

Creation of forest edges has a global impact on forest vertebrates

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Forest edges influence more than half of the world’s forests and contribute to worldwide declines in biodiversity and ecosystem functions. However, predicting these declines is challenging in heterogeneous fragmented landscapes. Here we assembled a global dataset on species responses to fragmentation and developed a statistical approach for quantifying edge impacts in heterogeneous landscapes to quantify edge-determined changes in abundance of 1,673 vertebrate species. We show that the abundances of 85% of species are affected, either positively or negatively, by forest edges. Species that live in the centre of the forest (forest core), that were more likely to be listed as threatened by the International Union for Conservation of Nature (IUCN), reached peak abundances only at sites farther than 200–400 m from sharp high-contrast forest edges. Smaller-bodied amphibians, larger reptiles and medium-sized non-volant mammals experienced a larger reduction in suitable habitat than other forest-core species. Our results highlight the pervasive ability of forest edges to restructure ecological communities on a global scale.

Fragmentation of forest ecosystems has critical and ongoing impacts that erode biodiversity and ecological processes^{1–6}. Fragmentation is a ubiquitous phenomenon, with nearly 20% of the world’s remaining forest now found within 100 m of an edge, 50% within 500 m and 70% within 1 km¹. Efforts to understand and manage the impacts of fragmentation have therefore become critical for effective conservation action⁷. Ecological effects arising from edges between forest and non-forest habitat change biophysical environments for species⁸ and can drive species that otherwise inhabit the centre of the forest (referred to as the forest core) to local extinction over spatial scales of more than 1 km⁹. Moreover, edge effects alter the amount of ‘effective’ habitat area in a landscape^{4,10}, suggesting that they are at least as important as habitat amount¹¹ as drivers of biodiversity responses to land-use change. However, our capacity to predict which species and ecosystem functions are likely to disappear first from edge-dominated landscapes is still limited. In particular, we lack consistent approaches to quantify the impacts of edge effects in a rigorous manner¹² across species¹³ and key functional groups¹⁴, leading to potentially distorted projections of overall changes in biodiversity in fragmented landscapes.

Frameworks^{15,16} around the traits of species should form a reliable, heuristic tool for predicting the sensitivity of different species to edge

effects in the same way as for predicting species’ extinction risks^{17,18}. A scarceness in meta-analyses in the fragmentation literature¹² has prevented such frameworks from being tested robustly, despite an abundance of hypotheses and data. We expect, for example, that species body size—a commonly measured vertebrate trait that correlates with many extinction-promoting traits¹⁸—will be significantly associated with how species respond to habitat edge effects. Forest ectotherms (that is, amphibians and reptiles) should have desiccation-driven relationships that respond to decreased humidity and increased temperature at forest edges and in the habitat that surrounds forests in human-modified landscapes (referred to as the matrix^{3,8}). Edge sensitivity should decrease with body size for amphibians as their desiccation tolerance increases due to a reduced surface-to-volume ratio in larger species¹⁹. The opposite should be true for reptiles (and in particular snakes), which often have an elongated body shape that does not allow a similar decrease in surface to volume ratio. By contrast, we expect mobility and metabolism to drive relationships between body size of forest endotherms (that is, mammals and birds) and their sensitivity to edges. Forest species that are larger or more mobile should have lower edge sensitivities compared to smaller-bodied species, because species that are larger or more mobile are better able to traverse and forage

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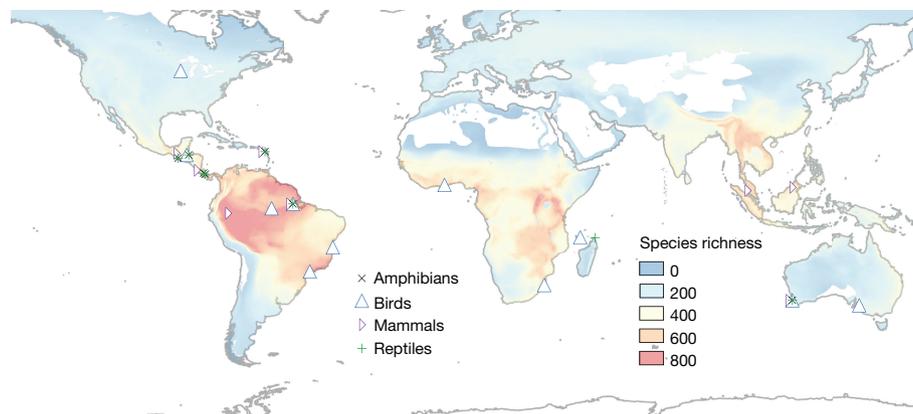


Figure 1 | Global distribution of the 22 study landscapes. Some of these were sampled for more than one vertebrate group. We sampled abundance data from a total of 1,673 vertebrate species (103 amphibians, 146 reptiles, 1,158 birds and 266 mammals). Landscape centroids are shown on the

in the matrix as well as to detect a suitable habitat and resources in a fragmented landscape^{20,21}.

Simple approaches to quantifying edge effects treat landscapes as binary entities (for example, forest versus non-forest) and quantify biodiversity responses to the nearest forest edge¹⁰. These approaches ignore the role of the habitat that surrounds forests²² in human-modified landscapes (the matrix^{3,8}), do not include the additive effects of multiple edges that arise in fragments with irregular shapes²³ and make no predictions about the identity of species that might go extinct²⁴. These simple approaches differ from widespread recognition that habitat quality varies continuously in space, shapes the contrast between forest and matrix^{25,26}, and therefore modulates edge impacts on the landscape. Habitats in the matrix can in some cases provide resources for some species²⁷, and in combination with species-specific requirements, may determine whether forest edges act as ‘hard’ or ‘soft’ boundaries to species populations²⁸. How species respond to edges affects their abundance and persistence in a landscape⁹, with declines in abundance reliably indicating that a species is at increased risk of local extinction²⁹.

We use a different approach to quantify the impacts of habitat edges on biodiversity. We map and quantify changes in the landscape-scale abundances³⁰ of 1,673 vertebrate species (103 amphibians, 146 reptiles, 1,158 birds and 266 mammals) that can be attributed to edge effects in fragmented forest landscapes, using data collected in 22 landscapes distributed across seven major biogeographic regions (Fig. 1 and Extended Data Tables 1, 2). Our approach defines two spatially explicit metrics, which together address two challenges that have so far prevented the detection of generalities in the edge responses of species. (1) Edge influence (I) assesses the configuration of landscapes and is calculated as a continuous, bounded spatial metric that quantifies local variations in percentage of tree cover (Methods). We developed this metric to specifically account for the cumulative effects of multiple edges (including edge shape and patch size) that exacerbate the realized impact of habitat edges on species^{4,12,23} (Methods). By computing I from continuous gradients in percentage tree cover (measured at the levels of pixels and ranging from 0 to 100%), as opposed to computing it from a binary classification of forest or non-forest habitat, we also account for variation in edge contrast and breadth (Methods) and therefore quantify the controlling influence of matrix habitat on the fragmented forest³. Absolute values of I range from 0 (when there are no edges within a 1-km radius) to 100 (when a pixel is surrounded by a different habitat for 1 km in all directions). I does not correlate closely with any single traditional landscape fragmentation metric, such as distance to the nearest edge, edge structure, fragment shape or fragment size, but rather aims to represent all of these previous metrics in a single metric. (2) We measured the edge sensitivity (S) of species as a biologically meaningful metric of changes in abundance¹². S is the

background of vertebrate species richness maps showing the total number of bird, mammalian and amphibian species³¹ combined using data from C. Jenkins, BirdLife, and IUCN. Credits: C. Jenkins, Instituto de Pesquisas Ecológicas/SavingSpecies.

proportion of the range of I that is avoided by the species (Methods). S is a bounded metric that ranges from 0.0 (inclusive) to 1.0 (exclusive). Species with an S equal to 0 show no change in local abundance owing to edge effects, whereas species with an S close to 1 are restricted to a specific habitat because of edge effects (for example, abundant only in the core habitat or at the edges). Because S is defined for a bounded landscape metric, it facilitates rigorous quantification and comparison of the edge responses of species between landscapes.

Pervasive impact of forest edges

For each species, we classified their observed abundance variations in the fragmented landscape with respect to I and percentage tree cover as one of seven categorical edge-response types⁹: forest core and matrix core (both edge-avoiding), forest edge and matrix edge (both edge-seeking), forest and matrix species with no preference regarding the edge, and generalist species (with no preference for either forest or matrix habitat). Edge responses of species that could not be classified into one of these types are referred to as unknown. We used a naive Bayes classifier to estimate the most likely edge-response type for each species from a training set comprising simulated abundance patterns that defined each edge-response type (Methods).

We found that the abundance of 85% of all vertebrate species were affected by forest edges (46% positively and 39% negatively), excluding 369 species with unknown edge responses. The most common edge-response type was forest core (519 species), followed by forest edge (338 species), matrix edge (165 species), forest and matrix with no preference regarding the edge (112 and 34 species), matrix core (80 species) and generalist (56 species). The result that marginally more species were positively rather than negatively impacted by edges should be interpreted with caution. When simply counting the number of positive versus negative impacts and assuming that one cancels the other out, one disregards the more important fact that 85% of species are impacted and that the resultant community that now persists near the edges bears little resemblance to those communities in the forest interiors. This large turnover in the composition of vertebrate communities at the edges of forests probably reflects pronounced changes in the ecological functioning of these modified forest habitats³¹. Species that are negatively affected by edges include threatened forest-core species of immediate conservation concern, such as the Sunda pangolin (*Manis javanica*, $S = 0.72$), the Bahia tapaculo (*Eleoscytalopus psychopompus*, $S = 0.88$), the long-billed black cockatoo (*Zanda baudinii*, $S = 0.77$) and Baird’s tapir (*Tapirus bairdii*, $S = 0.73$). Species that are positively affected by edges include invasive species, such as *Canis lupus* (forest edge, $S = 0.6$), the green iguana (*Iguana iguana*, matrix edge, $S = 0.56$) and the common boa (*Boa constrictor*, forest edge, $S = 0.61$).

