Species traits explaining sensitivity of snakes to human land use estimated from citizen science data

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ABSTRACT

Understanding how traits affect species responses to threats like habitat loss may help prevent extinctions. This may be especially true for understudied taxa for which we have little data to identify declines before it is too late to intervene. We used a metric derived from citizen science data on snake occurrences to determine which traits were most correlated with species' sensitivity to human land use. We found that snake species that feed primarily on vertebrates, that use a high proportion of aquatic habitats, and that have small geographic ranges occurred in more natural and less human-dominated landscapes. In contrast, body size, clutch (or litter) size, the degree of exposure to human-dominated landscapes, reproductive mode, habitat specialization, and whether a species was venomous or not had less effect on their sensitivity to human land use. Our results extend previous findings that higher trophic position is correlated with extinction risk in many vertebrates by showing that snake species that feed primarily on vertebrates are more sensitive to human land use – a primary driver of extinction. It is likely that conversion of natural landscapes for human land use alters biotic communities, causing losses of important trophic groups, especially in aquatic and riparian communities. Practitioners should therefore prioritize preserving aquatic habitat and natural landscapes with intact biotic communities that can support species at higher trophic levels, as well as focus monitoring on populations of range-restricted species.

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1. Introduction

Understanding how extinction risk is affected by species traits can guide conservation and monitoring of vulnerable species where it is needed most (Ribeiro et al., 2016). Linking traits to extinction risk may be especially important for preventing extinctions in understudied taxa for which we have little data to identify declines before it is too late. To date, several traits have been linked to increased extinction vulnerability in commonly studied vertebrates. For instance, extinction risk often increases with increasing habitat specialization, body size, and trophic level, but decreases with increasing range size and fecundity (Gaston and Blackburn, 1995; Purvis et al., 2000; Jones et al., 2003; Cardillo et al., 2005; Cardillo et al., 2008; Davidson et al., 2012; Tingley et al., 2013; Böhm et al., 2016). Ultimately, however, different suites of traits may underlie how species respond to a given threat (e.g., habitat loss, disease, overharvesting; Murray et al., 2014). Thus, understanding which traits directly link species responses to specific threats will provide clearer information with which to target conservation effort (Murray et al., 2011; Murray et al., 2014).

For most taxa, habitat loss is the primary threat driving their imperilment (Sala et al., 2000). However, the degree to which species are imperiled by habitat loss varies depending on their life histories and other traits. For example, species with small ranges, narrow niche breadths, and those at higher trophic levels are often among the first to disappear when habitat is lost (Laurance et al., 2002; Swihart et al., 2003; Barbaro and Van Halder, 2009). But research on which traits affect species responses to habitat loss have mostly focused on relatively visible and well-studied groups, such as birds, mammals, and butterflies (Swihart et al., 2003; Barbaro and Van Halder, 2009; Öckinger et al., 2010). Identifying traits linked to species declines from habitat loss may be especially valuable for preventing extinctions of understudied or hard-to-study taxa whose declines may go largely unnoticed.

Reptiles are perhaps one of the least studied vertebrate groups. For example, 65% of reptiles have not been evaluated in IUCN Red List assessments (Böhm et al., 2013). Additionally, of those species that have been evaluated, 20% of them have been deemed data deficient (Böhm et al., 2013). This is troubling given recent concerns that reptiles may be experiencing global declines on par with those in other taxa (Gibbons et al., 2000; Böhm et al., 2016). Among reptiles, snakes perhaps best epitomize the problem of both a considerable lack of data and recent enigmatic declines across several continents (Winne et al., 2007; Reading et al., 2010; Todd et al., 2010). Thus, identifying which

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traits in snakes are associated with sensitivity to human land use – defined here as the absence of a species from human-dominated landscapes, either because of habitat selection or because of local extirpations – may provide timely information to prevent declines of these often unnoticed or understudied species.

A major challenge to predicting how understudied taxa will respond to habitat loss or which traits affect their sensitivity to human land use is scarcity of data. One method scientists have used to address this lack of data in recent years has been to include volunteers from the public – citizen scientists – to increase the quantity of data that can be collected (Devictor et al., 2010; Dickinson et al., 2010). Citizen scientists can provide information for many understudied taxa that might otherwise escape research or management attention (Losey et al., 2007; Braschler, 2009; Barlow et al., 2015). Information obtained by citizen scientists for understudied taxa can in turn be used in species assessments or to direct management intervention and habitat preservation. For example, citizen science data were recently used to rank the sensitivity of reptile and amphibian species to human land use while accounting for inherent biases associated with these types of data (Todd et al., 2016); citizen science data can provide much-needed information for taxa that are difficult to study because of their cryptic behavior. One advantage of large data sets gathered from citizen scientists is that it is increasingly possible to examine how traits in understudied species are linked to their responses to habitat loss.

