

# Amphibian sensitivity to habitat modification is associated with population trends and species traits

A. Justin Nowakowski<sup>1</sup>  | Michelle E. Thompson<sup>2</sup> | Maureen A. Donnelly<sup>2</sup> |  
Brian D. Todd<sup>1</sup>

<sup>1</sup>Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA, USA

<sup>2</sup>Department of Biological Sciences, Florida International University, Miami, FL, USA

## Correspondence

A. Justin Nowakowski, Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA.

Email: Nowakowskia@gmail.com

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## Abstract

**Aim:** Habitat modification is causing widespread declines in biodiversity and the homogenization of biotas. Amphibians are especially threatened by habitat modification, yet we know little about why some species persist or thrive in the face of this threat whereas others decline. Our aim was to identify intrinsic factors that explain variation among amphibians in their sensitivity to habitat modification (SHM), factors that could help target groups of species for conservation.

**Location:** Global.

**Time period:** 1986–2015

**Major taxon studied:** Amphibians.

**Methods:** We quantified SHM using species abundances in natural and altered habitats as reported in published field surveys. We first examined associations between local SHM and range-wide threatened status, population trends and invasiveness. We then evaluated the importance of intrinsic and extrinsic variables in explaining species SHM using multiple comparative methods. Our analyses included over 200 species that could be ranked with confidence from 47 studies across five continents.

**Results:** Amphibians species varied considerably in local SHM. High SHM was associated with elevated range-wide extinction risk and declining population trends. Species that were tolerant of habitat modification were most likely to be invasive outside their native range. Geographical range size was the most important intrinsic predictor and was negatively associated with SHM. Larval habitat was also an important predictor, but was tightly coupled with phylogenetic position.

**Main conclusions:** Narrowly distributed species whose larvae develop on land or in lotic habitats are most sensitive to habitat modification. However, other unmeasured, phylogenetically constrained traits could underlie the effect of larval habitat. Species range size is frequently correlated with global extinction risk in vertebrates, and our analysis extends this macroecological pattern to the sensitivity of amphibians to local habitat loss, a proximate driver of extinction. These general patterns of SHM should help identify those groups of amphibians most at risk in an era of rapid habitat loss and scarce conservation resources.

## KEYWORDS

biodiversity, conservation, habitat loss, land use, life history, matrix tolerance, specialization, species traits, susceptibility, threatened

## 1 | INTRODUCTION

There is increasing evidence that human activities are ushering in a period of mass extinction (Ceballos et al., 2015). Among vertebrates, amphibians are most threatened with extinction [c. 30% of species], and recent estimates suggest as many as 200 amphibian species [3% of all amphibians] have already gone extinct (Alroy, 2015; Vié, Hilton-Taylor, & Stuart, 2009). For many amphibians, there is little information on population status with which to assess extinction risk or direct limited conservation resources—in part owing to rapid discovery of species and geographical research biases (Catenazzi, 2015; Gardner, Barlow, & Peres, 2007). Therefore, identifying which amphibian traits are associated with susceptibility to specific threats could help prioritize resources for species assessments and conservation action (Cooper, Bielby, Thomas, & Purvis, 2008; Murray, Rosauer, McCallum, & Skerratt, 2010).

Ecological and life-history traits have been correlated with extinction risk in multiple vertebrate groups, such as birds (Lee & Jetz, 2011), mammals (Davidson, Hamilton, Boyer, Brown, & Ceballos, 2009), reptiles (Böhm et al., 2016) and amphibians (Cooper et al., 2008). For many groups, including amphibians, species with smaller geographical ranges are more likely to be declining or at greater risk of extinction than species with larger ranges, even after excluding range-based assessments of extinction risk (Cooper et al., 2008; Davidson et al., 2009; Murray, Rosauer, McCallum, & Skerratt, 2010). Other variables, such as fecundity and microhabitat associations, have also been correlated with the decline of amphibians in regional-scale analyses (Lips, Reeve, & Witters, 2003; Murray et al., 2010). Extinction risk and population trends, however, often reflect a species' vulnerability to multiple underlying threats that each vary in severity or spatial extent (Murray, Verde Arregoitia, Davidson, Di Marco, & Di Fonzo, 2014). The susceptibility of species to different threats may therefore be determined by environmental context and unique suites of traits (Ruland & Jeschke, 2016). For example, large-bodied amphibians tend to be most vulnerable to overharvesting for consumption (Chan, Shoemaker, & Karraker, 2014), whereas, aquatic amphibians at high elevations appear particularly susceptible to declines associated with the fungal pathogen *Batrachochytrium dendrobatidis* (Bielby, Cooper, Cunningham, Garner, & Purvis, 2008). A recent review showed that failure to include specific threats in extinction risk analyses can lower the predictive accuracy of models and hinder effective prioritization of species for conservation (Murray et al., 2014). Future work should therefore integrate multiple threats into extinction risk analyses or, alternatively, examine variation in species sensitivity to the specific threats that underlie extinction risk.

The primary threat to amphibian diversity, affecting 60% of all amphibians, is loss of natural habitat (Vié et al., 2009). Human population growth drives habitat loss, largely via wholesale clearing of forests for establishment of agriculture, pastures, timber production and urbanization (FAO, 2011; Laurance, Sayer, & Cassman, 2014). Forest loss is a global phenomenon; however, rates of forest loss vary geographically, with species-rich tropical regions experiencing particularly high rates of loss (FAO, 2011; Hansen et al., 2013; Laurance et al.,

2014). In many regions, widespread forest conversion leads to biotic homogenization such that narrowly distributed habitat specialists are extirpated and widely distributed habitat generalists come to dominate local assemblages (Baiser, Olden, Record, Lockwood, & McKinney, 2012; Solar et al., 2015). When remaining tolerant species share similar traits, habitat modification can also result in functional homogenization of biotas and consequent decline in ecosystem function (Clavel, Julliard, & Devictor, 2011).

It remains unclear which traits generally predispose amphibian species to be sensitive to habitat modification. Several recent field studies, however, have reported decreases in functional diversity with decreasing habitat area as well as traits correlated with the dependence of species on forest habitat (Almeida-Gomes & Rocha, 2015; Trimble & van Aarde, 2014). For example, diversity of reproductive modes decreased in forest fragments and pastures compared with intact forest in Brazil (Almeida-Gomes & Rocha, 2015), and functional groups of amphibians characterized by ground-dwelling microhabitat use and terrestrial egg-laying were most sensitive to land use in South Africa (Trimble & van Aarde, 2014). A meta-analysis also reported that sensitivity of wetland vertebrates [including amphibians] to habitat loss was associated with low reproductive rates (Quesnelle, Lindsay, & Fahrig, 2014). However, we currently lack a comprehensive global assessment that identifies species traits associated with the responses of amphibians to habitat modification.