When taking into account sampling bias by computing species density (Methods) and excluding species with an unknown edge

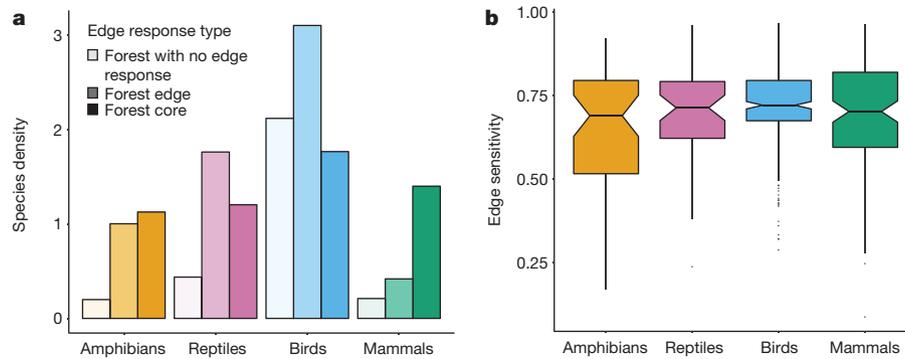


Figure 2 | Forest occupancy and edge sensitivities for forest-core species. **a**, Species density accounting for sampling bias in the datasets is shown for forest species, a subset of the seven edge-response types (see Methods for details). **b**, Edge sensitivity for ectotherms (forest-core amphibians ($n = 51$) and reptiles ($n = 49$)) and endotherms (forest-core

birds ($n = 296$) and mammals ($n = 123$)). Notched boxes show the median, 25th and 75th percentiles, error bars show 10th and 90th percentiles and points indicate the outliers. Notches display the 95% confidence interval around the median.

response, we found that most species found in the forest and classified as species that preferred forest (that is, forest core, forest edge, forest no preference) were sensitive to habitat edges, displaying either edge-seeking or edge-avoiding abundance distributions in the landscape (Fig. 2a). The abundances of 11%, 30%, 41% and 57% of birds, reptiles, amphibians and mammals, respectively, showed strong declines towards forest edges. We observed an analogous pattern for matrix-preferring species that were measured in the matrix (Extended Data Fig. 1a).

Edge sensitivities across species

As expected, species that were classified as having no preference for either edge or core habitat displayed the lowest edge sensitivities and were significantly less sensitive than species that were classified as preferring core habitats in either forest or matrix (Extended Data Fig. 2). The more edge-sensitive a species is, the less area it can use across fragmented landscapes. Although this is true for all edge-response types, quantifying sensitivity is particularly critical for forest-core species that are more likely to be threatened because of forest loss³² and whose suitable habitat area is decreasing due to fragmentation in addition to habitat loss resulting from deforestation⁵ (Methods). Therefore, we particularly focus our analyses on the 519 forest-core species (51 amphibians, 296 birds, 123 mammals and 49 reptiles; Extended Data Table 1).

Our data show that forest-core habitat supported a larger number of amphibian, reptilian and mammalian species compared with forest-edge, matrix-core or matrix-edge habitats (Extended Data Fig. 1b). Furthermore, forest-core species were 3.7 times more likely to be listed as threatened on the IUCN Red List compared with species with other edge-response types (two-sided two-sample test for equality of proportions with continuity correction, $P < 0.001$; see also Extended Data Table 3).

Edge sensitivities of forest-core species varied more within than among all four vertebrate groups (Fig. 2b). However, on average, forest-core species displayed edge sensitivities of around 0.7 across endotherms and ectotherms (Fig. 2b), and this corresponds to a peak (or plateau) in species abundance for a minimum of 200–400 m away from sharp and high-contrast forest edges (Methods). This highlights how the amount of optimal forest habitat within fragmented forest patches can be much smaller than the total land area encompassed by the patch.

Of 277 species with high edge sensitivity ($S \geq 0.8$) that have been assessed for the IUCN Red List (excluding ‘data-deficient’ species), 8.6% were listed as threatened compared with 3.3% of the 988 remaining species, demonstrating the conservation relevance of our edge-sensitivity metric. Forest-core species were more likely to have very high edge sensitivities (25.4% of forest-core species) compared

with forest species with other edge responses (20.6%; two-sided two-sample test for equality of proportions with continuity correction, $P < 0.05$). Very high edge sensitivities were particularly prevalent among forest-core mammals (30.1% of species) and birds (24.0%), compared with forest-core amphibian and reptilian species (9.8% combined).

Size and edge sensitivity of ectotherms

Edge sensitivity decreased with body size for forest-core amphibians (generalized additive models, deviance explained = 39.6%, $n = 32$, $P < 0.05$; Fig. 3a), but increased with body size for forest-core reptilian species (generalized additive models, deviance explained = 35.9%, $n = 45$, $P < 0.01$; Fig. 3b). Avoiding overheating and severe water loss is likely to be an important driver of edge responses in forest-core amphibians and reptiles, since most of the data were collected in tropical landscapes (Extended Data Tables 1, 2), where year-round

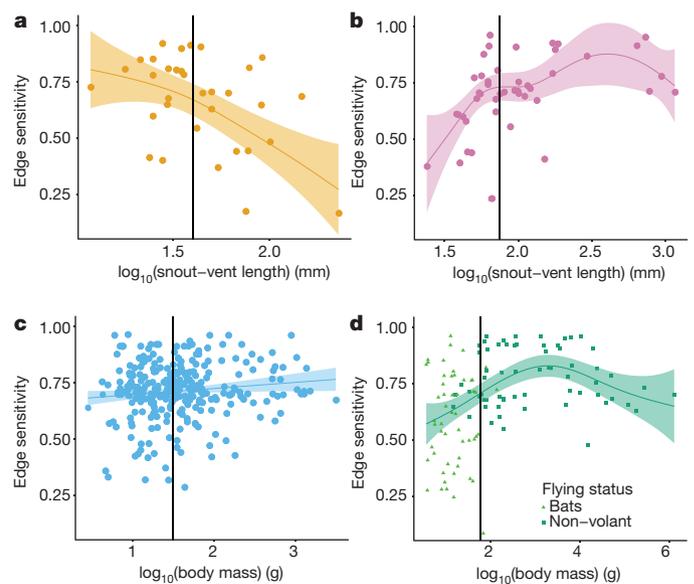


Figure 3 | Edge sensitivity and body size in forest-core vertebrates. **a–d**, Relationships are shown for forest-core amphibians (**a**, $n = 32$), reptiles (**b**, $n = 45$), birds (**c**, $n = 289$) and mammals (**d**, $n = 116$). Vertical lines indicate median body size of forest-core species (amphibians, 40.5 mm; birds, 31.0 g; mammals, 61 g; reptiles, 75 mm). We excluded two amphibian species of the order Gymnophiona, who have an elongated body shape. Smoothed curves and 95% confidence intervals were obtained from general additive models weighted by dataset reliability (Methods), which better explained the data than a null model for all taxa.

ambient temperatures are high but humidity can fluctuate considerably depending on microhabitat conditions³³. Amphibians require moisture to maintain gas exchange, cultivate bacterial symbionts with immune functions and protect their eggs³⁴. These physiological constraints make forest-core amphibians, adapted to the high humidity interior of forests, prone to desiccation in dry environments, such as habitats with lower tree cover at the forest edge and in the matrix³⁵. Small-bodied forest-core amphibian species are particularly sensitive to forest edges (Fig. 3a), because their high surface area-to-volume ratios¹⁹ (except perhaps for salamander and newts) make them more susceptible to desiccation. By contrast, the body shape of forest-core reptiles does not show a similar decrease in surface-to-volume ratio with increasing body size (Fig. 3b). Larger forest-core reptiles are therefore probably more vulnerable to overheating in sun-exposed environments, such as forest edges, particularly if they are too large to successfully use microhabitats, such as shaded leaf litter (Fig. 3b).

Size and edge sensitivity of endotherms

Edge sensitivity of forest-core mammals displayed a significant hump-shaped relationship with body mass (generalized additive models, deviance explained = 23.3%, $n = 116$, $P < 0.001$), a pattern driven mainly by non-volant species (Fig. 3d). We attribute this relationship to the compound effects of species-specific ways of locomotion (aerial or terrestrial) and energetic and other resource requirements. On average, forest-core bats displayed significantly lower edge sensitivities (S ; mean \pm s.e.m. = 0.59 ± 0.03 , $n = 53$) compared with non-volant forest-core mammals (0.77 ± 0.02 , $n = 63$; ANOVA with post hoc Tukey honest significant difference test, $P < 0.001$). This suggests that the ability to fly may make mammals that prefer the forest interior less sensitive to changes in habitat. But forest-core bats were also significantly smaller ($P < 0.001$), with only two species that were slightly larger, than the median body size of all studied forest-core mammals (Fig. 3d).

Energy demands and home-range size increase with body size in non-volant mammals³⁶. Larger forest-core mammals are less likely than smaller ones to meet their resource needs in highly fragmented landscapes that consist of small forest patches with many edges but little core habitat to provide those resources³⁷. Increasing energetic constraints are therefore hypothesized to account for the positive body size–edge sensitivity relationship for small-to-medium-sized forest-core species (Fig. 3d). However, larger species are also predicted to roam more widely in search of resources in fragmented landscapes if habitat loss results in a loss of resource density³⁸, decreasing their edge sensitivity in the landscape. This, together with other general features of large mammals, such as their lower vulnerability to predation³⁹, may explain why the largest forest-core mammals have lower edge sensitivities than medium-sized species (which are also susceptible to hunting¹⁷).

The combination of energetic constraints that are partly mitigated by dispersal capacity may also explain the similarly hump-shaped relationship of edge sensitivity with body mass in forest mammals that showed no edge preference (Extended Data Fig. 3). Conversely, dispersal capacity is likely to be the main driver explaining the decline in edge sensitivity with increasing body size in matrix-edge mammals (Extended Data Fig. 3), with the exception of *Bos javanicus*, a large but threatened wild cattle species that displayed high edge sensitivity.

Edge sensitivity of forest-core birds showed a weak increase with body size (generalized additive models, deviance explained = 1.5%, $n = 289$, $P < 0.05$). There was a tendency for small birds (less than 31 g, the median size of forest-core birds analysed in this study) to have more variable responses (Fig. 3c), as was also seen in bats (Fig. 3d). Some forest-core bird species certainly are sensitive to forest edges (Fig. 2b), especially in tropical landscapes and during the non-breeding period⁴⁰, but there is little evidence in our data to support a link between body size and edge sensitivity, probably because other traits, such as trophic guild are more important⁴¹.

Other species traits and edge sensitivity

The ability of some endotherms to adapt to a diverse range of environments²⁰ may enable them to respond better to habitat changes in a landscape²⁰. By contrast, many amphibian species are habitat specialists with small home ranges⁴² and these species are expected to be susceptible to changes in their environment. However, for both forest-core endotherms and forest-core ectotherms, our data do not support an effect of habitat specialization. Single-predictor models of habitat trait–edge sensitivity models were not significant, and the direction of the coefficient for habitat traits that were retained in multiple-predictor models could not be estimated with confidence, except for forest-core reptiles (Extended Data Table 4a–d). For forest-core endotherms, our data instead emphasize the importance of species locomotion, which correlates with the vulnerability of a species to hunting or predation when traversing non-forest habitats: edge sensitivity was consistently higher in non-volant mammals compared to volant species with similar habitat breadths (Extended Data Table 4c).

