


A shocking discovery of threat risks on newly described species of weakly electric fishes

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Abstract

This study aims to investigate relationships between species traits and publication date in the weakly electric osteoglossiform Mormyroidea (African knifefish and elephantfishes) and the ostariophysan Gymnotiformes (Neotropical knifefishes). It is investigated whether body size and geographic distribution area are correlated with publication date and whether extinction risk differs between both phylogenetically distant and geographically isolated clades. Statistical modelling indicates that the number of new species described annually is stable in mormyroids and clearly increasing in gymnotiforms. Best-fitting generalised linear models (GLM) indicate that the newly discovered species are more often of small-bodied, predominantly narrowly distributed and more likely to be threatened with extinction. These characteristics are more pronounced in mormyroids when compared with gymnotiforms, suggesting that some African electric fishes may live an ephemeral existence after formal description. Despite taxonomic work has been more intense in the Neotropics than in Africa in the recent decades, there is evidence that the African continent represents the next frontier of species descriptions. Taxonomic studies are fundamental for the understanding of richness and distribution and hence extinction risk assessment and conservation, of these remarkable convergent fish clades.

KEYWORDS

conservation, publication date, species discovery, taxonomy, traits, weakly electric fishes

1 | INTRODUCTION

Linnaean taxonomy began > 250 years ago and since then > 33,500 actinopterygians have been discovered and described worldwide, comprising 96% of all living fish species (Fricke *et al.*, 2018a). Taxonomically, actinopterygians are divided into the Cladistia, Chondrostei and Neopterygii (Betancur-R *et al.*, 2017; Near *et al.*, 2012), the latter being the largest clade encompassing a myriad of morphotypes and convergent forms. One of the most intriguing cases of convergent evolution in the Neopterygii is that of the osteoglossiform Mormyroidea (African knifefish and elephantfishes) and the ostariophysan Gymnotiformes (Neotropical knifefishes), both of which possess the ability to generate a weak electric signal for

environmental navigation and social communication (Albert, 2001; Alves-Gomes, 2001; Hopkins, 1995; Kirschbaum, 2008).

Ampullary electroreceptors and the ability to sense low-frequency electric fields evolved early in vertebrate history with the common ancestor of all gnathostomes (Betancur-R *et al.*, 2017; Near *et al.*, 2012). Active electroreception was lost twice, in the Amniota and at the origin of the Neopterygii and was reacquired in few lineages of the Teleostei (Figure 1). The osteoglossiform Notopteroidei (Mormyridae, Gymnarchidae, Xenomystidae, and Notopteridae) and the ostariophysan Siluriphysi (Siluriformes and Gymnotiformes) independently re-evolved ampullary electroreceptors and the ability to use passive electrolocation to detect biological sources of electric fields generated by prey organisms, predators, or conspecifics.

