



Completeness of national freshwater fish species inventories around the world

Patricia Pelayo-Villamil¹ · Cástor Guisande² · Ana Manjarrés-Hernández³ · Luz Fernanda Jiménez¹ · Carlos Granado-Lorencio⁴ · Emilio García-Roselló⁵ · Jacinto González-Dacosta⁵ · Juergen Heine⁵ · Luis González-Vilas² · Jorge M. Lobo⁶

Received: 4 January 2018 / Revised: 24 August 2018 / Accepted: 14 September 2018 /

Published online: 21 September 2018

© Springer Nature B.V. 2018

Abstract

The aim was to discriminate the countries with relatively comprehensive inventories of freshwater fishes from those with insufficiently prospected inventories. We used a data set of 16,734 freshwater fish species with a total of 1,373,449 occurrence records. Accumulation curves relating the increase in the number of species to the number of records, and completeness values obtained after extrapolating these curves to estimate the total number of predicted species were calculated for each country using the RWizard application *KnowBR*. Using the final slope values of the accumulation curves, the obtained completeness values, and the ratio between the number of records and the observed species, maps and plots representing the location of good, fair and poor quality inventories at country level were obtained. Inventory completeness ranged from 5.3% (Guinea-Bissau) to 108.4% (United Kingdom), with a pooled mean of 65.9%. We observed that a completeness higher than 90%, a slope lower than 0.02 and a ratio of records/species observed greater than 15 were good thresholds for identifying countries with good quality inventories; only 26 countries met these requirements, mainly located in Europe and North America. However, more than 71% of countries worldwide have inventories that can be categorised as of poor quality. Furthermore, even those countries with relatively accurate national inventories possess a high variability in the completeness of their provincial or regional inventories.

Keywords Biodiversity databases · Database records · Species richness estimators · Survey completeness · Well-surveyed territories

Communicated by Mark James Kennard.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10531-018-1630-y>) contains supplementary material, which is available to authorized users.

✉ Cástor Guisande
castor@uvigo.es

Extended author information available on the last page of the article

Introduction

The continuous and exponential evolution of data storage technology (Track et al. 2017) and processing power of computers (Swanson 2015), enables increased use of a vast amount of information compiled using non-digital tools over a long period of time. In the case of biological data that reflect our taxonomical and geographical knowledge of species, the Global Biodiversity Information Facility (GBIF; see www.gbif.org) is surely the most successful initiative for freely visualizing and managing primary biodiversity data. To date (December 2017), more than 870 million of occurrence records representing almost one million species are stored in the GBIF. However, the net result of this effort is that the obtained primary data are plagued with inaccuracies, incompleteness, biases and geographical or environmental data gaps (Anderson et al. 2016) due the unequal distribution of taxonomical resources and the preference for surveying under certain conditions (Hortal et al. 2015).

Taxonomical and geographical gaps and biases in primary biodiversity data in specific taxonomical groups need to be recognized and identified to guide future planning of resources (Lobo et al. 1997; Soberón et al. 2007; Sousa-Baena et al. 2014; Pelayo-Villamil et al. 2015; Sainge et al. 2017), which can be directed at obtaining a representative set of data capable of providing reliable macroecological and conservation guidelines. On a global scale, the completeness of inventories in regions, states or countries should be assessed to obtain a picture concerning the distribution of available knowledge and location of the most important gaps in data (Soberón et al. 2007; Rocchini et al. 2011; Meyer et al. 2015a, b; Ruete 2015). Additionally, within the context of the Species Distribution Models (Franklin 2010), the identification of these gaps and bias in the species inventories may also constitute a procedure for: (i) identifying relatively consistent absences (Lobo and Martín-Piera 2002; Anderson 2003; Hortal et al. 2008), and (ii) discriminating the areas in which predictions constitute extrapolated results beyond the observed range of conditions used in the process of model building (Hortal et al. 2015).

In this study, the most comprehensive set of information about freshwater fish worldwide was used to delimit present day gaps in fish inventories at country level. Taking into account that national resources maintain a large proportion of the task force on taxonomy and biogeography, our purpose is to provide a set of recommendations capable of better guiding future prospects and opportunities.

Materials and methods

Origin of freshwater fish species data

The data set of geographical records for freshwater fish developed by Pelayo-Villamil et al. (2015) were updated to reflect the taxonomic changes and new species described until the end of August 2017. Electronic supplementary material 1 shows a detailed description of all sources obtained from the GBIF used in this data set. Other sources used, such as web pages, museum collections and published manuscripts are described by Pelayo-Villamil et al. (2015). Records were downloaded and filtered using the data cleaning facilities available in ModestR software (García-Roselló et al. 2013, 2014, 2015). Records were filtered as follows: (i) records with the same latitude and longitude were excluded; (ii) records with latitude and longitude of 0° were excluded; and (iii) habitat data were cleaned in order to

eliminate occurrence in other habitats than those corresponding to terrestrial freshwater ecosystems (see García-Roselló et al. 2014 for details). At the end of August 2017, 16,734 species of freshwater fishes were recognized as valid by taxonomists and are available in Ipez (<http://www.ipez.es>, Guisande et al. 2010). Of these, 16,662 species (99.6% of the total) had associated geographical information with a total of 1,373,449 occurrence records (without duplication). The species with information about their distribution were used to identify the administrative areas (countries) with inventories that were probably reliable. See Electronic supplementary material 2 for a detailed description of the species included in the analysis.

