Figs. 3, S8 – S9). Tropical species have been confronted with less historical disturbance (Fig. 1b) and therefore tend to be more edge sensitive, and more likely to be associated with forest (Table S4, Fig. S8).

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The extinction filter hypothesis can be generalized beyond forest species to predict that in areas typified by large-scale historical disturbances, we should see a greater proportion of species that have evolved with non-forest land-cover types including disturbed habitats (hereafter the ‘matrix’). For example, a wide range of species in the Pacific Northwestern USA –where stand-

replacing crown fires are common– are associated with early successional ecosystems (22). Our
190 data supported this prediction; the odds of species using matrix habitat relative to using forest
habitat were estimated to be 644% higher in high disturbance regions than in low disturbance
regions (95% CI: [523%, 788%]; Fig. S5, Table S4). The proportion of matrix species also
strongly increased with latitude (Fig. S9, Table S4).

195 Our results support the extinction filter hypothesis; climatic, ecological and anthropogenic
disturbances have already filtered out many of the species that would be more susceptible to
forest edges and the process of fragmentation caused by deforestation (16). Proportions of forest
core species are substantially greater in regions that have not experienced large-scale historical
disturbances. This effect results in a latitudinal gradient in fragmentation sensitivity, and helps to
200 explain surprising rarity of extinctions following recent anthropogenic disturbance in Europe and
eastern North America (23). Species that were strongly sensitive to disturbance-created edges
have likely either undergone local extinction or adapted to repeated glaciation or historical land
clearance.

205 Our results partly reconcile the debate about the conservation importance of fragmentation and
its effect on biodiversity (6, 7). Many studies finding reduced fragmentation effects were
conducted in already denuded landscapes (24), in locations with stand-replacing disturbance
(glaciers, fire, 25) and at high latitudes, which experienced glacial advances and retreats (26).
Conversely, studies finding strong, negative fragmentation effects are often from the tropics
210 where broad-scale disturbance is rarer (27) or for matrix-associated temperate zone species –
which are adapted to unfragmented but disturbed habitat (28, 29). Exceptions to this general

215 pattern do, of course, exist (30, 31). Further, we caution that temperate species are not necessarily robust to anthropogenic change of other types, and synergistic effects of stressors may pose novel threats. For instance, climate change may interact with habitat loss and fragmentation to reduce species' capacity to adapt (32). Nevertheless, our data highlight a strong underlying pattern that has the potential to explain why fragmentation studies are known for generating such widely variable results. It will be essential to tie our broad-scale analyses to the analysis of the mechanistic underpinnings of fragmentation sensitivity to better generalize across biomes and taxa.

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These results indicate that conservation actions designed to mitigate edge-driven fragmentation effects can be tailored to the particular regions most likely to host sensitive species, rather than applying simple rules to the entire globe. Regions in temperate zones with greater historical disturbance might focus more on conserving mature forest habitat, regardless of its spatial configuration (6). On the other hand, efforts to reduce forest fragmentation should be concentrated in regions with low historical disturbance, particularly tropical forests (13) – especially those in biodiversity hotspots (33) – where fragmentation continues at a rapid rate and poses the greater extinction risk.