Our goal in this study was to determine which traits are linked with sensitivity of snakes to human land use, the primary driver of habitat loss globally. We used a quantitative measure of species sensitivity to land use recently developed from citizen science data collected in North and South Carolina (USA) to identify intrinsic factors of snakes that may help explain variation in their sensitivity to this major threat. Given earlier findings from other taxa discussed above, we predicted that snake species that feed primarily on vertebrates (i.e., at a higher trophic level than those feeding primarily on invertebrates), that have small ranges, produce small clutches (or litters for live-bearers), have large body sizes, and have narrow diet and habitat breadths would be more sensitive to human land use than other species. We also expected species that are highly aquatic and depend on streams and wetlands to be more sensitive to human land use than others because these habitats are often highly affected by human land use (Dahl, 2001; Allan, 2004). Several live-bearing snake species have longer generational times and we thus expected them to be sensitive to human land use because their populations may be slow to recover from disturbances. Finally, we expected that venomous snake species would be more sensitive to human land use because they are prone to human persecution and thus may disappear from areas where human land use dominates.

2. Methods

2.1. Data collection

We obtained data on the sensitivity of snake species to human land use from Todd et al. (2016). These data provide a quantitative ranking of the degree to which 33 snake species in North and South Carolina (USA) were associated with natural or human-dominated landscapes – defined as urban or built areas, agricultural areas, and roads. The 7684 snake occurrences were originally reported by citizen scientists to the Carolina Herp Atlas (www.carolinaherpatlas.org; Price and Dorcas, 2011) and included observations from every county across the two states. At each occurrence for each species, Todd et al. (2016) used the GIS layer of Theobald (2010) to extract a natural landscape value. Natural landscape values range from 1, representing an entirely natural 270-m cell with only natural landscapes neighboring it, to 0, representing an entirely human-dominated cell with only human-dominated landscapes neighboring it (Theobald, 2010). Todd et al. (2016) then calculated an effect size representing the sensitivity of snake species to human land use. The effect size was the difference between the mean natural

landscape value across all observations of a given species and 1000 bootstrapped means of an equal number of observations for all other snake species within the range of the focal species. This method addressed possible spatial biases in how users find and report observations to determine whether a snake species was observed in more or less natural landscapes than were all others given known sampling locations. Positive effect sizes indicate a species was found in more natural landscapes than was the average snake (i.e. more sensitive to human land use), and negative effect sizes indicate a species was found in more human-dominated areas (i.e., less sensitive to human land use). Although both agricultural and urban lands are treated as human-dominated (i.e., a score of 0), in practice, most agricultural areas include natural landscapes nearby whereas urban areas do not. Thus, the weighting schema of Theobald (2010) results in typically higher values for agricultural areas compared to urban areas, in line with the expectation that agricultural lands may be of higher quality for wildlife than urban lands would be. For complete details of how effect sizes were calculated, see Todd et al. (2016). Here, we use their effect size as the response variable in our analyses.

We obtained data on mean clutch or litter size (hereafter "clutch size") and minimum snout-to-vent length (SVL; "body size") of females at reproductive maturity for each species from Ernst and Ernst (2003), except for *Tantilla coronata*, for which we obtained mean clutch size from Todd et al. (2008). We categorized each species as live-bearing or not (hereafter "reproductive mode"), venomous or not ("venomous"), and either feeding primarily on vertebrates or invertebrates ("primary prey") following species accounts in Ernst and Ernst (2003). As a measure of "diet breadth", we included a count of the number of all taxonomic Classes reported as prey in species accounts in Ernst and Ernst (2003). As an index of habitat specialization/breadth ("habitat breadth"), we followed Böhm et al. (2016) and used a count of the number of habitat types inhabited by each species reported in IUCN species accounts (www.iucnredlist.org accessed 15 January 2016). We calculated the proportion of these habitats that were aquatic for each species as an index of the degree to which each species uses aquatic habitats ("aquatic index"), the results of which agreed well with life history accounts in Ernst and Ernst (2003) and the authors' personal observations. We downloaded geographic range shapefiles from IUCN and used ArcGIS 10.0 to calculate the total expanse of each species' geographic range ("range size"). Finally, we included as a covariate, thereby controlling for, each species' exposure to human land use ("exposure"). For this measure of exposure, we used ArcGIS 10.0 to calculate the mean natural landscape value of each species' range in the Carolinas from the Natural Landscape GIS layer of Theobald (2010). A lower value for exposure thus indicates less natural landscape within a species' range, whereas a higher value for exposure indicates more natural landscape within a species' range. Ultimately, because each species' occurrences were compared only to other snake occurrences within its range, its sensitivity response metric is not confounded by the mean exposure value of its range. In other words, a species whose range is predominantly natural landscape can still be found in more human-dominated areas compared with other snakes in its range.