One obstacle to identifying species traits associated with sensitivity to habitat modification [SHM] is that characterization of SHM is often subjective. Many studies rely on expert opinion or interpretation of natural history accounts to classify species as habitat specialists or generalists. A commonly used index of habitat specialization is the number of habitats used by a species, often taken from IUCN species assessments. In contrast, quantitative approaches to estimating habitat specialization require information on the relative abundances or occupancy of species across multiple habitats obtained from standardized sampling. The sampling-intensive nature of quantifying SHM typically limits these studies to local or regional scales (Julliard, Clavel, Devictor, Jiguet, & Couvet, 2006). Estimation of SHM for species sampled across continents and across the amphibian tree of life may provide new insights into which groups have particularly high SHM and which traits generally predispose those species to being sensitive to ongoing habitat modification.

Here we use data from published reports of species abundances in natural habitats and adjacent altered habitats to quantify SHM for species exposed to habitat modification across a range of climates and land-use types. Habitat modification is a primary process underlying extinction risk, but variation among species in their intrinsic SHM is understudied. We first examined the links between our response variable, SHM quantified from local data, and the most commonly analysed response variable in the extinction risk literature, IUCN Red List categories. Red List status represents an index of *global* extinction risk for a species [under criteria A–D; Collen et al. (2016)]; however, Red List assessments do not typically account for intrinsic SHM as estimated here, which provides an independent measure of species responses to

**TABLE 1** Intrinsic and extrinsic predictor variables in analyses of variation in amphibian sensitivity to habitat modification. For each variable, the expected mechanisms are listed

Predictor variable	Expected mechanism/prediction
<b>Intrinsic variables:</b>	
Body size	Body size scales with energetic needs and space-use requirements and is negatively correlated with population densities in some groups; large-bodied species may be more sensitive to habitat modification (Schmid, Tokeshi, & Schmid-Araya, 2000; Tamburello, Cote, & Dulvy, 2015)
Clutch size	Species with high fecundity/reproductive rates may be able to compensate for decreased survival in altered habitats, increasing population persistence (Quesnelle et al., 2014)
Larval habitat	Larval habitat type may contribute to the sensitivity of species to habitat modification when larvae/eggs require forest resources (e.g., phytotelmata or leaf litter; Trimble & van Aarde, 2014)
Microhabitat (stratum)	Species that use shrubs and trees as perches may be less common than ground-dwelling species in altered habitats where these substrates are scarce (Trimble & van Aarde, 2014)
Range size	Species with small range sizes tend to have narrow niches (e.g., thermal niche) and in turn may be more sensitive to local habitat modification than species with large ranges/broad niches. This differs from the role of range size in Red List assessments as an index of the spatial spread of risk from threats (IUCN, 2014; Slatyer et al., 2013)
<b>Extrinsic variables:</b>	
Human footprint	Areas heavily transformed by human activity may support a disproportionate number of disturbance-tolerant species if sensitive species have been locally extirpated (Swihart et al., 2003)
Land use	Land uses that exhibit high abiotic/biotic contrast with natural habitats are expected to have stronger negative effects on many species (Newbold et al., 2015; Thompson et al., 2016)
Mean annual temperature	Warmer climates may increase the magnitude of negative responses of species to habitat loss or fragmentation (Mantyka-Pringle et al., 2012)
Total precipitation	Drier climates may increase the magnitude of negative responses of species to habitat loss or fragmentation (Mantyka-Pringle et al., 2012)

local habitat modification. We then identified species traits and environmental variables correlated with SHM; the expected relationships between SHM and each species trait or environmental variable are provided in Table 1. The identification of intrinsic factors associated with SHM may help prioritize future conservation research and management in the absence of rigorous population data for many species.

## 2 | METHODS

### 2.1 | Characterizing the sensitivity of amphibians to habitat modification

We compiled data on the abundance of amphibians in natural habitat and nearby areas of land use from published field surveys in commonly studied land uses. We expanded on a previous global dataset that contained amphibian abundances records from 30 studies (Thompson, Nowakowski, & Donnelly, 2016); we included records from 22 of these studies [comprising 34% of the records in our final database] after excluding studies that focused on selective logging or regenerating forest [see Appendix S1 in the Supporting Information]. We added studies by searching the literature using ISI Web of Knowledge and Google Scholar entering various combinations of the following search terms: amphibian\*, in combination with land use, logging, silviculture, agriculture, crops, grazing, pasture, plantation, habitat disturbance, habitat alteration, habitat destruction, habitat modification, habitat loss, habitat fragmentation, or matrix. We also included studies found in reference sections of reviews and syntheses (Gardner et al., 2007; Newbold et al., 2015) as well as "latest papers" on amphibian conservation listed at Amphibiaweb.org. We included studies that reported species abundances in published data tables, figures or online appendices. We excluded studies that did not use standardized field sampling methods,

such as area- or time-constrained searches, or that did not report sampling effort and replication.

We used a multinomial logistic model to initially classify species as natural habitat specialists, generalists, altered habitat specialists or as too rare to classify based on their relative abundances in natural and altered habitats [see Chazdon et al. (2011) for a full description of the method]. The model is robust to unequal sampling effort among habitats, but most of the datasets analysed were generated using balanced sampling designs. Some studies, however, had unequal replication of sites [five studies] or unequal sampling effort among sites [six studies], and we corrected for this by using a random number generator to select an equal number of natural and altered-habitat sites [when site-specific abundances were reported] or by standardizing abundances by sampling effort [when only total abundances for a given habitat were reported]. We used a super-majority rule to classify species with at least two-thirds of individuals recorded in one habitat type as specialists for that habitat type [ $k = 0.667$ ] and others as generalist species or as too rare to classify. We used a significance threshold of  $p = .005$  to determine which species within an assemblage could be classified as specialists with confidence; Chazdon et al. (2011) suggest using this stringent significance threshold when classifying multiple species within an assemblage. We analysed datasets from each study separately, thereby classifying each species in the context of the local assemblage to which it belongs.