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Supplementary Materials

Materials and Methods
Supplementary Text
Figs. S1 to S9
Tables S1 to S9

Figures and Tables

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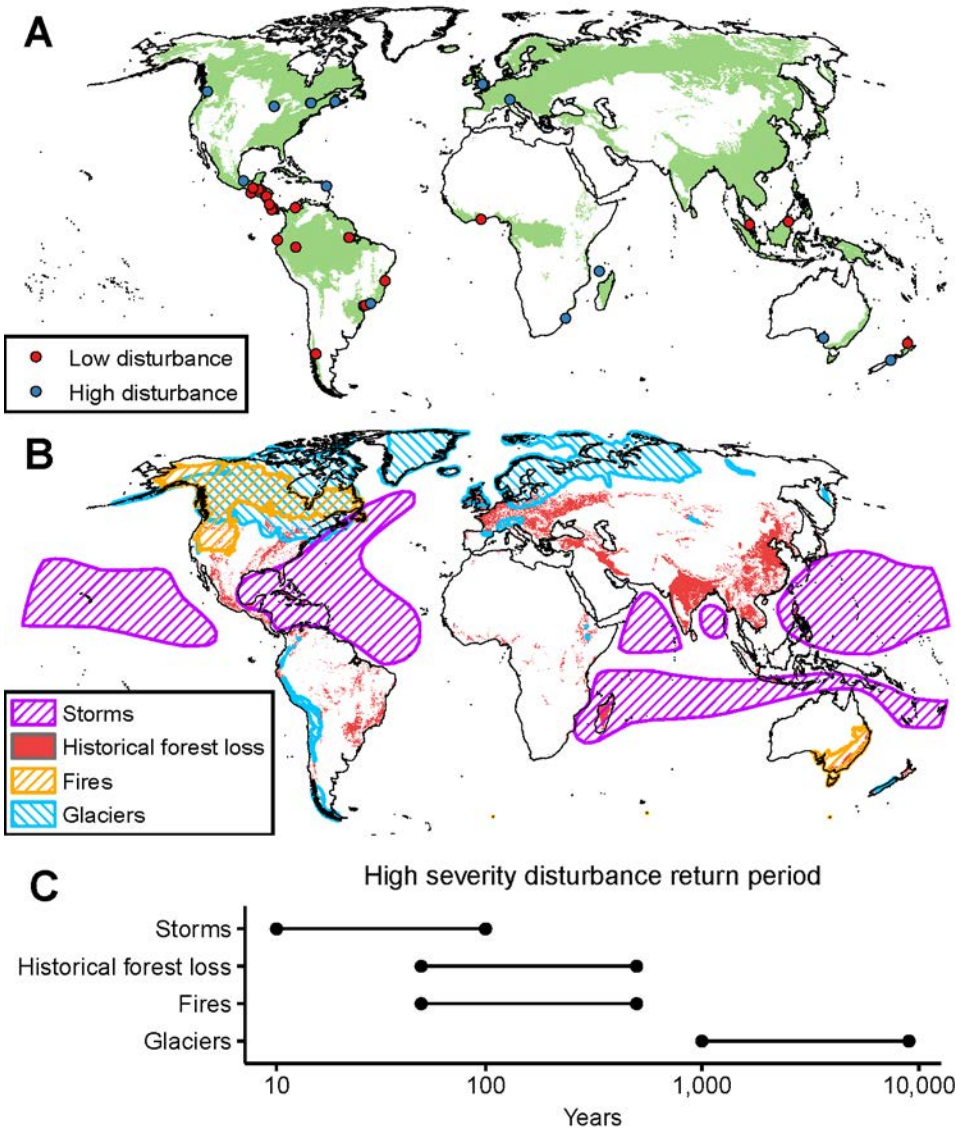


Fig. 1. Geographic distributions of sample study regions and historical disturbances.

(A.) Locations of the 35 regions where the 73 datasets included in our analysis were collected. Areas that can support forests are shown in green. The BIOFRAG regions are colored according to disturbance severity. (B.) Distributions of historical disturbances: tropical storms, historical (long-term) deforestation, high intensity-crown fires, and glaciation. (C.) Typical periods over which high-severity disturbances return to the same location.

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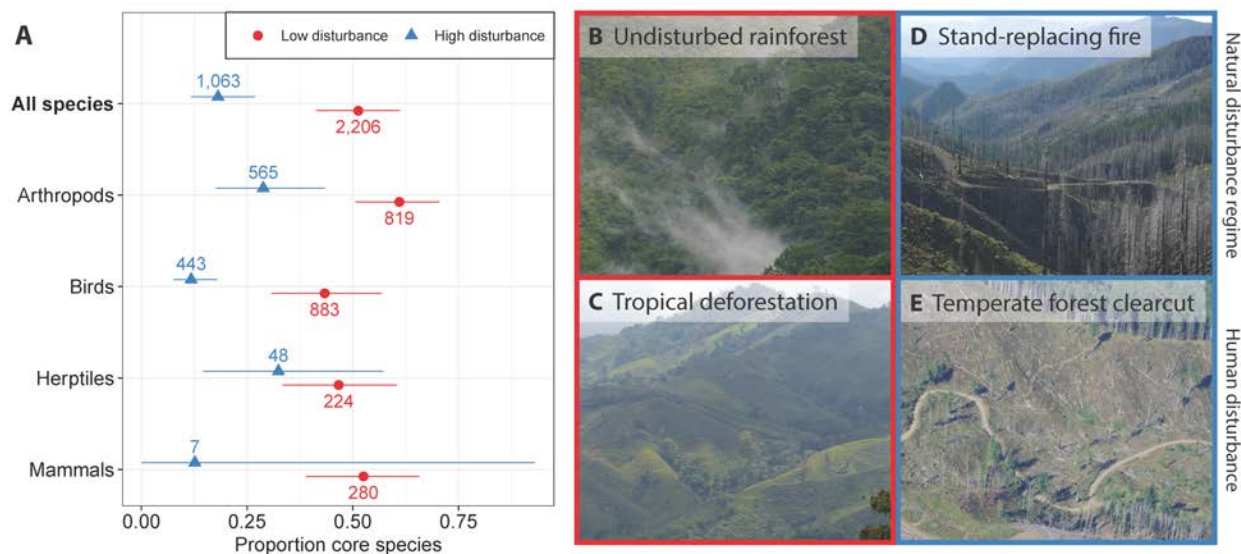


Fig. 2. (A) Estimated proportions (with 95% confidence intervals) of forest species associated with core habitat at low and high disturbance sites, according to mixed-effects logistic regression models. The binary 'disturbance' variable indicates whether or not each of the 73 BIOFRAG datasets comes from a location that has had high severity disturbances of any type (glaciation, tropical storms, crown fires, or greater than 50% historical forest loss). Numbers of species are shown beside point estimates. (B) Tropical rainforest, undisturbed by stand-replacing disturbance and (C) tropical deforestation for pastureland versus (D) temperate forest landscape that has been disturbed by wildfire and (E) temperate forest clearcuts. The extinction filter hypothesis predicts that species in disturbance-prone regions (D) should be less sensitive to habitat edges created by anthropogenic fragmentation (E) than species that have evolved in landscapes where disturbances are rare (B,C).