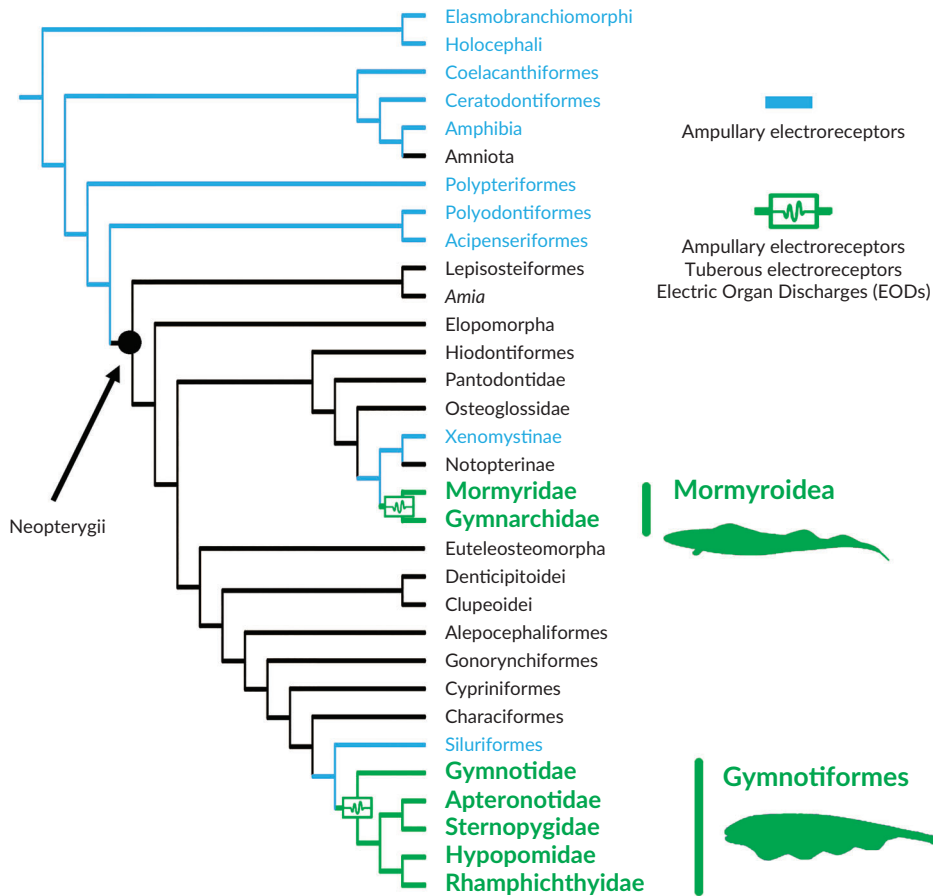


FIGURE 1 Cladogram of the gnathostomes highlighting the African Mormyroidea (Mormyridae and Gymnarchidae) and the Neotropical Gymnotiformes, depicting the evolution of ampullary and tuberous electroreceptor and myogenic electric organs (backbone tree from Betancur-R *et al.*, 2017; gymnotiform tree from Tagliacollo *et al.*, 2015)

Subsequently, active electrolocation evolved in the African Mormyroidea (Mormyridae and Gymnarchidae) and the Neotropical Gymnotiformes (Figure 1). These convergent groups are unique among all living vertebrates in possessing ampullary and tuberous electric organs, the latter being specialised for the detection of their own electric organ discharges (EOD). Therefore, they are the only vertebrates using self-generated electricity in both navigation and communication (Albert & Crampton, 2005; Bullock *et al.*, 1993; Kirschbaum, 2008; Lavoué *et al.*, 2012). The electric organ novelties appeared in both groups in approximately the same geological time-frame, during or probably immediately after the final separation of the South American and African continents in the early Cretaceous, c. 110 million years ago (Lavoué *et al.*, 2012).

In addition to electrolocation, mormyroids and gymnotiforms display an extraordinary array of convergent and parallel phenotypes. Convergences include striking morphological similarities in body shape and size, swimming behaviour (Hopkins, 1986; Nanjappa *et al.*, 2000), reproductive behaviour (Kirschbaum & Schugardt, 2002), and nocturnal foraging habits (Winemiller & Adite, 1997). These adaptations might have evolved secondarily, after the origin of electrolocation as a consequence of shifts in ecological niches and prey organisms exploited by the electrosensory systems (Lavoué *et al.*, 2012). Parallelism refers to independent but similar patterns of trait evolution from the same ancestral trait (Schluter *et al.*, 2004) and includes at least two instances: myogenic electric organs developmentally derived from

skeletal muscle progenitor cells or myoblasts (Kirschbaum, 1977; Kirschbaum & Schwassmann, 2008; Zakon & Unguez, 1999) and tuberous electroreceptors derived from similar lateral-line receptor precursors (Gibbs, 2004; Modrell *et al.*, 2011). The parallel origin of complex traits offers opportunities to investigate generalised patterns underlying the origins of evolutionary novelty between the African and Neotropical electric fishes.

Freshwater fishes are not only among the most diverse of all vertebrate groups, with nearly 16,000 described species, but they are also the most highly threatened (Winemiller, 2018). Although several studies have sought to assess risk by identifying characteristics that might favour extinction among certain groups of fishes or within specific geographic regions, none has succeeded in identifying a comprehensive and unifying set of such traits on a global scale (Duncan & Lockwood, 2001). Extinctions can be phylogenetically selective (Bennett & Owens, 1997; Purvis *et al.*, 2000; Russell *et al.*, 1998) and, because of their electrosensory systems, mormyroids and gymnotiforms are directly affected by the physico-chemical changes in the environment and could be easily extirpated after an environmental imbalance. However, increasing evidence from several clades (*e.g.*, fishes, reptiles, birds, mammals) has suggested that body size and the range area are good predictors of extinction risk (Cardillo *et al.*, 2005; Cooper *et al.*, 2008; Gaston & Blackburn, 1995; Meiri, 2016; Olden *et al.*, 2007). Interestingly, these traits are correlated with species description date, such that newly described species are usually

smaller in size, live in narrower geographical ranges and are more prone to be threatened with extinction, when compared with species described decades ago (Collen *et al.*, 2004; Diniz-Filho *et al.*, 2005; Meiri, 2016).

This study investigates relationships between species traits and publication date in the convergent weakly electric African mormyroids and Neotropical gymnotiforms. It is investigated whether maximum body size and geographic distribution area are correlated with publication date and whether extinction risk differs between both distantly related and geographically isolated clades.

2 | MATERIAL AND METHODS

2.1 | Random variables

To investigate the correlation between three species traits (maximum body size, geographic distribution area and threat risk) and publication date in the highly convergent African and Neotropical electric fishes, a comprehensive list of species names and publication dates was assembled for 221 and 249 mormyroids and gymnotiforms, respectively. The list and number of species described per year (cSPP) was derived from Bill Eschmeyer's Catalog of Fishes (Fricke *et al.*, 2018b), Carl Ferraris' checklist (Ferraris Jr *et al.*, 2017) and, when necessary, updates available in the literature.

