Rapoport's rule and determinants of species range size in snakes

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(A) Abstract

(B) Aim

Understanding determinants of species range size is paramount to explaining global ecological patterns and estimating extinction risk of species. Here, we examined whether a sample of 536 snake species exhibit a latitudinal gradient of range size in support of Rapoport's Rule, and determined predictors of range size from a set of environmental and biological factors.

(B) Location

Global

(B) Methods

Based on *a priori* hypotheses about the effects of latitude, environmental and biological factors on species' range, we calculated mid-latitudes of species ranges, and collected data on environmental factors (altitude, temperature, precipitation, size and number of ecoregions occupied) and biological traits (body size, fecundity, habitat breadth and species age) to construct multivariate models of snake range size. We used a recently-published dated consensus phylogeny to determine minimum adequate models of range size using phylogenetic generalised least squares models and establish correlations between range size and species description.

(B) Results

Range size increased significantly with latitude, consistent with Rapoport's rule, especially across mid- and high latitudes in the northern hemisphere. Habitat breadth, body size and altitude had a significant positive effect on range size, with minor negative effects on range size from mean altitude and reproductive output. Biological variables explained more variation in range size than environmental variables. Species' range size had a significant effect on species' description, with larger-ranged species having been described earlier.

(B) Main conclusions

Prediction of range size in lesser-known species such as snakes relies on a suite of factors. Species' with restricted habitat breadth, small body size and at high altitudes generally have smaller ranges, and are thus likely to have higher extinction risk. Our work illustrates that it is these species we are likely to under-report in extinction risk assessments.

(A) Introduction

Species' range size is a fundamental unit in ecology, biogeography and conservation and has received significant research attention throughout the decades. Rapoport's rule hypothesises that the latitudinal range of species distributions is greater at higher latitudes (Rapoport, 1982; Stevens, 1989; Brown *et al*., 1996). The Rule has received much debate over the years, however. It was originally proposed by Stevens (1989) in an attempt to explain latitudinal gradients in species diversity, with the most commonly cited hypothesis being that seasonal variability at higher latitudes selects for wider climate tolerance and therefore wider range size. Support for Rapoport's rule has been found in multiple studies, and especially across Northern latitudes, on damselflies (Swaegers *et al.*, 2014), Canadian freshwater fish (Blanchet *et al.*, 2013), plants (Morueta-Holme *et al.*, 2013), amphibians (Whitton *et al.*, 2012) and mammals (Arita *et al.* 2005); association with latitude in tropical regions and the Southern hemisphere appear to be less well defined. There are many studies which have shown complex, regional patterns, and provide only partial support for Rapoport's rule. For example, the smallest breeding ranges for birds were found on islands, mountains and primarily in the southern hemisphere, with no distinct latitudinal pattern (Orme *et al*. 2006).

Species' geographic range is determined by a complex interplay of species characteristics and environmental factors that limit viable dispersal (Gaston, 2003). Determining drivers of range size is important in a wider conservation context because small range size is one of the main predictors of elevated extinction risk of species (Purvis *et al.*, 2000; mammals: Davidson *et al*., 2009; birds: Lee & Jetz, 2010; reptiles: Böhm *et al*., 2016a), whereas large-ranged species tend to have high dispersal ability, broad environmental tolerances (Jablonski & Roy, 2003) and lower extinction risk. The IUCN Red List of Threatened Species incorporates range-based metrics as part of its extinction risk assessment; range-based metrics are of particular importance for less-well studied species groups (e.g. reptiles and non-vertebrates), for which data on population status and trends are often lacking (Böhm *et al*., 2013;

Collen *et al.*, 2016). Thus, understanding the drivers of range size in species can provide valuable information about appropriate conservation actions for range-restricted species. Range size has been associated with a number of biogeographical, environmental and life history factors, such as altitude (Stevens, 1989), body size (Blackburn & Gaston, 1996), fecundity (Blackburn *et al.*, 2006), and habitat breadth (Pagel *et al.*, 1991). These interactions between environmental and biological factors and range size result in frequency distributions of range size that are usually right-tailed; many species have small- to moderate-sized ranges, and few species have very large ranges (Brown *et al.*, 1996). This has been demonstrated across terrestrial vertebrate groups (birds: Orme *et al.*, 2006; Li *et al.*, 2016; mammals: Agosta *et al.*, 2013; Li *et al.*, 2016; amphibians: Whitton *et al.*, 2012; reptiles: Li *et al.*, 2016).

Body size appears to have a varying relationship with range size (e.g., positive in turtles: Hecnar, 1999; negative in British birds: Sutherland & Baillie, 1993; triangular in New World birds and mammals: Blackburn & Gaston, 1996; Davidson *et al.*, 2009). This variable relationship may be due the antagonistic effects of body size on factors that influence range size, such as fecundity and thermal biology. Large body size can increase thermal inertia (especially in ectotherms such as reptiles; Stevenson, 1985), enabling species to withstand a broader thermal regime for longer time periods. The opposite effect may be apparent in small-bodied species, which, if they only tolerate a narrow range of conditions, may be less able to colonise large geographic areas (Gaston *et al.*, 1997) and thus have smaller ranges. On the other hand, large body size is also correlated with low fecundity in many species, leading to low local abundances and smaller ranges, while high annual fecundity leads to high local abundances, which in turn are often correlated with large range sizes of species (Blackburn *et al.*, 2006). As a result, the combined effect of fecundity and body size on range size may not always be clear, given the inter-correlation between the two traits and their potential opposite impacts on range size.

