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META-ANALYSIS

A global analysis of traits predicting species sensitivity to habitat fragmentation

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ABSTRACT

Aim Elucidating patterns in species responses to habitat fragmentation is an important focus of ecology and conservation, but studies are often geographically restricted, taxonomically narrow or use indirect measures of species vulnerability. We investigated predictors of species presence after fragmentation using data from studies around the world that included all four terrestrial vertebrate classes, thus allowing direct inter-taxonomic comparison.

Location World-wide.

Methods We used generalized linear mixed-effect models in an information theoretic framework to assess the factors that explained species presence in remnant habitat patches (3342 patches; 1559 species, mostly birds; and 65,695 records of patch-specific presence–absence). We developed a novel metric of fragmentation sensitivity, defined as the maximum rate of change in probability of presence with changing patch size ('Peak Change'), to distinguish between general rarity on the landscape and sensitivity to fragmentation per se.

Results Size of remnant habitat patches was the most important driver of species presence. Across all classes, habitat specialists, carnivores and larger species had a lower probability of presence, and those effects were substantially modified by interactions. Sensitivity to fragmentation (measured by Peak Change) was influenced primarily by habitat type and specialization, but also by fecundity, life span and body mass. Reptiles were more sensitive than other classes. Grassland species had a lower probability of presence, though sample size was relatively small, but forest and shrubland species were more sensitive.

Main conclusions Habitat relationships were more important than life-history characteristics in predicting the effects of fragmentation. Habitat specialization increased sensitivity to fragmentation and interacted with class and habitat type; forest specialists and habitat-specific reptiles were particularly sensitive to fragmentation. Our results suggest that when conservationists are faced with disturbances that could fragment habitat they should pay particular attention to specialists, particularly reptiles. Further, our results highlight that the probability of presence in fragmented landscapes and true sensitivity to fragmentation are predicted by different factors.

Keywords
Amphibian, biodiversity, bird, conservation planning, island biogeography, mammal, patch size, peak change, vulnerability, reptile.

INTRODUCTION

In species conservation, sensitivity can be broadly defined as the degree to which species respond to changes in external stressors, with more sensitive species exhibiting larger responses than less sensitive species. Variation in species sensitivity to fragmentation translates directly to their probability of decline, endangerment and ultimately extinction. Although the effects of fragmentation on individual species are complex (Purvis *et al.*, 2005), ecological specialization (e.g. habitat use or diet; Sekercioglu, 2011; Bregman *et al.*, 2014; Newmark *et al.*, 2014), reproductive capacity (Polishchuk, 2002), geographical range (Davidson *et al.*, 2009), population density (Newmark, 1991) and body size (Cardillo *et al.*, 2005) have all been shown to predict species sensitivity for a variety of taxa. The use of such characteristics to inform conservation planning has become commonplace (Grammont & Cuaron, 2006), as have broad generalizations regarding specific relationships (e.g. species with low reproductive output are more sensitive to fragmentation).

In large part, generalizations regarding species sensitivity have derived from studies of broad taxonomic groups over broad geographical areas (e.g. continental or global) that use assessments of species endangerment as a response variable (Purvis *et al.*, 2005; Cardillo *et al.*, 2008; Davidson *et al.*, 2009). The most common of these assessments is the conservation status rank developed by the International Union for Conservation of Nature (IUCN) for its Red List of Threatened Species (IUCN, 2016). Although information from such broad studies is often applied to local and regional conservation, many studies exploring species sensitivity have also been done at more local levels (e.g. particular forests or management areas), investigating subsets of local fauna that track the responses of populations to specific stressors (e.g. Woodroffe & Ginsberg, 1998). Despite the need to generalize relationships between species characteristics and sensitivity, the factors that are important over broad areas and pertain to the endangerment of species may well differ from those that are important locally and pertain to the decline or extirpation of populations. This disconnect is evidenced by the fact that local studies often yield different conclusions from broad studies regarding which species characteristics are important (Fig. 1; Cardillo *et al.*, 2008). For instance, ecological specialization is often an important predictor of sensitivity in local studies (Fig. 1c), whereas body size and distributional patterns appear to be more important in broad studies (Fig. 1a & b). Perhaps more discouragingly, regardless of scale, individual studies often disagree regarding the direction of the effect of the same factor on sensitivity.

The disparate conclusions from broad studies of species endangerment and local studies of the decline or extirpation of populations could be methodologically induced or could indicate biologically meaningful differences. In either case, this conflicting information poses a challenge for wildlife managers when making conservation decisions. Because conservation action is often enacted by local and regional resource managers, the results of local studies would seem to be more applicable to conservation planning. Unfortunately, local studies are usually also of limited generality because they have a narrow biogeographical scope and frequently explore highly specific characteristics that are difficult to extrapolate to other areas and other taxa. Further, managers must often prioritize across disparate taxa (e.g. amphibians, birds, mammals and reptiles) which have never been comparably assessed in sensitivity studies.

The goal of our work was to bridge the gap between broad and local studies by analysing species responses to relatively local fragmentation across a broad range of taxa and landscapes, thereby providing a framework for better generalizations about how diverse wildlife will be differentially affected by such disturbance. To this end, we conducted a meta-analysis based on studies compiled from around the world that documented the presence and absence of species in remnant habitat patches following fragmentation, an empirical measure related to local extirpation that is directly linked to sensitivity. We incorporated these studies into a single, unified analysis that was global in scope and included all classes of terrestrial vertebrates. Thus, we conducted a broad analysis based upon local data rather than indirect assessments of extinction risk (Newbold *et al.*, 2013; Benchimol & Peres, 2014; Quesnelle *et al.*, 2014). We tested how a suite of species characteristics identified from previous empirical studies (Fig. 1) would influence sensitivity to local fragmentation. More specifically, we predicted that characteristics defining species ecology, which are important in local studies (e.g. Fig. 1c; habitat specificity, trophic level), would be more important in predicting species responses than the general life-history characteristics often deemed important in broad studies (e.g. Fig. 1a, d; body size, reproductive potential). Our inclusion of multiple taxonomic classes facilitated broad comparison across disparate taxonomic groups, life histories and body sizes. Additionally, the breadth of our analysis allowed us to explicitly consider interactions between local landscapes and species characteristics, which are likely to be important (Purvis *et al.*, 2005) but have rarely been tested in a generalizable way. In conducting these analyses, we also develop and use an approach for measuring sensitivity to fragmentation that distinguishes between two factors that can be conflated in broad studies of species sensitivity: overall probability of presence (i.e. rarity versus commonness) versus relative changes in occurrence due to different levels of disturbance (i.e. sensitivity).