The primary purpose of the classification step was to distinguish species that were abundant enough in samples to classify with confidence from those that were too rare to classify. For all further analyses we calculated a response ratio [a common effect-size metric] for each species that could be classified with confidence, which provided a continuous measure of SHM. We calculated response ratios for each species as  $\ln[(N_n + 1)/(N_a + 1)]$ , where  $N_n$  is abundance in natural habitat

and  $N_a$  is abundance in altered habitat. The response ratio summarizes the raw data used in classifying species. For species that were reported and classified from multiple studies [47 species], we randomly selected abundance records from a single study for further analyses. Although response ratios for these species were typically similar across different studies, we evaluated the sensitivity of our results to random selection of abundance records for species with multiple estimates of SHM.

## 2.2 | Intrinsic and extrinsic predictors of sensitivity to habitat modification

For each species, we compiled information on threatened status, population trend and whether the species is known to be invasive outside its native range from the IUCN Red List database (IUCN, 2015). Population trends included four categories: “declining,” “stable,” “increasing” and “unknown.” We classified species as either “threatened” or “not threatened,” combining the Red List designations of Critically Endangered, Endangered and Vulnerable into the “threatened” category, and Near Threatened and Least Concern into the “not threatened” category. We categorized species as “invasive” if they were established or considered invasive outside of their native range, and if not, the species was categorized as “non-invasive.” The Red List categories and our response variable, SHM, are derived from independent sources of information [Appendix S2]. Red List categories should be interpreted as general indices of range-wide population trends and extinction risk, which may include information on whether a species is exposed to habitat loss [Appendix S2] (Collen et al., 2016; IUCN, 2015), whereas SHM should be interpreted as a species’ intrinsic response to local habitat modification.

We compiled intrinsic variables for each species, including larval habitat, adult microhabitat, clutch size, maximum snout-to-vent length [SVL] and geographical range size, from species accounts from the IUCN Red List, AmphibiaWeb and the Encyclopedia of Life. If specific information could not be obtained from these online databases, we filled in missing cases using information from the primary literature. We categorized larval habitats as “lentic,” “lentic and lotic” [aquatic generalists], “lotic” and “terrestrial” [including species with direct development]. Adult microhabitats were categorized as “ground dwelling” if individuals primarily use ground stratum habitats and as “arboreal” if primary microhabitats include trees and shrubs. Because some of the species analysed in this study are rare, understudied and/or recently described, basic life-history data may have been scant or missing. For this reason, we binned clutch size into four categories reflecting order of magnitude: 1–9, 10–99, 100–999, or  $\geq 1000$  eggs. For some species, clutch size was unknown; we imputed these missing values using the *rflmpute* function in the “randomForest” package (Liaw & Wiener, 2002) in R 3.1.2 (R Development Core Team 2014), which assigned clutch classes using a proximity matrix of the observations based on taxonomy and intrinsic predictor variables listed above. We used the maximum reported SVL in analyses because this definition allows for inclusion of body length information reported in a variety of ways across species [e.g., ranges, means, maxima and SVLs for type specimens]. We calculated extent of occurrence [EOO] as a measure of

range size from IUCN EOO polygons, which encompass known locations and may also include areas of non-habitat (Joppa et al., 2016).

For each study location, we examined extrinsic variables including regional climate, the influence of human populations in the region [Human Footprint Index] and the type of land use compared with natural habitat. We did not include latitude in our models because it is typically a surrogate for more mechanistic variables [e.g., climate] and is often highly correlated with climate variables of interest, as in our data [Appendix S3]. To characterize the local climate of each study area, we extracted mean monthly temperatures and precipitation from 30-arc-sec resolution [c. 1 km<sup>2</sup>] Bioclim grids within a 5-km buffer around the centre of each study area (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). We included mean annual temperature and total annual precipitation in our models because the effects of habitat loss may be more severe in areas with drier or warmer climates (Mantyka-Pringle, Martin, & Rhodes, 2012). Because regions highly altered by human populations may support assemblages composed largely of species that tolerate disturbance (Swihart, Gehring, Kolozsvary, & Nupp, 2003), we accounted for regional context in our analyses by calculating the mean Human Footprint Index within a 10-km radius around each study area; this buffer size is approximately three to five times the distance at which many amphibian populations/assemblages are structured (e.g., Smith & Green, 2005; Nowakowski, DeWoody, Fagan, Willoughby, & Donnelly, 2015). The Human Footprint Index is derived from multiple global datasets, including human population density, land use, infrastructure and human accessibility; the index is normalized by biome (Sanderson et al., 2002). Finally, we included the type of land use paired with natural habitat in each study; these were categorized as agriculture, pastures, tree plantations and clear cuts.