2.2. Statistical analyses

We examined correlations among continuous predictor variables and variable inflation factors (VIF) for all variables, finding only weak-moderate correlations among variables, which did not meet thresholds for high multicollinearity (e.g., $r > 0.7$; Fig. S1; Zuur et al., 2009), and further supported by examination of VIF (≤ 4 for all variables). All continuous predictor variables were centered and scaled prior to analyses. We used generalized least squares (GLS) and phylogenetic GLS (PGLS) models to analyze variation in species sensitivity to human land use. First, we fit a global GLS model with clutch size, body size, reproductive mode, venomous, primary prey, diet breadth, habitat breadth, aquatic index, range size, and exposure as explanatory variables. We then fit

models with all additive combinations of explanatory variables, including an intercept-only model. We calculated the cumulative Akaike weights for models containing each focal variable and assessed significance of each predictor based on their model-averaged coefficients to evaluate relative variable importance in explaining variation in species sensitivity to human land use.

To account for potential phylogenetic non-independence in model residuals, we compared GLS results with those obtained from PGLS models, which included a phylogenetic correlation structure (Revell, 2010; Paradis, 2011). We obtained branch lengths for focal species from a large-scale squamate phylogeny (Tonini et al., 2016). Using these branch lengths, we first fit a global model with multiple phylogenetic correlations structures, selecting an appropriate correlation structure on the basis of AIC. Using the corPagel function in package ape, which produced the best fit, we generated variance-covariance matrices for all further models while simultaneously estimating phylogenetic signal (Paradis et al., 2004; Revell, 2010). We fit PGLS models, calculated variable importance, and evaluated significance of coefficients as described above for GLS models.

We tested for phylogenetic signal of individual variables, including species sensitivity to human land use, body size, clutch size, diet breadth, habitat breadth, aquatic index, range size, primary prey, venomous, and reproductive mode using Pagel's λ. Pagel's λ describes the transformation of the original phylogenetic tree that best fits the expected distribution of a given trait assuming a Brownian motion model of trait divergence. Values of λ typically range between 0 and 1, with values near 1 indicating strong phylogenetic signal, whereas values near 0 indicate that trait values are independent of phylogeny. We determined significance of phylogenetic signal using a likelihood-ratio test that compared the λ-transformed tree for a given trait to a star-phylogeny (a null model where λ = 0). We assessed phylogenetic signal for continuous traits using the phylosig function in package phytools (Revell, 2012) and for discrete traits using the fitDiscrete function in package Geiger (Harmon et al., 2008). We conducted all analyses in R (version 3.1.2, R Development Core Team, 2014).

3. Results

The relative importance of variables in explaining species sensitivity to human land use in the GLS model set was greatest for primary prey, followed by aquatic index, with range size the third most important variable (Fig. 1). Species whose primary prey are vertebrates were more sensitive to human land use than were those whose primary prey are invertebrates (p = 0.009; R^2 = 0.20; Fig. 2A). Species that used more aquatic habitats were also more sensitive to human land use than were those that used few or no aquatic habitats (p = 0.004; R^2 = 0.31; Fig. 2B). In contrast, species with greater range sizes were less sensitive to human land use than were those with smaller range sizes (p = 0.027; R^2 = 0.17; Fig. 1B). Model-averaged coefficients for all other variables in the GLS model set had P-values > 0.05.

Results of PGLS analyses were largely concordant with those of GLS analyses, likely owing to weak phylogenetic signal (λ < 0.001) in global model residuals despite strong signal associated with some individual variables (see below). Primary prey (p = 0.007; R^2 = 0.18), aquatic index (p = 0.007; R^2 = 0.32), and range size (p = 0.019; R^2 = 0.15) had the most support and followed the same patterns of correlation with a species' sensitivity to human land use as in the GLS analyses (Fig. 1). Model-averaged coefficients for all other variables in the PGLS model set had P-values > 0.05.

We found no phylogenetic signal associated with sensitivity to human land use (λ < 0.001, P = 1.0; Fig. 3). We found moderate-strong phylogenetic signal associated with the aquatic index (λ = 1.07, p < 0.001; Fig. 3), clutch size (λ = 1.02, p = 0.06), venomous (λ = 1.0, p < 0.001), and reproductive mode (λ = 1.0, p < 0.001). All other intrinsic variables, including primary prey, exhibited weak or no phylogenetic signal (λ < 0.25, p > 0.10; Fig. 3).

