

CONSERVATION ECOLOGY

Extinction filters mediate the global effects of habitat fragmentation on animals

Matthew G. Betts^{1,*}†, Christopher Wolf^{1,*}†, Marion Pfeifer², Cristina Banks-Leite³, Víctor Arroyo-Rodríguez⁴, Danilo Bandini Ribeiro⁵, Jos Barlow^{6,7}, Felix Eigenbrod⁸, Deborah Faria⁹, Robert J. Fletcher Jr.¹⁰, Adam S. Hadley¹, Joseph E. Hawes¹¹, Robert D. Holt¹², Brian Klingbeil¹³, Urs Kormann^{1,14,15}, Luc Lens¹⁶, Taal Levi¹, Guido F. Medina-Rangel¹⁷, Stephanie L. Melles¹⁸, Dirk Metzger¹⁹, José Carlos Morante-Filho^{9,20}, C. David L. Orme³, Carlos A. Peres²¹, Benjamin T. Phalan²², Anna Pidgeon²³, Hugh Possingham^{24,25}, William J. Ripple¹, Eleanor M. Slade²⁶, Eduardo Somarriba²⁷, Joseph A. Tobias³, Jason M. Tylianakis²⁸, J. Nicolás Urbina-Cardona²⁹, Jonathon J. Valente^{1,30}, James I. Watling³¹, Konstans Wells³², Oliver R. Wearn³³, Eric Wood³⁴, Richard Young³⁵, Robert M. Ewers³

Habitat loss is the primary driver of biodiversity decline worldwide, but the effects of fragmentation (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 to, and therefore species' evolutionary responses to disturbance. Using a database containing 73 datasets collected worldwide (encompassing 4489 animal species), we found that the proportion of fragmentation-sensitive species was nearly three times as high in regions with low rates of historical disturbance compared with regions with high rates of disturbance (i.e., fires, glaciation, hurricanes, and deforestation). These disturbances coincide with a latitudinal gradient in which sensitivity increases sixfold at low versus high latitudes. We conclude that conservation efforts to limit edges created by fragmentation will be most important in the world's tropical forests.

Global biodiversity loss is occurring at more than 100 times the prehuman background extinction rate (1), and there is general consensus among scientists 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). Resolving 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 most intact forest

landscapes—the tropics—is predicted to accelerate over the coming five decades (10).

The variation across taxa and regions in species' responses to fragmentation and edge effects in particular is central to the fragmentation debate (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 multiple taxa on a global scale.

Species' evolutionary histories can shape their capacity to respond to 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 distur-

bances, 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, 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 disturbances (such as wildfires and glaciation) and anthropogenic ones (such as logging, burning, and 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.

We used 73 datasets collected worldwide containing 4489 species from four major taxa [2682 arthropods, 1260 birds, 282 reptiles (reptiles and amphibians), and 265 mammals] (Fig. 1, fig. S1, and tables S1 and 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 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.

We used a recently developed approach to quantify the landscape-scale impacts of forest edges on biodiversity (13, 18). 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