Three species traits were selected: maximum body size (MBS), geographic distribution area computed as extension of occurrence (EOO), and threat risks (THR). MBS was measured as the total length as defined in *FishBase*, the global species database of fishes (Froese & Pauli, 2018). The MBSs were obtained from *FishBase* or from the largest individual measured in the original descriptions. Some MBSs were updated with information obtained from the examination of specimens deposited in museum collections. To minimise the effect of outliers (*e.g.*, species having MBS larger than 2 SD), an annual median of MBS per clade was calculated for the statistical analyses.

The geographic distribution area was estimated as EOO following the criterion used by IUCN Standards and Petitions Subcommittee (2017). Each species' EOO was calculated as a convex polygon encompassing the known, inferred, or projected regions of present occurrence of a taxon, excluding cases of vagrancy. The EOOs were calculated using GPS coordinates or digitised maps from the IUCN Red List database (IUCN, 2018) when GPS coordinates were unavailable. The majority of the coordinates were compiled from the literature and museum records. Few others were acquired from meta-databases such as Global Biodiversity Information Facility (GBIF, 2018) and SpeciesLink (SpeciesLink, 2018), particularly those GPS coordinates extending species ranges with vouchered specimens identified by a qualified taxonomist. The GPS coordinates were plotted on maps and thoroughly inspected for any obvious errors. The occasional errors (*e.g.*, replacing of longitude by latitude) were rectified as appropriate or, in cases of dubiety, excluded completely. Point localities were converted to EOO polygons using the WGS84 coordinate reference system. It was assumed that each species must occupy a minimum EOO of 10 km²; this assumption was applied to species

reported from a single GPS coordinate, most frequently the type locality (*e.g.*, *Apteronotus ferrarisi* de Santana & Vari 2013, *Megadontognathus cuyuniense* Mago-Leccia 1994, *Sternarchogiton zuanoni* de Santana & Vari 2010).

Extinction Risk was obtained from the IUCN Red List database (IUCN, 2018) for mormyroids and from the Brazilian Ministry of Environment Red List of endangered species for gymnotiforms (ICMBio, 2014). Newly described species awaiting formal evaluation were categorised according to the IUCN categories and criteria (IUCN Standards and Petitions Subcommittee, 2017). THR was defined as a binary variable where 0 is non-threatened and 1 is threatened, in order to increase sample sizes per group and to enhance statistical power. THR was determined by the extinction risk of each species considered to be threatened (*i.e.*, Vulnerable, VU; Endangered, EN; or Critically Endangered, CR) or non-threatened (*i.e.*, Least Concern, LC; Near Threatened, NT; or Data Deficient, DD).

2.2 | Statistical analyses

The GLM was used to infer relationships between the response and explanatory variables. Each of the three response variables (*i.e.*, MBS, EOO and THR) was explained by publication date. The GLM was chosen because of its flexibility for dealing with heterogeneous variances and skewed error distributions.

It is acknowledged that some species-level traits (*e.g.*, body size) should be controlled for phylogenetic affinities (Felsenstein, 1985; Symonds & Blomberg, 2014). Nonetheless, some traits are not always expected to be inherited from common ancestors (*e.g.*, species range, threat risk) and, therefore, they probably lack a phylogenetic signal that would need to be accounted for. In this study, one practical limitation in controlling for evolutionary relationships is that the published species-level trees of mormyroids (Sullivan *et al.*, 2000) and gymnotiforms (Tagliacollo *et al.*, 2016) include less than 40% of the species richness in each clade; *i.e.*, several threatened and newly described species are often not included in the available trees, thus precluding the inference of meaningful conclusions.

A GLM has three components: (1) an equation specifying the linear relationships between the response and the explanatory variables; (2) a distribution family that assumes some mean-variance relationship in the error distribution conditional on the explanatory variables (*e.g.*, γ -distribution); (3) an associated link function that transforms the expected value of the response variable (Nelder & Baker, 2004). Here, model specifications included the combination of three family distributions (Poisson, gamma and binomial) and six link functions (identity, square-root, log, inverse, logit, probit). The link function identity uses the raw, non-transformed values. GLMs with Poisson distribution were applied to investigate the relationship of discrete response variables. GLMs with γ -distribution were applied to investigate relationships of continuous, non-negative response variables. GLMs with binomial distributions were applied to investigate relationships of categorical binary response variables.

For the discrete variable cSPP, the GLMs assuming Poisson distributions were evaluated (hereafter, PoisGLM) with three alternative

link functions (identity, square-root, log). For the continuous variables MBS and EOO, the GLMs assuming γ -distributions were evaluated (hereafter, GamGLM) with three alternative link functions (identity, inverse, log). The shape and scale parameters of the distributions were estimated by maximum likelihood. The GamGLMs were used for MBS and EOO because both variables comprised continuous and positive numbers, with skewed residuals and an implied mean–variance relation. For the categorical variable THR, the GLM assuming binomial distributions were evaluated (hereafter, BinGLM) with two link functions (logit, probit). These two link functions have similar properties differing only in which cumulative distribution function each one applies; *i.e.*, the logistic distribution or standard normal distribution.

2.3 | Model selection

The GLMs were fitted using maximum likelihood (ML) estimation and compared using the Akaike information criterion with correction for small sample sizes (AICc; Hurvich & Tsai, 1989). The AICc is less likely to select an over-parameterized model when compared to the AIC method. All GLMs with $\Delta\text{AICc} < 2.0$ were considered equally supported.