4. Discussion

Despite many studies linking species traits to extinction risk in several taxa, few have evaluated how these traits directly predispose species to risk from specific conservation threats. Given that species likely differ in how they respond to specific threats, linking their traits to known causes of decline can provide more concrete information with which to prioritize conservation effort. Such information may be especially useful in preventing losses of species that are understudied, given that there is rarely sufficient data with which to identify declines and mobilize action to preserve these species. Our results suggest that for snakes, a relatively understudied group (Bonnet et al., 2002), several traits are linked to sensitivity to human land use in the Carolinas. It is unclear whether the results found here are more broadly representative of snakes in general, or at least those across North America. However, the community assemblage in the present study is both highly characteristic of the southeastern US and it includes many species widely distributed across North America, where threats like urbanization, wetland loss, and land conversion for agriculture are all common. Nevertheless,
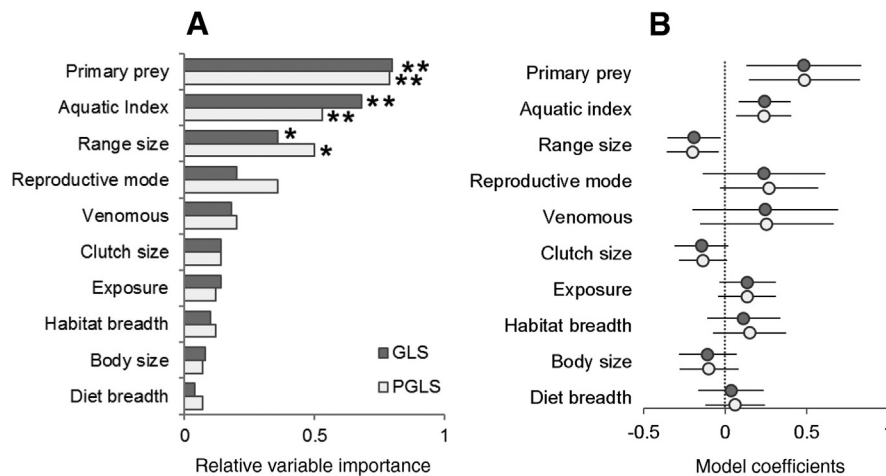

Fig. 1. Relative variable importance, calculated as the sum of Akaike weights, for variables in the generalized least squares (GLS) and phylogenetic GLS (PGLS) model sets, (A) and a plot of model-averaged coefficients (i.e., effect sizes) and confidence intervals for each variable (B). An asterisk '*' denotes p < 0.05 and a double-asterisk '**' denotes p < 0.01. The reference variable for Primary prey was invertebrate (compared with vertebrate), for Reproductive mode was egg-laying (compared with live-bearing), and for Venomous was non-venomous. Variables are sorted by mean variable importance.
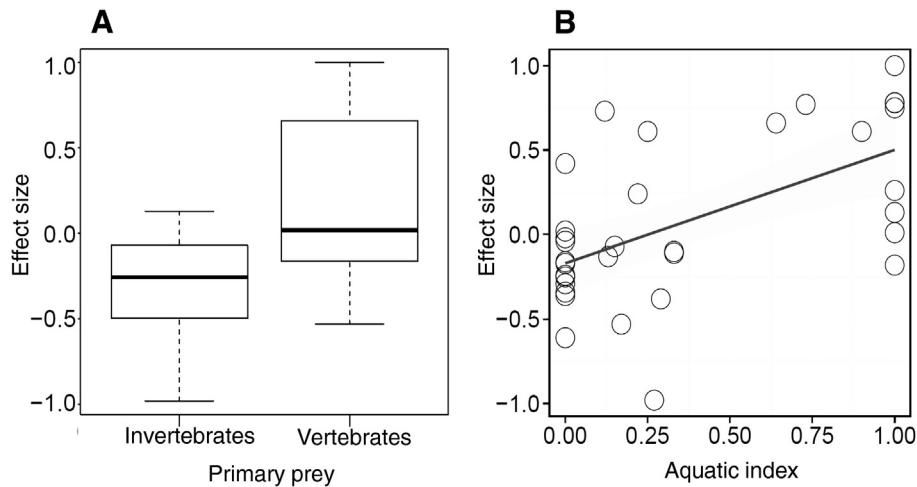
A **B**

Fig. 2. Comparison of effect sizes from a generalized least squares model for snakes whose primary prey type is invertebrates or vertebrates (A) and as a function of the proportion of aquatic habitats used by a species out of all habitats listed in IUCN RedList account for each species (B). Positive effect sizes indicate greater sensitivity to human land use and negative effect sizes indicate lower sensitivity to human land use. The box and whisker plots show medians, interquartile ranges, and ranges.

at least one study provides caution that results from any single state may not reflect nationwide trends (Cosentino et al., 2014).

Previous studies have identified that species at higher trophic levels are often more imperiled than are species at lower trophic levels (Pimm et al., 1988; Purvis et al., 2000), likely because they are more sensitive to cumulative threats that affect species lower down the food web (Crooks and Soule, 1999). This in turn can lead to the erosion of food webs and the loss of species in upper trophic levels before those at lower trophic levels (Brezonik et al., 1993; Terborgh et al., 2001; Purtauf et al., 2004; Dobson et al., 2006). Additionally, predators at higher trophic levels may need more space to meet resource demands and are thus less likely

Fig. 3. Cladogram adapted from Tonini et al. (2016) showing the degree to which snake species are more sensitive (positive effect sizes) or less sensitive (negative effect sizes) to human land use. Also shown for each species is its primary prey type (Vertebrate or Invertebrate) and Aquatic index (proportion of aquatic habitats used by each species out of all habitats listed in IUCN RedList species accounts).

to persist in small fragments (Laurance et al., 2002). Collectively, these studies agree with our finding that snakes that feed primarily on vertebrates were sensitive to human land use, in contrast to those at a lower trophic level who feed primarily on invertebrates. We suggest, therefore, that the habitat degradation, alteration, and fragmentation that accompany human land use likely lead to trophic collapses that disproportionately affect vertebrate-feeding snakes, causing declines in these species in areas where human land use dominates. In contrast, many of the primarily invertebrate-feeding snakes remain disproportionately common in areas of high human land use.