## 2.3 | Statistical analyses

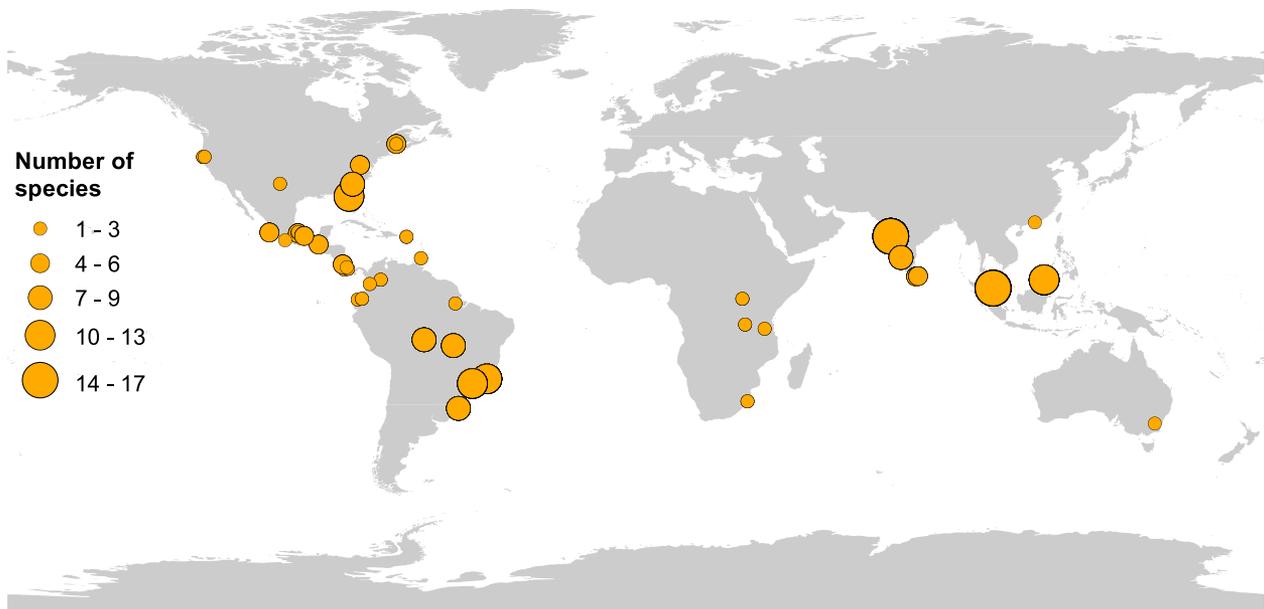
To analyse variation in SHM with respect to species status [population trends, threatened status and invasive status] we used linear mixed effects models [LMMs] fitted separately with each individual species’ status variable as a fixed effect. We fitted models with random effects of family, accounting for broad phylogenetic associations, and source study, accounting for potential non-independence of records from the same study, using the “lme4” package (Bates, Maechler, Bolker, & Walker, 2014) in R. Multiple comparisons among factor levels were conducted using Tukey contrasts. To determine the relative importance of intrinsic and extrinsic variables in explaining SHM, we employed three modelling approaches commonly used in quantitative syntheses and in the comparative extinction risk literature (Murray et al., 2014), LMMs, phylogenetic generalized least squares [PGLS] models and decision tree methods. The use of multiple analytical methods allowed us to assess the robustness of our results to the modelling approach. Prior to analyses, we centred and scaled all continuous predictor variables and assessed correlations among them, finding a lack of strong multicollinearity among variables [Appendix S3] (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We then fitted and compared LMMs and PGLS models. For LMMs, we fitted a global additive model with family and source study as random effects and all predictor variables as fixed

effects. We then fitted all possible subsets of predictors. We calculated relative single variable importance as cumulative Akaike weights for models containing each variable. We assessed the significance of individual variables based on their model-averaged coefficients. We examined possible interactions among pairs of variables by comparing additive and interactive linear models using the Akaike information criterion [AIC]. We also examined potential spatial autocorrelation by examining correlograms of Moran's  $I$  calculated from the residuals of the global model. To evaluate the robustness of our model results we conducted a series of cross-validation and sensitivity analyses. First, we refitted all models after dropping each of 10 random partitions of the dataset; we then assessed geographical influence by dropping data from each region and refitting the models (e.g., Newbold et al., 2015). Next, we refitted our models after iteratively shuffling and randomly selecting abundance records for species reported from multiple studies. Finally, we constructed funnel plots to evaluate the presence of publication bias.

To account for phylogenetic associations of species (Purvis, 2008), we fitted PGLS models using the "nlme" package (Pinheiro, Bates, DebRoy, & Sarkar, 2016). We obtained branch lengths from a time-calibrated phylogenetic tree containing 2871 extant amphibian taxa (Pyron & Wiens, 2011). We added species from our database that were not in the phylogeny [17% of species in our dataset] by randomly attaching branches along subtrees that included all members of the genus of given species. Most variation in branch lengths should be attributable to variation among higher-order clades [e.g., genera and families]. However, we assessed sensitivity to branch placement within genera for missing taxa by generating 10 trees as described above and repeating our analyses. We compared the fit of alternative phylogenetic correlation structures using the AIC [Table S1] and fitted final

PGLS models with a correlation structure derived from the Ornstein-Uhlenbeck model of trait evolution using the *corMartins* function in the "ape" package (Paradis, Claude, & Strimmer, 2004). We assessed phylogenetic signal associated with intrinsic variables by estimating Pagel's  $\lambda$  and conducting likelihood ratio tests using the *phylosig* function of the "phytools" package (Revell, 2012) for continuous variables and the *fitDiscrete* function of the "geiger" package (Harmon, Weir, Brock, Glor, & Challenger, 2008) for discrete variables.

There is some debate over the appropriateness of phylogenetic methods in comparative extinction risk analyses because these models often include non-heritable predictors, such as climatic variables (Bielby, Cardillo, Cooper, & Purvis, 2009; Grandcolas, Nattier, Legendre, & Pellens, 2011; Murray et al., 2014). We further validated our LMM and PGLS analyses by using decision tree methods implemented in the "randomForests" package (Liaw & Wiener, 2002). Random forest [RF] is a nonparametric method that makes no assumption about error distributions and is robust to correlated predictor variables (Liaw & Wiener, 2002; Prasad, Iverson, & Liaw, 2006). The method generates many decision trees by taking bootstrap samples of the dataset. The RF model then aggregates estimates across the many trees that comprise the "forest" to improve prediction of a given response. In addition to the predictor variables examined in the LMM and PGLS analyses, we also included family as a factor representing broad phylogenetic associations among species. We assessed variable importance for each predictor in the RF analysis as the percentage increase in mean squared error when a given variable was randomly permuted (Liaw & Wiener, 2002). Finally, we conducted an additional exploratory analysis to determine which amphibian families are overrepresented by species with high or low SHM by plotting mean effect sizes [SHM response ratio] by family.



**FIGURE 1** Map of studies reporting abundances of amphibian species in both natural and altered habitats. The size of the circles indicates the number of species from each study included in analyses of sensitivity to habitat modification; these species could be ranked with confidence according to their sensitivity to habitat modification (a total of 204 species from 47 studies)