3 | RESULTS

The African superfamily Mormyroidea and the Neotropical order Gymnotiformes possess many similarities in richness and conservation status. Considering the vast variation in richness among fish clades, these two groups have similar species richness, with gymnotiforms currently composed of five families, 34 genera and 249 species, while mormyroids include two families, 22 genera and 221 species. The mean extinction risks of the African and Neotropical electric fishes are also surprisingly similar. A total of 19 gymnotiforms (8% of the species) and 20 mormyroids (9% of the species) are currently assessed as threatened with some degree of extinction risk. All larger species (MBS > 50 cm, range 5–250 cm) are either LC or DD, with the exception of the *Sternarchorhynchus axelrodi* de Santana & Vari 2010 (MBS 60 cm) categorised as NT. When comparing distribution area with

extinction risk, all widespread species are listed as LC. All species listed as DD, NT or VU have distribution areas below 10^6 km² and species listed as EN occur in areas up to 128,000 km². The four species listed as CR are gymnotiform fishes known from the type-locality only. The investigation of the relationships between the species traits and the publication date of the two distant clades revealed further remarkable similarities.

With regard to the Mormyroidea traits investigated and their correlation to date of publication, it was found that for the variable cSPP, all three evaluated PoisGLM were supported (Table 1). These estimates suggested that the number of mormyroid descriptions was constant through time, with an average of 2–3 species described per year; *i.e.*, the variable publication date was not considered to be a predictor of the count of species per year (Figure 2). For the variable MBS, one GamGLM was supported (Table 2). Its gamma-parameter shape and scale were estimated to be 2.94 and 0.42, respectively. The best-fitting model assumed an inverse link function. Its estimates suggested that the MBS of mormyroids decreased with date of species description (Figure 3). For the variable EOO, one GamGLM was supported (Table 3). Its gamma-parameter shape and scale were estimated to be 0.97 and 0.14, respectively. The best-fitting model assumed a log-link function. Its estimates suggested that the EOO of mormyroids had decreased with date of species description (Figure 4). For the variable THR, two best-fitting BinGLMs were supported (Table 4). The best-fitting models assumed logit or probit link functions. Their estimates suggested a steeper increase of threat risk in mormyroids in the last century (Figure 5). Converting probabilities to odds ratios, it is expected that for every two species of mormyroids one might become threatened shortly after its description (odds ratio 2:1).

In Gymnotiformes, a single PoisGLM was supported for the variable cSPP (Table 1). Its estimates suggested that the number of gymnotiform species descriptions increased at a logarithmic scale. The best-fitting model assumed a log-link function. Its estimates suggested that the number of gymnotiform descriptions increased through time especially in the last century (Figure 2). For the variable MBS, one GamGLM was supported (Table 2). Its gamma-parameter shape and scale were estimated to be 6.98 and 1.14, respectively. The best-fitting model assumed a log-link function. Its estimates suggested that

TABLE 1 Model selection among PoisGLMs applied to evaluate relationships between species count (cSPP) and publication date of the African Mormyroidea and Neotropical Gymnotiformes. Each model only differs in its link function (Link FUN). The PoisGLMs with $\Delta\text{AICc} < 2.0$ were considered equally supported

| cSPP | Clade | GLM family | Link FUN | logLik | pars | AICc | ΔAICc | wAIC |
|---------|---------------|------------|----------|--------|------|-------|---------------------|-------|
| Model 1 | Mormyroidea | Poisson | identity | −186.8 | 2 | 377.6 | 0.0 | 0.33 |
| Model 2 | Mormyroidea | Poisson | sqrt | −186.8 | 2 | 377.6 | 0.0 | 0.33 |
| Model 3 | Mormyroidea | Poisson | log | −186.8 | 2 | 377.6 | 0.0 | 0.33 |
| Model 1 | Gymnotiformes | Poisson | identity | −190.7 | 2 | 385.5 | 27.6 | ~0.00 |
| Model 2 | Gymnotiformes | Poisson | sqrt | −184.1 | 2 | 372.4 | 14.5 | ~0.00 |
| Model 3 | Gymnotiformes | Poisson | log | −176.9 | 2 | 357.9 | 0.0 | ~1.00 |

GLM, Generalised linear model; logLink, log likelihoods; pars, number of parameters; AICc, Akaike information criterion for small sample sizes; wAIC, weighted AICc.