Time since speciation has also been related to range size, although a number of theories have emerged: range size increasing with lineage age (Willis, 1922; Taylor & Gotelli, 1994), remaining static over time (Jablonski, 1987), or decreasing with age (Ricklefs & Bermingham, 1999). For some taxa, there is no evidence of a clear

relationship between lineage age on range size (e.g., aquatic beetles: Abellán & Ribera, 2011).

Other factors influencing species range size include physical or climatic biogeographic restrictions. For example, topography and spatial differences in average annual temperature can reduce the expansion opportunity for a given species. Therefore, species living in ecoregions with a large spatial extent often have larger range sizes than species found in small biogeographic provinces (Pagel *et al.*, 1991; Roy *et al.*, 1994; Smith *et al.*, 1994; Gaston *et al.*, 1998; Fortes & Absalão, 2004; Boehning-Gaese *et al.* 2006), because minimal environmental variability within large ecoregions facilitates colonization of larger areas. Support for a positive relationship between elevation and range size was low across an analysis of vertebrates, although there was greater support in some reptile species (McCain & Knight, 2013).

Finally, range size itself may be in part determined by factors such as time since species' description (e.g. Collen *et al.*, 2004; Meiri, 2016). For example, larger-ranged species were described earlier than smaller-ranged species in lizards, carnivores and primates (Collen *et al.*, 2004; Meiri, 2016). Species with larger ranges are more likely to be encountered, whereas species with small ranges are more likely to be overlooked. This may present knock-on effects for our knowledge on species' extinction risk, due to more recently described species generally having smaller ranges and thus likely heightened extinction risk. This effect needs to be accounted for when examining the likely outcome on extinction risk in any assessment of drivers of species' range size.

Of the 3,619 snake species currently described (Uetz & Hošek, 2016), 55% have been assessed for the IUCN Red List (IUCN, 2016), and have been assessed as threatened primarily based on restricted range size (Böhm *et al.*, 2013). Snakes were found to have larger ranges and thus lower extinction risk compared to lizards (Böhm *et al.*, 2013). Here, we build on previous regional studies (e.g., Reed, 2003) to investigate the global pattern of range size variability within snakes, a species group that is difficult to monitor, for which data are sparse and that relies primarily on distribution metrics for its assessment of extinction risk. First, we test whether latitudinal range

size in snakes follows Rapoport's Rule to find evidence for a global gradient in snake range sizes which can underpin our knowledge on ranges for species with minimal locality data, such as snakes. We then investigate the contribution of environmental and biological variables towards determining species' range size using phylogenetic comparative analysis. We assess the: (1) influence of environmental factors such as altitude, climatic factors, size or number of ecoregions occupied on species' range size; and (2) the effect of specific biological traits such as habitat specialism, body size, fecundity or age of lineage on species' range size. Lastly, we assess the relationship between range size and species' description dates. We place our findings in the context of their effects on conservation assessments and current macroecological knowledge, specifically since our knowledge on extinction risk in snakes greatly depends on our ability to define the extent of species' geographic ranges and to deduce aspects of a species' range from broad-scale macroecological patterns to fill in data gaps.

(A) Methods

(B) Species ranges

We obtained species ranges for 536 non-marine snake species from a recent IUCN Red List assessment (Böhm *et al.*, 2013; see Supplementary Materials for a detailed description of the species set). Distribution mapping followed the species mapping protocol of the IUCN Red List. Distributions were based on polygon maps created from georeferenced locality data, which were then further refined based on expert opinion and published distribution maps to exclude unsuitable habitats, altitudes, etc. (Böhm *et al*., 2013). Therefore, mapping of species was standardised across taxonomic groups but may be affected by our level of knowledge on a species' habitat requirements. Only current, extant ranges were included in the analysis (i.e. excluding extinct, possibly extinct and uncertain parts of the range). For each species, range area (in km^2) was calculated in an equal area projection in ArcGIS v. 9.3.

(B) Examining snake ranges for Rapoport's latitudinal pattern

We calculated the latitudinal midpoint for each species range. We then allocated species to 5 degree latitudinal bins based on the location of their latitudinal range midpoints, and plotted the median range area of the species in each bin against the

latitudinal midpoint of that bin (Rohde *et al.*, 1993). We carried out a series of univariate phylogenetic generalised least square models (pGLS) to assess correlations between latitude and species range size. We subset our data into all possible latitudinal ranges at 5 degree intervals to investigate whether Rapoport's rule was evident across any subsets of the data (Figure S2).

(B) Explanatory variables of range size
We collected data on extrinsic environmental and geographic factors (altitude, temperature, precipitation, size and number of ecoregions occupied) and intrinsic biological traits (body size, fecundity, habitat breadth and species age) to test our hypotheses about the predictors of range size (Table 1).

We summarised the climatic aspects of a species' range in two ways, as the 1) mean monthly temperature and precipitation, and 2) the average absolute deviation (AAD, calculated using function 'aad' in R package 'lsr'; Navarro, 2014) of monthly temperature and precipitation. Climatic data was derived from Hijmans *et al.* (2005) at 10 minute resolution across each species' range. We also calculated 1) mean and 2) AAD for altitude (elevation above sea level), again using data at 10 minute resolution (Hijmans *et al.*, 2005).