Snake species in the Carolinas that rely on a greater proportion of aquatic habitats were more sensitive to human land use than were more terrestrial species. Being highly aquatic was also strongly correlated with phylogeny, suggesting that highly aquatic clades in the Carolinas may be disproportionately affected by land use. Nevertheless, there was no direct phylogenetic association with sensitivity to human land use, suggesting that, although being highly aquatic may engender greater sensitivity to human land use, additional traits likely mediate overall sensitivity of aquatic snakes to human land use.

There are at least two mechanisms that may explain the greater sensitivity of aquatic snakes to human land use seen here. First, many isolated freshwater wetlands in the US have been lost (Dahl, 2001), in part because they are not protected under federal Clean Water Act provisions because they do not share a significant nexus with navigable waters (Downing et al., 2003; Leibowitz et al., 2008). Many of the snakes sensitive to habitat loss in the present study rely on freshwater wetlands; as these wetlands have disappeared from human-dominated landscapes, species that depend on them have likely disappeared as well, being found now primarily in more natural landscapes where aquatic habitat remains intact. Second, it is likely that species that rely on aquatic habitats suffer from degradation that occurs in both aquatic and terrestrial areas. That is, in addition to directly losing aquatic habitat, the loss of natural upland areas and concomitant increases in impervious surfaces also degrades watersheds, reducing the quality of aquatic habitat. For example, urbanization – a prominent feature in human-dominated landscapes – causes decreases in water quality with associated declines of many aquatic species like fish and stream salamanders (Wang et al., 2001; Willson and Dorcas, 2003; Price et al., 2012), two common prey types for aquatic snakes. Our results suggest that highly aquatic snakes may also suffer from overall degradation of watersheds, and apparently more so than terrestrial snakes.

Small range size is a factor commonly linked to increased imperilment in many species (Jones et al., 2003; Tingley et al., 2013; Böhm et al., 2016). This increased imperilment has been attributed to multiple
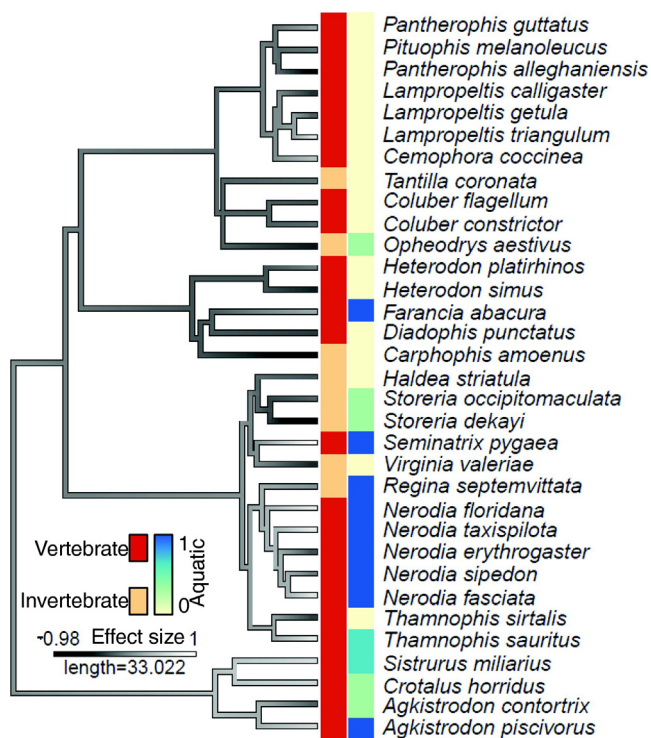
factors, including smaller populations and narrower overall niche breadths (Purvis et al., 2000; Slatyer et al., 2013). In the present study, species ranges varied from as little as 173,131 km^2 for *Nerodia floridana* to as much as 7.8 million km^2 for *Thamnophis sirtalis*. Because even the species at the lower end of this range still has a large range compared to IUCN metrics of imperilment risk (e.g., 5000 km^2; IUCN, 2016), it is unlikely that small population sizes contribute to the sensitivity to human land use observed in this study. Instead, it is more likely that species with larger ranges have greater niche breadths that allow them to persist across a broader array of habitats (Slatyer et al., 2013), including both disturbed and undisturbed habitats. Although we did not find support for a specific link between habitat breadth or diet breadth and species sensitivity, a species' niche reflects many other unmeasured tolerances and factors that can play a role in how well species tolerate habitat loss or degradation (Slatyer et al., 2013). Thus, species with large ranges who are capable of inhabiting diverse habitats across broad environmental gradients should be relatively less sensitive to the habitat alteration that occurs in human-dominated landscapes compared to species with smaller ranges.

