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BIODIVERSITY RESEARCH

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Extinct, obscure or imaginary: The lizard species with the smallest ranges

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Abstract

Aim: Small geographic ranges make species especially prone to extinction from anthropogenic disturbances or natural stochastic events. We assemble and analyse a comprehensive dataset of all the world's lizard species and identify the species with the smallest ranges—those known only from their type localities. We compare them to wide-ranging species to infer whether specific geographic regions or biological traits predispose species to have small ranges.

Location: Global.

Methods: We extensively surveyed museum collections, the primary literature and our own field records to identify all the species of lizards with a maximum linear geographic extent of <10 km. We compared their biogeography, key biological traits and threat status to those of all other lizards.

Results: One in seven lizards (927 of the 6,568 currently recognized species) are known only from their type localities. These include 213 species known only from a single specimen. Compared to more wide-ranging taxa, they mostly inhabit relatively inaccessible regions at lower, mostly tropical, latitudes. Surprisingly, we found that burrowing lifestyle is a relatively unimportant driver of small range size. Geckos are especially prone to having tiny ranges, and skinks dominate lists of such species not seen for over 50 years, as well as of species known only from their holotype. Two-thirds of these species have no IUCN assessments, and at least 20 are extinct.

Main conclusions: Fourteen per cent of lizard diversity is restricted to a single location, often in inaccessible regions. These species are elusive, usually poorly known and little studied. Many face severe extinction risk, but current knowledge is inadequate to properly assess this for all of them. We recommend that such species become the focus of taxonomic, ecological and survey efforts.

KEYWORDS
accessibility, endemism, extinction, geckos, holotype, range size, skinks, threat, type locality

1 | INTRODUCTION

A prominent feature of the distribution of biodiversity is the extreme variation in species range sizes. Within the same lineage, some species have continental-wide distributions whereas others are restricted to a single locality (Gaston, 2003). Although ranges can be very labile (e.g., Chen, Hill, Ohlemuller, Roy, & Thomas, 2011; Currie & Venne, 2017; Lyons, 2003; Meiri, Lister, et al., 2013), range size is thought to be the product of ecologically relevant traits such as body size, population density and dispersal ability (Brown, 1984; Pimm & Jenkins, 2010; but see Novosolov et al., 2017). Crucially, from a conservation perspective, range size is known to influence extinction risk. Species with small ranges have, everything else being equal, fewer individuals and lower genetic variation than wide-ranging relatives, often leading to elevated extinction probabilities (Caughley, 1994; MacArthur & Wilson, 1967). Threats such as new (or introduced) predators, pathogens and competitors, severe climatic events (e.g., droughts), cataclysms (e.g., fires and volcanic eruptions) and population-level phenomena (e.g., inbreeding depression) can rapidly wipe out narrow-ranging species (Purvis, Gittleman, Cowlinshaw, & Mace, 2000). Habitat loss and collection for the pet trade can likewise easily cause species with tiny ranges to go extinct. The elevated threat these species face makes them particularly relevant for conservation efforts.

The importance of range size is reflected in the way extinction risk is evaluated by the International Union for Conservation of Nature (IUCN) Red List assessments. One of the five criteria the IUCN (2017) uses to evaluate threat, criterion B, uses estimates of range size to designate extinction probabilities. Although range size per se is insufficient to designate threat, species with ranges (defined as the extent of occurrence) smaller than 20,000 km^2 can qualify as vulnerable under criterion B. To qualify as endangered under criterion B, range size cannot exceed 5,000 km^2, whereas to qualify for the highest level of threat—critically endangered, the threshold is lowered to 100 km^2 (IUCN, 2017).

Although we are often ignorant regarding the true extent of a species' geographic range (because not observing a species somewhere is not sufficient evidence of its absence), we know that ranges can be even smaller than 100 km^2. Many Southeast-Asian geckos, for example, seem to be confined to isolated karst outcrops (e.g., Ellis & Pauwels, 2012; Wood et al., 2017), never venturing far into the surrounding forest. At the minimum, species must be known from one locality, and a single individual, the holotype, on which the species description is based.

Species known only from small ranges are likely to be either difficult to observe, difficult to distinguish from others or genuinely rare. They may even already be extinct. Several studies have tried to link range size to biological attributes such as body size (e.g., Agosta & Bernardo, 2013) or to geographic attributes such as latitude (Rapaport's Rule; Ruggiero & Werenkraut, 2007). A common finding, however, associates range size not with particular biological attributes, but with the year, a species was described (e.g., Costello, Lane, Wilson, & Houlding, 2015; Gaston, Blackburn, & Loder, 1995). Generally, scientists observed, distinguished and described the widely distributed species early. In fact, range size consistently emerges as the key correlate of description date in all tests we know that examined this link (e.g., Collen, Purvis, & Gittleman, 2004; Colli et al., 2016; Costello et al., 2015; Diniz-Filho et al., 2005). Species that were discovered and described (as opposed to being split from other species) relatively recently are poorly known almost by definition, given that not enough time has lapsed for biologists to study their biology, abundance and true range extent. Thus, many recently discovered species may have larger ranges than are currently known.