We calculated the number of ecoregions overlapping each species' range and the area of each of these ecoregions for terrestrial (Olson *et al.*, 2001) and freshwater species (Abell *et al.*, 2008). A previous study examined the relationship between median area of all ecoregions overlapping a species' range with species' range size (Boehning-Gaese *et al.* 2006); however, ecoregion variables may be highly correlated with species' range size simply by chance, as larger ranges are likely to encompass larger and more ecoregions. Thus, any significant relationship between ecoregion variables and species' range size may simply reflect this chance pattern. We therefore investigated the validity of including ecoregion variables within our model by randomly plotting 1,000 circular ranges of varying radius onto the global map of ecoregions and investigating the resulting relationships between a set of possible ecoregion variables and range size: the number of ecoregions occupied, the summed area of all ecoregions overlapping a species' range (reflecting the maximum potential

range size of a species, if a species were to spread across each ecoregion within its range), the maximum area of all ecoregions a species' range overlaps, and the median ecoregion area (Boehning-Gaese *et al.* 2006). Any indication that correlations between ecoregion variables and range size may simply arise by chance resulted in the exclusion of these variables from further analyses. A detailed description of the simulation and analyses is given in the Supplementary Materials (Appendix S2).

We collated data on the body size of snakes from the published literature (Böhm *et al.*, 2016b), using maximum snout-vent length (SVL, in mm), which presents a better predictor of squamate body mass than total length measures (Feldman & Meiri, 2013). To estimate annual number of offspring, we collected data on the number of young (viviparous species) or clutch size (oviparous species) and number of clutches or groups of neonates per year. Habitat breadth was calculated as the number of habitats recorded for each species in its IUCN Red List assessment, based on the second hierarchical level of the IUCN habitat classification (Table S2; IUCN, 2013).

(B) Snake phylogeny

We used the recently published dated consensus phylogeny of Squamata (Tonini *et al.*, 2016) to account for shared ancestry within our data. The phylogeny represents 523 of the 536 non-marine snake species in our original dataset – the remaining species were missing from the phylogeny. We extracted terminal branch lengths for all species from the original phylogeny ('phytools' package v. 0.5-20; Revell, 2016), defining species age as the estimated age of the most recent node that connects it to another taxon or clade.

(B) Data analysis

Statistical analyses were carried out in R (version 3.2.2; R Development Core Team, 2015). Variables were log- or square-root-transformed as appropriate, to follow assumptions about normality of data.

We tested for multicollinearity by computing variance inflation factors (VIF) for all predictors and excluded variables with a VIF>5 from further analysis. We followed Revell (2010) and simultaneously estimated phylogenetic signal (Pagel's λ, using

maximum likelihood) and regression parameters, an approach shown to outperform equivalent non-phylogenetic approaches. We implemented this using phylogenetic generalised least square (pGLS) models in the R package 'caper' (Orme *et al*., 2012).

First, we tested for latitudinal effects on all biological and taxonomic variables in order to assess whether any underlying latitudinal patterns may affect our results on range size predictors. We used all remaining explanatory variables in univariate pGLS to assess relationships between predictor variables and species range size. We determined minimum adequate models (MAM) of range size in snakes using multivariate pGLS and multi-model inference for model selection based on AICc, as implemented in the R package MuMIn (Barton, 2015).

We assessed how much variation in species range size is explained by biological versus environmental predictors using partial regression of species range size and two sets of explanatory variables: 1) biological predictor variables retained in the MAM and 2) environmental predictor variables retained in the MAM. The resulting variance partitioning (Legendre & Legendre, 1998) shows the shared variance between these two sets of explanatory variables, plus each set's independent contribution to species range size. Variance partitioning was run in the package 'vegan' (Oksanen *et al*., 2015).

(B) Impact of range size on species description

Finally, we investigated the relationship between range size and species description date, to assess the indirect impact that drivers of range size may have on species description. We calculated years since description and hypothesised that species with a larger range size have earlier description dates. We tested this hypothesis using 1) a simple pGLS with range size as the explanatory and years since description as the dependent variable, and 2) bivariate pGLS using additive models of range size and range size correlates to examine effects on years since description.

(A) Results

(B) The distribution of snake range size and Rapoport's Rule

The distribution of the species' range areas for all 536 species of non-marine snakes

in our analysis was strongly right-skewed (Figure 1A), with the mean range area (874,849 km^2) markedly larger than the median (113,161 km^2). The spatial distribution of range sizes showed no consistent spatial pattern (Figure 1B), with larger average range sizes found at lower latitudes, specifically in Africa and the Neotropics, as well as at higher latitudes in the Palearctic and southern Africa. However, ranges were on the whole smallest between 0˚ and 20˚C latitude north, and largest towards high latitudes in the Northern hemisphere (Figure 1C).