Birds particularly may also be more susceptible to biophysical drivers, such as disturbance history⁵, confounding the detection of patterns between life-history traits and species responses to edges separating forest from non-forest habitat. This may explain why we found no evidence for direct effects of diet, range size, migratory status or clutch size on edge sensitivities of forest-core birds in single-predictor models (Methods). Multiple-predictor models for edge sensitivities of forest-core birds retained range size, body mass, migratory status, forest dependency and number of habitats (Extended Data Table 4d). However, none of the predictor coefficients were significant and the overall deviance explained by the model was negligible.

A ubiquitous phenomenon

Tracking changes in the abundances of species in response to edge effects allows us to predict biodiversity responses to forest loss and fragmentation at scales that are useful for land management. This is an important difference compared with previous global analyses and projections of biodiversity responses to global land-use changes⁴³ that do not account for the continuous variation in habitat quality of either matrix or forest habitat²⁴ that are known to affect the species and the ecosystem processes, which they control⁴⁴.

Considering edge effects (and therefore the landscape configuration and forest–matrix contrast) is at least as important as the amount of habitat when predicting species richness from habitat distribution in a landscape. Although forest-core endotherms and ectotherms vary greatly in how their abundance changes in response to edge effects, on average they reach peak abundances in forest habitats farther than 200–400 m from sharp high-contrast forest edges. This seems to corroborate the traditional perception that edge effects operate within a relatively small spatial window of just a few hundred metres^{45–47}. We cannot, however, exclude the possibility that the effect of edges on core species extends further within the forest, but rigorously testing this would require data from many more studies that examine edge effects over scales of one kilometre or more⁹, which are currently rare. Regardless of whether larger-scale edge effects are as ubiquitous as small-scale effects, our data strongly suggest that small forest fragments with no forest located farther than 200–400 m from sharp high-contrast edges (or alternatively, with no forest located farther than 100 m from low-contrast edges) should probably be seen as extended forest-edge habitats⁴⁸. Such habitats may support lower abundances of forest-core species and may act as a stepping stone or corridor for improving patch interconnectedness⁴⁹, but maximum abundances for many species will only be achieved within much larger forest-core fragments. The distances to edges given here are, however, only indicative. In practice, to account for multiple edges and forest–matrix contrast, it will be necessary to compute a map of I , using, for example, our BioFrag software³⁰, and delineate forest areas of $I < 30$ as suitable for most forest-core species.

Anthropogenic disturbances to tropical forests were recently shown to double biodiversity losses incurred directly from deforestation⁵.

Our data demonstrate this pattern, observed in the Amazon, holds globally. Approximately half of the global forest area lies within 500 m of a forest edge¹, and across these edges, the abundances of many forest-core species can be diminished. The direct implication is that less than 50% of Earth's remaining forests can be considered free from edge effects, but even those forests are under threat from the chaotic expansion of road networks, selective logging, wildfires, widespread hunting and other human encroachment into the last intact forest frontiers⁵⁰.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions M.P., V.L. and R.M.E. designed the study and wrote the first draft of the manuscript. M.P. conducted all analyses and V.L. developed the methodology. R.M.E. and all other authors contributed data. All authors commented on manuscript drafts.

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METHODS

Data reporting. No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment.

Species abundance data and species traits data. We compiled primary biodiversity datasets containing abundance measurements at plot level acquired in 22 anthropogenically fragmented forest landscapes around the world (BIOFRAG database²). All landscapes encompassed anthropogenic forest edges and—except for one landscape, which is dominated by forests with only a small amount of habitat conversion in the north-west corner—a mosaic of natural forests and other land uses (Extended Data Table 2). In seven landscapes, the natural forests were bordered at least in part by managed, plantation forest. Eighteen landscapes were from continents and the remaining four were from islands, and six landscapes could reasonably be described as coastal (Extended Data Table 2). For our analysis, we only used datasets that measured abundance of vertebrates in at least nine plots per landscape. We only used datasets for which geographic coordinates of plots were provided at high spatial accuracy by the authors of the dataset, because the location of each plot in relation to the forest edges was important. Datasets represented full gradients of distance to edge and edge influence. All datasets in our analysis were from community-level surveys of a focal taxonomic group (rather than sampling for a target list of species). The final datasets used in this analysis came from 22 landscapes, with some landscapes sampled for more than one taxonomic group in separate or combined studies^{51–71} (Fig. 1).

The majority of taxa represented in the datasets were true species (that is, not morpho-species; Extended Data Table 1). We matched taxonomic names given by the dataset author using steps outlined in ref. 2 to obtain the full taxonomic classification for each species. We used `lets.iucn` and `let.iucn` functions in the `letsR72` package to extract, for each true species from the IUCN online database, the Red List conservation status (IUCN status) and habitat information (IUCN Tree: species present in forests and savannah or shrub habitats only; IUCN Forest: species present in forests only; IUCN Habitat: number of main IUCN habitat categories listed).

For each species, we extracted life-history trait data from literature and database sources. For amphibians and reptiles, we extracted trait data (body size: maximum snout-vent length in mm and maximum total length in mm for snakes, mean clutch size, thermal niche: average temperature and temperature range, adult and larvae habitats and vertical stratification (that is, arboreal, semi-arboreal or terrestrial) from academic literature^{73–113}, region-specific guide books^{114–116}, text books^{117–119} and websites (all last accessed on 24 June 2016), including <http://amphibiaweb.org/>, <http://frogs.org.au/>, <http://www.anolislizards.myspecies.info/>, <http://www.reptile-database.org/db-info/news.html>, <http://www.iucnredlist.org/>, <http://research.amnh.org/vz/herpetology/amphibia/index.php>, <http://eol.org/> and <http://tolweb.org/tree/>. For birds, we extracted information on body size (mean body mass in g), range size, migratory status (not migrating, altitudinal migrant, full migrant or nomadic), generation length in years and mean clutch size from the trait database compiled by BirdLife International (<http://www.birdlife.org/>). We extracted information on bird diet from a global dataset¹²⁰, focusing on the Diet-5Cat attribute (that is, assignment to the dominant category among five categories based on the summed scores of constituent individual diets: plant- and seed-eating species; fruit- and nectar-eating species; invertebrate-eating species; vertebrate-, fish-eating and scavenging species; and omnivores). For mammals, we extracted body size (mean body mass in g), trophic status, litter size and litter numbers per year, maximum longevity in months, migratory behaviour, range extent in km and age at first birth from the PanTHERIA database¹²¹ complemented by information from <http://animaldiversity.org/accounts/Mammalia/> (last accessed on 11 May 2016). We also recorded whether or not species can fly (volant, all from the order Chiroptera; non-volant, all other orders).

Quantifying abundance responses to variations in tree cover. We analysed a species' abundance distribution in the landscape with respect to two spatial variables, percentage of tree cover (C) and edge influence (I), to characterize both the species' edge response and the species' habitat preference. For each landscape we obtained 30-m pixel resolution percentage C maps¹²², which were generated from Landsat imagery using the percentage tree cover training data and decision trees classification algorithm implemented in the Google Earth engine. These maps define tree cover in the year 2000 as canopy closure for all vegetation taller than 5 m, encoded as a percentage per output grid cell and ranging between 0 and 100%. **Quantifying I within and among landscapes.** We computed the I metric from the regional standard deviation of C (σ_C , a measurement of regional heterogeneity) and the regional average of C (\bar{C}) subtracted by the individual values of C (a measure of point heterogeneity and direction)³⁰. I is the maximum of regional and point heterogeneity for each pixel and has the sign of the point heterogeneity (equation (1)).

$$I = \max(\sigma_C, |\bar{C} - C|) \times \text{sign}(\bar{C} - C) \quad (1)$$

where I , C , σ_C and \bar{C} are matrices. \bar{C} and σ_C were computed using a Gaussian filter with a 1-km radius, the distance previously shown to impact animal abundance⁹, to ensure that all C variations (that is, edges) contained within a window of 1-km radius contributed to the value of I . Absolute values of I range from 0 (no edges within a 1-km radius) to 100 (one pixel surrounded by a different habitat for 1-km in all directions). The sign of I is determined by the point heterogeneity ($\bar{C} - C$): forest habitat near the matrix has a negative I and matrix habitat near the forest has a positive I (Extended Data Fig. 4).

The amplitude of I depends on the landscape configuration (Extended Data Fig. 5a) and forest-matrix contrast (Extended Data Fig. 5b). I measured at a focal point increases as the point approaches all nearby edges, and therefore varied with the shape and size of the forest patch (Extended Data Fig. 5a). I also varied with the contrast between forest and matrix habitats, that is, the contrast in C (Extended Data Fig. 5b). Therefore, there is no general relationship between I and the distance to a defined edge, and no direct relationship between the percentage of forest cover in a buffer as I is sensitive to contrast in C whereas the percentage of forest cover is computed from a binary forest-non-forest map.

Categorizing species into edge-response types. Species abundance within each landscape was plotted in a two-dimensional space based on C and I values ($C - I$ graph in universal transverse mercator WGS 84 projection; Extended Data Fig. 6c). We defined seven edge-response types⁹: forest-core, forest-edge, forest no preference, matrix-core, matrix-edge, matrix no preference and generalist species.