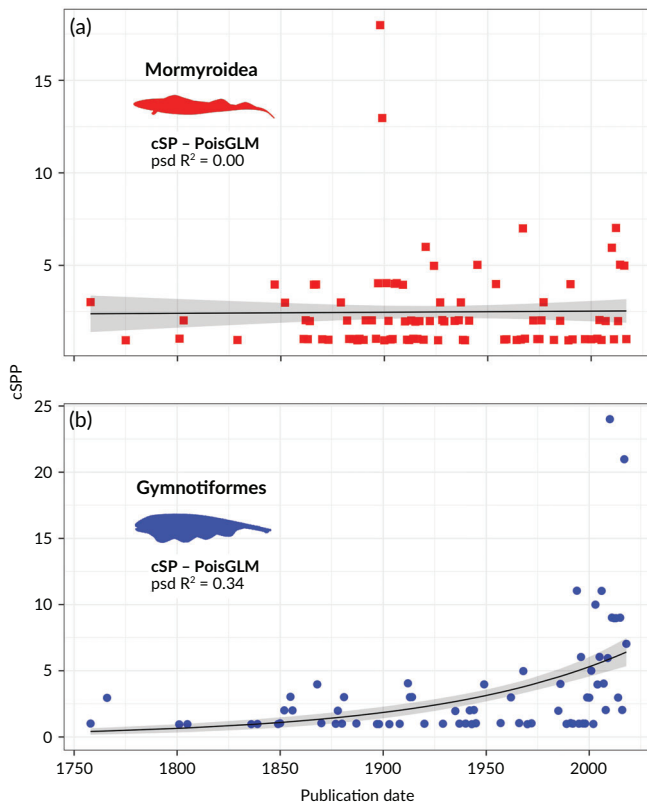


FIGURE 2 Species count (cSPP) explained by publication date of (a) the African Mormyroidea, which shows a constant count of species descriptions, and (b) Neotropical Gymnotiformes, which shows a logarithmic increase. For mormyroids, the best-fitting PoisGLM indicates a pattern standard deviation (psd) $R^2 = 0.00$, which means that the variable publication date does not explain species count; *i.e.*, according to the model, on average, species count (between 2–3 spp. per year) have not changed in mormyroids since 1758 (for more details see Table 1)

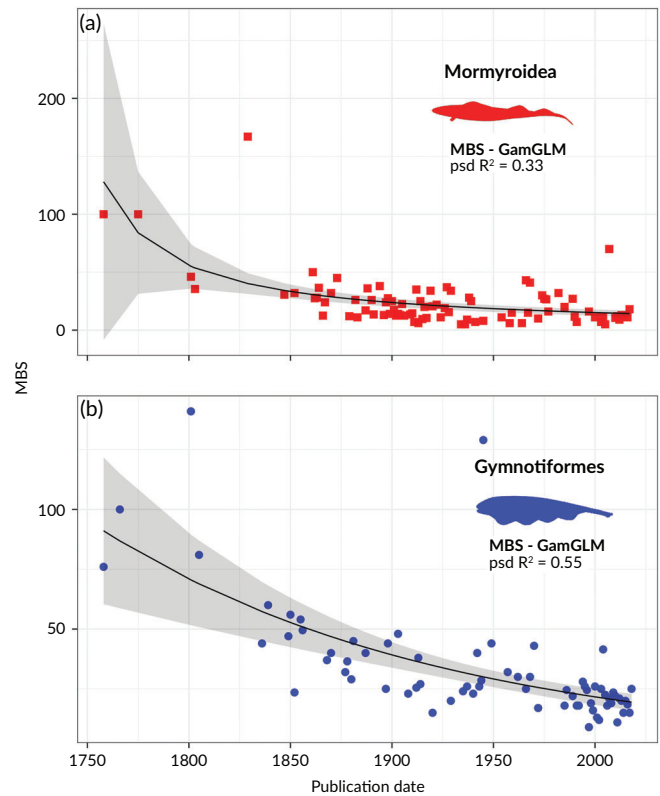


FIGURE 3 Maximum body size (MBS) explained by publication date of (a) the African Mormyroidea, showing a negative gamma-like slope, and (b) Neotropical Gymnotiformes, which shows a negative logarithmic-like gamma slope. On average, mormyroids are smaller than gymnotiforms (~24 v. 33 cm total length, respectively). Pseudo- R^2 indicates that the variable publication date explains better changes in body size in gymnotiforms (0.55) than mormyroids (0.33). (For more details of gamma shape and scale parameters see Table 2)

TABLE 2 Model selection among GamGLMs applied to evaluate relationships between maximum body size (MBS) and publication date of the African Mormyroidea and Neotropical Gymnotiformes. Each model only differs in its link function (Link FUN). The GamGLMs with $\Delta AICc < 2.0$ were considered equally supported

| MBS | Clade | GLM Family | Link FUN | shape | scale | logLik | pars | AICc | $\Delta AICc$ | wAIC |
|---------|---------------|------------|----------|-------|-------|--------|------|-------|---------------|--------|
| Model 1 | Mormyroidea | Gamma | identity | 2.58 | 0.34 | -344.9 | 3 | 696.2 | 13.1 | ~ 0.00 |
| Model 2 | Mormyroidea | Gamma | inverse | 2.94 | 0.42 | -338.4 | 3 | 683.1 | 0.0 | 0.96 |
| Model 3 | Mormyroidea | Gamma | log | 2.75 | 0.39 | -341.7 | 3 | 689.7 | 6.6 | 0.04 |
| Model 1 | Gymnotiformes | Gamma | identity | 6.74 | 1.10 | -272.7 | 3 | 551.7 | 2.5 | 0.18 |
| Model 2 | Gymnotiformes | Gamma | inverse | 6.77 | 1.11 | -272.5 | 3 | 551.4 | 2.2 | 0.21 |
| Model 3 | Gymnotiformes | Gamma | log | 6.98 | 1.14 | -271.4 | 3 | 549.2 | 0.0 | 0.62 |