¹Forest Biodiversity Research Network, Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA. ²School of Natural and Environmental Sciences, Newcastle University, Newcastle Upon Tyne NE1 7RU, UK. ³Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, UK. ⁴Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México (UNAM), Campus Morelia, Antigua Carretera Patzcuaro no. 8701, Ex-Hacienda de San José de la Huerta, 58190 Morelia, Michoacán, Mexico. ⁵Instituto de Biotecnología, Universidade Federal de Mato Grosso do Sul, Caixa Postal 549, 79070-900 Campo Grande, Brazil. ⁶Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK. ⁷Setor Ecologia, Departamento de Biologia, Universidade Federal de Lavras, 37200-000, Lavras, MG, Brazil. ⁸Geography and Environmental Sciences, University of Southampton, Southampton SO17 1BJ, UK. ⁹Applied Conservation Ecology Lab, Programa de Pós-graduação em Ecologia e Conservação, da Biodiversidade, Universidade Estadual de Santa Cruz, Rodovia Ilhéus-Itabuna, km 16, Salobrinho, 45662-000 Ilhéus, Bahia, Brazil. ¹⁰Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611, USA. ¹¹Applied Ecology Research Group, School of Life Sciences, Anglia Ruskin University, Cambridge CB1 1PT, UK. ¹²Department of Biology, University of Florida, Gainesville, FL 32611, USA. ¹³School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849, USA. ¹⁴Swiss Ornithological Institute, Sempach, Switzerland. ¹⁵Division of Forest Sciences, School of Agricultural, Forest and Food Sciences HAFU, Bern University of Applied Sciences, Zollikofen, Switzerland. ¹⁶Ghent University, Department of Biology, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium. ¹⁷Grupo de Biodiversidad y Conservación, Reptiles, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Ciudad Universitaria, Edificio 425, Bogotá, Distrito Capital, Colombia. ¹⁸Department of Chemistry and Biology, Ryerson University, 350 Victoria Street, Toronto, ON M5B 2K3, Canada. ¹⁹Department of Science and Education, Field Museum of Natural History, Chicago, IL 60605, USA. ²⁰Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, Avenida Transnordestina, s/n - Novo Horizonte, 44036-900 Feira de Santana, Bahia, Brazil. ²¹Centre for Ecology, Evolution and Conservation, School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK. ²²Instituto de Biologia, Universidade Federal da Bahia, Salvador, 40170-115 Bahia, Brazil. ²³Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA. ²⁴School of Biological Sciences, University of Queensland, St Lucia, Queensland, Australia. ²⁵The Nature Conservancy, Arlington, VA 22203, USA. ²⁶Asian School of the Environment, Nanyang Technological University, 62 Nanyang Dr., 637459 Singapore. ²⁷Centro Agronómico Tropical de Investigación y Enseñanza, Turrialba, Costa Rica. ²⁸School of Biological Sciences, University of Canterbury, Private bag 4800, Christchurch 8140, New Zealand. ²⁹Department of Ecology and Territory, School of Rural and Environmental Studies, Pontificia Universidad Javeriana, Bogotá, Colombia. ³⁰Smithsonian Conservation Biology Institute, Migratory Bird Center, National Zoological Park, Washington, DC 20013, USA. ³¹Department of Biology, John Carroll University, University Heights, OH 44118, USA. ³²Department of Biosciences, Swansea University, Swansea SA2 8PP, Wales, UK. ³³Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK. ³⁴Department of Biological Sciences, California State University Los Angeles, 5151 State University Drive, Los Angeles, CA 90032, USA. ³⁵Durrell Wildlife Conservation Trust, Les Augres Manor, Trinity, Jersey JE3 5BP, UK.

*Corresponding author. Email: matt.betts@oregonstate.edu (M.G.B); wolffch@oregonstate.edu (C.W) †These authors contributed equally to this work.

biodiversity (13), and the approach we use comprehensively captures the process of fragmentation at the landscape scale (17) (figs. S2 and 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 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 on the basis of variation in percentage of forest cover (13, 17). This metric accounts for the cumulative effects of multiple edges (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 or between edge avoidance and edge preference, we also used abundance, percentage of tree cover within 30 m of sample points, and EI to classify species as forest, nonforest matrix, or generalist habitat users and as core, edge, or no preference (17) (fig. S4). We did this 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 on the basis of abundance versus point cover and EI relationships. By definition, forest core species are those that are restricted to forest areas distant from the edge; hence, these species are sensitive to fragmentation of large patches into smaller ones (figs. S2 and S3). We used this classification as the basis for our statistical models, focusing on both 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 available data on forest fire severity (19), whether or not its location was glaciated in the last glacial maximum (20), whether or not it experienced tropical storms (21), and if historical anthropogenic forest loss at the site exceeded 50% (3, 17) (Fig. 1).

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 classified as forest core were 79.0% (95% confidence interval: 65.9 to 87.0%) lower in study regions that have experienced historically severe disturbances ($P < 0.001$) (Fig. 2 and table S3). A substantial 51.3% of forest species tended to avoid edges in low-disturbance regions, whereas only 18.1% of forest species in high-disturbance regions avoided edges (Fig. 2).