METHODS

Scope and data

We compiled data from studies that documented the presence and absence of terrestrial vertebrate species in patches of native habitat remaining after fragmentation (see Appendix S2 in Supporting Information). We drew roughly half the studies from those compiled by Prugh *et al.* (2008), to which we added studies from a Web of Science™ search for titles containing the keywords 'patch, fragment or remnant' AND
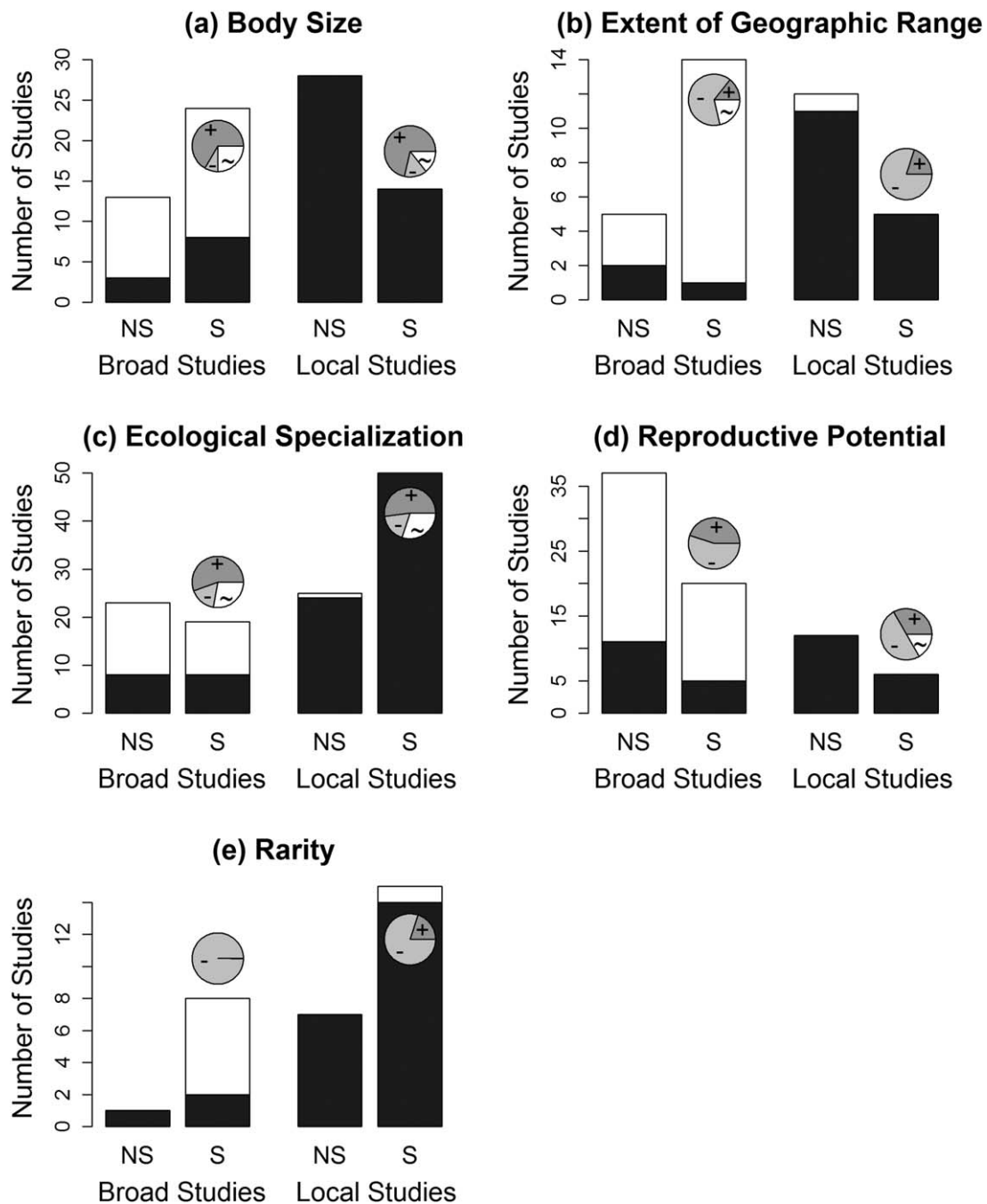
Figure 1 Numbers of studies showing significant (S) versus non-significant (NS) results for tests investigating the ability of species characteristics to predict sensitivity. Studies were compiled from a standardized Web of Science search (Appendix S1). While local studies generally use local measures of decline as their response variable (black shading; e.g. abundance trends), broad studies more often use synthetic risk scores (grey shading; e.g. IUCN Red List categories). Species body size and range size are more often found to be important in broad studies that use risk scores as their response variables (a, b), whereas ecological specialization tends to be more important in local studies (c). Despite being a widely accepted predictor of sensitivity, measures of reproductive potential have mixed support at both levels, with most studies showing non-significant effects (d). In contrast, rarity is broadly supported at all levels of analysis (e). Directions of effect for significant results are displayed in pie charts as the proportion of studies where the characteristic increased sensitivity (+), decreased sensitivity (−) or had a complex effect (∼). Additional details of how studies were classified can be found in Appendix S1.

'species, community, diversity or richness' AND 'bird, avian, mammal, amphibian, reptile, herp* or wildlife'. We filtered search results by focusing on relevant subject categories (e.g. ecology, biodiversity conservation) and eliminating studies that did not incorporate multiple habitat patches, did not document the presence and absence of individual species in all patches or for which raw data were not available in the published article or directly from the authors.

Table 1 Landscape and species characteristics included in analyses of species sensitivity to habitat fragmentation.