We used a naive Bayes classifier to estimate the most likely edge-response type for each species from a training set of simulated abundance patterns on the $C - I$ graph (see Extended Data Fig. 4 for the $C - I$ graph, Extended Data Fig. 6d for an illustration of a training set and ref. 30, particularly pages 23 and 24 of the user manual for an illustration of classification). The training set contained, on average, 15 different abundance patterns for each edge-response type to fully describe each type (spanning all possible patterns that may be classified as a specific type when measured on the $C - I$ graph). We created the training sets using sigmoidal surfaces of varying means (location of maximum abundance) and standard deviations (spread) along the C and I axis, thereby defining areas of high and low abundance on the $C - I$ graph. For forest and matrix types, the location of maximum abundance along the C axis ranged from 60% to 100% and from 0% to 20%, respectively. We defined the training set by assuming that a species that is most abundant for $C > 60$ has a high probability to be a forest species, whereas a species most abundant for C around 50 is likely to be a forest species but retains a significant probability to be a matrix species (sigmoidal threshold). The classification of the preferred habitat depends on the full shape of the species abundance curve along the C axis and how it compares to the training set patterns that we defined. Similarly, we defined core and edge types in the training set with the location of a maximum abundance range of $|I| = 0-10$ and $|I| = 30-100$, respectively. By definition, types of no preference have a flat abundance along the I axis, whereas generalist types have a flat abundance along the C axis. The location and spread parameters of sigmoid curves along the C and I axis were combined to create an ensemble of abundance surfaces describing each categorical edge-response type in the $C - I$ graph (see examples provided in Extended Data Fig. 6d). The collection of these simulated abundance patterns on the $C - I$ graph forms the training set. The classifier compares the measured abundance distribution of each species to the ensemble of abundance patterns for each type in the training set and estimates the most likely match, depending on the area (or areas) in which the species was most abundant on the $C - I$ graph and the shape of the abundance surface. For example, species with abundances that increase with C are very likely to be classified as forest even if they are mostly abundant for a $C < 60\%$.

Species that did not match any defined type were classified as unknown (for example, species that are abundant in both the matrix core and forest edge but not on the matrix edge). Our approach of defining a training set to use a classifier is effective for the categorization of species with similar edge responses pertaining to known types and is more flexible than fitting a parametric model to each species' abundance distribution or using thresholds.

Quantifying S for each species. We developed the edge sensitivity (S) metric to quantify and compare the edge responses of species that were measured in different landscapes but on the same scale, and to do so independently of landscape configuration¹²³. S is derived from comparing the abundance surface of a species on the $C - I$ graph (A_s) with the abundance surface the species would have if it was insensitive to edge effects (A_i). A species' S therefore corresponds to the proportion of the I spectrum that is not occupied by this species.

We obtained the A_s for each species by linearly interpolating its abundance to the full graph (for $C \in [0, 100] \in \mathbb{N}$, and $I \in [0 - C, 100 - C] \vee C$), assuming zero abundance for locations with no measurements. We estimated the A_i for each species by obtaining the maximum abundance at each C value, and replicating this maximum abundance along the I axis of the graph, so that A_i varied with C only, and not with I . We then computed S from the ratio of the sum of the species

abundance surface on the $C - I$ graph (A_s) and the sum of the abundance surface the species would have if it was insensitive to edge effects (A_i):

$$S = 1 - \frac{\sum \sum A_s}{\sum \sum A_i} \quad (2)$$

where A_s and A_i are matrices and S is a scalar. Because A_i is computed from the maximum for each C of A_s , its sum is larger or equal to that of A_s , therefore S is bounded between zero and one. Species with S values equal to zero are species for which the abundance is not influenced by the presence of habitat edges. Species with S values larger than zero are species that either increase or decrease in abundance in response to edge effects. Species with values close to one are species that are only abundant for a specific edge influence value.

S does not quantify the abundance variation of a species directly, as this depends on the configuration of the landscape. Also, S does not quantify whether the species abundance increases or decreases with the presence of edges, as this depends on the I values preferred by the species (that is, low values for core species, high values for edge species). S quantifies the length of the range of I values for which a species is abundant: if the range is as wide as the I spectrum (that is, the species is abundant for large portions of the I domain), then the species is not sensitive to edge effects and S is low (and the species has a high tolerance to habitat change). If the range is small compared to the I spectrum (that is, the species is abundant at a small portion of the I domain only), then the species is sensitive to I , and S is high (and the species has a low tolerance to habitat change). Species for which the S value is close to one can only be abundant in narrow ranges of I , for example, $|I| < 10$ (core species) or $45 < |I| < 55$ (edge species).

The S metric is useful to compare species sensitivity for edges, and its computation is independent of the species categorization described in 'Categorizing species into edge-response types'. Two species with the same S may have different predictions about the spatial distribution of their preferred habitat if they belong to different edge-response types. Forest-core species with $S > 0.7$ will only be found within the forest interior far away from edges, whereas forest-core species with S of around 0.6 will be found near edges of large forest patches, but not in peninsulas or small forest patches. Forest-core species with $S < 0.6$ will be found throughout the forest and in large forest patches, but not in the smallest forest patches (size depending on the window size used to compute I , which was 1 km in this study). We compared the distribution of S for forest-core species within taxonomic groups using notched box plots (Fig. 2b), thereby notches display the 95% confidence interval around the median. If box notches do not overlap there is strong evidence that medians differ.

S cannot generally be converted to a 'distance to nearest edge' equivalent, as it is based on I , which varies depending on landscape configuration (Extended Data Fig. 5a) and patch contrast (Extended Data Fig. 5b). However, in the special case that a species' abundance was measured across a straight edge of constant and maximum contrast, forest-core species with $S = 0.5$ will be abundant up to this edge, and forest-core species with $S = 0.7$ will be abundant up to 400 m from this edge (for an I computed with a 1-km window). A forest-core species of low sensitivity would also be found near edges and even in small forest patches, albeit with a lower abundance.

We provide these distance estimates as an indication only, because there is no direct relationship between distance to the nearest edge and I . In practice, instead of computing the distance to nearest edges using binary forest-non-forest maps, we urge decision makers to utilize I maps computed from bounded landscape measurements (for example, percentage tree cover) using the provided software³⁰. This would allow them to identify areas where I is below 30 as suitable for most forest-core species (with a S around 0.7) thereby taking into account edges varying in contrast, breadth and shape.

Rating datasets based on their capacity to assess species' responses to edges.

Each dataset was rated based on the accuracy of its C map and the distribution of sampling points within the C and I spectra. To evaluate C map accuracy, we computed the proportion of sampling points with a C value that matches the description given by the dataset authors (for example, the C value of points identified as 'forest' should be over 50%). We also rated the sampling design based on the distribution of plots on the $C - I$ graph, because accurate classification of species responses requires data to be collected from each habitat type (forest core, forest edge, matrix edge and matrix core). We downgraded the dataset rating for each missing category. Dataset ratings were then used as weights when comparing the S of each species across datasets.

Estimating the relative number of species belonging to edge-response types.

Owing to sampling bias present in most datasets (for example, many datasets include more sample sites in the forest core compared to forest edges), simple counts of the number of species belonging to each edge-response type partly reflect the relative abundance of measurement locations within different habitat categories (Extended Data Table 1). For example, out of 103 amphibian species, 49 were

categorized as forest-core species. This could arise either because $49 / 103 = 48\%$ of amphibian species show a preference for forest-core habitats, or alternatively because 48% of sampling locations were in forest-core habitats, or a mixture of both. Therefore, the number of sampling sites within different habitat categories must be considered when estimating the number of species belonging to each edge-response type.

We addressed the ambiguity resulting from sampling bias across different habitat categories by computing the mean number of species per site (termed 'species density' or D). D was computed separately for sites located within each of the four habitat categories (H : forest core, forest edge, matrix edge and matrix core) and for species classified in each of the seven edge-response types. Therefore, for each H and each species edge-response type (T) we computed the mean number of species of type T recorded per site located in H , formally termed 'species density of species of type T in habitat H ' and denoted D_H^T :

$$D_H^T = \frac{\sum_{i=1}^{\text{number of sites in } H} \text{number of } T \text{ species in } H_i}{\text{number of sites in } H} \quad (3)$$

where i indicates a site in the habitat H . For example, the mean number of species of type forest-core (T_{FC}) recorded in sites located in forest-core habitat (H_{FC}) was calculated as (with i indicating a site in the forest-core habitat ($H_{FC, \text{number of}}$):

$$D_{H=FC}^{T=FC} = \frac{\sum_{i=1}^{\text{number of sites in } H_{FC}} \text{number of } T_{FC} \text{ species in } H_{FC,i}}{\text{number of sites in } H_{FC}} \quad (4)$$

the mean number of forest-core species recorded in sites located in the forest-edge habitat (H_{FE}) as:

$$D_{H=FE}^{T=FC} = \frac{\sum_{i=1}^{\text{number of sites in } H_{FE}} \text{number of } T_{FC} \text{ species in } H_{FE,i}}{\text{number of sites in } H_{FE}} \quad (5)$$

the mean number of forest-edge species (T_{FE}) recorded in sites located in the forest-core habitat as:

$$D_{H=FC}^{T=FE} = \frac{\sum_{i=1}^{\text{number of sites in } H_{FC}} \text{number of } T_{FE} \text{ species in } H_{FC,i}}{\text{number of sites in } H_{FC}} \quad (6)$$

and so on for each combination of T and H .

Species densities within the forest habitat, including the density of forest-core species in the forest (F), were determined as the average of species densities for the forest-core and forest-edge habitats:

$$D_{H=F}^{T=FC} = \frac{D_{H=FC}^{T=FC} + D_{H=FE}^{T=FC}}{2} \quad (7)$$

Similarly, the mean number of forest edge species in the forest was given by

$$D_{H=F}^{T=FE} = \frac{D_{H=FC}^{T=FE} + D_{H=FE}^{T=FE}}{2} \quad (8)$$

and the mean number of forest no preference species in the forest (F_{NP}) was given by

$$D_{H=F}^{T=F_{NP}} = \frac{D_{H=FC}^{T=F_{NP}} + D_{H=FE}^{T=F_{NP}}}{2} \quad (9)$$

This corresponds to the mean number of species of edge-response type T per forest site weighted by the number of sites in the forest core and the forest edge (Fig. 2a: forest occupancy per edge-response type). If there were the same number of sites in the forest core and the forest edge then $D_{H=F}^T$ would simplify to the mean number of species of type T per site in the forest. However, we weighted the mean number of species per forest site (number of forest sites $n = 4,359$: 203 for both amphibians and reptiles, 1,805 for birds, 2,148 for mammals) so that the contributions of core and edge habitats were equivalent. The weighted mean allows us to compare, for example, the number of F_C and F_E species in the forest as if the same areas of edge and forest-core habitats had been sampled (Fig. 2a).

We also quantified the mean number of species (regardless of edge-response type) per dataset in each habitat category to identify the habitat that can support the largest number of species:

$$D_H = \frac{\sum_{i=1}^{\text{number of sites in } H} \text{number of species in } H_i}{\text{number of sites in } H} \quad (10)$$

D_H was computed for all four habitat categories (Extended Data Fig. 1b). To compute D , sampling sites and species were pooled from all landscapes used in this study, that is, the s.d. was computed across rather than within landscapes.

Modelling edge sensitivity as a function of species life-history traits. To test whether body size predicts species responses to edges, we used general additive models implemented in the *mgcv* package¹²³ (using \log_{10} -transformed body size as predictor), with smoothers fitted separately for each taxonomic group. We used dataset ratings (see 'Rating datasets based on their capacity to assess species' responses to edges') as a weighting factor for the smoothing. Data were visualized using the R package *ggplot2*¹²⁴.