Absolute latitude had a significant positive effect on snake range size across the full dataset (t=2.34, d.f. = 521, p=0.02; Table S3). For latitudinal subsets of the data, latitudinal effects were greatest in subsets spanning 15 to 45°N latitude (15 to 35°N: t = 5.31, d.f. = 157, p<0.001; 15 to 40°N: t = 4.57, d.f. = 169, p<0.001; 15 to 45°N: t = 5.22, d.f. = 174, p<0.001; Figure 1D). Significant relationships between absolute latitude and range size for subsets entirely contained within the Southern hemisphere were negative (e.g., 40 to 25°S: t = -2.41, d.f. = 38, p=0.02).

(B) Relationship between ecoregion variables and range size from simulated data
All ecoregion variables were significantly correlated with range size in our simulation (number: t = 50.9, res. d.f. = 998, p<0.001; summed area: t = 33.4, res. d.f. = 998, p<0.001; maximum ecoregion size: t = 11.7, res. d.f. = 998, p<0.001; median ecoregion size: t = -13.7, res. d.f. = 998, p<0.001). However, while all ecoregion variables were positively correlated with range size in our real dataset, median ecoregion area was negatively correlated with range size in our simulated data (Figure S3). This resulted in a negative relationship between median ecoregion area and number of ecoregions occupied (Figure S4A). Due to these significant relationships between ecoregion variables and range size in our simulations, we subsequently excluded these variables from our main analyses, as any patterns between these variables in our real data set may occur by chance.

(B) Variation in range size with extrinsic and intrinsic variables
We excluded AAD for temperature and precipitation from further analysis due to collinearity. Absolute latitude had a significant positive effect on habitat breadth only (t = 4.7, d.f. = 490, p<0.001). Univariate pGLS found positive relationships between

range size and 1) body size ($t = 9.2$, d.f. = 400, $p<0.001$), 2) habitat breadth ($t = 11.3$, d.f. = 490, $p<0.001$) and 3) altitude (AAD: $t = 13.3$, d.f. = 521, $p<0.001$; Figure 2). This suggests that larger species occupying a larger number of habitats over a larger range of altitudes have larger ranges.

In the MAM, habitat breadth, body size and altitude (AAD) retained significant effects on species range size (Table 2), while mean altitude and offspring per year were also retained as variables (although both were non-significant in the full multivariate model). Overall, the MAM explained just less than 25% of variation in species range size. Variance partitioning showed that biological factors alone contributed 13% of variation in range size to our MAM, while another 4% of variation in range size was explained by environmental factors alone. All MAM variables combined contributed 7% of variation in range size to our model. Unexplained residual variance was the main contributor to our model. The residuals of the MAM were normally distributed with no phylogenetic structuring ($\lambda = 0.000$, $p = 0.62$) (Figure S5). Inclusion of offspring per year in the MAM greatly reduced the sample size available for analysis, so that we re-ran the analysis with this variable excluded. The overall pattern remained the same, though the data explained more of the variance than when offspring per year was included (39%; Table 2).

(B) Impact of range size on species description
Species range size was significantly positively correlated with years since species' description ($t = 16.5$, d.f. = 521, $p< 0.001$; Figure 4). Controlling for the effect of range size, offspring per year ($t = 2.7$, d.f. = 93, $p = 0.007$), mean altitude ($t = -2.3$, d.f. = 520, $p= 0.021$) and habitat breadth ($t = 6.2$, d.f. = 489, $p<0.001$) correlated significantly with years since species' description in bivariate pGLS.

(A) Discussion
Given the importance of species' range size as a fundamental unit in ecology, biogeography and conservation, we examined patterns and drivers of range size in a previously understudied group, snakes. Our findings suggest evidence for a latitudinal gradient in snakes, especially significant across latitudes from 15 to 45°N, with ranges larger at higher latitudes. Small-bodied habitat specialists which occur over a limited

altitudinal range have smaller ranges than large-bodied generalist species. Our results also suggest that given the positive effect of years since species' description on species range, species at lower altitudes, with larger reproductive output and larger habitat breadth are described earlier.

(B) Rapoport's rule in snakes

Latitude had a significant positive effect on range size across the full set of species, and in regional subsets, especially above 15°N latitudes. Our results support previous studies that have shown the latitudinal effect to be strongest in the northern hemisphere (Fortes & Absalão, 2004; Whitton *et al.*, 2012; Blanchet *et al.*, 2013; Morueta-Holme *et al.*, 2013; Swaegers *et al.*, 2014), including for North American snakes (Reed, 2003). The Rapoport phenomenon in species is thought to be local to the northern hemisphere (Gaston *et al.*, 1998), particularly above 40°N, due to range expansion following the glacial retreat at the end of the last ice age (Price *et al.*, 1997). Although the effect of post-glacial expansion is likely to be less pronounced within snakes than within more mobile groups (e.g., mammals, birds), we found that latitudinal gradient in the geographic ranges of snakes was most obvious in latitudinal subsets spanning 15°N to 45°N latitude (Figure 1E), suggesting a similar, primarily regional, effect which becomes evident at lower latitudes than in other species groups.

Given our randomly sampled species set, and the resulting lack of high-altitudinal species in the Northern hemisphere, especially in Europe and Northern Asia, we would have expected latitudinal gradients towards higher latitudes to be less distinct in our dataset (Figure 1B). The random sampling procedure we used to obtain the original dataset ensures that patterns in species extinction risk are broadly representative of reptiles overall (Böhm *et al.*, 2013). Using random sampling, other patterns observed within the species set, including geographical patterns of range size, should be broadly representative of true patterns across the whole species groups, although at present we do not know if our sample size is large enough to detect trends and patterns in phenomena other than extinction risk. However, spatial patterns based on samples of 1,500 randomly selected species provided good agreement of patterns observed across the full datasets in mammals and amphibians, respectively (B. Collen, unpublished data). Our evidence for a latitudinal gradient in range size

towards higher latitudes despite obvious data gaps suggests that our randomly sampled species set can pick up on broad global patterns which have been previously observed in other species groups.