Characteristic	Code	Category	Description
Patch area	PLnPSize	Patch metrics	Continuous variable representing the contiguous area of a remnant habitat patch, measured in hectares
Habitat type	LHSt	Landscape metrics	Categorical variable indicating the major habitat type of patches included in a study. Categories are forest, grassland and shrubland
Matrix type	LMatrix	Landscape metrics	Categorical variable representing the major driver of fragmentation for a study. Categories are urban, agriculture (e.g. crops, livestock) and semi-natural (e.g. burn, flood)
Number of patches	LPNum	Landscape metrics	Ordinal variable indicating the number of habitat patches assessed within a study
Landscape size	LLnLandSize	Landscape metrics	Continuous variable indicating the spatial extent of the landscape over which a study was conducted, measured in km^2
Landscape impact	LLnLandImp	Landscape metrics	Continuous variable representing the relative proportion of the landscape disturbed, calculated as the total area of patches divided by the landscape size
Time since fragmentation	LLnFragTime	Landscape metrics	Continuous variable representing the approximate time since habitat fragmentation, measured in years
Latitude	LLatitude	Landscape metrics	Continuous variable indicating the distance from the equator at which the study occurred, measured in degrees
Litter size	RLnLS	Species trait	Continuous variable indicating the typical number of offspring per litter, measured as number of eggs or live-born young (typically clutch size for birds and herpetofauna)
Litters per year	RLnLPY	Species trait	Ordinal variable indicating the typical number of litters per calendar year (typically clutches per year for birds and herpetofauna)
Age at first reproduction	RLnAFR	Species trait	Continuous variable indicating the typical age at which a species first produces offspring, measured in years
Life span	RLnML	Species trait	Continuous variable indicating the typical age of death for a species in the wild, measured in years
Body mass	SLnBM	Species trait	Continuous variable indicating the typical adult body mass of a species, measure in grams
Taxonomic class	TC	Species trait	Categorical variable indicating whether a species is an amphibian, bird, mammal or reptile
Primary habitat	SHSt	Species trait	Categorical variable representing habitat type with which a species is most commonly associated. Categories are forest, shrubland, grassland, general and specific feature (e.g. caves, cliffs, rock-outcrops)
Habitat specificity	SHSp	Species trait	Categorical variable representing the degree of habitat specialization for a species. Categories are high specialization (only one primary habitat occupied), moderate specialization (two primary habitats occupied) or low specialization (more than two primary habitat types occupied)
Diet class	SDC	Species trait	Categorical variable representing the primary diet of a species. Categories are carnivore, herbivore and omnivore
Wetland obligation	SW	Species trait	Binary variable indicating whether a species requires wetland habitats (e.g. rivers, lakes, marshes)
Flight	SF	Species trait	Binary variable indicating whether a species is capable of sustained flight
Migratory status	SM	Species trait	Categorical variable representing whether species exhibits seasonal movements of long distances (> 200 km), short distances (20–200 km), or is essentially resident (< 20 km)
Range size	SLnSArea	Species trait	Continuous variable indicating the geospatial extent of a species global range, measured in km^2. For long-distance migrants, the smaller of breeding versus non-breeding range was used

We developed a set of characteristics describing each study landscape and each focal species (Table 1). Landscape characteristics were obtained from descriptions in the articles containing species presence and absence data (Appendix S2). Although many species characteristics have been evaluated for their influence on sensitivity to fragmentation, we focused on a set that has been widely addressed in the literature, was available for most species and could be effectively generalized across disparate taxa. We obtained avian life-history data from Bird Life International (2013) and Sekercioglu (2012), with additions from the Handbook of the Birds of the World series (Del Hoyo *et al.*, 2011). Mammal data were drawn from the Pantheria database (Jones *et al.*, 2009), with additions from primate data maintained

by the authors (e.g. Deaner *et al.*, 2007). Most amphibian and reptile data, as well as supplementary data for mammals and birds, were drawn from the studies containing species presence and absence data (Appendix S2), IUCN Red List accounts (IUCN, 2014), the AmphibiaWeb database (Lannoo, 2005; AmphibiaWeb, 2013), the Animal Diversity Web database (Myers *et al.*, 2013), the Encyclopedia of Life database (Parr *et al.*, 2014) and primary literature. Additional demographic data for all species were obtained from the Animal Aging and Longevity database (Tacutu *et al.*, 2013). Body size for reptiles and amphibians was generally reported as snout-to-vent length, so we used published relationships to covert these values to body mass (Lagler & Applegate, 1943; Blakey & Kirkwood, 1995; Deichmann *et al.*, 2008; Meiri, 2010; Feldman & Meiri, 2013). A complete set of variables influencing fecundity (i.e. age at first reproduction, litters/clutches per year, litter/clutch size and maximum life span) was not available for all species. We used linear regressions to estimate missing values based on body size within taxonomic order and family, which yielded generally good predictions ($r^2 = 0.71 \pm 0.18$ SD; Appendix S3). We log-transformed all continuous variables to correct for skewness and conducted tests of variable collinearity that showed no two variables had a Pearson's correlation coefficient greater than 0.49.

Analysis and sensitivity index

We evaluated the influence of landscape and species characteristics on species occurrence in remnant patches using generalized linear mixed-effect models (Gurevitch *et al.*, 2001). All analyses were conducted in R version 3.1.1 (R Development Core Team, http://www.r-project.org) using the glmer function in the lme4 package to fit models (Bates *et al.*, 2015) and the glmulti package (Calcagno, 2014) to conduct model selection in an information theoretic framework (Burnham & Anderson, 2002). When comparing models, we only varied fixed effects (Bolker *et al.*, 2009; Muller *et al.*, 2013). We guarded against over-fitting by limiting model complexity to 12 terms at each step and comparing competing models using the Bayes information criterion (BIC; Burnham & Anderson, 2004; Muller *et al.*, 2013; Aho *et al.*, 2014). Models were deemed well supported if they had BIC weights within 10% of the top model, and variables were included in subsequent analysis if they had a cumulative BIC weight greater than 0.5 over the resulting confidence set (Burnham & Anderson, 2004; Johnson & Omland, 2004).