We also wanted to know whether we can use additional species' traits, in particular their habitat specialization, as a proxy for abundance when predicting sensitivities to habitat edge. Within each taxonomic group, we first tested for single-predictor relationships between edge sensitivity of forest-core species and their life-history traits (see 'Species abundance data and species traits data'). We then fitted multiple-predictor general linear models using the automated model selection through information theoretic approaches and multi-model averaging using maximum likelihood. First, we constructed a global model for each taxonomic group, modelling S as a function of predictors. We excluded highly inter-correlated predictors ($V > 0.5$, $R^2 > 0.5$, $P > 0.6$) from these models using Pearson's χ^2 test with Yates' continuity correction and Cramer's V measure of association to test for correlations among categorical predictors (*lsr* package), Pearson's product-moment correlation P for associations between numeric predictors and the coefficient of determination R^2 of linear models for relationships between numeric and categorical predictors. For each global model, we used the dredge function in the R *MuMIn* package v.1.10.5¹²⁵, which constructs models using all possible combinations of the explanatory variables supplied in each global model. These models were ranked, relative to the best model, based on the change in the Akaike information criterion (ΔAIC). A multi-model average (final model) was calculated across all models with $\Delta AIC < 2$.

Global models were restricted to a subset of life-history traits in mammals, amphibians and reptiles due to a large number of missing values. Predictors in the global models for ectotherms include IUCN Habitats, IUCN Forest, IUCN Tree (this variable correlated strongly with IUCN Forest and was excluded together with its two-way interaction from the models for mammals and amphibians), body size (decadic logarithmic; in mm), and two-way interactions of body size with each habitat trait. Predictors in the global models for endotherms include IUCN Habitats, IUCN Forest (this variable correlated strongly with IUCN Habitats and was excluded together with its two-way interaction from the model for reptiles), IUCN Tree, body mass (decadic logarithmic; in g), and two-way interactions of body mass with each habitat trait. For mammals, we also included body mass squared (given the hump-shaped relationship with edge sensitivity; Fig. 3d), flying status and two-way interactions of flying status with body mass and habitat traits. For birds, we also included: range size, mean clutch size, migratory status, diet and two-way interactions of migratory status with body mass and habitat traits, and of body mass with diet and extent of occurrence.

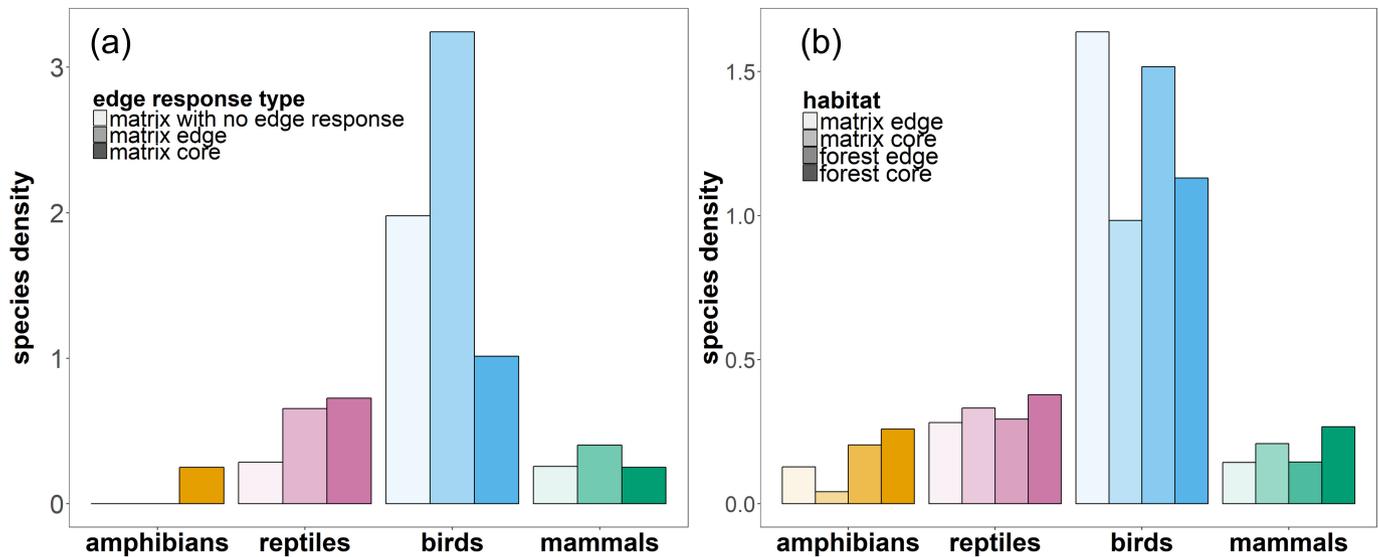
Code availability. We used the statistical software R version 3.2.1 for all statistical analyses. We used in-house generated software for analyses central to the manuscript: computing edge influence, categorizing species into edge-response types, quantifying edge sensitivity, rating datasets and estimating the relative number of species belonging to edge-response types. Details of the analyses can be found in the Methods. The software itself is accessible at <https://github.com/VeroL/BioFrag> (see ref. 30).

Data availability. The .xls and .kml data that support the findings of this study are available in Figshare (https://figshare.com/articles/Pfeifer_etal_2017_Nature/4573504). Original BIOFRAG data are available upon request from the corresponding author, but restrictions apply to the availability of these data, which are not publicly available. Data are, however, available from the authors upon reasonable request and with permission of dataset authors as specified in the BIOFRAG database² (<https://biofrag.wordpress.com/>).

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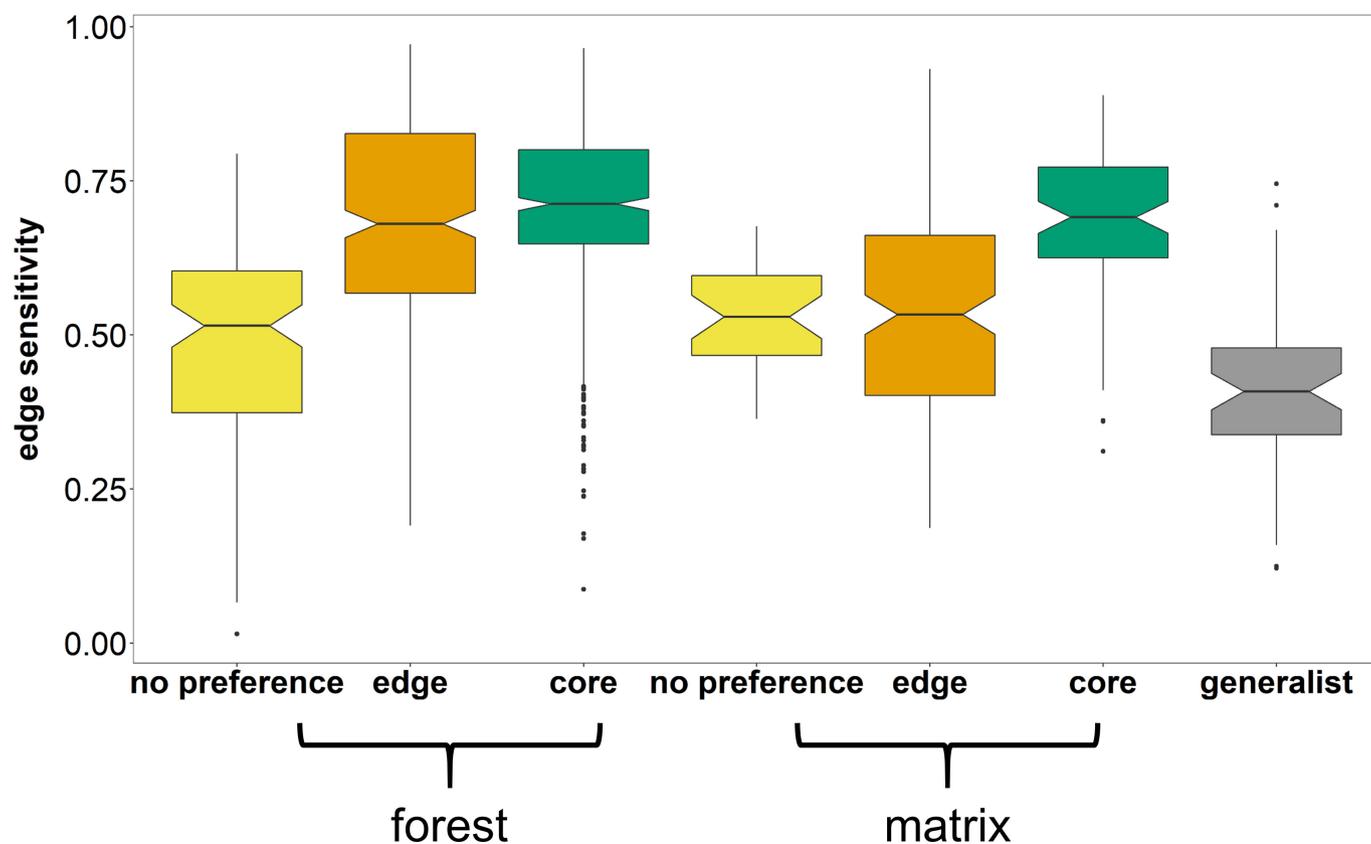
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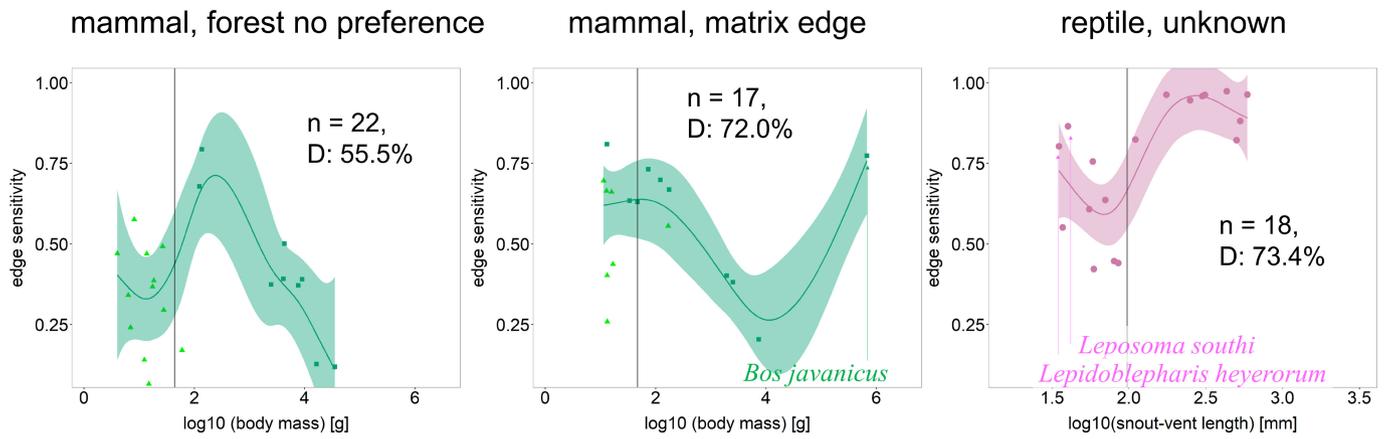
Extended Data Figure 1 | Matrix occupancy by matrix species per edge-response type and mean number of species per habitat category. **a**, Mean number of species per matrix site (number of matrix sites = 727; 7 for amphibians, 659 for birds, 51 for mammals and 10 for reptiles), weighted so that the contributions of core and edge habitats are equivalent (Methods, equations (7)–(9)). Only species classified as preferring the matrix are shown (that is, matrix core, matrix edge, matrix with no edge response). **b**, Mean number of species (regardless of edge-response type) in each habitat category showing which habitat can support the largest number of species after addressing the ambiguity resulting from sampling