Snakes may avoid some of the effects of higher latitudes, especially lower temperatures, through estivation, retreating into shelter deep enough to avoid temperature fluctuation (Cloudsley-Thompson, 1999) or by reducing their metabolic response to temperature (Wang, 2002). However, despite the potential importance of estivation as a coping mechanism for extreme environmental conditions and its possible impact on global range size patterns in snakes, species-specific data on estivation is sparse in the literature, especially when species sets are selected randomly and may include many relatively poorly-studied species. Recent work showed that basic biological data on reptiles, such as critical temperature, is lacking for many reptile species (Böhm *et al.* 2016c). As such, it was not possible to assess the effects of estivation in our present study.

(B) Variation in range size with extrinsic and intrinsic variables
We found a significant positive relationship of range size with altitudinal range, but a negative relationship with mean altitude. This suggests that species with a larger altitudinal range though at lower mean altitudes have larger ranges. Previous studies showed evidence of larger reptile range sizes at higher altitudes (McCain & Knight, 2013).

Of our biological factors, body size and habitat breadth were significantly positively correlated to range size. The number of habitats a species has been recorded in reflects a species' habitat breadth, and was a highly significant factor affecting range size, with species occurring in a larger number of habitats also occupying larger ranges. Habitat was also found to be a significant factor in studies on other taxa (e.g., mammals: Pagel *et al.*, 1991; plants: Morueta-Holme *et al.*, 2013). For example, habitat area (represented through environmental variation in space), in conjunction with climate stability, determined range size pattern in New World plants (Morueta-Holme *et al.*, 2013), with smaller habitat area coupled with climate stability relating to smaller mean range sizes. Focusing conservation efforts on reptile species which

are habitat specialists has also previously been suggested as a strategy to reduce species loss (Böhm *et al.*, 2016a), and given our current results, is at least partly driven by the effect of habitat specialism on range size. As opposed to the inclusion of ecoregion variables, which are directly derived from range data, habitat breadth was derived from the non-spatial IUCN Red List database, thus avoiding the inherent bias introduced when deriving range size-dependent data such as variables summarising ecoregion extent or number.

As in other taxa (e.g., birds: Gaston & Blackburn, 1996), larger-sized snakes had significantly larger geographic ranges. Body size was shown to relate positively with range size in turtles (Hecnar, 1999) and New World snakes (Reed, 2003). Small-bodied species (especially ectotherms such as reptiles) may be sensitive to temperature fluctuations across large geographical areas (Gaston, 1990), while large animals require large home ranges to acquire sufficient resources. Hence, large areas needed to maintain minimum viable population sizes lead to large overall geographic range. Interestingly, reproductive output was negatively related to species' range size which was contrary to our hypotheses; this was likely a reflection of the interplay between fecundity and body size than a genuine relationship with range area.

(B) Relationship between range size and ecoregion variables
Unsurprisingly, we found a strong positive relationship between ecoregion area metrics and range size (Figure S3): species occupying smaller or fewer ecoregions had correspondingly small geographic range sizes. We predicted this would be the case because species that exhibit strong specificity to a certain ecoregion can be limited in their ability to expand their range if it requires crossing ecoregion boundaries (Pagel *et al.*, 1991; Roy *et al.*, 1994; Smith *et al.*, 1994; Gaston *et al.*, 1998; Fortes & Absalão, 2004). However, simulations showed that for a random set of ranges with varying range sizes, a species' range encompasses more and larger ecoregions simply by chance with increasing range size. As a result, including ecoregion variables in the analysis did not explain causality of observed range size patterns, but rather a consequence of variation in range size.

(B) Effects of range size on species description
We found that years since description correlated with larger range size in snakes.

Other studies have previously shown similar positive relationships between time since description and range size: larger range and body size were related to earlier description dates in carnivores and primates (Collen *et al.*, 2004). Our results suggest that snake species described today are more likely to be small-ranged habitat specialists, found in understudied areas, such as at high altitude. In lizards, new descriptions are similarly disproportionally biased in favour of understudied species such as nocturnal species (although surprisingly not subterranean forms), and also species found in the developing world, with more new species being described in the Oriental Realm than in Africa (Meiri, 2016). Given that many of these regions suffer from severe habitat degradation, it is also likely that some of our effect of smaller range size in newly described species and towards lower latitudes stems from the fact that, given anthropogenic pressures on species' habitats, ranges have already declined for many species (Di Marco & Santini, 2015).