There were many variables with literature support to consider in our models, and no justifiable rationale for specifying particular combinations of interactions in the candidate set of models. Further, given the large number of variables, it was not possible to exhaustively compare combinations and their interactions. We therefore used a multistep process to construct a best-supported model, an approach that has been used successfully in other studies with many possible explanatory factors (Yamashita *et al.*, 2007; Caldwell *et al.*, 2013). All candidate models at each step contained a base model that included taxonomic class and patch size as fixed effects, because these variables were of primary interest in our analysis, and study as a random factor, to control for interstudy variation. First, we identified important landscape characteristics by comparing models that differed only in their combinations of landscape fixed effects and their interactions, including species as a random effect in all candidate models. Second, having used the first part of our analysis to identify key landscape variables, we then removed species as a random effect and identified important species characteristics by comparing models that differed only in combinations of species main effects and their interactions. Third, with important landscape variables and species characteristics thus identified, we compared models differing only in two-way interactions between those variables and variables in the base model (i.e. interactions with patch size and taxonomic class). Fourth, we compared models that differed only in combinations of two-way interactions between the landscape variables and species characteristics. To create a best-supported model, we combined the base model with terms identified as most important at each of these steps (Appendix S4). To synthesize and present the results of the optimal model, we evaluated the importance of individual parameters by running the model on a centred and scaled dataset (Kutner *et al.*, 2005; Grueber *et al.*, 2011).

Coefficients from the best-supported scaled model indicated the magnitude of the effect of each term on the overall probability of presence of species in patches of disturbed landscapes, and thus the relative strength of different main effects and interactions. The use of probability of presence alone to assess sensitivity potentially confounds aspects of species biology and the landscape context of studies with sensitivity to changes in the level of habitat fragmentation. For example, intrinsically sparse species or species that are locally rare because they are part of studies conducted in landscapes with less habitat across patches may be less likely to be present, even in relatively large patches within a given study. In such cases, a low probability of presence may not truly indicate sensitivity to habitat fragmentation, particularly across studies. To address this problem, we derived a novel metric that separates rarity from sensitivity per se. In considering how best to measure sensitivity, we were particularly interested in interactions with patch size, because such interactions indicate a differential sensitivity to degrees of habitat loss that are largely independent of biases introduced by factors like the inherent rarity of species on the landscape. Therefore, for variables that had a significant interaction with patch size, we calculated the peak proportional change in the probability of presence with changing patch size (i.e. the maximum slope in plots of probability of presence against area divided by the area-specific prediction; see Fig. 4 for an illustration). To simplify discussion, we refer to this metric of peak proportional change in the probability of presence as 'Peak Change'.

Peak Change is an informative index of sensitivity to fragmentation for broad analyses, because it is largely
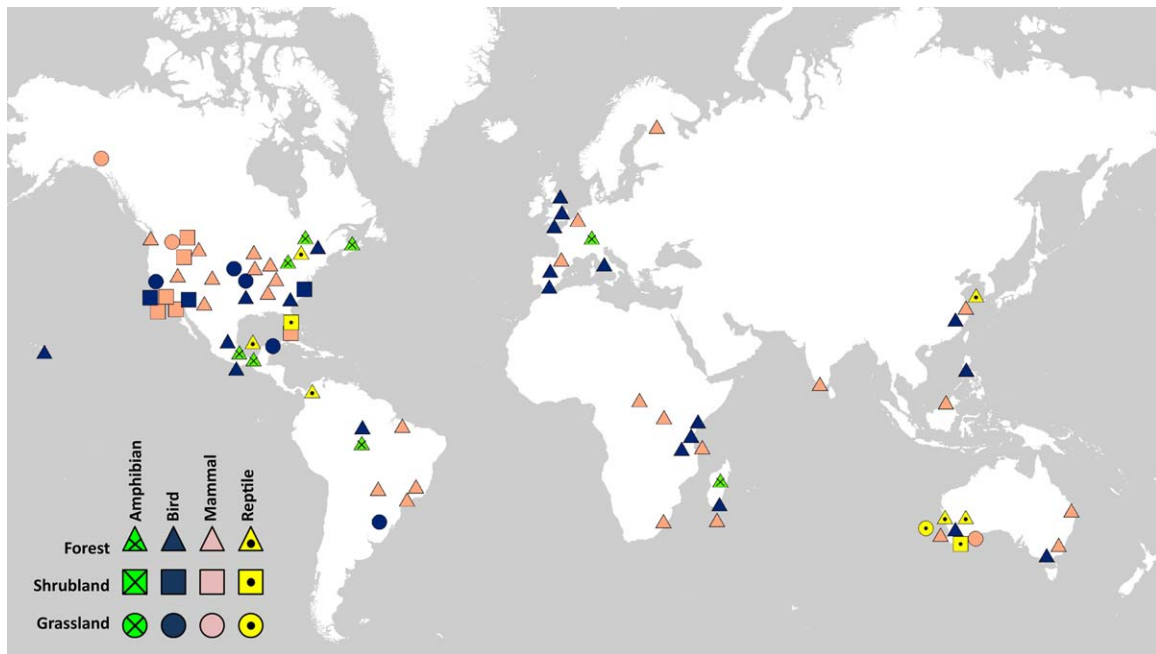
Figure 2 Map of the studies used in this meta-analysis, displayed with their habitat type and taxonomic focus. As discussed in the text, we were unable to find appropriate studies that represented all taxonomic groups in all regions, with gaps in Africa and most of Asia being especially notable.

independent of the actual amount of habitat remaining in patches. It is, therefore, less likely to be biased by variation in the size range of patches across disparate species in disparate landscapes, which can make other indices, such as patch size thresholds, problematic. The coefficients of our optimal model indicated effects that influenced the probability of presence in disturbed landscapes, while Peak Change indicated drivers of species sensitivity to fragmentation that are less confounded with the drivers of simple probability of presence. While other indices of sensitivity to fragmentation are possible if sufficient data are available (Newmark, 1995; Woodroffe & Ginsberg, 1998), Peak Change is informative, less prone to bias and better able to distinguish rarity and sensitivity in broad, synthetic analysis than other alternatives we explored.