GLM, Generalised linear model; logLik, log likelihoods; pars, number of parameters; AICc, Akaike information criterion for small sample sizes; wAIC, weighted AICc.

the MBS of gymnotiforms decreased with date of species description (Figure 3). For the variable EOO, one GamGLM was supported (Table 3). Its gamma-parameter shape and scale were estimated to be 0.34 and 0.04, respectively. The best-fitting model assumed an

identity-link function. Its estimates suggested that the EOO of gymnotiforms also decreased with date of species description (Figure 4). For the variable THR, two best-fitting BinGLMs were supported (Table 4). The best-fitting models assumed logit or probit-

TABLE 3 Model selection among GamGLMs applied to evaluate relationships between extension of occurrence (EOO) and publication date of the African Mormyroidea and Neotropical Gymnotiformes. Each model only differs in its link function (Link FUN). The GamGLMs with $\Delta\text{AICc} < 2.0$ were considered equally supported

| EOO | Clade | GLM Family | Link FUN | shape | scale | logLik | pars | AICc | ΔAICc | wAIC |
|---------|---------------|------------|----------|-------|-------|--------|------|-------|---------------------|--------|
| Model 1 | Mormyroidea | Gamma | identity | 0.88 | 0.13 | -64.2 | 3 | 134.7 | 9.6 | ~ 0.00 |
| Model 2 | Mormyroidea | Gamma | inverse | 0.78 | 0.11 | -69.9 | 3 | 146.2 | 21.1 | ~ 0.00 |
| Model 3 | Mormyroidea | Gamma | log | 0.97 | 0.14 | -59.4 | 3 | 125.1 | 0.0 | ~ 1.00 |
| Model 1 | Gymnotiformes | Gamma | identity | 0.34 | 0.04 | -3.6 | 3 | 13.6 | 0.0 | ~ 1.00 |
| Model 2 | Gymnotiformes | Gamma | inverse | 0.30 | 0.04 | -11.4 | 3 | 29.2 | 15.7 | ~ 0.00 |
| Model 3 | Gymnotiformes | Gamma | log | 0.31 | 0.04 | -8.4 | 3 | 23.2 | 9.7 | ~ 0.00 |

GLM, Generalised linear model; logLink, log likelihoods; pars, number of parameters; AICc, Akaike information criterion for small sample sizes; wAIC, weighted AICc.

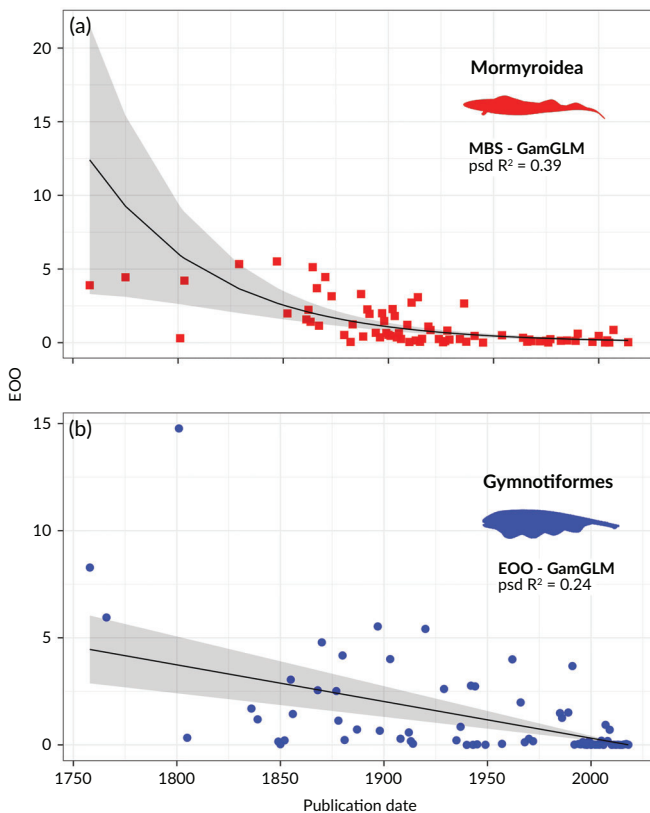


FIGURE 4 Extension of occurrence (EOO) explained by publication date of (a) the African Mormyroidea, showing a negative logarithm-like gamma pattern, and (b) and Neotropical Gymnotiformes, which show a negative linear-like gamma reductions of EOO. On average, mormyroids occupy slightly smaller geographic areas than gymnotiforms (~1.21 v. 1.35 million km²). Pseudo R^2 indicates that the variable publication date explains better changes in EOO in mormyroids (0.39) than gymnotiforms (0.24). (For more details of gamma shape and scale parameters see Table 3)

link functions. Their estimates suggested a slight increase in threat risks in gymnotiforms (Figure 5). Converting probabilities to odds ratios, it is expected that for every 10 species of gymnotiforms one might become threatened shortly after its description (odds ratio 10:1).