(B) Importance for conservation and future steps

Geographic range size is a fundamental unit in ecology and conservation, but is a complex trait combining aspects of environmental variability and species' biology. We show that this is also the case in snakes, a group that is understudied and often overlooked in conservation efforts. Our findings at present are based on a random sample of snakes from across the globe. As more and better distribution information of reptiles becomes available, we will be able to assess the representativeness of this sample for depicting global range size patterns in snakes, and better assess correlates of range size (and extinction risk) in this little-known group of species. Meanwhile, and directly relevant to extinction risk assessments, we have shown that a number of factors are related to range size in this group, namely altitude, habitat breadth and body size. This aids better understanding of range size patterns in snakes and can guide assessment of range size in snakes, a vital metric in conservation assessments of reptiles (Böhm *et al.*, 2013). Given the observed relationship between range size and description date, it is highly likely that snake species which are yet to be discovered are more likely to be at a high risk of extinction, because they will generally have smaller ranges. This indicates that current levels of threat reported in snakes are likely to be underestimates of extinction risk for this group, with an expected shift of range size distribution in snakes towards smaller ranges when new species are described.

Given the impact of coarse range maps on macroecological studies (e.g. Hurlbert & Jetz, 2007), more detailed information on snake distributions may help to further support the presence of general macroecological patterns, and improve our understanding of drivers of range size and, by extension, extinction risk. This is likely to be an important consideration for similar studies in other lesser-known species groups, including extinction risk assessments. Our ability to predict species' extinction risk greatly depends on our ability to define the extent of species' geographic ranges, which may be greatly affected by the intensity of data collection for locality records. As an understudied group, it should be noted that many snakes in this study are relatively poorly known and may thus be associated with missing trait and/or occurrence data. There is often marked expansion of known geographic ranges as sampling improves (Gaston, 2003). As greater numbers of poorly-known species are assessed for the IUCN Red List of Threatened Species – particularly invertebrates – and often under range-based criteria, there is a more pressing need to investigate the way in which spatial data for species are gathered over time, how much these data accumulation patterns affect macroecological patterns and extinction risk assessments, and whether we can deduce certain aspects of a species' range size from broad-scale macroecological patterns to fill in data gaps.

(A) Acknowledgements

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(A) Biosketch

The researchers involved in this analysis (the Indicators and Assessments Unit at the Zoological Society of London (http://www.zsl.org/indicators) and their collaborators at University College London, Stony Brook University and Universidad Nacional Autonoma de Mexico) share their interest in understanding global change in biodiversity using extinction risk analyses, monitoring of global population trends and ecosystem-level studies. Author contributions: M.B., R.K. and B.C. conceived the ideas; M.B., R.K., R.W., H.B., K.M.M., A.D. and A.G. collected the data; M.B. and R.K. analysed the data; and M.B., A.D. and R.K. led the writing.

(A) Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Species data set and trait data

Appendix S2. Additional methods and analyses

Appendix S3. References

Appendix S4. Species list and data used in the analysis (Excel file)

Table S1. Variables considered as predictors of range size in snakes

Table S2. Habitat classification used by the IUCN

Table S3. Effect of absolute latitude on snake range size for latitudinal subsets of snake range sizes

Figure S1. Histogram of mid-latitudes of the 536 non-marine snakes in our dataset

Figure S2. Schematic for testing for Rapoport's Rule across all possible latitudinal ranges

Figure S3. Real versus simulated relationships between range size and ecoregion variables

Figure S4. Relationship of number of ecoregions occupied versus number of median ecoregion area in km^2, from simulated and real data

Figure S5. Normality plot for phylogenetic residuals for minimum adequate model

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Tables

Table 1. Summary of hypotheses for the link between environmental, biological life history, and taxonomic variables with species' range size. '+' and '–' represent an expected positive or negative correlation, respectively.

Variable	Prediction	Hypothesis
Elevation	+	Species living at high altitudes have larger ranges due to climatic and environmental variability
Temperature	-	Species in higher temperature areas have smaller ranges, potentially as a consequence of Rapoport's rule or increased climatic stability
Precipitation	+	Species in areas with higher levels of rainfall have larger ranges, potentially as a consequence of Rapoport's rule
Size of ecoregions	+	Species overlapping larger ecoregions have broader access to similar environmental conditions, hence possibility to expand to larger ranges
Number of ecoregions	+	Species overlapping more ecoregions may have broader tolerance to different environmental conditions, hence possibility to expand to larger ranges
Body size	+	Larger-bodied snakes may use thermal inertia to be active in more extreme environments, enabling species' range extension towards extreme latitudes
Habitat breadth	+	Species with less specificity to a certain habitat type have the possibility to expand to larger ranges
Fecundity	+	Species with larger reproductive output can expand over larger areas
Lineage age	+	Older species had longer period of time to expand range post-speciation

Table 2. Minimum adequate models for the phylogenetic analysis of range size determinants in freshwater and terrestrial snakes, based on the phylogeny by Tonini *et al.* 2016; *p<0.05, **p<0.01, ***p<0.001. Other variables considered were body size, habitat breadth, mean altitude and mean temperature, but none of these were significant in the final MAM. MAM1 sample size = 91; MAM2 sample size = 383.