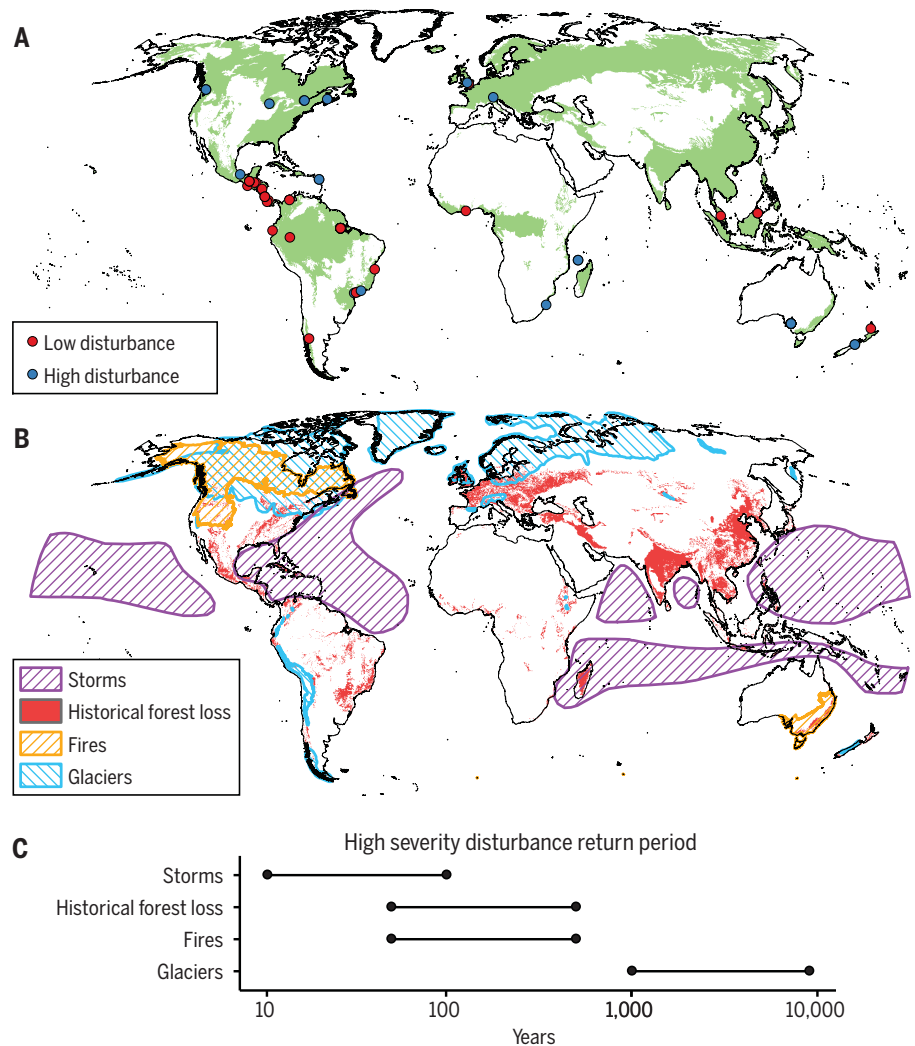


Fig. 1. Geographic distributions of sample study regions and historical disturbances. (A) Locations of the 35 BIOFRAG regions where the 73 datasets included in our analysis were collected. Areas that can support forests are shown in green. The regions are colored according to disturbance severity. (B) 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.

Edge-sensitive species are therefore largely absent from communities in historically disturbed locations, suggesting that they have either disappeared from these regions or adapted to become less edge sensitive. This result was particularly strong for arthropods and birds, and the results were in the same direction for herptiles and mammals, though nonsignificant, 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% credible interval: 608 to 891%) higher in low-disturbance versus high-disturbance regions (fig. S5 and table S4).

Edge sensitivity (S) of forest core species tended to be 1.16 times as high in low-disturbance

regions [$S = 0.660 \pm 0.004$ (standard error)] as in high-disturbance regions ($S = 0.568 \pm 0.004$). This effect size is considerable; species with values of $S > 0.75$ are found only within the forest interior far away from edges, whereas forest species with $S = 0.5$ are abundant up to the edges (13). Additionally, 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 of forest species in high-disturbance regions are not driven solely by anthropogenic habitat loss and fragmentation.

The effects of disturbance on edge influence sensitivity and the proportion of forest core species are unlikely to be an artifact of undersampling in high-disturbance regions (fig. S6). Also,