A concern in comparative studies is that treating species as independent data points may increase the risk of bias and Type I errors, because species characteristics may not be independent of phylogeny (Felsenstein, 1985; Harvey & Pagel, 1991; McKinney, 1997). Although studies on species and disturbance focused on collections of species with well-resolved phylogenies have modelled phylogenetic signals in the data (Woodroffe & Ginsberg, 1998; Purvis *et al.*, 2000), in our case, accounting for phylogeny is especially problematic because there is no current, well-resolved phylogeny that is consistent across all four taxonomic classes in our analysis. Although we could do separate analyses within each class incorporating phylogenetic information, doing so would defeat the purpose of our goal of comparing sensitivities across groups as assessed by Peak Change. Further, recent

studies similar to ours have found that the results of trait-based analysis can be largely unchanged by phylogenic consideration (Newbold *et al.*, 2013). Nevertheless, in addition to explicitly modelling the major classes in our analysis, we evaluated the potential importance of taxonomy on our results by replicating our final model with taxonomic family nested within class as an additional random variable and then comparing the results with those without this additional taxonomic information.

RESULTS

The final dataset included 77 studies from around the world (Fig. 2, Appendix S2) that documented the occurrence of 1559 species across 3342 habitat patches, resulting in 65,695 records of patch-specific presence and absence. Avian species ($n = 924$) represented the majority of the compiled data, followed by mammals ($n = 330$), reptiles ($n = 166$) and amphibians ($n = 139$). Studies in forest ecosystems ($n = 57$) were more common than those in shrublands ($n = 11$) or grasslands ($n = 9$).

Our model selection procedure (Appendix S4) yielded a final model containing four landscape characteristics, seven species characteristics and 13 interaction terms (Fig. 3). There were no differences in interpretation caused by including additional taxonomic data (Appendix S5). The fact that family did not influence our model suggests that our results were not unduly biased by lack of quantitative phylogenetic information, so we based the remainder of our results and discussion on the analysis without this variable. The final model demonstrated a
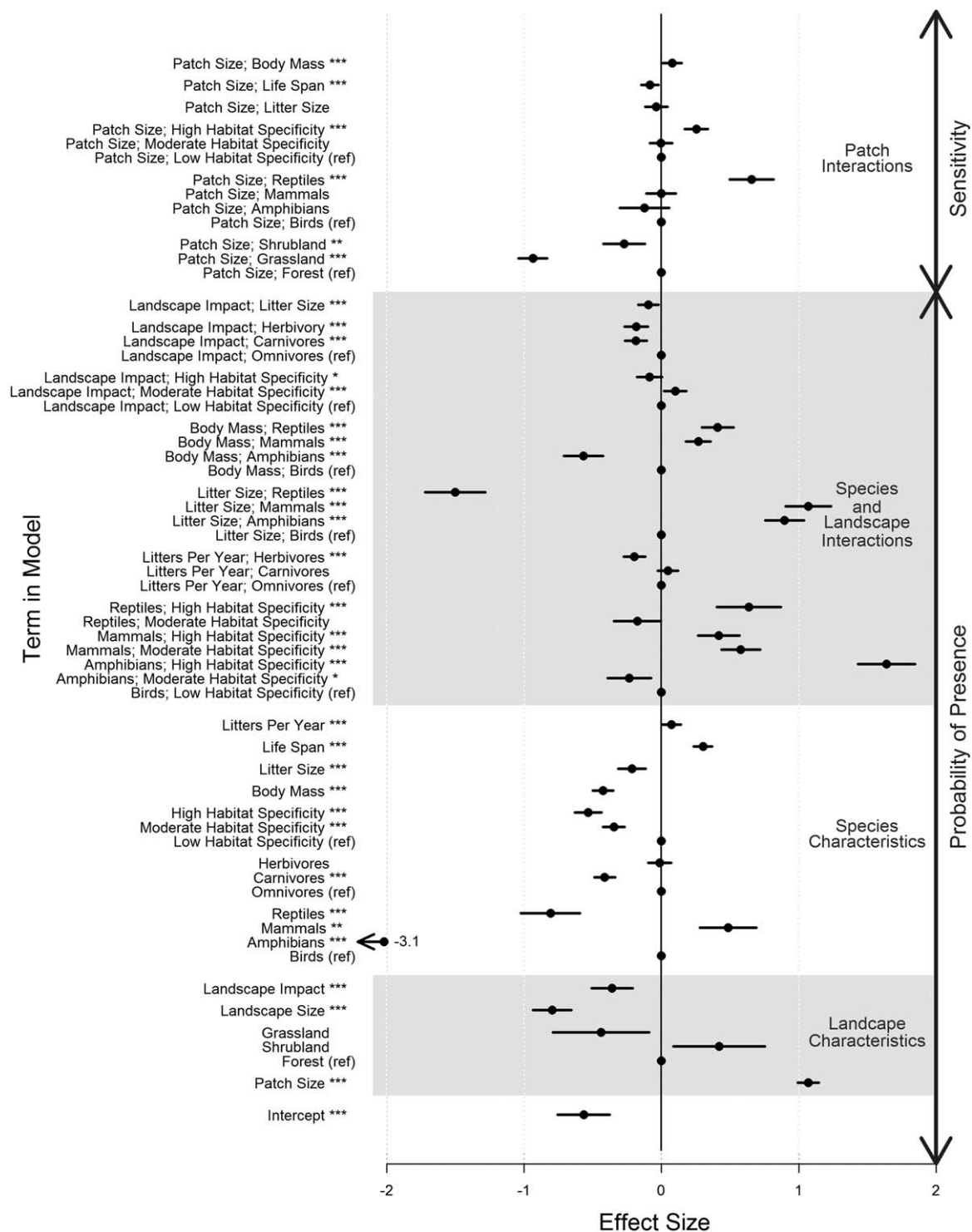
Figure 3 Effect sizes, standard errors, and significance for terms in the final model predicting patch occupancy as a function of scaled landscape and species characteristics. Significance is noted on the vertical axis (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$). Reference values for factors are specified by '(ref)' and are displayed with an effect size of zero. All variables influence the probability of presence, while interactions with patch size are drivers of sensitivity to changes in patch area (see Fig. 4 for illustration).