Model	*Estimate*	*SE*	*t*	*R^2*	*λ*
MAM 1: including offspring/year					
Intercept	3.60	3.02	1.19	0.244	0.000
No. habitats	0.77	0.33	2.35*		
SVL	1.31	0.44	2.97**		
Altitude (AAD)	0.15	0.06	0.01***		
Altitude (mean)	-0.57	0.30	-1.89		
Offspring/year	-0.10	0.34	-0.30		
MAM 2: excluding offspring/year					
Intercept	4.01	1.67	2.40	0.392	0.422
No. habitats	1.20	0.20	6.11***		
SVL	1.27	0.21	6.13***		
Altitude (AAD)	0.23	0.03	9.02***		
Altitude (mean)	-0.99	0.16	-6.07***		

Figure legends

Figure 1. Geographic range area distribution for freshwater and terrestrial snakes in our study. (A) Frequency of range sizes across species; (B) Frequency of log range sizes across species; (C) Spatial distribution of range size in a sample of 536 non-marine snakes, shown as the average weighted mean of species range size (log) per grid cell (approximately 7,700 km^2), calculated as explained in the Supplementary Materials; (D) Median range size of snakes across the latitudinal gradient; (E) Summary of significant relationships and their direction across latitudinal subsets; data are plotted as the model coefficient for absolute latitude obtained in univariate pGLS versus latitudinal range extent (in degrees) of the subset.

Figure 2. Relationship between extrinsic factors of habitat breadth (A), body size (B) and average absolute deviation of altitude (C) and species range size in snakes.

Figure 3. Variation partitioning within minimum adequate model (MAM) of range size, showing the different contributions of biological versus environmental variables, as well as their shared contribution, to range size. Biological variables retained in the MAM: habitat breadth, body size, reproductive output; environmental variables: mean altitude and altitudinal AAD. Area of overlap: shared contribution of all MAM variables. Unexplained (residual) variance in the model is 0.76.