Species that were described early, and remain poorly known (with few or even just a single observation locality), are more likely to truly occupy small ranges, rather than just poorly known ones. They may even already be extinct. Importantly, however, some may not be real species. Recent species descriptions often follow modern integrative taxonomic practices, compare more species and specimens, and examine more characters than previous descriptions. The species that remain known only from single specimens sometimes turn out to be based on aberrant or juvenile specimens, or belong to congenerics or even to distantly related species, especially if they were described long ago. For example, *Oreodeira gracilipes* was described as an Australian species based on a single specimen, but was in fact a juvenile African *Agama* (Moody, 1988). *Scelotes schebeni* was described based on a single specimen from Namibia, but was later found to be a *Melanoseps occidentalis*, probably from Cameroon (Bauer, 2016).

Correctly identifying the species with the smallest ranges is important to uncover the factors affecting geographic range size. It is also of paramount importance from a conservation perspective, as it can suggest how to correctly allocate limited resources to the most threatened species. Many narrow-ranging species are among those in greatest need of conservation effort. Some may already be extinct without us knowing they are (cryptic extinctions). If some of these species are not valid taxonomic entities, we may be wasting conservation resources. Elucidating the ecological and distributional patterns of species known only from their type localities to establish the roles of true rarity, lack of records and taxonomic ambiguities in generating them is thus crucially important.

We identify all the species of lizards (Reptilia: Squamata, excluding snakes) that are known only from their type locality (the *terra typica*), the place where the species was described from (henceforth "TL-species"). We examine whether these species are taxonomically or geographically clustered (especially in poorly surveyed regions) and whether they share attributes that may make them easy to overlook, such as small size, fossorial habits (or their correlate: reduced limbs) or nocturnal activity. We compare relevant traits of these TL-species to those of all other lizard species, to highlight the attributes associated with small ranges.

We pay special attention to these TL-species that were described relatively early, using an arbitrary cut-off time of 50 years from the present (i.e., 1967 or earlier versus 1968 or later), and compare these species' traits to those of TL-species described more recently.

2 | METHODS

To identify the lizard species known only from their type localities, we reviewed and refined a dataset containing range sizes of all the world's lizards (Roll et al., 2017). We manually reviewed the ranges of all species with ranges smaller than the median size in the global dataset of Roll et al. (2017) to determine whether they are known only from their type locality. For these, we manually searched for additional geographic data in the primary and grey literature using the Reptile Database (Uetz, 2017) and Google Scholar), meta-datasets such as GBIF (www.gbif.org), Vertnet (www.vertnet.org) and the Atlas of Living Australia (www.ala.org.au), IUCN assessments, field guides and our own observations. We further systematically searched data on these species in scientific journals that have dedicated sections for publishing reptile range extensions (e.g., Herpetological Review, Check List, Mesoamerican Herpetology). In addition to the geographic data, we further extracted from these sources the latest year in which individuals of each species were observed alive. We used the latest version (May 2017) of the Reptile Database for taxonomy (Uetz, 2017) and excluded all species known only from fossils or subfossils. We identified all species that are known only from their type locality. We arbitrarily defined a type locality as having a maximum latitudinal and longitudinal range of <10 km or <0.1 degrees because this represents an extent of occurrence smaller than 100 km^2—fitting the IUCN's criterion B1 for an extent of occurrence of a critically endangered species (IUCN, 2017. Note that as this criterion cannot be applied alone, such species are not necessarily classified as threatened). Species inhabiting more than one island were excluded even if the islands are small and close to each other, as these species cannot be said to inhabit a single locality.

We distinguished between species that are only known from old records and those known from recent records (either having been repeatedly found at their type locality or having been described from specimens observed there recently). We arbitrarily placed the cut-off between old and recent records at 50 years ago (1967). We further distinguished species known from multiple specimens and those known only from a single specimen, the holotype. Data and metadata of traits used in our comparisons and analyses of lizard groups can be found in Meiri, Brown, and Sibly (2012); Meiri, Lister, et al. (2013); Meiri, Bauer, et al. (2013); Scharf et al. (2015), Feldman, Sabath, Pyron, Mayrose, and Meiri (2016) and Vidan et al. (2017).

2.1 | Statistical analyses

Only 12% of the species we identified as known only from their type locality are represented in the large-scale squamate phylogeny of Pyron and Burbrink (2014), effectively preventing us from running phylogenetically informed tests. Instead, we explored the effects of individual traits on our classifications of lizards. We used a machine learning procedure to classify lizard species to groups (TL-species versus broad ranged species, and single specimen versus multiple specimens). We explored the relative importance of the different traits when used together in these classification procedures. We used a gentle adaptive stochastic boosting classification model (ADA-Boost; Friedman, Hastie, & Tibshirani, 2000) as our classification mechanism. ADA-Boost distinguishes between cases by combining the outputs of many weak classifiers to achieve, through iterations, a powerful classification with low error rates. This procedure has been successfully applied in a wide variety of fields, outperforming many other classifiers (Hastie, Tibshirani, & Friedman, 2001).

To test our predictions, we used the following predictors in the classification procedure: description year, the biogeographic realm (Wallace, 1859, 1876) in which a species reside (using the maps of Olson et al., 2001), its activity period (day or night, with cathemeral species counted in both categories), whether it is terrestrial, fossorial, saxicolous or arboreal, whether or not it has reduced legs, its infraorder, body mass, if it is an insular endemic and the latitudinal centroid of its range. Our modelling was conducted using the “ada” package in R (Culp, Johnson, & Michailidis, 2016) and incorporated an exponential loss function with 50,000 iterations.