bias across different landscape configurations (Methods, equation (10)). Plots were categorized by their locations into forest-core ($n = 2,955$), forest-edge ($n = 1,404$), matrix-core ($n = 388$) and matrix-edge plots ($n = 339$). For each configuration we computed the mean number of species present per habitat category plot, which identifies the habitat that can support larger numbers of species. For amphibians, reptiles and mammals, forest-core habitats supported more species than did forest-edge, matrix-core or matrix-edge habitats. By contrast, bird species were found in larger numbers in edge habitats (in forest and matrix) than in core habitats.



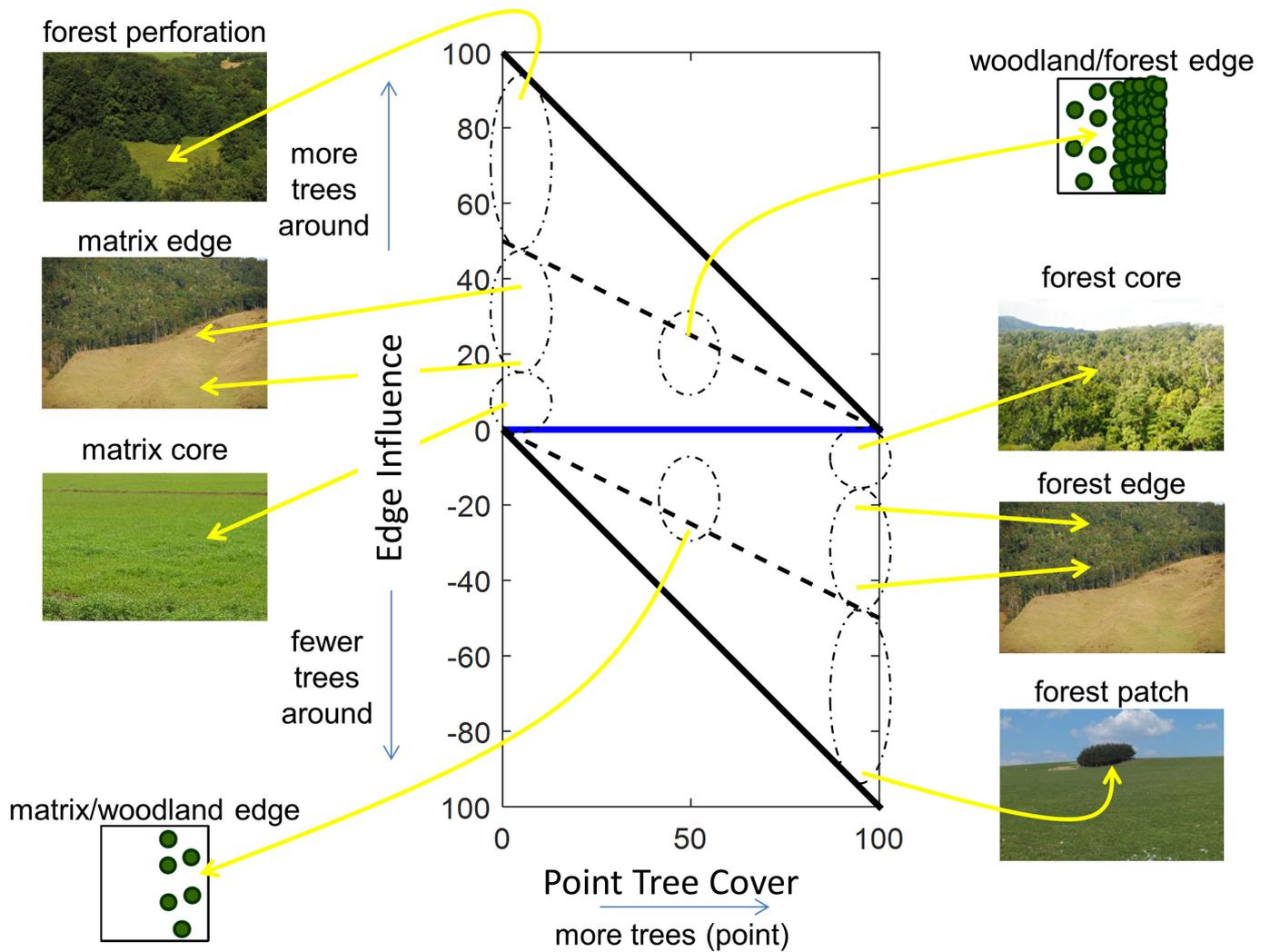
Extended Data Figure 2 | Distribution of edge sensitivities for seven recognized edge-response types. Forest-core ($n = 519$) and matrix-core species ($n = 80$) displayed significantly higher edge sensitivities compared to generalists ($n = 56$) and to forest ($n = 112$) and matrix species ($n = 34$), with no preference for either edge or core habitats (two-sided pairwise Wilcoxon signed-rank test with Bonferroni correction: $P < 0.001$). We excluded species that could not be classified ($n = 113$). Forest-edge species ($n = 338$) had significantly higher edge sensitivities compared

to forest no preference, matrix no preference, generalist and matrix-edge species ($P < 0.001$). Matrix-edge species ($n = 165$) also displayed significantly lower edge sensitivities compared to matrix-core species and higher edge sensitivities compared to generalists ($P < 0.001$). Notched boxes show the median, 25th and 75th percentiles, error bars show 10th and 90th percentiles, and points indicate outliers. Notches display the 95% confidence interval around the median.



Extended Data Figure 3 | Significant relationship between edge sensitivity and body size across edge-response types. This excludes forest-core species that are shown in Fig. 3. Vertical lines indicate median body size of the species per taxonomic group and edge-response type (mammals forest no preference, 43.8 g; mammals matrix edge, 47.0 g; reptiles, unknown 97.5 mm). Smoothed curves and 95% confidence

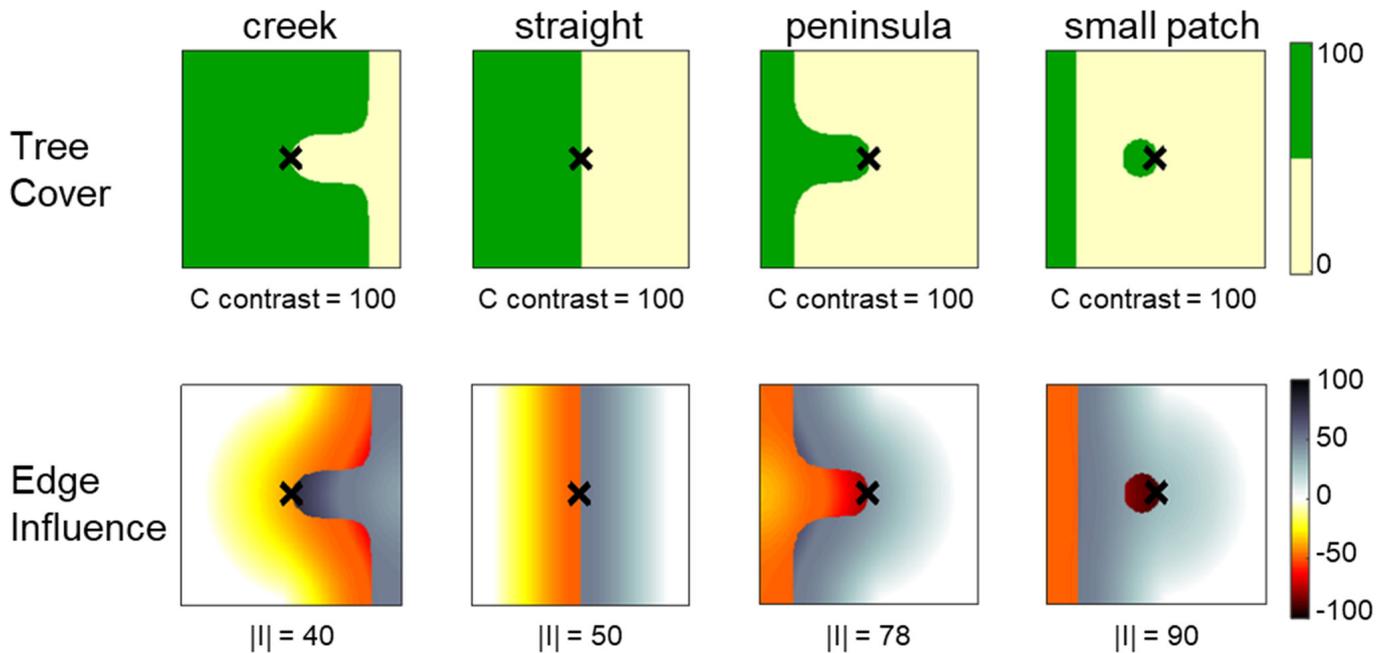
intervals were obtained from general additive models, with the model weighted by a variable that reflects dataset reliability (Methods). General additive models better explained the data than a null model for taxa and edge-response types shown. Edge sensitivity ranges from 0.0 (no declines in local abundance due to edge effects) to 1.0 (local extinction due to edge effects).