Several traits that have been linked to species imperilment in other studies were only poorly correlated with the sensitivity of snakes to human land use in the present study. For example, imperilment has been shown almost universally to increase with body size for most species (e.g., Purvis et al., 2000; Cardillo et al., 2008), including reptiles (Tingley et al., 2013; Böhm et al., 2016). Nevertheless, a direct link between body size in vertebrates and sensitivity to habitat loss or human land use has proven elusive across many taxa (Swihart et al., 2003; Meyer et al., 2008; Thornton et al., 2011; Vetter et al., 2011; Quesnelle et al., 2014), and our results agree with these earlier findings. Body size may not generally correlate well with sensitivity to habitat loss because it is linked to many other life-history attributes that more directly predispose species to imperilment risks, including trophic level and fecundity, among others (Henle et al., 2004). Species with high fecundities, for example, should have a low risk of imperilment because they can respond rapidly to perturbations in their environment (Bennett and Owens, 1997; Larson and Olden, 2010). In the present study, however, clutch size, which is linked to fecundity, was not correlated with sensitivity to habitat loss. This may result from the fact that many additional factors, including clutch frequency (Reed and Shine, 2002), age at maturity, and longevity, among others, collectively determine fecundity, making clutch size alone a poor proxy. Low annual reproductive frequency can be common among live-bearing snakes (Seigel and Ford, 1987), especially venomous species that have slow life histories and who may face heightened human persecution (e.g., Dunham et al., 1988; Means, 2009). Here again, however, we found no support for a link between reproductive mode or being venomous and a species' sensitivity to human land use. In the present study, trophic level – i.e. primary prey type – appears to be a more direct link that predisposes some snakes to greater sensitivity to habitat loss.

5. Conclusions

An effective first step in preventing losses of biodiversity is predicting which species are at risk before they are listed as threatened. By understanding which intrinsic traits are linked with species responses to conservation threats, it may be possible to better prioritize monitoring and management efforts, something especially valuable for understudied species. Our study provides new insights into which traits are linked with species sensitivity to human land use for snakes, an understudied group. Using a metric developed from an extensive data set collected by citizen scientists, we found that snake species that feed primarily on vertebrates, that are highly aquatic, and that have small geographic ranges are more sensitive to human land use than are other sympatric snake species. For these reasons, such species will likely be the first to disappear as natural habitats continue to be lost or converted for human use. We suggest, therefore, that practitioners and managers prioritize preserving aquatic habitat and natural landscapes with intact biotic communities that can support species at higher trophic levels, as well as focus monitoring on populations of range-restricted species.

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References

Allan, J.D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annu. Rev. Ecol. Evol. Syst. 35, 257–284.

Barbaro, L., Van Halder, I., 2009. Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. Ecography 32, 321–333.

Barlow, K.E., Briggs, P.A., Haysom, K.A., Hutson, A.M., Lechiara, N.L., Racey, P.A., Walsh, A.L., Langton, S.D., 2015. Citizen science reveals trends in bat populations: the national bat monitoring programme in Great Britain. Biol. Conserv. 182, 14–26.

Bennett, P.M., Owens, I.P.F., 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? Proc. R. Soc. Lond. B Biol. Sci. 264, 401–408.

Böhm, M., Williams, R., Bramhall, H.R., McMillan, K.M., Davidson, A.D., Garcia, A., Bland, L.M., Bielby, J., Collen, B., 2016. Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. Glob. Ecol. Biogeogr. 25, 391–405.

Böhm, M., et al., 2013. The conservation status of the world's reptiles. Biol. Conserv. 157, 372–385.

Bonnet, X., Shine, R., Lourdais, O., 2002. Taxonomic chauvinism. Trends Ecol. Evol. 17, 1–3.

Braschler, B., 2009. Successfully implementing a citizen-scientist approach to insect monitoring in a resource-poor country. Bioscience 59, 103–104.

Brezonik, P.L., et al., 1993. Experimental acidification of Little Rock Lake, Wisconsin: chemical and biological changes over the pH range 6.1 to 4.7. Can. J. Fish. Aquat. Sci. 50, 1101–1121.

Cardillo, M., Mace, G.M., Gittleman, J.L., Jones, K.E., Bielby, J., Purvis, A., 2008. The predictability of extinction: biological and external correlates of decline in mammals. Proc. R. Soc. Lond. B Biol. Sci. 275, 1441–1448.

Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species. Science 309, 1239–1241.