We further tested whether species only known from type localities are found in remote, difficult to access, regions. To do this, we compared the locations of the type locality-restricted lizard and amphisbaenians for which we had precise locality information (Appendix S1) to the point localities of all ~4,550 lizard and amphisbaenians known to be more wide-ranging (Roll et al., 2017). For each point, we extracted its accessibility as measured by the travel time (in minutes, by land or water) to major cities (Nelson, 2008). We then compared the distributions, means and medians of accessibility between point localities of species known only from their type localities with wide-ranging species (whose localities were obtained from literature, observations and museum data; Roll et al., 2017). Extraction of the accessibility information was performed using ArcGIS (ESRI, 2011); statistical analyses were conducted using R.

3 | RESULTS

3.1 | The dataset

We identified 927 species of lizards that are, as far as we know, restricted to their type locality (i.e., an area with a linear extent no larger than 10 km or 0.1 of a degree; Appendix S1). They represent fully 14.1% of all lizard diversity (6,569 species, Uetz, 2017; supplemented with additional species described until 1 September 2017). Of these 927 species, 756 were observed in the wild in the last 50 years (since 1968), whereas 171 were last seen between 1830 (*Diploglossus microlepis* (Gray, 1831)) and 1967 (e.g., *Calotes bhutanensis*, Biswas, 1975). Only 191 of the TL species were seen alive after they were described, whereas the other 736 (79%) were last seen alive when the holotype

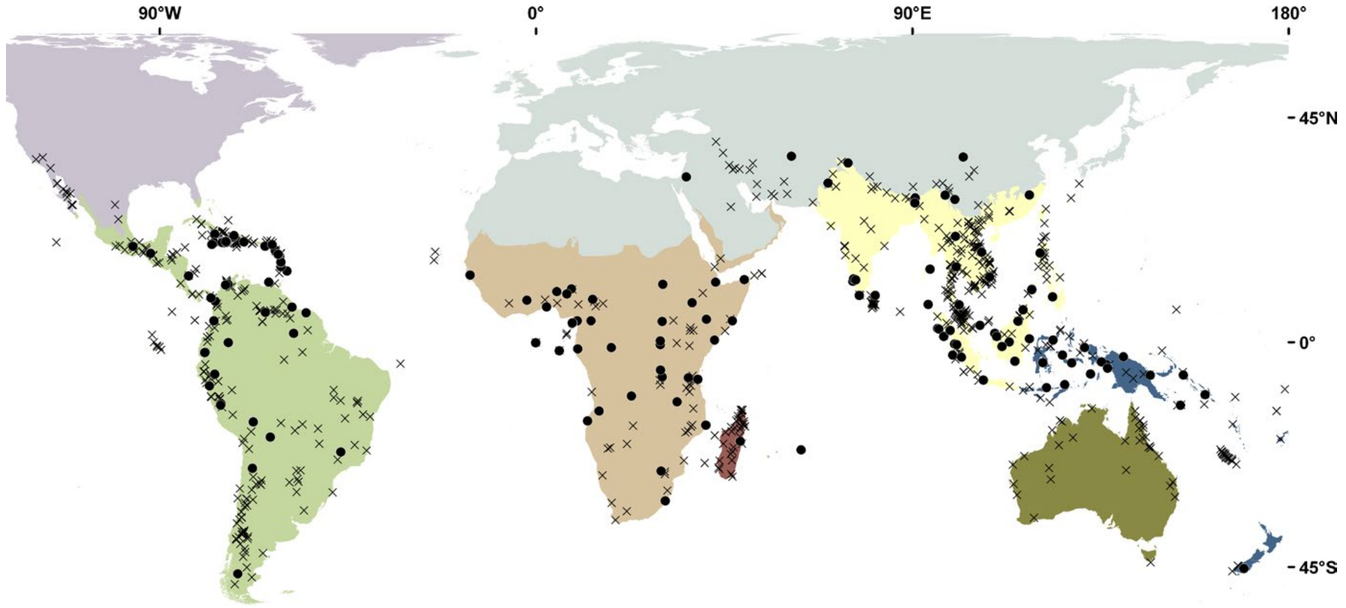

FIGURE 1 Lizard species known only from their type localities. Circles: species not observed after 1967 ($n = 151$). Crosses: species observed after 1967 ($n = 754$). Eighteen species could not be mapped. Underlying colours represent the biogeographic realms. Equal-area Behrmann projection

TABLE 1 Lizards known only from their type localities versus wider ranging species within families

Family	TL-species	Holotype only	Wider ranging species	Proportion of TL-species
Gekkonidae*	261	33	867	23%
Scincidae	210	72	1,414	13%
Dactyloidae	58	15	361	14%
Liolaemidae	52	6	255	17%
Agamidae	48	16	439	10%
Gymnophthalmidae	42	13	220	16%
Amphisbaenidae	31	13	147	17%
Sphaerodactylidae*	31	7	184	14%
Chamaeleonidae	28	3	178	14%
Anguidae	23	11	106	18%
Tropiduridae	20	3	116	15%
Lacertidae	15	6	311	5%
Phyllodactylidae*	15	2	122	11%
Diplodactylidae*	12	3	137	8%
Dibamidae	11	5	12	48%
Eublepharidae*	8	0	28	22%
Carphodactylidae*	7	0	23	23%
Phrynosomatidae	7	0	147	5%
Teiidae	7	0	149	4%
Leiocephalidae	6	1	25	19%
Varanidae	6	2	73	8%
Xantusiidae	6	0	28	18%
Cordylidae	5	0	63	7%
Hoplocercidae	5	0	14	26%
Iguanidae	5	0	38	12%
Gerrhosauridae	3	2	34	8%
Anniellidae	2	0	4	33%
Leiosauridae	1	0	32	3%
Pygopodidae*	1	0	45	2%
Xenosauridae	1	0	10	9%
Bipedidae	0	0	4	0%
Blanidae	0	0	6	0%
Cadeidae	0	0	2	0%
Corytophanidae	0	0	9	0%
Crotaphytidae	0	0	12	0%
Helodermatidae	0	0	2	0%
Lanthanotidae	0	0	1	0%
Opluridae	0	0	8	0%
Polychrotidae	0	0	7	0%
Rhineuridae	0	0	1	0%
Shinisauridae	0	0	1	0%
Trogonophiidae	0	0	6	0%