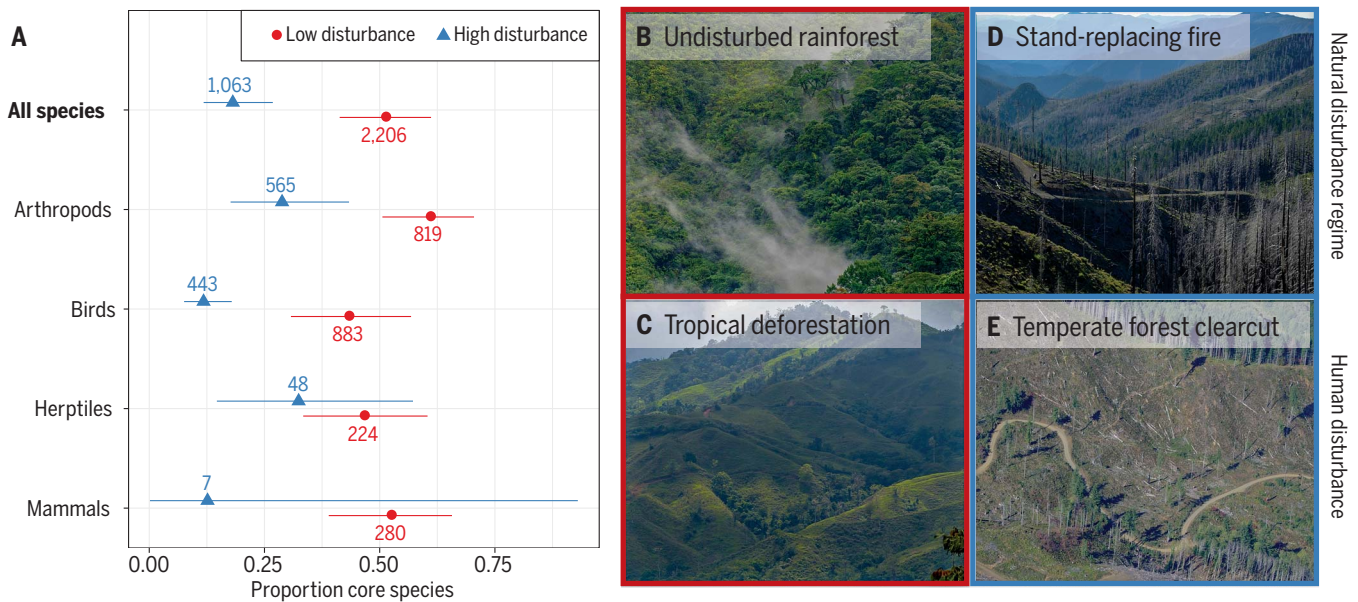


Fig. 2. The proportion of forest species associated with core habitat is mitigated by historical exposure to disturbance. (A) Estimated proportions (with 95% confidence intervals) are based on mixed-effects logistic regression models. The binary disturbance variable (low- versus high-disturbance sites) indicates whether 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 >50% historical forest loss). Numbers of species are shown beside point

estimates. (B) Tropical rainforest, undisturbed by stand-replacing disturbance. (C) Tropical deforestation for pastureland. (D) Temperate forest landscape that has been disturbed by wildfire. (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) and (C)]. [Photos: (B) C. Ziegler; (C) to (E) M. G. Betts]

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). Notably, the strong disturbance effect could not be reproduced when species were categorized using forest amount alone (6), indicating that our findings relate primarily to fragmentation in addition to landscape-scale forest loss (tables S7 and S8). The disturbance effect generally remained after statistically accounting for absolute latitude (table S9); the proportion of forest core species declined roughly sixfold and the proportion of forest-associated species declined 1.5-fold over the entire absolute latitudinal gradient observed (0.7° to 51.8°) (Fig. 3 and figs. S8 and 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 and fig. S8).

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 nonforest land-cover types, including disturbed habitats (hereafter, the matrix). For example, a wide range of species in the Pacific Northwestern United States—where stand-replacing crown fires are common—is associated with early successional ecosystems (22). Our data support 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% credible interval: 523 to 788%) (fig. S5 and table S4). The proportion of matrix species also strongly increased with latitude (fig. S9 and table S4).