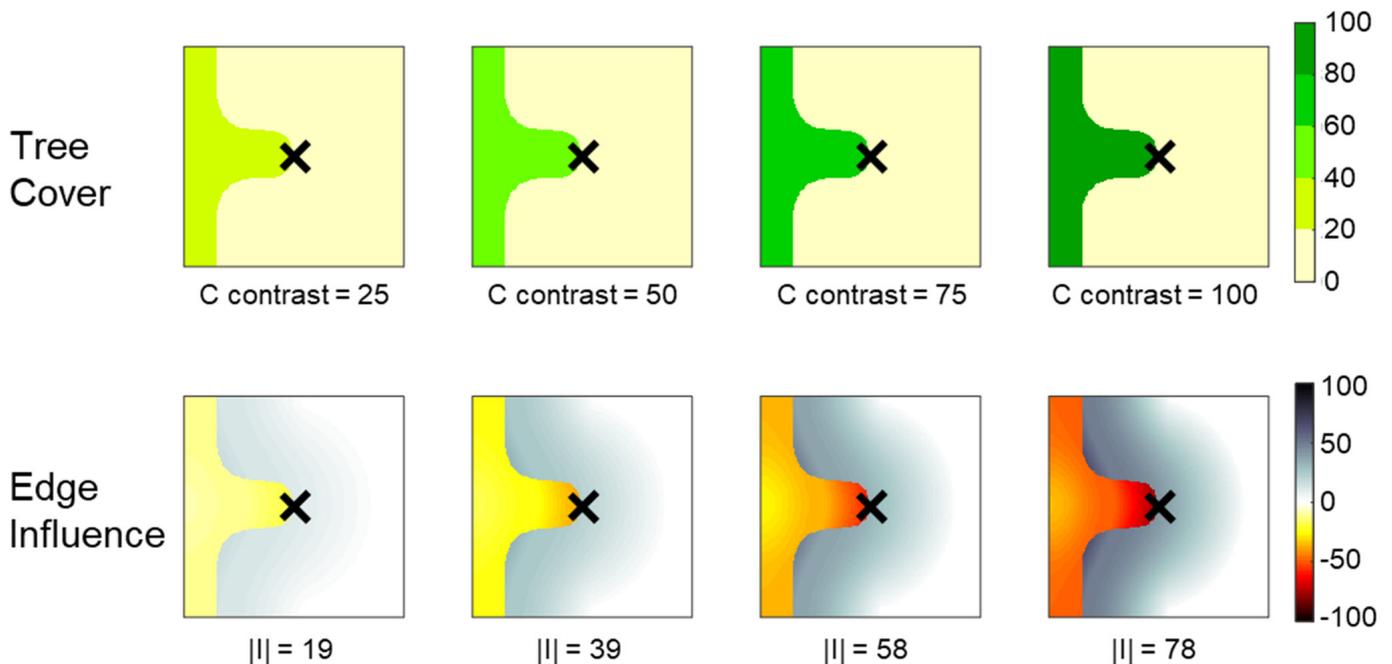
Extended Data Figure 4 | Illustration of the graph of $C - I$. Combinations of C and I values characterize different landscape configurations, although some combinations are impossible by design (areas outside of the bold lines (upper right and lower left corners)). The x axis represents the percentage of tree cover at the scale of a pixel.

The y axis represents I , computed from the regional standard deviation of C (a measurement of regional heterogeneity) and the regional average of C subtracted by individual values of C (a measurement of point heterogeneity and direction).

(a) Landscape configuration and the amplitude of the Edge Influence

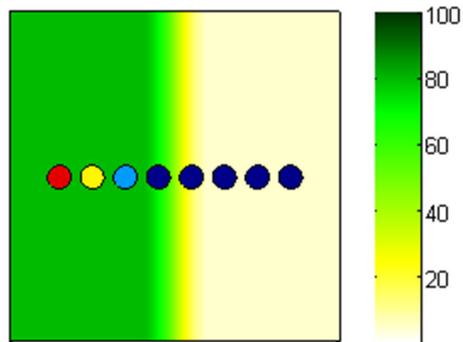
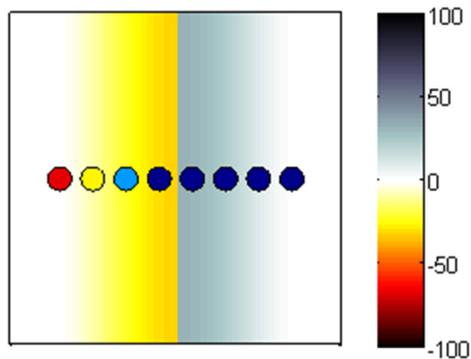
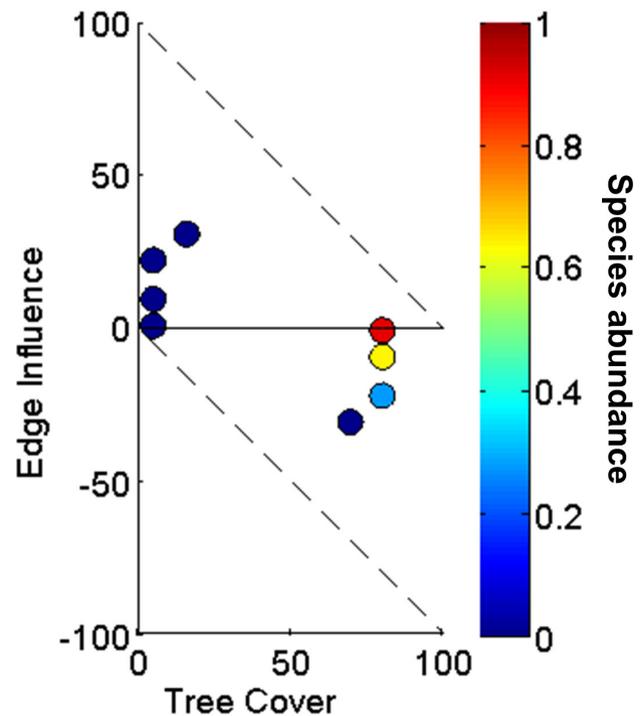
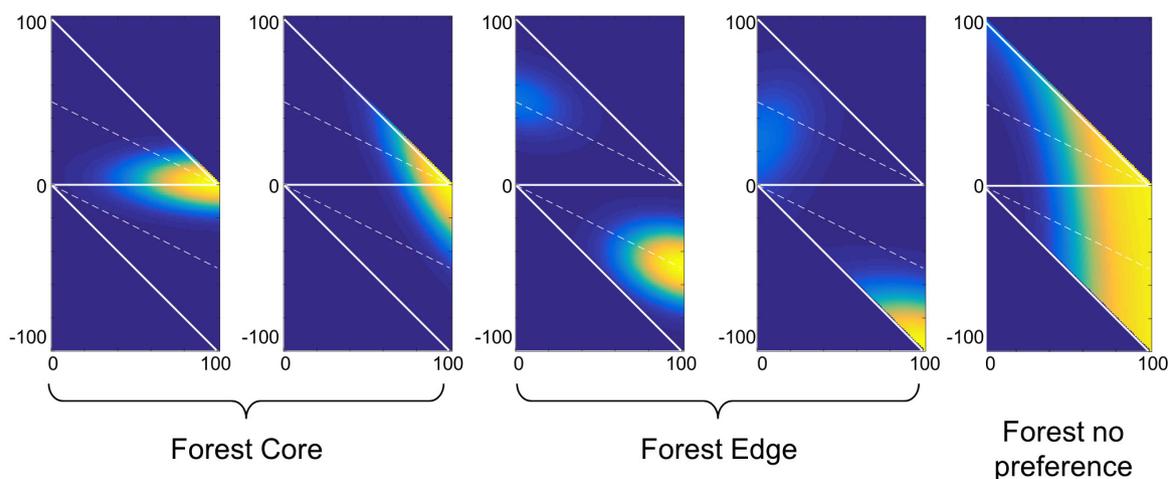


(b) Forest – matrix contrast and the amplitude of the Edge Influence



Extended Data Figure 5 | Variations of I with C configuration and contrast. **a.** Landscape configuration and the amplitude of I . Top, four examples of landscape configurations comprising dense tree cover habitats (green) and matrix (cream). From left to right: creek edge, straight edge, peninsula edge and small forest patch. Bottom, maps of I that correspond to the above landscape configurations. The value of I at the central point (cross) is given for each configuration. The central point is always located on an edge and its distance to the nearest edge is always zero. Nonetheless, I increases in absolute value as the central point is increasingly surrounded

by a different type of habitat. **b.** Forest–matrix contrast and the amplitude of I . Top, Four examples of peninsula edges between matrix (cream, $C = 0\%$) and habitats of varying tree density (shades of green). From left to right: $C = 25\%$, 50% , 75% and 100% . Bottom, maps of I that correspond to the above landscape contrasts. The value of I at the central point (cross) is given for each configuration. The central point is always located on an edge and its distance to nearest edge is always zero. I increases as the edge contrast increases.

(a) 'Forest Core' species abundance on the **Tree Cover (C)** map(b) 'Forest Core' species abundance on the **Edge Influence (I)** map(c) 'Forest Core' species abundance on the **C – I** graph(d) **Illustration of training set of edge response types**

Extended Data Figure 6 | Computing species abundance surfaces and simulated edge-response types on the graph of $C - I$. **a**, Plots superimposed on a hypothetical map of C . Marker colours correspond to the abundance of a hypothetical species and follow the colour bar shown in **c**. **b**, Map of I corresponding to **a**. **c**, Graph of $C - I$: species abundance (warm colour, higher abundance) is plotted as a function of C and I measured at the species' plots. In this example, the species is predominantly found in sites characterized by a high C and low $|I|$, and

would be classified as a forest-core species. **d**, Illustration of the training set of edge-response types used for classification. Each of the seven response types has around 15 patterns associated with it in the training set; here we show two examples for the forest-core and forest-edge type and one example for the forest no-preference type. Each graph is a graph of $C - I$ with C on the x axis and I on the y axis. Warmer colours indicate a high abundance, dark blue is 0.

Extended Data Table 1 | Summary statistics of species and landscapes assessed in our study

Taxon	n	n, true	n, IUCN	LS (tropical)	n, fc (tropical)	n, fc + true (tropical)
Amphibians	103	72	72	7 (6)	51 (48)	35 (32)
Birds	1158	1139	1139	11 (7)	296 (275)	293 (273)
Mammals	266	260	258	8 (7)	123 (121)	118 (117)
Reptiles	146	124	49	8 (7)	49 (41)	45 (37)

We include information of the number of species measured across datasets (*n*), the number of those species that were not morpho-species (*n, true*) and that were assessed by IUCN (*n, IUCN*), and the number of landscapes (LS) sampled overall and in the tropics only (in parentheses). The number of forest-core (*n, fc*) species (all and true species only) after grouping species into edge-response types based on their abundance distribution in the fragmented landscapes is also shown. Note that 299 birds (25.8%), 35 mammals (13.2%), 21 reptiles (14.4%) and 14 amphibians (13.6%) could not be categorized, as their abundance in the landscape was either too low or too variable to reliably classify them into any of the edge-response types.