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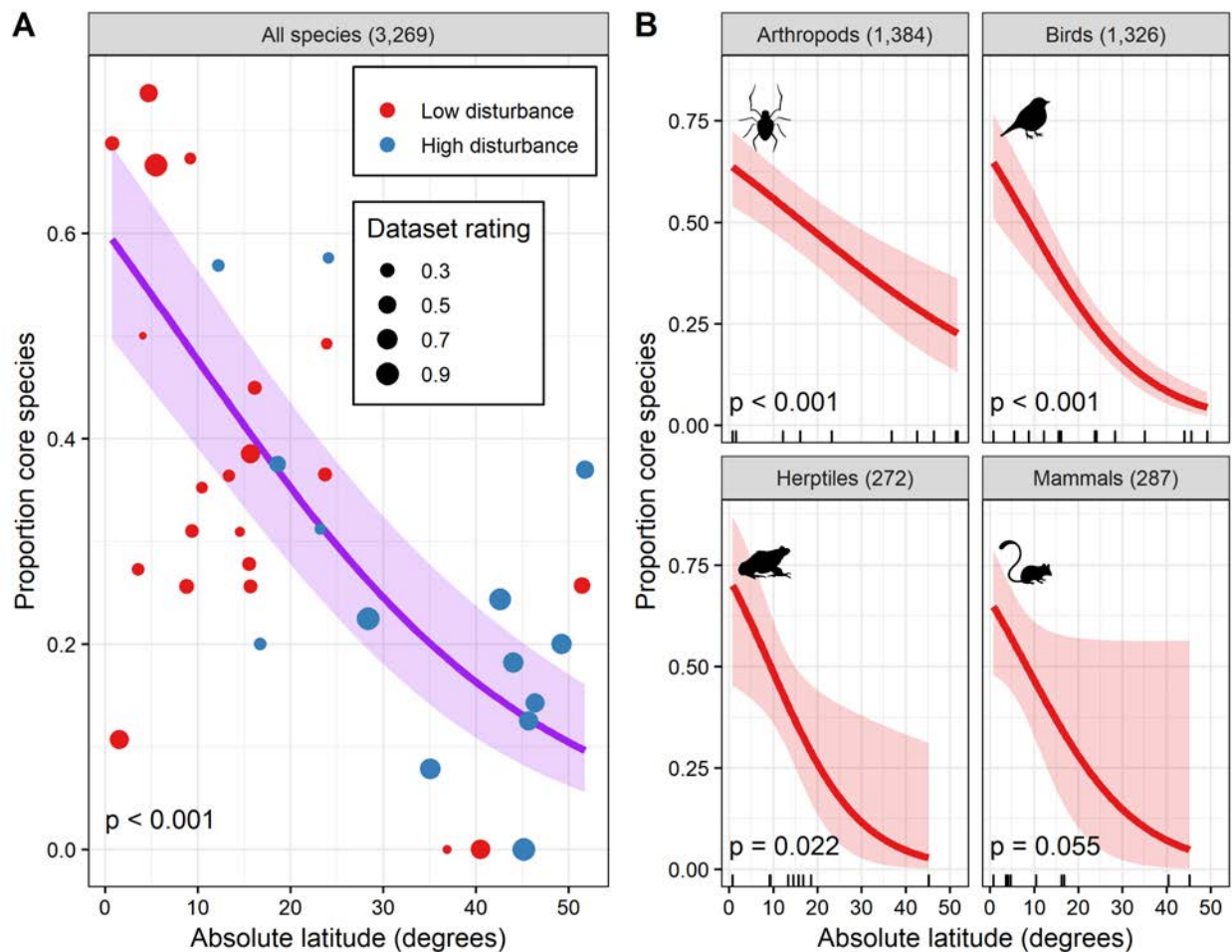


Fig. 3. Logistic regression models used to estimate the proportion of forest core species as a function of absolute latitude. In panel (A), each point shows the proportion of species classified as core within each BIOFRAG region. Point sizes indicate the dataset rating, with higher values reflecting better estimation of edge sensitivity. Point colors indicate disturbance level associated with each region. The response variable is whether or not a species was classified as preferring forest core habitat. 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 in panel titles. Study region absolute latitudes are shown using black tick marks (panel B). All p -values were false discovery rate (FDR) adjusted to control the expected proportion of Type I errors, and taxonomic class was included as a random effect in the "All species" model.

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