Cosentino, B.J., Marsh, D.M., Jones, K.S., Apodaca, J.J., Bates, C., Beach, J., Beard, K.H., Becklin, K., Bell, J.M., Crockett, C., Fawson, G., Fjelsted, J., Forys, E.A., Genet, K.S., Grover, M., Holmes, J., Indeck, K., Karraker, N.E., Kilpatrick, E.S., Langen, T.A., Mugel, S.G., Molina, A., Vonesh, J.R., Weaver, R.J., Willey, A., 2014. Citizen science reveals widespread negative effects of roads on amphibian distributions. Biol. Conserv. 180, 31–38.

Crooks, K.R., Soule, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400, 563–566.

Dahl, T.E., 2001. Status and Trends of Wetlands in the Conterminous United States 2004 to 2009. US Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

Davidson, A.D., Boyer, A.G., Kim, H., Pompa-Mansilla, S., Hamilton, M.J., Costa, D.P., Ceballos, G., Brown, J.H., 2012. Drivers and hotspots of extinction risk in marine mammals. Proc. Natl. Acad. Sci. 109, 3395–3400.

Devictor, V., Whittaker, R.J., Beltrame, C., 2010. Beyond scarcity: citizen science programmes as useful tools for conservation biogeography. Divers. Distrib. 16, 354–362.

Dickinson, J.L., Zuckerberg, B., Bonter, D.N., 2010. Citizen science as an ecological research tool: challenges and benefits. Annu. Rev. Ecol. Evol. Syst. 41, 149–172.

Dobson, A., et al., 2006. Habitat loss, trophic collapse, and the decline of ecosystem services. Ecology 87, 1915–1924.

Downing, D.M., Winer, C., Wood, L.D., 2003. Navigating through clean water act jurisdiction: a legal review. Wetlands 23, 475–493.

Dunham, A.E., Miles, D.B., Reznick, D.N., 1988. Life history patterns in squamate reptiles. In: Gans, C., Huey, R.B. (Eds.), Biology of the Reptilia. John Wiley and Sons, New York, NY, USA, pp. 441–522.

Ernst, C.H., Ernst, E.M., 2003. Snakes of the United States and Canada. Smithsonian Institution Press, Washington, D.C., USA.

Gaston, K.J., Blackburn, T.M., 1995. Birds, body size, and the threat of extinction. Philos. Trans. R. Soc. Lond. B 347, 205–212.

Gibbons, J.W., et al., 2000. The global decline of reptiles, déjà vu amphibians. Bioscience 50, 653–666.

Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E., Challenger, W., 2008. GEIGER: investigating evolutionary radiations. Bioinformatics 24, 129–131.

Henle, K., Davies, K.F., Kleyer, M., Margules, C., Settele, J., 2004. Predictors of species sensitivity to fragmentation. Biodivers. Conserv. 13, 207–251.

IUCN, 2016. Using the IUCN Red List Categories and Criteria. Version 12. Standards and Petitions Subcommittee. http://www.iucnredlist.org/documents/RedListGuidelines.pdf.

Jones, K.E., Purvis, A., Gittleman, J.L., 2003. Biological correlates of extinction risk in bats. Am. Nat. 161, 601–614.

Larson, E.R., Olden, J.D., 2010. Latent extinction and invasion risk of crayfishes in the southeastern United States. Conserv. Biol. 24, 1099–1110.

Laurance, W.F., et al., 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv. Biol. 16, 605–618.

Leibowitz, S.G., Wigington, P.J., Rains, M.C., Downing, D.M., 2008. Non-navigable streams and adjacent wetlands: addressing science needs following the Supreme Court's Rapanos decision. Front. Ecol. Environ. 6, 364–371.

Losey, J.E., Perlman, J.E., Hoebeke, E.R., 2007. Citizen scientist rediscovers rare nine-spotted lady beetle, Coccinella novemnotata, in eastern North America. J. Insect Conserv. 11, 415–417.

Means, D.B., 2009. Effects of rattlesnake roundups on the eastern diamondback rattlesnake (Crotalus adamanteus). Herpetological Conservation and. Biology 4, 132–141.

Meyer, C.F.J., Fründ, J., Lizano, W.P., Kalko, E.K.V., 2008. Ecological correlates of vulnerability to fragmentation in Neotropical bats. J. Appl. Ecol. 45, 381–391.

Murray, K.A., Rosauer, D., McCallum, H., Skerratt, L.F., 2011. Integrating species traits with extrinsic threats: closing the gap between predicting and preventing species declines. Proc. R. Soc. Lond. B Biol. Sci. 278, 1515–1523.

Murray, K.A., Verde Arregoitia, L.D., Davidson, A., Di Marco, M., Di Fonzo, M.M.I., 2014. Threat to the point: improving the value of comparative extinction risk analysis for conservation action. Glob. Chang. Biol. 20, 483–494.

Öckinger, E., et al., 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecol. Lett. 13, 969–979.

Paradis, E., 2011. Analysis of Phylogenetics and Evolution with R. Springer, London.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: Analyses of phylogenetics and evolution in R language. Bioinformatics 20, 289–290.