fair fit to the data, with an area under the curve (AUC) from the receiver operating characteristic of 0.77 and a true positive classification rate (TPR) of 0.68 based on a threshold that maximized training sensitivity plus specificity. Cross-

validation suggested that this fit was robust, because models built by removing one study were able to predict the presence of species in patches of the withheld study with similar accuracy (AUC = 0.66 ± 0.12, TPR = 0.65 ± 0.12; mean ± SD).
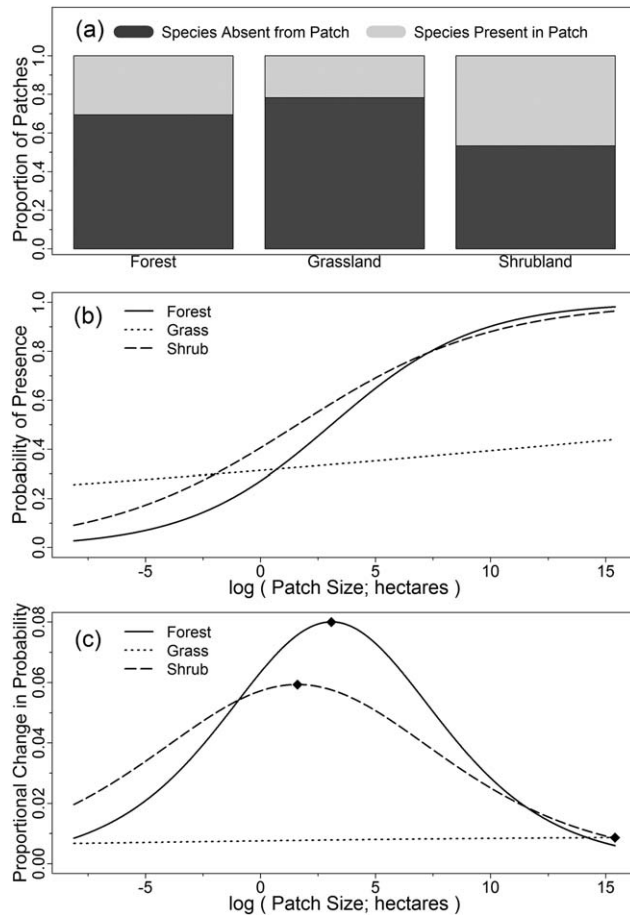
Figure 4 Relationship between probability of presence and sensitivity to remnant patch size across habitat types. (a) Species in grasslands exhibited a lower probability of presence, or a lower proportion of patches with species present. (b) The probability of presence of species in forests (solid line) and shrublands (dashed line) changed markedly with patch size, but far less so in grasslands (dotted line). (c) The proportional change in probability of presence (i.e. the slope of the lines in b divided by the predicted value) typically showed a peak value (diamonds) that we used as a measure of sensitivity to changing habitat area (Peak Change). Grassland species thus exhibited lower sensitivity than either forest or shrubland species, as shown by a smaller maximum proportional change in probability of presence. The lines from (b) displayed against a representation of the raw data can be found in Appendix S2 (Fig. S2-2).

Unsurprisingly, patch size had the largest main effect in predicting the probability of presence in patches following fragmentation, with species more likely to be present in larger patches (Fig. 3; Arrhenius, 1921; Connor & McCoy, 1979). The main effects having the second and third largest absolute values were both landscape characteristics: habitat type (grassland species were less likely to be present) and landscape size (species assessed over larger landscapes were less likely to be present). Main effects of some species characteristics also had a large influence. In particular, amphibian and reptile species were less likely to be present than birds or mammals, and habitat specialists were less likely to be present than generalists. Species with longer life spans and more litters per year were more likely to be present. Carnivores, larger species and species with larger litter sizes were less likely to be present, the latter effect being driven largely by reptiles, as shown by the interaction between taxonomic class and litter size, where amphibians and mammals with larger litters had markedly higher probabilities of presence than

either birds or reptiles. Other interaction terms had marginal effects, but several were comparable in size to the main effects they modified. Notably, the interaction between taxonomic class and species habitat specificity substantially influenced probability of presence, with amphibian specialists more likely to persist in remnant habitat patches than other classes and non-specialists (Fig. 3).

Several variables affected differential sensitivity to habitat patch size, as assessed by Peak Change (e.g. Fig. 4). These variables included habitat type, taxonomic class, habitat specialization, litter size, life span and body mass, all of which (except for litter size) had significant interactions with patch size in the optimal model (Fig. 3). Species in forest and shrubland were more sensitive to changes in patch area than those in grasslands (Fig. 4). Species with high habitat specificity were more sensitive than either generalists or moderately specialized species, and reptilian habitat specialists were the most sensitive collection of species in the study (Fig. 5d). Although amphibian habitat specialists were more sensitive
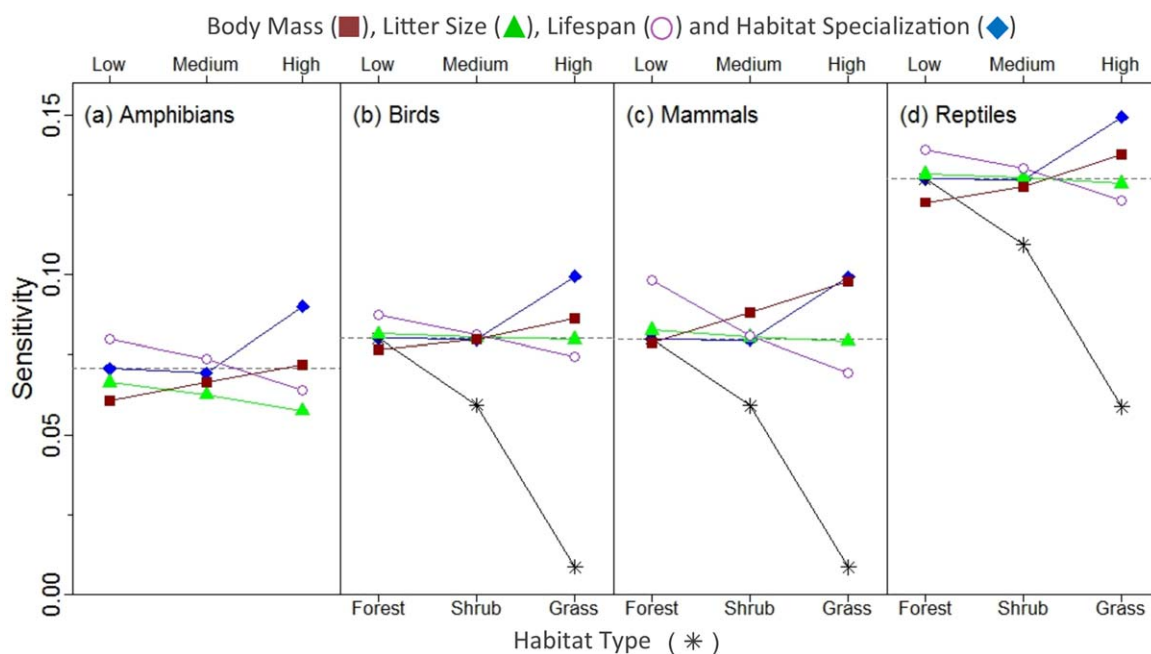
Figure 5 Relative impact of species and landscape characteristics on sensitivity (i.e. maximum proportional change in probability of presence, or Peak Change; Fig. 4c) graphed separately for each taxonomic class. Habitat type categories are indicated on the lower axis, except for amphibians for which there were no grassland or shrubland studies. Values for the continuous species characteristics are plotted on the upper axis, where low, medium and high signify 10th, 50th and 90th quantiles. Dashed lines are reference values generated for a habitat-generalist omnivore in forested habitat using median values of all continuous variables. Habitat type had a substantial impact on sensitivity for all classes where such data were available. Habitat specialization increased sensitivity, which led to particularly high values for reptiles. Large body mass increased sensitivity for mammals in particular.