Extended Data Table 2 | Attributes describing the geographical context for each landscape

Landscape	Ocean present in landscape	Geographic context	Forest within & outside PAs	Plots within & outside PAs	Land use in the matrix
LS_01	yes	Africa	pw	wo	Crops, Plantation forest
LS_02	no	S America	wo	wo	Clear cuts
LS_03	yes	Island^a	o ^e	o	Clear cuts, Crops, Cattle pasture, Settlements
LS_06	no	S America	o	o	Clear cuts, Crops
LS_10	yes	Australia	pw	wo	Clear cuts, Crops, Settlements
LS_15	no	Island^b	o ^e	o	Clear cuts, Grassland, Settlements
LS_16	no	SE Asia	wo	wo	Plantation forest (oil palm rubber)
LS_18	no	S America	o	o	Clear cuts, Crops, Plantation forest (Eucalyptus)
LS_25	no	N America	o	o	Savannah, Grassland
LS_30	no	Island^c	o ^{ef}	o	Clear cuts, Orchards
LS_37	no	C America	wo	wo	Grassland
LS_38	no	C America	wo	wo	Crops, Plantation forest, Settlements
LS_39	no	C America	wo	wo	Clear cut, Settlements
LS_40	yes	C America	wo	wo	Clear cut, Crops, Settlements
LS_42	yes	C America	pw	wo	Cattle pasture, Crops, Plantation forest
LS_44	no	Australia	wo	wo	Plantation forest
LS_46	no	C America	wo	wo	Crops, Grassland, Settlements
LS_47	no	S America	wo	wo	Clear cuts, Settlements
LS_57	no	C America	wo	wo	Crops, Pasture, Settlements
LS_59	no	Island^d	wo	wo	Clear cuts, Plantation forest (oil palm)
LS_60	no	S America	w	w	Pasture, Plantation forest (rubber, eucalyptus, cocoa)
LS_62	yes	Africa	wo	wo	Crops, Plantation forest

PA, protected area; o, outside; pw, primarily within; w, within; wo, within and outside. Islands are shown in bold in the column 'Geographic context'. Landscape minimum convex polygons created to encompass the plots sampled in each landscape are available for display as.kml. All landscapes have anthropogenic forest edges present in them. The majority encompass a mosaic of natural forests and other land uses. Only one landscape (LS_30, Madagascar) is forest-dominated with few anthropogenic edges present at the northern edge.

Extended Data Table 3 | Number of threatened and not-threatened species for forest-core and all other species in each taxonomic group

Taxon	<i>P</i>	Forest core species		Not forest core species	
		Not threatened	Threatened	Not threatened	Threatened
Amphibians	1.0	32	3	32	3
Birds	< 0.01	280	13	835	10
Mammals	< 0.05	92	21	120	11
Reptiles	1.0	9	0	37	1

We excluded species that were not assessed or that were listed as data deficient by the IUCN Red Lists (IUCN status data were not accessible for the majority of reptilian species). We used a two-sided two-sample test for equality of proportions with continuity correction and confidence level = 0.95. The *P* value is significant if forest-core species were more threatened than species of other edge-response types.

Extended Data Table 4 | Importance of predictor variables in explaining edge sensitivities of forest-core ectotherms and endotherms

4a Predictors retained, Reptiles	I	Coeff	P	2.5%	97.5%
Body size	-	3.11	< 0.01	2.33	3.89
IUCN Tree	-	2.94	< 0.01	2.02	3.86
IUCN Habitats	-	2.53	< 0.01	1.88	3.17
Body size : IUCN Tree	-	-1.54	< 0.01	-2.04	-1.04
IUCN Habitats : Body size	-	-1.34	< 0.01	-1.69	-1.00

4b Predictors retained, Amphibians	I	Coeff	P	2.5%	97.5%
IUCN Habitats	1.00	0.03	0.73	-0.16	0.23
Body size	1.00	-0.02	0.77	-0.17	0.13
IUCN Forest	0.89	-0.36	0.07	-0.75	0.02
Body size: IUCN Habitats	0.56	-0.03	0.18	-0.07	0.01
Body size: IUCN Forest	0.45	-	L	-	-

4c Predictors retained, Mammals	I	Coeff	P	2.5%	97.5%
Non-volant	1.00	0.20	< 0.001	0.10	0.30
IUCN Habitats	0.24	0.02	0.40	-0.03	0.07
IUCN Forest	0.23	-0.04	0.39	-0.14	0.06
(Body size) ²	0.13	-0.00	0.55	-0.01	0.00
IUCN Habitats : Non-volant	0.12	-0.04	0.16	-0.10	0.01
IUCN Forest : Non-volant	0.11	0.09	0.21	-0.05	0.23
Body size	0.11	-0.01	0.78	-0.04	0.03

4d Predictors retained, Birds	I	Coeff	P	2.5%	97.5%
IUCN Forest	0.51	-0.04	0.27	-0.10	0.03
IUCN Tree	0.29	0.00	0.97	-0.16	0.17
Body size	0.26	0.01	0.36	-0.02	0.04
Migrant = Full Migrant	0.16	0.13	0.10	-0.03	0.29
Migrant = Nomadic	-	0.06	0.70	-0.24	0.35
Migrant = Not migrating	-	0.13	0.08	-0.02	0.28
Range size	0.09	0.00	0.50	-0.00	0.00
IUCN Habitats	0.08	0.00	0.93	-0.02	0.02
Mean clutch	0.08	-0.01	0.55	-0.02	0.01
IUCN Forest : Full Migrant	0.07	0.05	0.45	-0.08	0.19
IUCN Forest : Full Nomadic	-	0.30	0.04	0.02	0.58
IUCN Forest : Body size	0.05	0.04	0.23	-0.02	0.10
IUCN Tree : Full Migrant	0.05	-0.12	0.45	-0.42	0.18
IUCN Tree : Nomadic	-	0.12	0.56	-0.27	0.51
IUCN Tree : Not migrating	-	-0.18	0.21	-0.46	0.10

I, importance; Coeff, coefficient; P, significance of coefficient estimate; 2.5% and 97.5%, lower and upper limits for coefficient estimates; outputs as conditional average. L, only one species identified as IUCN forest dependent. We fitted two-sided general linear models and selected models from a global model for edge sensitivity via information theoretic approaches and multi-model averaging. Predictors in global models are detailed in the Methods. This yielded 1 model for reptiles ($n = 9$ species), 5 models for amphibians ($n = 34$ species), 7 models for mammals ($n = 111$ species) and 20 models for birds ($n = 190$). The deviance explained by the final model was 98% (reptiles), 31% (amphibians), 24% (mammals) and 3% (birds).

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▶ Experimental design

1. Sample size

Describe how sample size was determined.

For our analysis, we extracted datasets from the BIOFRAG database only using datasets that measured abundance of vertebrates in at least nine plots per landscape. We subsequently analysed the abundance responses of all unique species measured in a total of 22 landscapes. Sample size is given as n. Sample sizes are described in the relevant text sections in the manuscript (Lines 223,225,244,248,249, 274), in the legends of Figures (1 to 3) and of Extended Data (Tables 1 and 4 and Figures 1 to 3). We used non-parametric tests for pair-wise comparisons. To test whether body size predicts species responses to edges, we used general additive models implemented in the mgcv package of the R statistical software.

2. Data exclusions

Describe any data exclusions.

In the analyses of threatened versus non-threatened species, we excluded species that have not been assessed for IUCN Red Lists or that were listed as data deficient (Extended Data Table 3, Lines 200-203). In the gam models linking body size of amphibians to their edge sensitivity, we excluded two species of the order Gymnophiona, as their body shape resembles that of worms or snakes (Fig. 3 Legend and Lines 223-224). When modelling edge sensitivity as a function of multiple predictors, we excluded highly inter-correlated predictors ($V > 0.5$, $R^2 > 0.5$, $P > 0.6$) from these models using Pearson's Chi-squared test with Yates' continuity correction and Cramer's V measure of association to test for correlations among categorical predictors (lsr package), Pearson's product-moment correlation P for associations between numeric predictors and the coefficient of determination R^2 of linear models for relationships between numeric and categorical predictors (Extended Data Table 4, see Methods for details - Lines 777-782, 791). When comparing edge sensitivities among edge response types, we excluded species that could not be classified ($n = 113$).

3. Replication

Describe whether the experimental findings were reliably reproduced.

Experimental replication was not attempted.

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

Samples were not randomized for the experiments.

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

We did not use techniques to blind the investigators to the experimental groups.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

- | | |
|-------------------------------------|--|
| n/a | Confirmed |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> The <u>exact sample size</u> (n) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.) |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> A statement indicating how many times each experiment was replicated |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section) |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> A description of any assumptions or corrections, such as an adjustment for multiple comparisons |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> The test results (e.g. P values) given as exact values whenever possible and with confidence intervals noted |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> A clear description of statistics including <u>central tendency</u> (e.g. median, mean) and <u>variation</u> (e.g. standard deviation, interquartile range) |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Clearly defined error bars |

See the web collection on [statistics for biologists](#) for further resources and guidance.

► Software

Policy information about [availability of computer code](#)

7. Software

Describe the software used to analyze the data in this study.

We used R 3.2.1 statistical software for all our analyses: proportion tests, multiple pairwise comparisons between groups, general additive models (mgcv package), multi-model averaging (MuMin package and lsr package). We used in house generated software for analyses central to the manuscript. Details on these analyses are described in the Methods section of the manuscript. The software itself is accessible at <https://github.com/VeroL/BioFrag> (see reference 29 in the manuscript).

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* [guidance for providing algorithms and software for publication](#) provides further information on this topic.

► Materials and reagents

Policy information about [availability of materials](#)

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

NA

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

NA

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

NA

b. Describe the method of cell line authentication used.

NA

c. Report whether the cell lines were tested for mycoplasma contamination.

NA

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by [ICLAC](#), provide a scientific rationale for their use.

NA

► Animals and human research participants

Policy information about [studies involving animals](#); when reporting animal research, follow the [ARRIVE guidelines](#)

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.

NA

Policy information about [studies involving human research participants](#)

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

NA