4 | DISCUSSION

Some of the traits exhibited by African mormyroid and Neotropical gymnotiform species differ based on their date of publication. The annual number of species descriptions is not decreasing in either of the groups, but it is stable in mormyroids and increasing in gymnotiforms (Figure 2). Furthermore, newly described electric fishes are more often small-bodied species occupying narrow geographical ranges and are more likely to be threatened with extinction. This scenario applies to both groups, but it is more pronounced among mormyroids (Figures 3–5), suggesting that some African electric fishes may live an ephemeral existence after formal description. The Neotropical gymnotiforms, by contrast, appear to be less vulnerable to extinction and recent taxonomic studies have greatly improved our understanding of species delimitation and distribution (Albert & Crampton, 2001, 2003; Craig *et al.*, 2017; Crampton *et al.*, 2016; de Santana & Crampton, 2011; de Santana & Vari, 2010).

The rate at which new taxa are described has been steadily increasing since 2000 in several actinopterygian groups (Ota *et al.*, 2015; Reis *et al.*, 2016). A similar pattern is demonstrated for gymnotiforms, in which annual rates of species description are increasing at a logarithmic rate (Figure 2). These recently described gymnotiform species rarely comprise new morphotypes with no correspondent congeneric forms (Albert & Crampton, 2006; Maldonado-Ocampo *et al.*, 2014; Meunier *et al.*, 2011). Instead, most of them are morphological variations of the well-known forms derived from previously known species that have been split after extensive taxonomic revisions (Albert & Crampton, 2003; Crampton *et al.*, 2016; de Santana & Vari, 2010). Therefore, forthcoming discoveries in gymnotiforms are more likely to be made from taxonomic studies evaluating species complexes with widespread distributions. Even though the annual number of species descriptions has not increased within the African mormyroids for over 250 years (Figure 2), there is evidence that additional species will be discovered in the continent after poorly explored regions become logistically and legally more accessible to taxonomists. The African continent represents the next frontier of species descriptions (Clark *et al.*, 2011), therefore the inferred absence of correlation between species number and

TABLE 4 Model selection among BinGLMs applied to evaluate relationships between Threat risks (THR) and publication date of the African Mormyroidea and Neotropical Gymnotiformes. Each model only differs in its link function (Link FUN). The BinGLMs with $\Delta AICc < 2.0$ were considered equally supported. logLink: log likelihoods, pars: number of parameters

| THR | Clade | GLM Family | Link FUN | LogLik | scale | pars | AICc | $\Delta AICc$ | wAIC |
|---------|---------------|------------|----------|--------|-------|------|-------|---------------|------|
| Model 1 | Mormyroidea | Binomial | Logit | -38.1 | 0.13 | 2 | 80.3 | 0.8 | 0.40 |
| Model 2 | Mormyroidea | Binomial | Probit | -37.7 | 0.11 | 2 | 79.5 | 0.0 | 0.60 |
| Model 1 | Gymnotiformes | Binomial | Logit | -65.3 | 0.04 | 2 | 134.7 | 0.1 | 0.48 |
| Model 2 | Gymnotiformes | Binomial | Probit | -65.2 | 0.04 | 2 | 134.5 | 0.0 | 0.52 |

GLM, Generalised linear model; logLink, log likelihoods; pars, number of parameters; AICc, Akaike information criterion for small sample sizes; wAIC, weighted AICc.

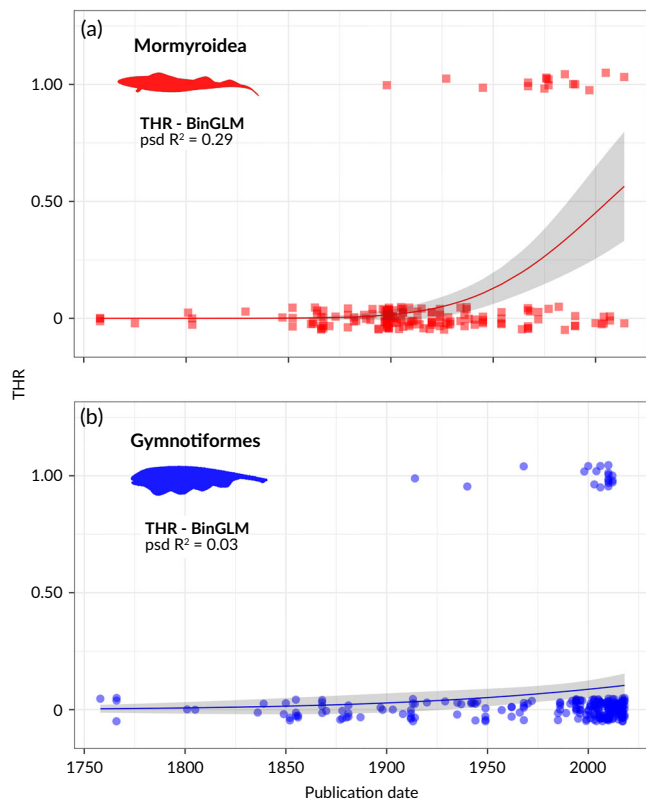


FIGURE 5 Threat risks (THR) predicted by publication date of (a) the African Mormyroidea, which are c. five times more pronounced than in (b) the Neotropical Gymnotiformes. When converting probabilities to odds ratios it is possible to predict that for every two newly described mormyroids one might be assessed as threatened. For gymnotiforms, the pseudo- R^2 estimates indicate that the variable publication date is a poor predictor of THR. (For more details see Table 4)