Lizard species in each family that are known from their type locality only ("TL-species," maximum linear extent of <10 km; 1st column), and only known from the holotype (2nd column), versus the number of more widely ranging species (3rd column; maximum linear extent >10 km). The fourth column is the proportion of species known from their type locality out of all species in the family. Gecko families are marked with an asterisk.

or type series was collected. Two hundred and thirteen species are only known from their holotype (Appendix S1; 112 species observed during the last 50 years, 101 species only observed earlier).

3.2 | The geography of small-ranged lizards

Lizards known only from their type localities inhabit mostly tropical regions and some arid regions (although the Sahara and Sahel, for example, have few TL-species). Those known only from old records show a more restricted, almost entirely tropical, distribution (mean absolute value of latitude: 11.3 ± 9.2° *SD*), especially in Indonesia, equatorial Africa, northern and western South America and the Caribbean (Figure 1). More recently observed species have additional hotspots, in both tropical and desert regions (e.g., in Australia, Argentina and Chile, Madagascar, New Caledonia, Iran, north-western Mexico and southern Asia; mean of absolute value of latitude: 15.7 ± 9.6°; Figure 1).

Overall, TL-species tend to inhabit somewhat lower latitudes than large-ranged species (absolute latitude 14.9° vs. 18.5°, $t_{905,5607} = 9.40$, $p < .0001$). They are relatively rare in the Nearctic, the Palaearctic and Australia (8%, 5% and 5% of the lizard fauna, respectively), but comprise 28% of the lizard species in the Oriental realm.

3.3 | Taxonomic composition

Geckos (Gekkota) dominate the list of TL-species (335 of 927 species, 36%), followed by skinks (210, 24%) and anoles (58, 6%; Table 1). The list TL-species not observed in the last 50 years, however, is dominated by skinks (69 of 171 species, 40%), followed by geckos (31 species, 18%) and amphisbaenians (14, 8%). Interestingly, this is mirrored in the taxonomic composition of the species known only from their type specimen (regardless of when it was collected), for which skinks are the largest group (72 of 213 species, 34%), followed by geckos (45 species), agamids (16), anoles (15) and both gymnophthalmids and amphisbaenians (14; Table 1). The Dibamidae has the highest proportion of species only known from the type locality (11 of 23 species; 48%), followed by Anniellidae (two of six species; 33%), Hoplocercidae (26%) and three gecko families: Gekkonidae (23%), Carphodactylidae (23%) and Eublepharidae (22%). Twelve of 42 families have no TL-species, but these are species poor (the largest is the 12-species Crotaphytidae).

3.4 | Traits of lizards known only from their type localities

Lizards known only from their type localities have generally been described later than wide-ranging species (by 58 years on average, $t_{927,5641} = 27.3$, $p < .0001$; Figure 2). Most (3,142 of 4,366; 72%) of the wide-ranging species for which we have data are diurnal (22% nocturnal, 6% cathemeral). Those known only from their type localities tend more towards nocturnality (232 of 612 species, 38%, vs. 59% diurnal, and 3% cathemeral; $\chi^2 = 73.9$, $p < .0001$; all χ^2 values are for 2 × 2 tables). This is especially the case for the TL-species observed in the last 50 years (39% nocturnal), as would be expected by the high proportion of geckos among them. We only know the activity times of 46 TL-species that were last seen before 1968, whereas those of 127 of them (73%) are unknown.

Contrary to our expectations, fossorial species were not more dominant among species known only from the type locality. Assuming all amphisbaenians and dibamids are fossorial, 12.2% (86 of 701 species with known habits) of the TL-species are fossorial versus 10.2% (557 of 4,913) lizards with wider ranges ($\chi^2 = 0.46$, $p = .53$). Species known only from their type localities were more associated with rocky substrates (39% species fully or partially saxicolous, versus 26% of the wider ranging species; $\chi^2 = 52.5$, $p < .0001$). The maximum body mass of wider ranging species is 71% higher, on average, than those known only from their type localities (back-transformed from logarithms: average 10.2 ± 5.0 g vs. 6.0 ± 4.2 g, $t_{910,5634} = 9.38$, $p < .0001$; Figure 3; non-transformed averages are 135 and 32 g, respectively). This difference is retained when we compare sizes within families (as recognized by Uetz, 2017; average difference 41%, $t = 7.84$, $p < .0001$).

3.5 | Classifications analysis

We used our classification procedure to distinguish between TL-species and species with wider ranges for which we had data for all the traits we coded (4,237 wider ranging species, 555 TL-species). Our model managed to classify the two groups nearly perfectly, with a cross-validated training error of 0% and an out-of-bag error rate of 1.7%. These traits can thus be used to successfully distinguish TL-species from wider ranging species. Figure 4 depicts the relative importance of the different traits in the classification procedure, and the associated partial dependence plots are shown in Appendix S2. They highlight the importance of low latitude and infraorder affiliation in the classification, as well as the roles of biogeographic realm, low body mass and late description year.