### 3 | RESULTS

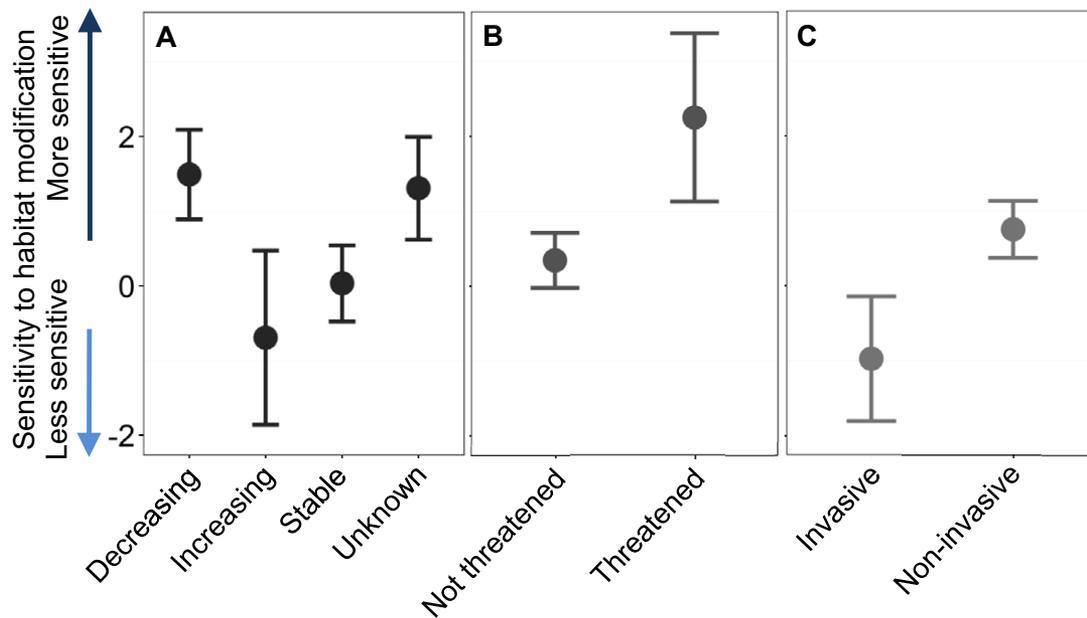
Our literature search produced 861 species abundance records in natural and modified habitats from 47 studies across five continents [Figure 1, Appendix S1]. Of these, 34% of species by study records could be classified with confidence using the multinomial model. After randomly eliminating duplicate species records from multiple studies, our dataset contained 204 unique species records for further analysis. Our LMM analyses showed that population trend was a significant predictor of species SHM [ $p = .007$ ; Figure 2a]; species with decreasing population trends were more sensitive to habitat modification than species with stable population trends [ $p = .012$ ; Figure 2a]. Other pairwise comparisons were non-significant [at  $\alpha = 0.05$  and  $p > .1$ ] as determined by multiple contrasts. Threatened species were more sensitive to habitat modification on average than species that are not threatened [ $p = 0.0203$ ; Figure 2b], and species that were invasive outside of their native range were less sensitive to habitat modification than non-invasive species [ $p = .00196$ ; Figure 2c].

Analyses of intrinsic and extrinsic variables using all additive subsets of the full LMM indicated that range size was the most important predictor of SHM and larval habitat was the second most important predictor; these were the only predictors with significant model-averaged coefficients [Figure 3a]. The best supported model included range size and larval habitat; however, a model with comparable support [ $\Delta AIC < 2$ ] included range size, larval habitat and microhabitat [Table S2]. Range size was negatively correlated with SHM [ $p = .0097$ ; Figure 4a]. Multiple comparisons for a single model fit with larval habitat showed that species with lentic larval habitats were less sensitive to habitat modification than species with lotic [ $p = .0114$ ] or terrestrial [ $p = .003$ ] development [Fig-

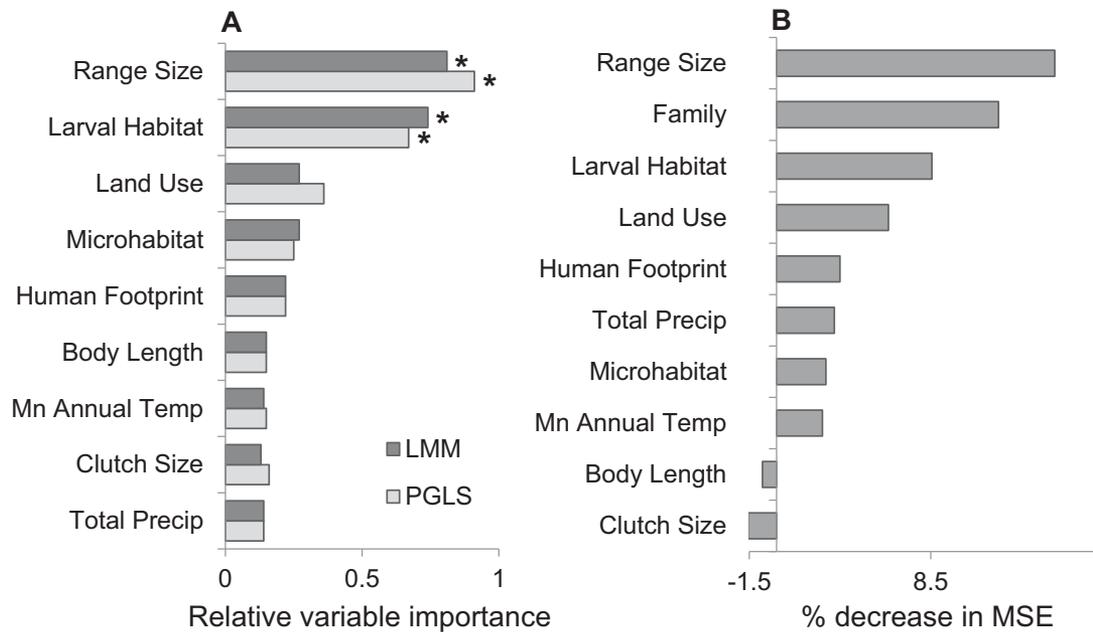
ure 4b]. Inclusion of interaction terms between combinations of top-ranked variables [range size and larval habitat], as well as human footprint and land-use type, did not improve model fit. There was no significant spatial autocorrelation in the residuals of the global model [Appendix S4]. Sensitivity analyses and cross-validation showed that results were robust to random selection of species records and to omitting random and geographical partitions of the dataset [Appendix S5]. We found no evidence of publication bias [Appendix S6].

Variable importance and mean model-averaged coefficients from PGLS models also indicated that range size and larval habitat were the most important predictors of SHM and had the only statistically significant model-averaged coefficients [ $p < .05$ ; Figure 3a]. The best-supported model in the PGLS analysis included range size and larval habitat; however, a model with comparable support [ $\Delta AIC < 2$ ] included range size, larval habitat and land-use type. Sensitivity analysis showed that mean variable importance was robust to the random placement of branches within genera for missing taxa [Appendix S5]. There was significant phylogenetic signal associated with all intrinsic variables [Table S3], including a moderate to strong phylogenetic signal of range size [ $\lambda = 0.76$ ;  $p < .001$ ] and a strong phylogenetic signal associated with larval habitat [ $\lambda = 0.96$ ;  $p < .001$ ; Table S3].