to changes in patch size than non-specialists, they were still less sensitive than generalists from other classes (Fig. 5). Compared with habitat type and habitat specialization, the effects of life-history characteristics (i.e. life span, litter size and body mass) were relatively small, although large body size increased sensitivity in mammals as much as habitat specialization (Fig. 5c).

DISCUSSION

As the well-known species–area relationship would predict, remnant patch size was a key driver of the probability of species presence in disturbed landscapes, which was evidenced by the large effect size in our best-supported model (Fig. 3). This finding reinforces the notion that the amount of habitat loss is of paramount importance in predicting species responses (Watling & Donnelly, 2006; Prugh *et al.*, 2008). Species characteristics also had notable effects on the probability of presence and on sensitivity to remnant patch size (as demonstrated by Peak Change), with characteristics defining ecological relationships (e.g. habitat type in combination with specialization) being consistently important drivers. Habitat specialization, often in combination with other life-history parameters, was largely related to species being both rare in the landscape and sensitive to fragmentation (Fig. 6). Habitat specialists were generally less prevalent across landscapes, and thus more likely to be absent in remnant patches,

and they were also more sensitive than generalists to changes in the amount of available habitat (i.e. the proportional change in their probability of occurrence with increasing patch size was greater; Fig. 5). This pattern lends support to the idea that habitat specialists may be particularly impacted by land-altering disturbance and should in turn receive heightened conservation attention to mitigate loss of habitat (Matthews *et al.*, 2014; Newbold *et al.*, 2014).

The sensitivity of habitat specialists, however, must be considered with respect to taxonomic class, as indicated by a significant interaction between these two factors (Fig. 3). Birds generally had a lower probability of presence than mammals, but a higher probability of presence than reptiles or amphibians. Habitat specialization decreased the probability of presence of birds more than other classes, although this pattern did not translate into higher sensitivity (Fig. 5). Reptiles, however, exhibited the lowest probability of presence across habitat remnants and showed the highest sensitivity to patch size among the classes, with habitat specificity further increasing sensitivity (Figs 5d & 6). Our results thus indicate that reptiles are more sensitive to fragmentation than the other classes, while amphibians may be less sensitive than the other classes. This finding accords with recent analyses indicating that negative responses of reptiles to habitat loss have increased more than those of other taxa in the face of climate change (Mantyka-Pringle *et al.*, 2012), and that reptiles respond more to changes in patch characteristics than do
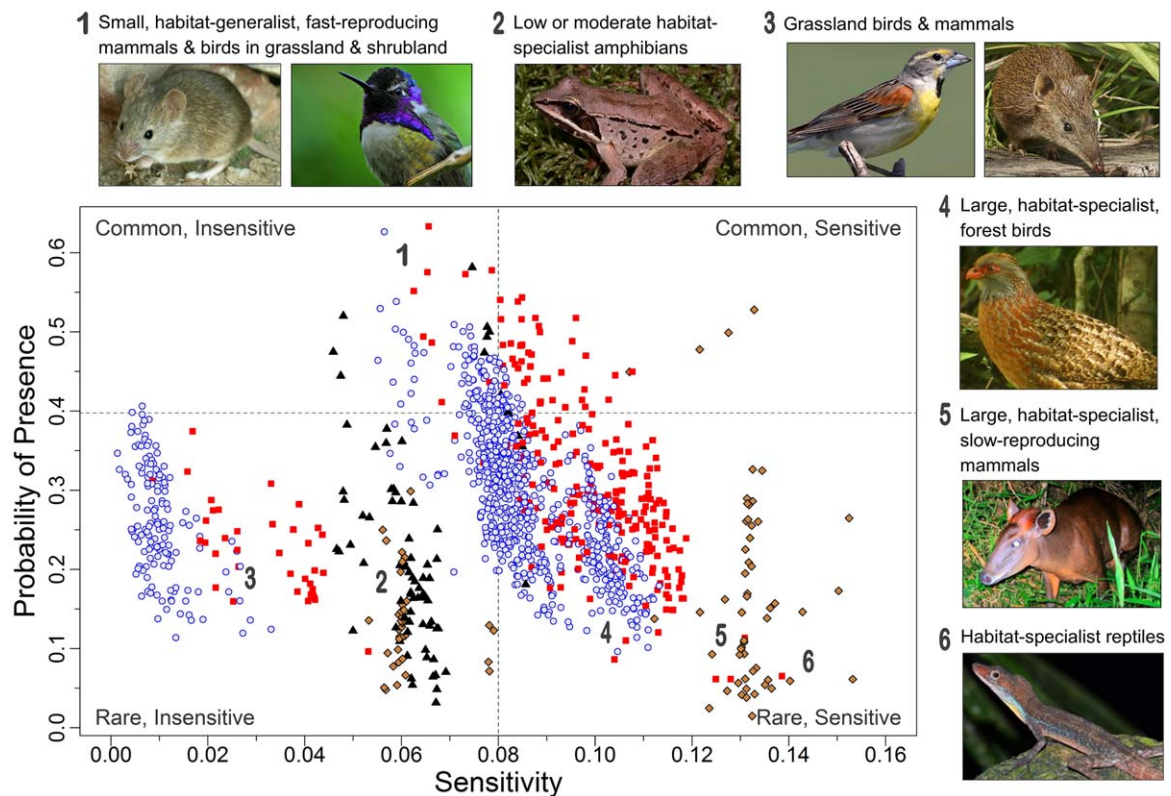
Figure 6 Probability of presence versus sensitivity for amphibians (triangles), birds (circles), mammals (squares) and reptiles (diamonds) analysed in this study. Dashed lines are reference values for a habitat-generalist, omnivorous, forest bird using median values of all continuous variables. Marginal descriptions highlight species characteristics that predispose animals to be in regions of the graph indicated by corresponding numbers on the plot. Photographs are of representative species included in this study; clockwise from upper left: house mouse (*Mus musculus*), Costa's hummingbird (*Calypte costae*), wood frog (*Lithobates sylvaticus*), southern brown bandicoot (*Isoodon obesulus*), bearded tree-quail (*Dendrortyx barbatus*), Abbott's duiker (*Cephalophus spadix*) and Barker's anole (*Anolis barkeri*). See Acknowledgements for photo credits.