In our classification of TL-species known either from one (62 species) or multiple specimens (493 species), the model achieved perfect classification between the groups with a cross-validated error of 0% (both training and out of bag). For this classification, most attributes played an important role. Realm and infraorder affiliation, fossoriality and the degree of leg reduction (species known only from their holotype tend to be fossorial, limbless or with reduced legs; see Appendix S3 for variable importance) were the best classifiers.

3.6 | Accessibility and threat

The accessibility (time to major cities, in minutes) of the localities of the 868 TL-species in our database, for which such data could be calculated, ranged from 8 min for the aptly named *Cyrtodactylus metropolis* (Grismer, Wood, Onn, Anuar, & Muin, 2014) to 7,432 min (=5.16 days) for the Venezuelan *Adercosaurus vixadnexus* (Myers & Donnelly, 2001). These 868 points are generally found in inaccessible places compared to the 136,840 unique localities for which we have data for wide-ranging lizard species (Figure 5). The mean (518 min = 8.6 hr) and median (319 min = 5.3 hr) inaccessibility values are greater for species known only from their type localities

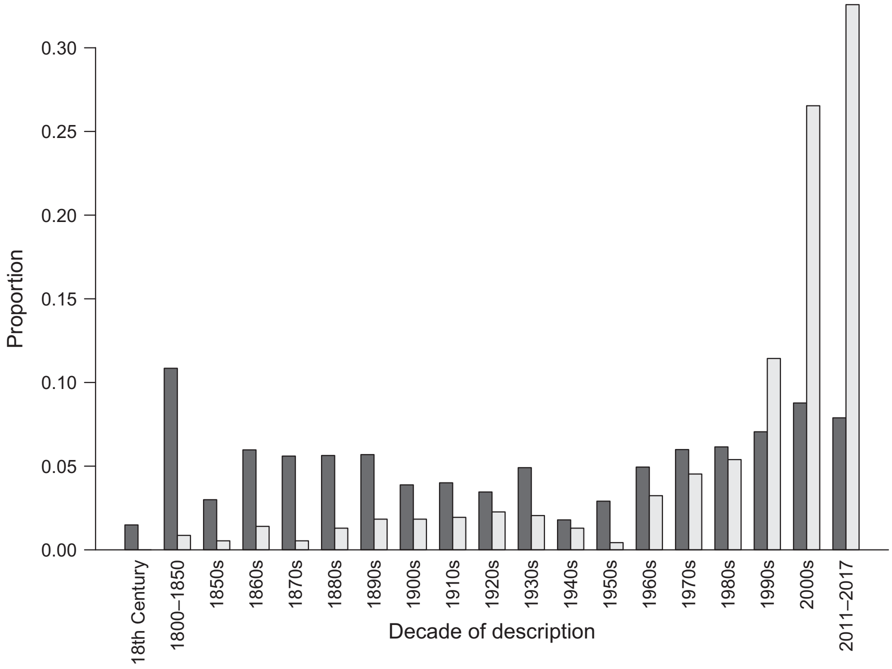

FIGURE 2 Decades when wide-ranging lizards (dark grey; 5,641 species) and species known only from their type localities (light grey; 927 species) were described. Frequency is the proportion of species in each category (TL-species and wider ranging species) described in a given decade

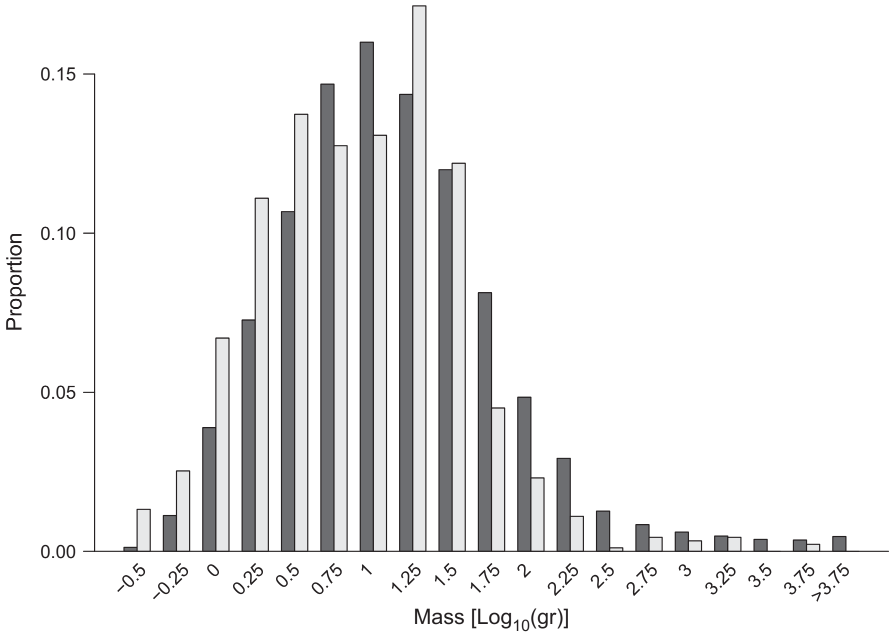

FIGURE 3 Maximum body masses of wide-ranging lizard species (dark grey, 5,634 species) and species known only from their type localities (light grey, 910 species). Frequency is the proportion of species in each category (TL-species and wider ranging species) in a given mass bin. Masses (in grams) are log-10 transformed

than those of wide-ranging species (by 34% and 49%, respectively; $t = -5.16$, $df = 873.8$, $p < .0001$).