Pimm, S.L., Jones, H.L., Diamond, J., 1988. On the risk of extinction. Am. Nat. 132, 757–785.

Price, S.J., Dorcas, M.E., 2011. The Carolina Herp Atlas: an online, citizen-science approach to document amphibian and reptile occurrences. Herpetological Conservation and. Biology 6, 287–296.

Price, S.J., Browne, R.A., Dorcas, M.E., 2012. Evaluating the effects of urbanisation on salamander abundances using a before-after control-impact design. Freshw. Biol. 57, 193–203.

Purtauf, T., Dauber, J., Wolters, V., 2004. The response of carabids to landscape simplification differs between trophic groups. Oecologia 142, 458–464.

Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. Proc. R. Soc. Lond. B Biol. Sci. 267, 1947–1952.

Quesnelle, P.E., Lindsay, K.E., Fahrig, L., 2014. Low reproductive rate predicts species sensitivity to habitat loss: a meta-analysis of wetland vertebrates. PLoS ONE 9, e90926.

R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Reading, C.J., Luiselli, L.M., Akani, G.C., Bonnet, X., Amori, G., Ballouard, J.M., Filippi, E., Naulleau, G., Pearson, D., Rugiero, L., 2010. Are snake populations in widespread decline? Biol. Lett. 6, 777–780.

Reed, R.N., Shine, R., 2002. Lying in wait for extinction: ecological correlates of conservation status among Australian elapid snakes. Conserv. Biol. 16, 451–461.

Revell, L., 2010. Phylogenetic signal and linear regression on species data. Methods Ecol. Evol. 1, 319–329.

Revell, L., 2012. Phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3, 217–223.

Ribeiro, J., Colli, G.R., Caldwell, J.P., Soares, A.M.V.M., 2016. An integrated trait-based framework to predict extinction risk and guide conservation planning in biodiversity hotspots. Biol. Conserv. 195, 214–223.

Sala, O.E., et al., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.

Seigel, R.A., Ford, N.B., 1987. Reproductive ecology. In: Seigel, R.A., Collins, J.T., Novak, S.S. (Eds.), Snakes: Ecology and Evolution. Macmillan, New York, NY, USA, pp. 210–252.

Slatyer, R.A., Hirst, M., Sexton, J.P., 2013. Niche breadth predicts geographical range size: a general ecological pattern. Ecol. Lett. 16, 1104–1114.

Swihart, R.K., Gehring, T.M., Kolozsvary, M.B., Nupp, T.E., 2003. Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. Divers. Distrib. 9, 1–18.

Terborgh, J., Lopez, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D., Balbas, L., 2001. Ecological meltdown in predator-free forest fragments. Science 294, 1923–1926.

Theobald, D.M., 2010. Estimating natural landscape changes from 1992 to 2030 in the conterminous US. Landsc. Ecol. 25, 999–1011.

Thornton, D., Branch, L., Sunquist, M., 2011. Passive sampling effects and landscape location alter associations between species traits and response to fragmentation. Ecol. Appl. 21, 817–829.

Tingley, R., Hitchmough, R.A., Chapple, D.G., 2013. Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. Biol. Conserv. 165, 62–68.

Todd, B.D., Rose, J.P., Price, S.J., Dorcas, M.E., 2016. Using citizen science data to identify the sensitivity of species to human land use. Conserv. Biol. 30, 1266–1276.

Todd, B.D., Willson, J.D., Gibbons, J.W., 2010. The global status of reptiles and causes of their decline. In: Sparling, D.W., Linder, G., Bishop, C.A., Krest, S. (Eds.), Ecotoxicology of Amphibians and Reptiles, second ed. CRC Press, Pensacola, FL, USA, pp. 47–67.

Todd, B.D., Willson, J.D., Winne, C.T., Semlitsch, R.D., Gibbons, J.W., 2008. Ecology of the Southeastern Crowned Snake, Tantilla coronata. Copeia 2008, 388–394.

Tonini, J.F.R., Beard, K.H., Ferreira, R.B., Jetz, W., Pyron, A., 2016. Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. Biol. Conserv. 204, 23–31.

Vetter, D., Hansbauer, M.M., Végvári, Z., Storch, I., 2011. Predictors of forest fragmentation sensitivity in Neotropical vertebrates: a quantitative review. Ecography 34, 1–8.

Wang, L., Lyons, J., Kanehl, P., Bannerman, R., 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. Environ. Manag. 28, 255–266.

Willson, J.D., Dorcas, M.E., 2003. The effects of habitat disturbance on stream dwelling salamander populations: implications for buffer zones and watershed management. Conserv. Biol. 17, 763–771.

Winne, C.T., Willson, J.D., Todd, B.D., Andrews, K.M., Gibbons, J.W., 2007. Enigmatic decline of a protected population of Eastern Kingsnakes, Lampropeltis getula, in South Carolina. Copeia 2007, 507–519.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.Z., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, NY, USA.