In our RF model, range size was again the most important variable. Other top-ranked variables, in order of importance, were family, larval habitat and land-use type [Figure 3b]. The remaining predictor variables were of relatively marginal or low importance in the model. The importance of specific variables from the RF model was generally consistent with LMM and PGLS analyses, highlighting the associations of SHM with range size and larval habitat as well as some phylogenetic patterns of SHM [the latter indicated by the importance of family in the RF



**FIGURE 2** Mean sensitivity to habitat modification for amphibian species grouped by their IUCN population trend (a), threatened status (b), with Critically Endangered, Endangered and Vulnerable species grouped as “Threatened,” and invasive status (c). Sensitivity to habitat modification was measured for each species as the natural log of the ratio of their abundance in natural habitat to their abundance in altered habitat (i.e., effect size), using data from published field surveys. Error bars represent 95% confidence intervals

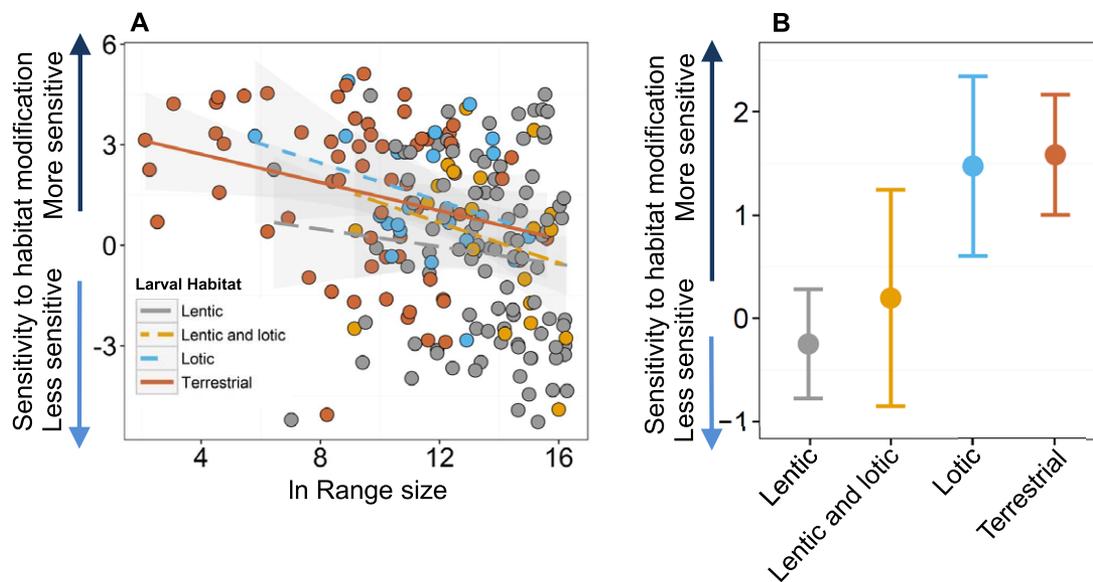


**FIGURE 3** Relative importance of intrinsic and extrinsic variables in explaining the sensitivity of amphibians to habitat modification: results from (a) linear mixed effects models (LMM), phylogenetic generalized least squares (PGLS) models and (b) random forest (RF) analysis. For LMM and PGLS analyses, relative variable importance is the cumulative Akaike weights for models containing each variable from all additive subsets of the full model. Asterisks indicate significant model-averaged coefficients ( $p < .05$ ). For RF analysis, variable importance is the percentage increase in mean squared error (MSE) when a given variable was randomly permuted

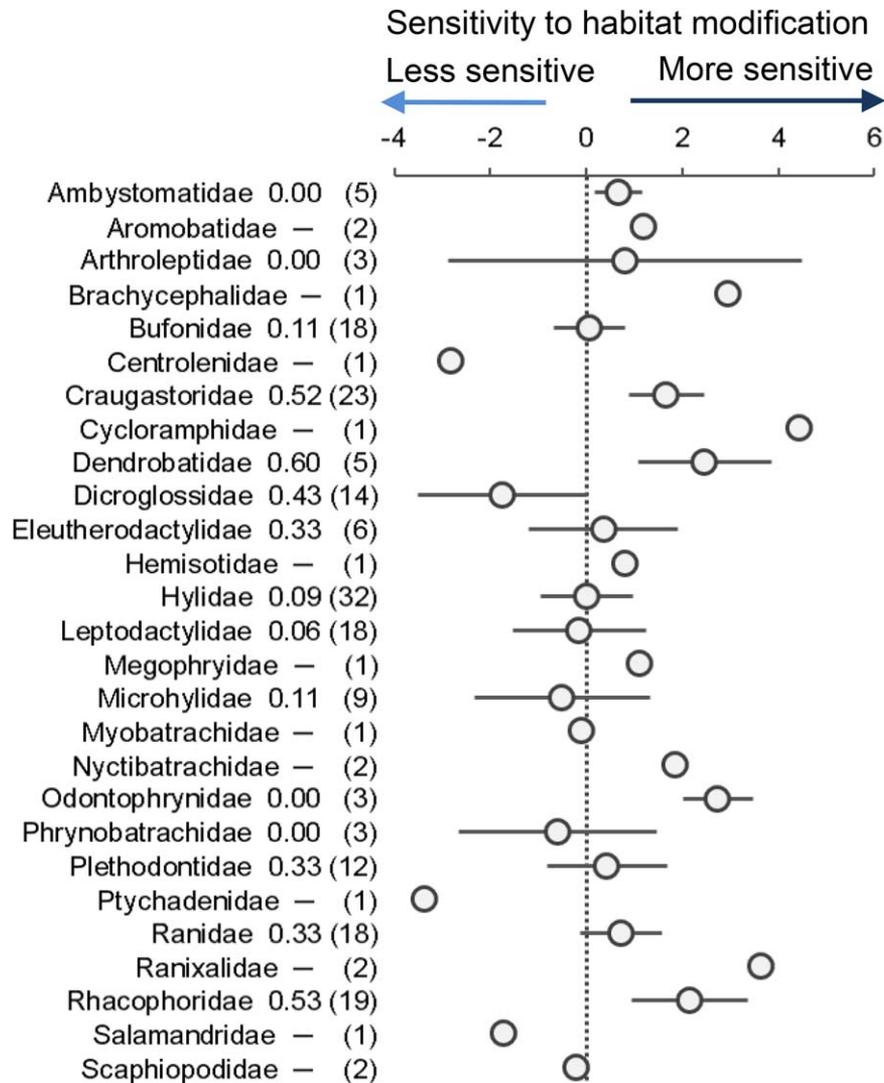
model]. By plotting mean effect sizes [SHM response ratios] by families, we found that several families have mean SHM values significantly greater than zero, indicating that constituent species are often associated with natural habitat; these families included Ambystomatidae, Craugastoridae, Dendrobatidae, Odontophrynidae and Rhacophoridae [Figure 5].