Of the 927 species known only from their type locality, 625 (67%) have no IUCN assessment (as of September 2017). Of the 302 assessed species, 126 (42%) are data deficient (DD) and 93 (31%) are listed as threatened: 35 vulnerable (VU), 16 endangered (EN) and 42 critically endangered (CR). Seventy-seven species are classified as non-threatened (25%): 61 least concern (LC) and 16 near threatened (NT; IUCN 2017). The respective proportions for wide-ranging lizards are 11% DD, 19% threatened and 69% non-threatened species. The populations of 26 species are assessed as decreasing, and of 58 (including *Lipinia zamboangensis*, last seen in 1959, and the extinct *Tachygyia microlepis*) as stable. For most species, the population status is unknown (202 species) or has not been assessed (625 species). None are increasing.

Of the 171 species seen only before 1968, sixty-five have been assessed. Fifty-one are listed as data deficient. One African skink, *Panaspis helleri* (Loveridge 1932), is classified as least concern although as far as we are aware it is only known from its holotype (although a specimen in the Royal Museum for Central Africa [RMCA] from 2.70°S, 27.33°E, ~450 km from the type locality of *P. helleri* in Bugongo Ridge, Mt. Ruwenzori, DRC, may prove to also belong to this species, Danny Meirte, personal observation). Seven are listed as threatened (2 VU, 1 EN and 4 CR). Finally, the IUCN lists six species in our list as extinct

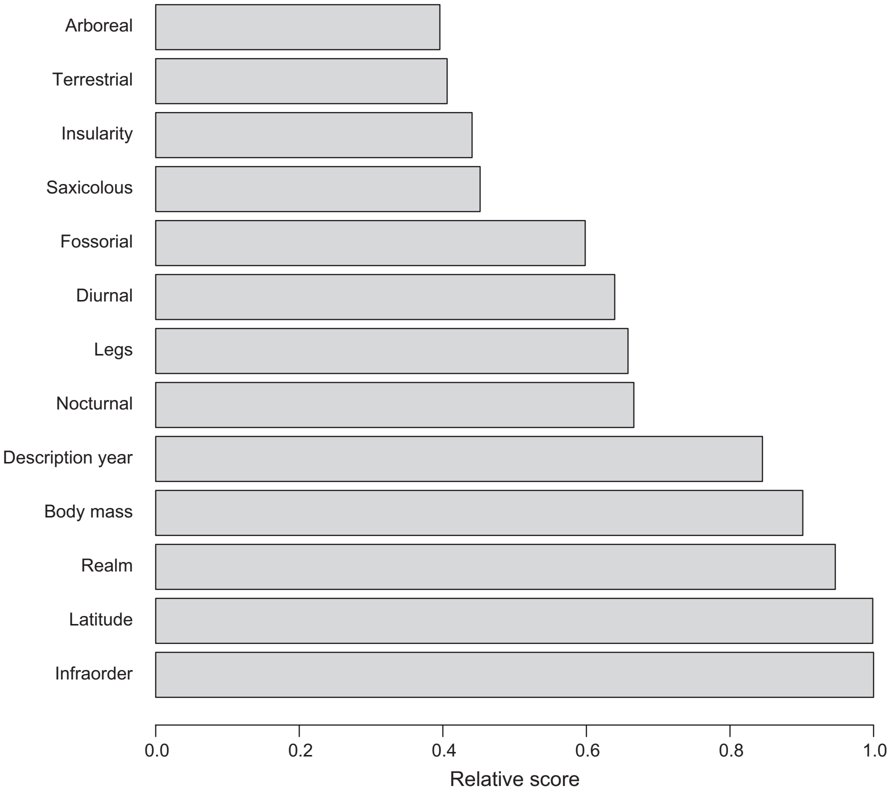

FIGURE 4 The relative importance of different traits in classifying lizards to the TL-species versus wider ranging species groups (555 and 4237 species in each group, respectively, for which data on all traits are known)

(*Celestus occiduus*, *Hoplodactylus delcourti*, *Leiocephalus herminieri*, *Leiocephalus eremitus*, *Tachygyia microlepis* and *Tetradactylus eastwoodae*). Slavenko, Tallowin, Itescu, Raia, and Meiri (2016), however, lists 20 species known only from their type localities (2.2%) as extinct (as well as 20 extinct wide-ranging species; 0.4%).

4 | DISCUSSION

We found that 927 of the world's lizard species—nearly one in seven of the currently recognized 6,568 species—are known only from the lowest end of the range size spectrum, basically from their type locality alone. Furthermore, 736 of them have never been recorded after being described, which was more than 50 years ago for 162 of them. No fewer than 213 species are only known from a single specimen.

Many species may indeed have extremely small ranges, particularly the 64 species residing on islands with <10 km maximum linear extent (e.g., *Anolis ernestwilliamsi*, Lazell, 1983), as well as cave and rock-associated endemics (e.g., *Cyrtodactylus hontreensis*, Ngo et al., 2008). Others may be more wide-ranging but were either only recently described or elevated to species level, have cryptic lifestyles, or inhabit poorly surveyed or difficult-to-access regions. Our results highlight those species of lizards (and those regions, e.g., Indonesia; see Figure 1) that are in most desperate need of further work to assess their true ranges.