publication date in mormyroids (Figure 2) should be interpreted carefully. Future collecting expeditions and taxonomic studies can possibly change the flat regression pattern of species description through time in mormyroids, especially if relevant institutional and governmental support is granted to the few practising systematists in Africa (Skelton & Swartz, 2011).

There is a general tendency for larger species of organisms to be described before smaller species, resulting in a decline of the mean body size of named species over time (Collen *et al.*, 2004; Diniz-Filho

et al., 2005; Gaston, 1991; Meiri, 2016). According to Gaston (1991), most of the evidence for an influence of body size upon the likelihood of species being described was, at that time, somewhat anecdotal as few studies had sought systematic trends in the dates of description of species of different body sizes for a particular taxon. Although considerable advances have been achieved since the 1990s (Reed & Boback, 2002; Stork *et al.*, 2015; Vilela *et al.*, 2014), this correlation is usually not formally investigated using statistical tests, as are performed here. This generalised pattern was found in both mormyroids and gymnotiforms, in which the small-bodied species were often described later (Figure 3). Thus, some convergences between the two groups might be the direct consequence of having comparable body size ranges.

As with body size, the most recently described mormyroids and gymnotiforms also frequently have smaller geographical ranges than their relatives described decades ago (Figure 4). Not surprisingly, similar relationships between geographical range and publication date have been demonstrated in other taxonomic groups (*e.g.*, Collen *et al.*, 2004; Diniz-Filho *et al.*, 2005; Meiri, 2016). Extinction risk and body size have been found to be related in various vertebrate groups, with larger species being more at risk than smaller ones (Vilela *et al.*, 2014). Body size is a fundamental ecological variable correlated with natural mortality rates, longevity, age at maturity and reproductive output (Olden *et al.*, 2007; Peters & Wassenberg, 1983; Pimm, 1982). According to Olden *et al.* (2007), although body size can be predictive of extinction risk for freshwater and marine species, linkage between fish body size and conservation status is more evident in marine ecosystems. These authors compared body-size distribution of freshwater and marine fishes under different levels of global extinction risk and concluded that global fish extinction risk does not universally scale with body size.

In African and Neotropical electric fishes, new discoveries have been primarily of small-bodied species, predominantly occupying small ranges, which are thus more likely to be threatened with extinction (Figures 3–5). For this reason, contrary to the general tendency, many of the smaller species described in recent years are threatened. Approximately half of mormyroids described in the past few decades are assessed as threatened, while about 10% of gymnotiforms described in the same period have the same status. Publication date is expected to predict their conservation status (Figure 5) and this

scenario is more concerning in mormyroids because undescribed species might be already threatened.

Indeed, gymnotiforms show a much higher number of species described annually in recent decades, which is certainly a reflection of the much greater effort in exploring the habitat and documenting the biodiversity of these fishes by a larger number of taxonomists in the Neotropics than those working in Africa (Skelton & Swartz, 2011). As an effect of this dissimilar state of taxonomic knowledge, recent estimates of the final number of freshwater fishes in South America and in Africa are highly contrasting. Reis *et al.* (2016) recorded over 5600 valid species for South America with a rate of annual new species description of 104 year⁻¹ and estimated that 34%–42% of the species are still awaiting to be discovered, reaching to a final richness between 8000 and 9000 species. Conversely, in Malawi, Pavanelli *et al.* (2018) recorded over 3200 valid species and estimated that 66% of the species are still undiscovered, the final number possibly reaching over 9000 species. This imbalance in biodiversity knowledge in Africa and South America has deep roots in the very history of scientific exploration of the continents and highlights the importance of the taxonomic work for conservation. Considering the high estimate of freshwater fish species yet to be described in Africa and the prediction that the new species will have narrow geographical ranges and will probably be threatened, high concerns about their conservation status arise. Although taxonomy and conservation are clearly distinct disciplines, a certain level of taxonomic knowledge is required to ensure success in target species conservation (Ely *et al.*, 2017; Greenwood, 1992). Therefore, the complementarity of taxonomy and conservation is a necessary prerequisite to stronger and more effective conservation actions (Collares-Pereira *et al.*, 2016; Dubois, 2003; Ely *et al.*, 2017; Skelton & Swartz, 2011). To prevent the extinction of the weakly electric fishes, strong action should be taken to protect the river channels and floodplains of tropical ecosystems and to support more surveys and taxonomic studies, especially in Africa.

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CONTRIBUTIONS

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