#### 4 | DISCUSSION

Habitat modification is the leading driver of global biodiversity declines, but species vary considerably in their susceptibility to this threat. Identifying groups of species that are most sensitive to habitat modification [natural habitat specialists] is a critical first step in conservation triage,



**FIGURE 4** (a) Relationship between sensitivity to habitat modification and geographical range size of amphibian species grouped by their larval habitat. (b) Mean sensitivity to habitat modification for species grouped by their larval habitat. Error bars represent 95% confidence intervals. Sensitivity to habitat modification was measured for each species as the natural log of the ratio of their abundance in natural habitat to their abundance in altered habitat (i.e., effect size), using data from published field surveys



**FIGURE 5** Mean sensitivity to habitat modification for each amphibian family. Sensitivity to habitat modification was measured for amphibian species as the natural log of the ratio of their abundance in natural habitat to their abundance in altered habitat (i.e., effect size) using data from published field surveys. The proportion of species in the dataset with declining population trends directly follows the family name. The number of species in the dataset from each family is in parentheses. Error bars represent 95% confidence intervals

allowing prioritization of understudied species for proactive conservation research and action. Despite many studies of the effects of habitat loss on amphibian assemblages, little is currently known about the taxonomic groups or traits associated with susceptibility to habitat modification. Here, we report, to our knowledge, the first global-scale analysis of variation in SHM among amphibian species using data on relative abundances in natural and modified habitats. By characterizing general associations between species SHM and other intrinsic factors, we hope to provide a point of departure for future research on the mechanisms underlying species SHM that could help predict and protect those species most vulnerable to habitat modification.

#### 4.1 | Sensitivity to local habitat modification and amphibian population status

We found that amphibian species that are declining or threatened range-wide were more sensitive to local habitat modification than spe-

cies with stable populations. It is also noteworthy that species for which population trends were unknown also tended to be sensitive to habitat modification. By comparing a quantitative measure of SHM with Red List categories, our results further support the general efficacy of Red List assessments while providing information beyond that available from assessments. Owing to the scarcity of quantitative population data for many species, most threatened amphibians have been assessed under Red List criteria that largely account for range size [as a measure of the spatial spread of risk] and whether a population is fragmented and/or experiencing habitat loss [criteria B or D] (Stuart et al., 2008). Subsequent analyses of the Red List have revealed geographical and taxonomic patterns of range-wide extinction risk and exposure to habitat loss (Stuart et al., 2004; Vié et al., 2009). However, we found that while all species in our dataset were *exposed* to habitat modification not all species were *sensitive* to habitat modification. For multiple species experiencing the same level of habitat modification, some species possess characteristics—other than their spatial spread of risk or

exposure to threats—that predispose them to decline or local extirpation, such as life-history traits or specialized niche requirements.

Habitat fragmentation and modification have been widely identified as major drivers of population declines and extirpations (Newbold et al., 2015; Vié et al., 2009; Watling & Donnelly, 2006); however, most research treats species as uniformly sensitive to these processes [e.g., metapopulation and island biogeography research; Ewers & Didham, 2006]. Studies of habitat loss and fragmentation frequently focus on species richness, abundance, or occupancy responses and commonly report a mixture of positive, negative or negligible effects on assemblages and species (Ewers & Didham, 2006; Kurz, Nowakowski, Tingley, Donnelly, & Wilcove, 2014; Thompson et al., 2016). Many of these conflicting results, including variable population trends (Murphy, 2003), may be attributable to marked differences among species in SHM and associated traits (Newbold et al., 2013; Ockinger et al., 2010; Thompson et al., 2016). For example, the strength of fragmentation effects [i.e., area, isolation and edge effects] may depend on the degree to which species in patches can tolerate and use matrix habitat (Ewers & Didham, 2006). Therefore, species-centred approaches that account for variable SHM and traits may help resolve apparent idiosyncrasies in the responses of species to habitat modification (Betts et al., 2014). Our results link the SHM of amphibian species to their population status, highlighting important variation among amphibians in their susceptibility to habitat modification and the consequences for their populations.

As habitat loss continues unabated in many regions, natural habitat specialists are likely to decline and habitat generalists and invasive species are likely to dominate newly impoverished assemblages, a process known as biotic homogenization (Olden, 2006; Solar et al., 2015). Our results support the biotic homogenization hypothesis in amphibians by showing that species that are now established outside their native range are significantly more tolerant of habitat modification than non-invasive species. In other words, invaders tend to be more abundant in human land uses [i.e., matrix habitat] than in natural habitats. Research focused on intrinsic factors associated with invasive amphibians has found that small body size (Allen et al., 2013; but see Tingley et al., 2010), large brain size (Amiel, Tingley, & Shine, 2011) and large range size (Allen et al., 2013; Tingley et al., 2010) predict invasiveness.

#### 4.2 | Intrinsic and extrinsic variables associated with sensitivity to habitat modification

Geographical range size is the most important intrinsic predictor of extinction risk in many vertebrate groups, even after controlling for range-based extinction risk assessments (e.g., Cooper et al., 2008); species with restricted ranges are generally at greater risk of extinction than species with large ranges. Our results extend this general macroecological pattern to the vulnerability of species to local habitat modification, which is the primary threat underlying extinction risk for amphibians and many other taxa (Vié et al., 2009). Range size is also an important sub-criterion [measured as EOO] in many Red List assessments [under criterion B] (IUCN, 2014). The use of range size [or EOO] in global extinction-risk assessments is intended as an index of population redundancy or “insurance” against localized threats (Collen et al.,

2016; IUCN, 2014); it does not reflect the likelihood that a localized response is greater or lesser for any given species. In this sense, we would not expect range size as a measure of the spatial spread of risk to be associated with *local* responses to habitat modification. However, we found that even at local scales [i.e., a given study site], species with small geographical ranges are intrinsically more sensitive to habitat modification than wide-ranging species, possibly owing to niche specialization.