Figure 4. Relationship between range area and time since species description (in years) in snakes.
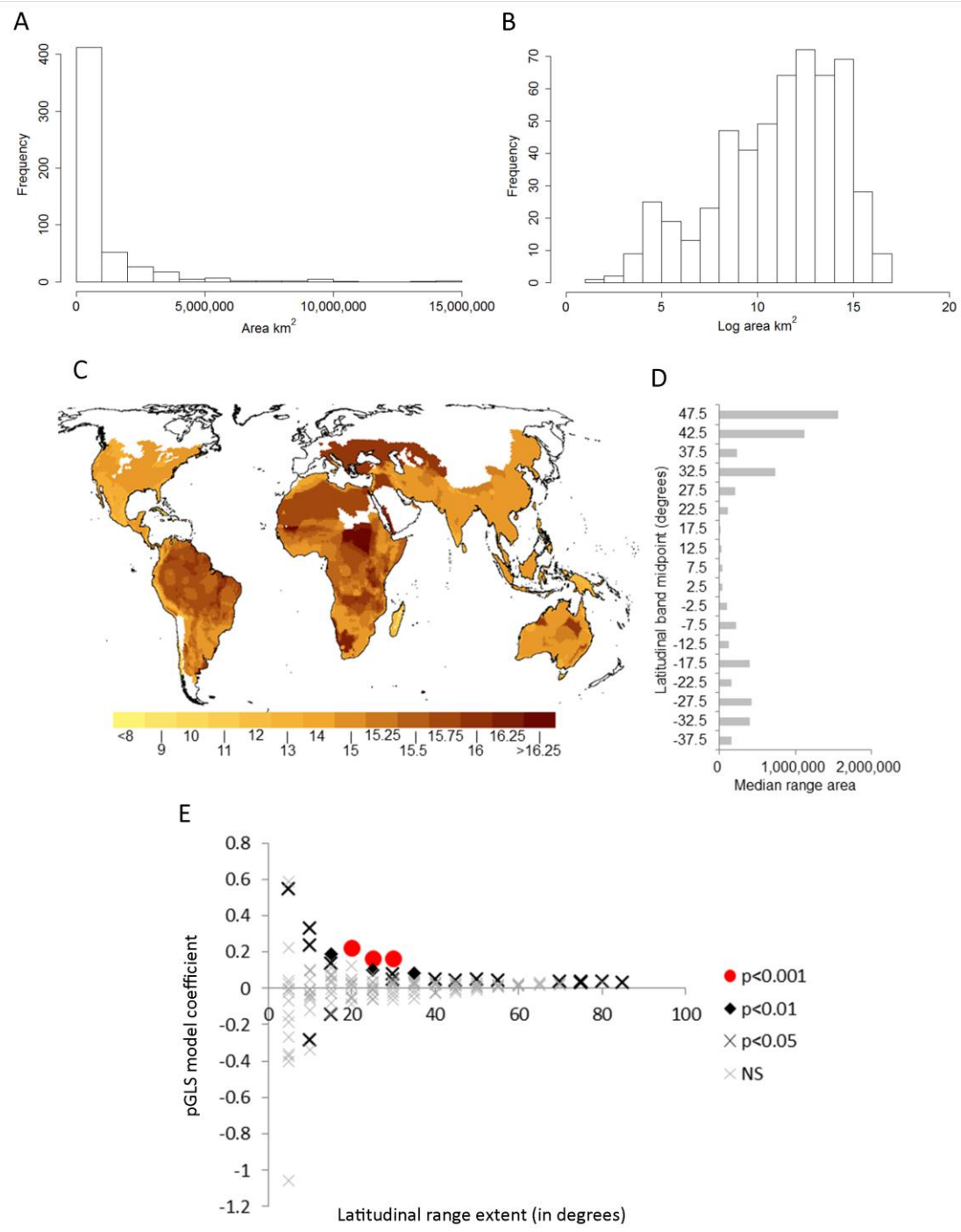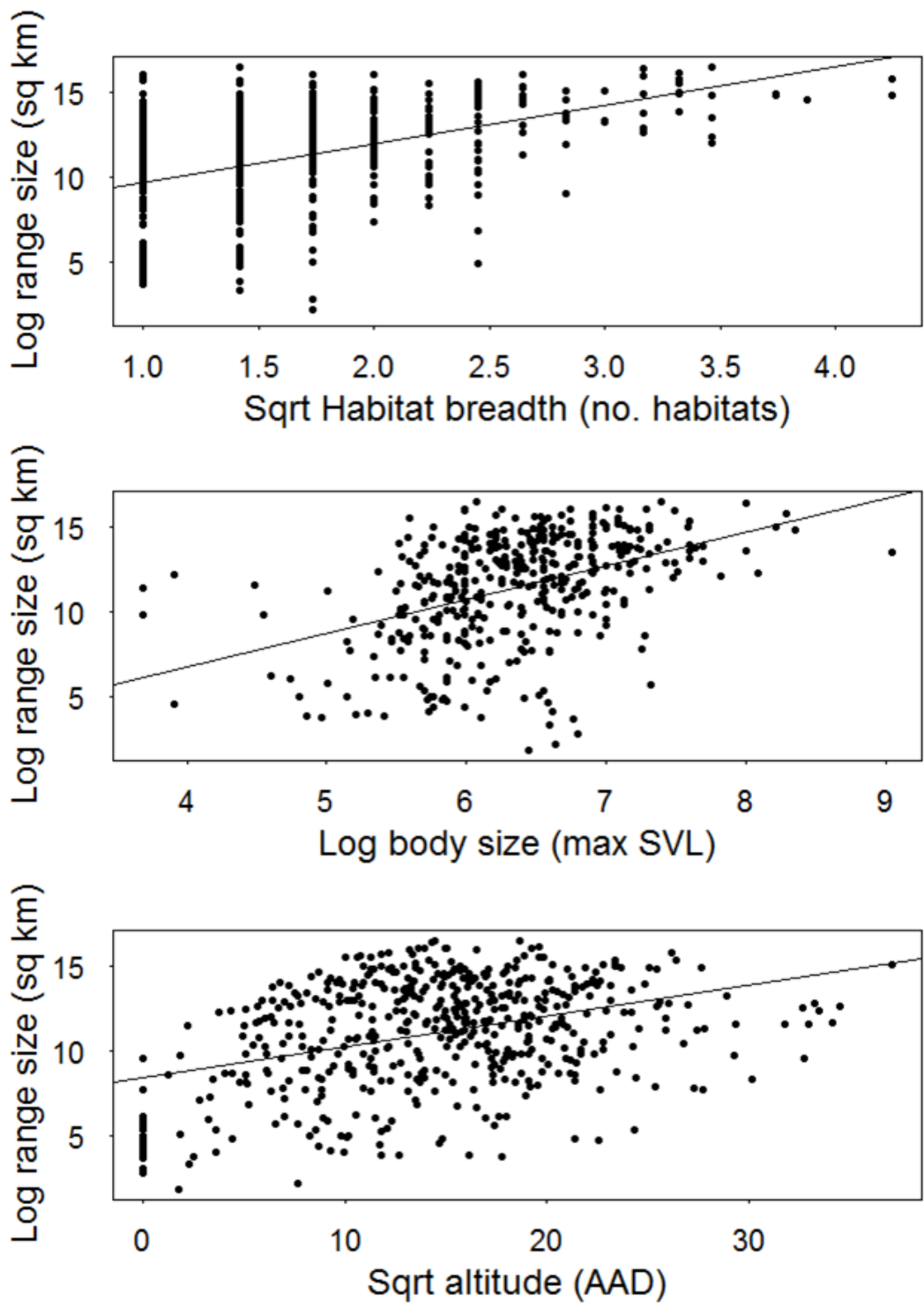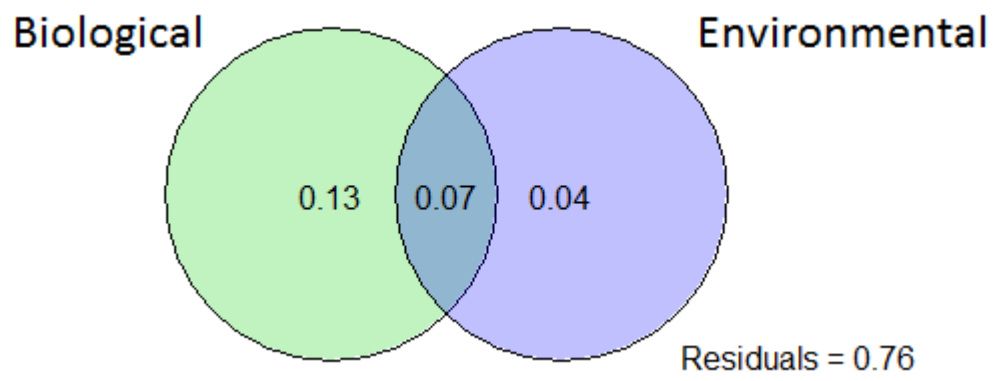
Figure 1

Figure 2.

Figure3.

Figure 4.