Our definition of a type locality, as an area with a maximum known linear extent of less than 10 km, is arbitrary. The range sizes of lizards in general, however, are distinctly bimodal, with a pronounced mode of tiny ranges (<30 km^2), followed by a relatively symmetrical distribution around 100,000 km^2 (Roll et al., 2017). Thus, although a type locality versus wider ranging dichotomy of some sort seems justified, there is nothing special about our chosen cut-off. A similar argument can be made regarding our decision to place the early versus late cut-off at 50 years ago. We arbitrarily chose this value to represent a time span that is about the same as a long career in herpetology and much longer than the lifespan of nearly all lizards (Scharf et al., 2015). It also approximately marks an era of expanded research into lizard systematics, with 44% of all lizard species described since 1967 (the median year is 1947). The 1950s and 1960s were a time of few lizard species descriptions (Figure 2, see also Pincheira-Donoso, Bauer, Meiri, & Uetz, 2013), and the 1960s and 1970s are often thought to be when global warming started to strongly affect the phenology and ranges of organisms (e.g., Walther et al., 2002). Thus, contrasts based on these arbitrary numbers serve to illustrate important points: many lizards are known from single localities, and many of them have not been seen for a very long time, during which many important changes (e.g., habitat loss, climate change) have occurred.

4.1 | Taxonomic considerations

Some of the species in our dataset may not be real species but belong to other, better known and more widely ranging species (Isaac, Mallet, & Mace, 2004; Meiri & Mace, 2007). Many of the 'older' species we list here are known from very few specimens, and some have been lost. For example, the holotype (and only specimen) of *Chalcides pentadactylus* (Beddome, 1870) was lost before 1935 (Smith, 1935), and the holotype of *Lipinia miangensis* (Werner, 1910) was destroyed during World War II. Others are in a poor state of preservation (e.g.,

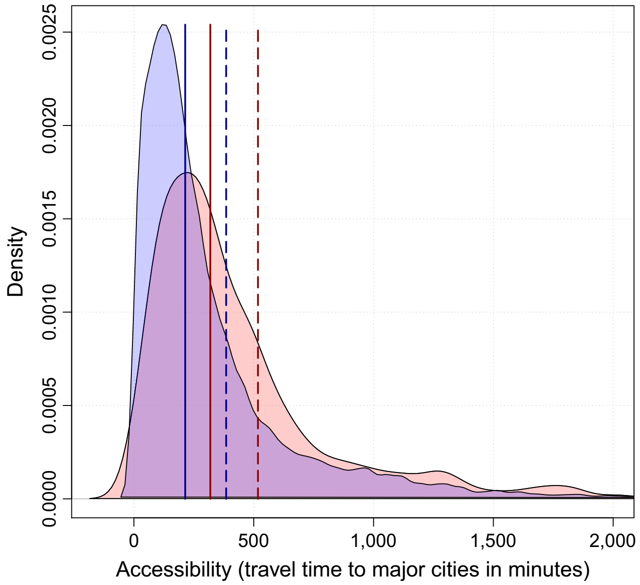

FIGURE 5 Accessibility of lizard species known only from type localities (pink, red lines) versus wide-ranging species (blue). The plots depict histograms of accessibility (= travel time to major cities, in minutes) of localities from which TL-species and wider ranging lizards are known (dashed lines: mean values, full lines: median values)

Liolaemus melanopleurus, Pincheira-Donoso & Nuñez, 2005; *Capitellum parvicruzae*, Hedges & Conn, 2012). This makes it difficult to assess whether they are indeed distinct from other, better known and more widely ranging species. Even some recently described species are known from very old specimens that long remained unidentified in scientific collections. For example, *Mabuya guadeloupae* (Hedges & Conn, 2012) and *Hemidactylus endophis* (Carranza & Arnold, 2012) are based on specimens dating back to 1892 and 1887, respectively (Hedges & Conn, 2012; and Salvador Carranza, personal communication to Shai Meiri). This also likely means that they were kept in preservatives that left little DNA accessible for genetic analysis. That said, some of the species we identify as being known only from their type locality—especially those known just from the holotype—have long been known as requiring further taxonomic evaluation (e.g., *Leiolopisma fasciolare*, *Salea gularis* and *Trachylepis betsileana*; Zug, 1985; Smith, 1935; Nussbaum, Raxworthy, & Ramanamanjato, 1999; respectively). Together with more survey work, taxonomic revision of some of these lizards is strongly warranted.

4.2 | Traits of lizards known only from their type localities

In general, TL-species have a unique set of attributes that distinguishes them from wider ranging species. We identify some traits that may make these species difficult to find, such as relatively small body size and nocturnal behaviour. It is important to interpret these findings cautiously given that, for example, the apparently small body size of most TL-species we list may be an artefact of the use of maxima to represent lizard sizes (Meiri, 2008). Coupled with small sample size, this will automatically result in small inferred body sizes (Meiri, 2007). That said, the large effect size we identify (see above) makes it unlikely that all the size differences could be ascribed to sampling. Nocturnality may make lizards more difficult to detect, possibly meaning that the recent increased rate of finding nocturnal TL-species could reflect the increased use of head torches (which also resulted in finding new species of diurnal lizards, e.g., anoles and chameleons, which were detected sleeping on branches, e.g., Poe, Latella, Ayala-Varela, Yanez-Miranda, & Torres-Carvajal, 2015). It may also reflect the propensity of geckos to have narrow ranges, tropical distribution and nocturnal behaviour (Gamble, Greenbaum, Jackman, & Bauer, 2015; Meiri, 2016; Vidan et al., 2017). Indeed, the propensity of geckos to specialize in using specific and naturally isolated substrates (usually rocks; e.g., Giri, Bauer, Vyas, & Patil, 2009; Grismer, 2010; Heinicke, Jackman, & Bauer, 2017; Oliver, Bourke, Pratt, Doughty, & Moritz, 2016; Oliver & Doughty, 2016; Pauwels & Sumontha, 2014; Wood et al., 2017) and speciate where these are found may often predispose them to have very small ranges. Large, relatively continuous patches of habitat, such as Amazonia and the Sahara, on the other hand, harbour many lizard species (Roll et al., 2017), but relatively few TL-species (Figure 1).