Range size is generally correlated with niche breadth [i.e., dietary specialization and environmental tolerances] (Slatyer, Hirst, & Sexton, 2013), but also reflects the evolutionary and biogeographical histories of species [e.g., lineage age, dispersal and glaciation] (Hodge & Bellwood, 2015; Whitton, Purvis, Orme, & Olalla-Tárraga, 2012). Range sizes are expected to increase with latitude following Rapaport's rule, possibly owing to physiological adaptations to variable-temperate climates (Whitton et al., 2012). In support of a potential link between range size and thermal physiology, studies have shown that the thermal niche breadth of amphibians decreases toward the tropics (Sunday et al., 2014) and acclimation potential increases with range size (Bozinovic, Calosi, & Spicer, 2011). In the present study, range size was positively correlated with latitude and negatively correlated with SHM; however, there was no direct association between latitude and SHM [Appendix S3]. It is plausible, therefore, that at any given latitude species with relatively large ranges and broad niches may tolerate habitat alteration better than species that have small ranges and narrow niches. Multiple niche axes probably enable species to expand and occupy a broad geographical range (Slatyer et al., 2013). Future work should therefore focus on identifying which niche axes are most important for explaining variation in species SHM [e.g., thermal tolerance and dietary breadth].

Relative to other vertebrate groups, many amphibian species have small geographical ranges (Grenyer et al., 2006), which may contribute to the high proportion of species that are threatened with extinction. Nearly a quarter of all amphibians also do not receive habitat protection, and approximately half of all species with small ranges [ $<1,000 \text{ km}^2$ ] do not occur in any protected area, creating a substantial conservation gap for these ancient vertebrates (Nori et al., 2015; Rodrigues et al., 2004). Many range-restricted amphibians do, however, occur in parts of the world with accelerated rates of habitat loss (FAO, 2011; Grenyer et al., 2006). Our results demonstrate that these range-restricted species are more sensitive to local habitat modification than are wide-ranging species.

Certain clades may be particularly sensitive to habitat modification. Family was ranked as an important variable in our RF model, and further exploratory analysis showed that several amphibian families were overrepresented by species with relatively high SHM. In three of these families—Craugastoridae, Dendrobatidae and Rhacophoridae—over half of the species in our database had declining population trends. Craugastorids and rhacophorids are mainly composed of species with terrestrial larval development [or direct development]. Dendrobatids have highly derived reproductive modes that often include terrestrial oviposition, aquatic larval development in phytotelmata and obligate parental

care (Myers & Daly, 1983). Although species with high SHM are distributed across the amphibian tree of life, extinctions resulting from habitat modification are likely to disproportionately affect some clades (Stuart et al., 2004), possibly owing to shared traits that increase their vulnerability.

Larval habitat may directly affect species SHM or could be correlated with other phylogenetically constrained traits for which data were unavailable for many species [e.g., thermal tolerances or diet]. Species with larvae that develop in terrestrial or lotic systems were more sensitive to habitat modification, on average, than species with larvae that develop in lentic systems. One possible explanation for a direct effect of larval habitat on SHM is that terrestrial breeders often depend on forest resources for reproduction, such as moist leaf litter for oviposition (Wells, 2007); in some systems, stream-breeding amphibians also depend on forested stream reaches for population persistence (Becker, Fonseca, Haddad, Batista, & Prado, 2007), suggesting they may rely on relatively unaltered, low-order streams. In contrast, populations of pond breeders appear to be more likely to persist in altered habitats such as pastures and clear cuts (Harper, Patrick, & Gibbs, 2015; Neckel-Oliveira & Gascon, 2006). Interestingly, egg laying with larval development in lentic habitats is an ancestral reproductive mode that persisted through the last mass extinction at the end-Cretaceous, and lineages with terrestrial development [e.g., Craugastoridae] have evolved multiple times from this ancestral mode (Gomez-Mestre, Pyron, & Wiens, 2012; Wells, 2007; Wiens, 2007). When considered alongside the findings of the present study, it is plausible that species with larvae that develop in lentic water bodies are more likely to endure the current extinction crisis than species with derived reproductive modes.

An alternative explanation for the effect of larval habitat on SHM is that larval habitat is correlated with other phylogenetically constrained traits. Terrestrial breeders tend to have smaller clutches than aquatic breeders; however, clutch size was not an important predictor of SHM in our analyses, possibly because lotic-breeding species did not have smaller clutches than lentic-breeding species. Alternatively, thermal niche breadths or tolerances could be correlated with reproductive modes. A recent study found that terrestrial-breeding species typically had lower upper thermal tolerances than aquatic breeders, and upper thermal tolerances predicted susceptibility to infection with *B. dendrobatidis* (Nowakowski, Whitfield et al., 2016). Species with high thermal tolerances may be able to exploit altered habitats with higher temperatures than those found in forests (Nowakowski, Watling et al., 2017).

## 5 | CONCLUSIONS

Efforts to target groups of species that are highly susceptible to a given threat can add a valuable layer to prioritization schemes in an era of increased extinction risk (Murray et al., 2011, 2014; Stuart et al., 2004). A recent review, however, concluded that comparative analyses that identify traits correlated with extinction risk have

had little influence on conservation practice, in part because they often do not account for specific threats that drive extinction and that can each require different management strategies (Cardillo & Meijaard, 2012). We addressed this concern by identifying intrinsic factors that are correlated with the vulnerability of species to habitat modification, a direct driver of species extinctions. We found that species with increased SHM had small geographical ranges; because SHM is a measure of the localized responses of species to habitat modification, the importance of range size probably reflects niche specialization of range-restricted species (Slatyer et al., 2013) rather than the spatial spread of risk from threatening processes [i.e., the role of range size in IUCN assessments; IUCN, 2014]. We also identify global patterns of SHM associated with larval habitat, suggesting that further prioritization of amphibians for assessment, research and action could be guided by the combination of range size and larval habitat information. Future research focused on the traits and mechanisms underlying variation in SHM will help close the conservation gap for amphibians by allowing managers to better target both species and habitats for protection (Murray et al., 2010, 2014; Nori et al., 2014; Nowakowski & Angulo, 2015).

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#### BIOSKETCH

The authors have shared interests in the effects of global change on biodiversity and the ecological principles relevant to biodiversity conservation, with particular focus on amphibian and reptile systems.

#### SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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