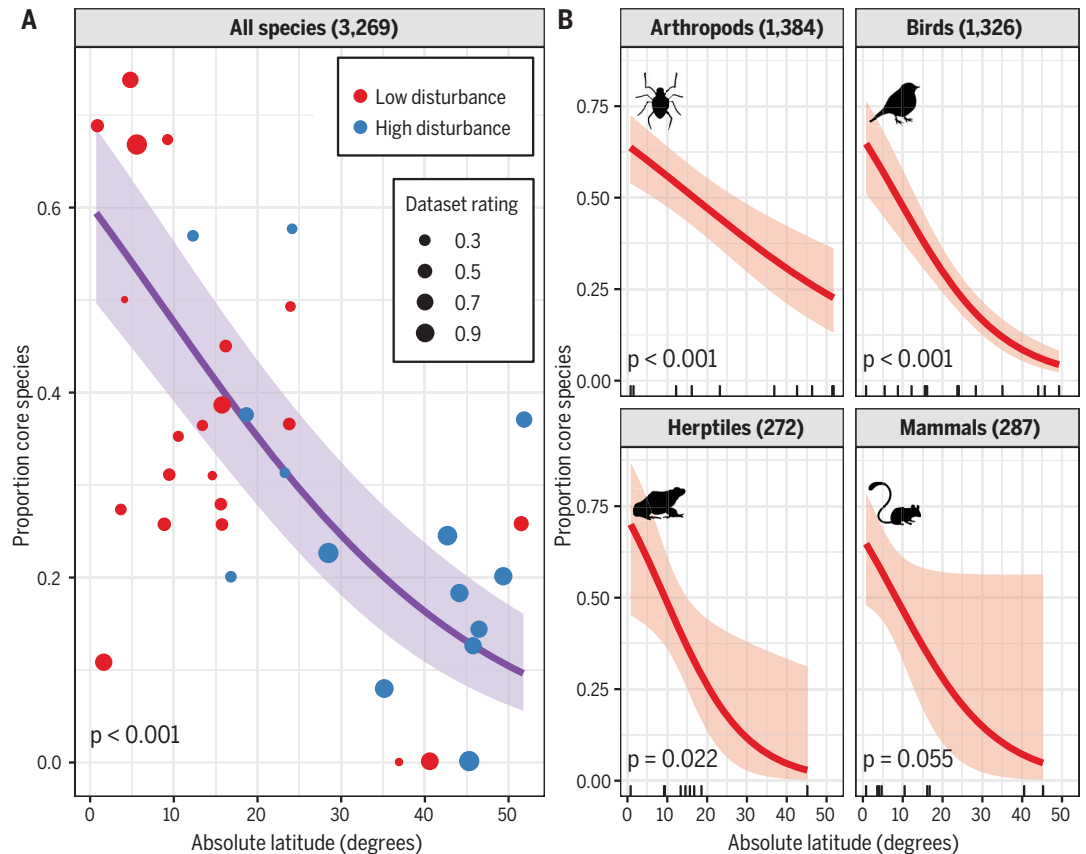
Our results support the extinction filter hypothesis; climatic, ecological, and anthropogenic disturbances have already filtered out many of the species that would be more susceptible to forest edges and the process of fragmentation caused by deforestation (16). Proportions of forest core species are 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 explain the 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.

Our results partly reconcile the debate about the conservation importance of fragmentation and its effect on biodiversity (6, 7). Many studies that have found reduced fragmentation effects were conducted in already-denuded landscapes (24), in locations with stand-replacing disturbance [glaciers or fire (25)], and at high latitudes, which experienced glacial advances and retreats

(26). Conversely, studies that have found strong, negative fragmentation effects are often from the tropics, where broad-scale disturbance is rarer (27), or are for matrix-associated temperate zone species, which are adapted to unfragmented but disturbed habitats (28, 29). Exceptions to this general pattern do, of course, exist (30, 31); 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 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.

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. In regions in temperate zones with greater historical disturbance, efforts might be focused 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

Fig. 3. Logistic regression models used to estimate the proportion of forest core species as a function of absolute latitude. In (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 (B). All *P* values were false discovery rate (FDR)-adjusted to control the expected proportion of type I (false positive) errors, and taxonomic class was included as a random effect in the “All species” (A) model. Shaded portions represent 95% confidence bands.



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

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Materials and Methods
Supplementary Text
Figs. S1 to S9
Tables S1 to S9
References (35–60)

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Vulnerability to habitat fragmentation

Habitat fragmentation caused by human activities has consequences for the distribution and movement of organisms. Betts *et al.* present a global analysis of how exposure to habitat fragmentation affects the composition of ecological communities (see the Perspective by Hargreaves). In a dataset of more than 6500 animal species, regions that historically experienced little disturbance tended to harbor a higher proportion of species vulnerable to fragmentation. Species in more frequently disturbed regions were more resilient. High-latitude areas historically experienced more disturbance and harbor more resilient species, which suggests that extinction has removed fragmentation-sensitive species. Thus, conservation efforts to limit fragmentation are particularly important in the tropics.

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