Surprisingly, we did not find that burrowing lifestyle makes lizards more likely to have tiny ranges. Living underground may not only make species difficult to find, but may also seriously limit their dispersal abilities. The obligatory fossorial amphisbaenians, however, have a similar proportion of species known only from the type locality to that of non-fossorial lizards (31 species, 2.2% vs. 166, 3.3% of the more wide-ranging species). The mostly fossorial and secretive dibamids, however, have the highest ratio of TL-species of all lizard families. The high percentage of recently described geckos could have ‘diluted’ the signal of fossorial taxa. On the other hand, habitats used by fossorial reptiles are often extensive, whereas some exposed rock escarpments that specialized saxicolous lizards (e.g., many geckos) use are small and relatively stable over evolutionary time, mediating persistence. It should be noted, however, that many species known only from their type localities, especially some of the skinks, are so poorly studied that we have no data indicating whether they are fossorial or not.

4.3 | Threat status

By definition, species known from only a few specimens are also relatively little known. This is especially true for species known only from old records and from few or even single specimens. Thus, even though the IUCN guidelines explicitly say that “the liberal use of ‘Data Deficient’ is discouraged”; IUCN, 2017), DD is the most commonly ascribed status for the species we analysed here, and rightfully so. We suggest that DD species are probably rare (or they would be easier to ascribe to another category; cf. Bland & Bohm, 2016). We think that, until more data are gathered, species known only from a single specimen cannot be ascribed any status other than DD—or extinct. They may reasonably be listed as threatened if their habitat is known to be deteriorating, but then perhaps they are already extinct. If their habitat is large and relatively intact they may well be doing fine, but current knowledge probably precludes us from making any strong inference. Forty-six species in our list (Appendix S1) are assessed as non-threatened despite being known only from their original description. Four of them (*Panaspis helleri*, *Liolaemus lopezi*, *Adercosaurus vixadnexus* and *Loxopholis hoogmoedi*) are assessed as least concern while being known from just one individual (but see above for *P. helleri*). We suggest they may not be sufficiently well known to merit such a positive assessment.

Species known only from a single locality, especially if they have not been seen for a long time, may already be extinct. Only six species in our list are formally recognized as extinct by the IUCN. Red listing is not yet complete for reptiles (only 51%, 5,338 of >10,500 species as of May 2017), and several species most likely extinct (e.g., *Phelsuma edwardnewtoni*) are not yet listed by the IUCN. Twenty species we identify here (Appendix S1) as being known only from their type localities were listed as extinct by Slavenko et al. (2016). These include forms that have not been seen for decades, despite repeated surveys (e.g., *Alinea lanceolata*, Hedges & Conn, 2012), and species that were recently described based on old specimens (e.g., *Tarentola albertschwartzi*, Sprackland & Swinney, 1998; and many of the skinks described by Hedges and Conn (2012), such as *Mabuya guadeloupae* and *Capitellum parvicruzae*). In contrast, Slavenko et al. (2016) identify exactly the same number (20) of extinctions in species we consider more wide ranging. Thus species known only from the type locality are seven times more likely to have gone extinct than wider ranging ones. Even these numbers may underestimate the actual extinction rates of species known only from the type locality—as many of them were not seen for decades. We suggest that species not seen for 50 years or more should be reviewed as a matter of priority by the IUCN and are surveyed for in their last (and only) known locality by conservation agencies and herpetologists alike.

5 | CONCLUSIONS

Range-restricted species, i.e. true narrow endemics, are critical for the study of evolution, bioregionalization processes, small-population ecology and conservation (Nogueira, Ribeiro, Costa, & Colli, 2011; Whittaker, Araújo, Jepson, Ladle, & Willis, 2005). In general, lizards (and amphibians) have much smaller ranges than other vertebrates (e.g., Anderson, 1984; Lewin et al., 2016; Roll et al., 2017). They may thus be particularly important proxies for patterns of endemism in other, poorly known narrow-ranging taxa (e.g., most invertebrate taxa). Our work demonstrates that we still poorly understand the status of even the narrow-ranging taxa already described—many may well be threatened, or even extinct, but at the moment, we simply lack adequate data to assess their status. At the same time, the rate of accumulation of newly described endemics is increasing (Figure 2), suggesting that endemism levels in many regions and habitats remain underestimated. Thus, above all else, this work underlines the critical importance of careful, targeted surveys in nature and of integrated taxonomic analyses, to refine our understanding of which narrow-ranging lizards are valid species, which are likely to be already extinct and which are in dire need of protection.

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DATA ACCESSIBILITY

All data and references on the species known only from their type localities are included in Appendix S1.

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BIOSKETCH

The research team is dedicated to the study of lizard taxonomy, biology and biogeography, as well as to lizard conservation.

Author contributions: S.M. conceived and designed the study, U.R. and S.M. analysed the data, all the authors helped collect and verify the data, S.M. wrote the manuscript. All the authors helped the writing.

SUPPORTING INFORMATION

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

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