amphibians (Larson, 2014). The congruence of results across these disparate studies strongly suggests that reptiles are indeed more sensitive to changes in patch characteristics than other taxa, which may help explain their pronounced global declines (Gibbons *et al.*, 2000). The mechanistic underpinning of reptilian sensitivity may stem from thermoregulatory constraints combined with morphological specialization and dispersal limitations (Böhm *et al.*, 2013).

Amphibians had low and variable probability of presence across patches (Fig. 6), but contrary to expectations the probability of presence was not markedly reduced by habitat specialization and amphibians showed lower sensitivity to patch size than did the other classes (Figs 5a & 6). In other words, despite amphibians being more likely to be absent across all patch sizes, amphibian habitat specialists seemed more capable of persisting in small patches relative to generalist species. Although not intuitive, this finding agrees with evidence suggesting that amphibians are relatively more likely to be impacted by habitat loss at larger patch sizes (Mantyka-Pringle *et al.*, 2012), and that they can be less sensitive to changes in patch characteristics than reptiles (Larson, 2014). We hypothesize that the generally lower probability of

presence of amphibians may result from amphibians being particularly affected by expansive stressors (e.g. climate change, disease; Collins & Storfer, 2003), so local effects of habitat change tend to occur against a backdrop of widespread population declines (Houlahan *et al.*, 2000). It is also possible that the apparently low sensitivity of amphibians in this analysis is because their presence depends more on whether existing patch mosaics maintain connectivity between their aquatic and terrestrial life-forms than it does on coarse metrics such as patch size (Becker *et al.*, 2007). These differences among classes highlight the importance of using a multitaxon approach to analysis of species sensitivity.

Forest species were the most sensitive to habitat fragmentation (Fig. 4). This sensitivity was moderately greater than that of shrubland species. By comparison, grassland species had a consistently lower probability of presence across a range of patch sizes, but were less sensitive to changes in patch size (Figs 5 & 6). In other words, species in forests and shrublands had a relatively low probability of presence at small patch sizes that markedly increased with increasing patch size, while species in grasslands had a low probability of presence that did not change strongly with patch size. In terms of species response to habitat

fragmentation, shrublands could be considered more similar to forests than grasslands. The consistently low probability of presence of grassland species across a range of patch sizes accurately reflects widely observed declines of grassland species resulting from habitat loss and degradation (Hill *et al.*, 2014). Further, we suspect that the low sensitivity of grassland species demonstrated here may underlie the results of studies investigating fragmentation in grasslands, wherein even grassland specialists often show mixed responses to habitat fragmentation and degradation (Benson *et al.*, 2013).

Birds and mammals are well-studied compared with herpetofauna, and research in forested ecosystems is more prevalent than other biomes. This state of the science is reflected in the distribution of studies in our meta-analysis (Appendix S2), so our results are most robust with respect to these taxa and ecosystems. In fact, the final dataset did not include any studies of amphibians in either grasslands or shrublands. Similarly, data are sparse for Africa and parts of Asia, particularly, once again, for herpetofauna. Direct inference to areas with such data gaps should be made with caution. Ideally, analyses of species sensitivity would take into account patterns of species presence prior to disturbance for each patch within each study before the landscape in question was fragmented. Unfortunately, this information is almost never available. As a result, it is possible that especially sensitive species could be missing from some of the assemblages reported in this meta-analysis. Even if our data do not perfectly represent pre-disturbance conditions in all constituent studies, this does not hinder the interpretation of our results regarding the sensitivities of locally extant fauna.

Conservation of biodiversity in the face of habitat disturbance generally occurs at relatively local levels, so generalizable patterns in the response of species to local fragmentation are likely to be more applicable for conservation planning than those derived from studies using coarse response metrics. Here, we have presented a global analysis of local data that demonstrates the complex interaction of species and landscape characteristics that influence the responses of wildlife to habitat fragmentation. Our results further stress that conservationists should pay particular attention to habitat specialists, notably habitat-specific reptiles and forest specialists, when considering suites of species potentially most affected by habitat loss and fragmentation (Fig. 6). Moreover, after decades of searching for cross-taxon generalities, our work reveals important differences among taxa in how they respond to habitat loss, depending upon habitat specialization and life history. Our work also emphasizes the need to distinguish between the factors that determine whether species are sparse and those determining their sensitivity to habitat fragmentation.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1 Studies used to create Figure 1.
Appendix S2 Studies included in the meta-analysis and summary of dataset.
Appendix S3 Results of regressions used to estimate missing species data.
Appendix S4 Model selection.
Appendix S5 Results of analysis exploring potential impact of phylogeny.

BIOSKETCH

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