Quantification of completeness

Completeness of freshwater fish inventories at country level was estimated using the RWizard (Guisande et al. 2014) application *KnowBR* (Lobo et al. 2018; www.ipez.es/RWizard), also available as an R package on CRAN (Guisande and Lobo 2018). This application enables the use of the information from database records to build species accumulation curves which describe the relationship between the accumulated number of species and a surrogate of survey effort (database records; see Lobo 2008) for different spatial units (such as cells, basins or countries, as is the case here) at the same time. The final slope of each of these accumulation curves (i.e. the final rate at which species accumulate) is calculated to determine the comprehensiveness of a country's inventory. Additionally, these accumulation curves are adjusted to different asymptotic or quasi-asymptotic functions in order to estimate the predicted number of species when the survey effort is almost "infinite" (Clench 1979; Soberón and Llorente 1993; Hortal and Lobo 2005). This value is used to derive a completeness value, namely the percentage of observed species with respect to predicted species. Conclusions on the adequacy or not of each territorial unit (countries in this case) for studying biodiversity variations according to the quality of its inventory are based both on the final slope of the accumulation curve and on the completeness values.

Species accumulation curves are constructed following the *specaccum* function of the *vegan* R package (Oksanen et al. 2017), according to the analytical formula of Ugland et al. (2003) for the *exact* estimator (default option). Extrapolated richness and completeness values were calculated using the four adjustment functions available in *KnowBR*: Clench, exponential, saturation and rational (see Flather 1996; Mora et al. 2008). For further information about these functions and the use of *KnowBR*, see Lobo et al. (2018).

Additionally, a new application (*Survey Quality*) included in the package *KnowBR* allows identification and plotting the cells or polygons with good, fair and poor quality inventories. This function uses the file called "Estimators" obtained from the functions of *KnowBR* that operate with geographical squares (*cell*) or any type of vectorial features (*polygon*). Using the final slope values of the accumulation curves, the obtained completeness values and the ratio between the number of records and the observed species (R/S ratio), *Survey Quality* provides a map with the location of the good, fair and poor quality spatial units. The default values are used to distinguish the cells or polygons with good, fair and poor quality surveys are: slope < 0.02, completeness > 90% and R/S ratio > 15 for good quality surveys, and slope > 0.3, completeness < 50% and R/S ratio < 3 for poor quality surveys. In the case of polygons, a plot representing the values of the three parameters is depicted by using polar coordinates (Van Sickle 2010). The order of the variables is important for the estimation of the polar coordinates because a different angle is assigned to each variable. Therefore, the variables must be introduced in the following order: slope,

completeness and R/S ratio. All variables are transformed to a scale of between -1 and 1. For each value, the X and Y polar coordinates are estimated using the following equations:

$$X = \sum_{j=1}^3 |(z_j)| \cos(\alpha_j) \quad Y = \sum_{j=1}^3 |(z_j)| \sin(\alpha_j)$$

where z is the value of the variable j .

Each variable is assigned an angle (α). The increment value of the angle is always 60. Therefore, for the first variable (slope), if the transformed value is ≥ 0 , then α is 60 and, if the transformed value is < 0 , then α is 240. For the second variable (completeness), if the transformed value is ≥ 0 , then α is 120 and, if the transformed value is < 0 , then α is 300. For the third variable (R/S ratio), if the transformed value is ≥ 0 , then α is 180 and, if the transformed value is < 0 , then α is 360. Conversion of degrees to radians angle is carried out by assuming that 1 degree = $\frac{\pi}{180}$ radians.

Results

Figure 1 shows a schematic representation of the polar coordinates obtained with the function *Survey Quality*. In the upper right of the plot are located the countries with the lowest quality of survey (high slope, low completeness and a R/S ratio ~ 1). In the lower medium side of the plot are located the countries at the interface between poor and fair quality surveys. Finally, in the upper left corner of the plot are located the countries with highest quality surveys (slope ~ 0 , completeness $\sim 100\%$ and a R/S ratio > 200). The variation between countries in the number of records, observed richness, and final slope of the accumulation curve is shown in Electronic supplementary material 3, as well as predicted richness values according to the extrapolation of accumulation curves, their completeness, standard errors

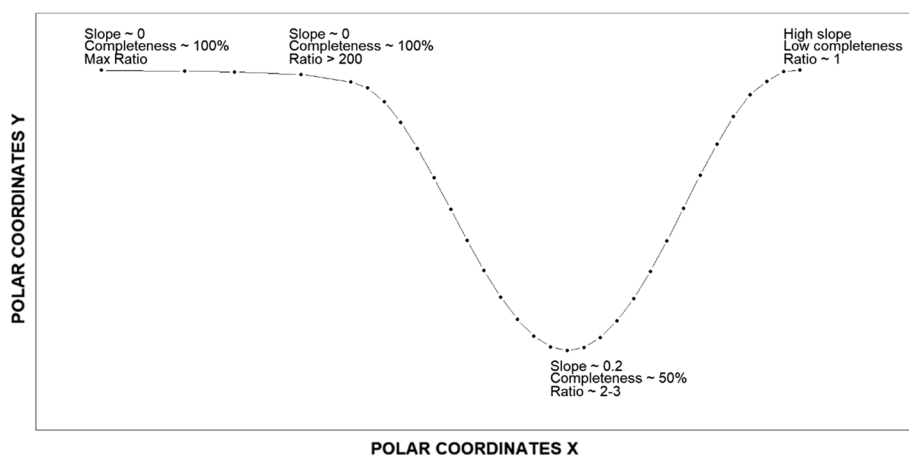


Fig. 1 Schematic representation of the polar coordinates obtained with the function *Survey Quality* of the package *KnowBR*, when the ratio between the number of records and the observed species richness, the slope of the accumulation curve and completeness values based of richness predictions are considered together

and R^2 values for the four adjustment functions. The slopes of the accumulation curves are negatively and highly correlated with the four obtained completeness values; from Pearson $r = -0.95$ in the case of Clench and Rational adjustments to -0.99 in the case of Saturation and exponential adjustments, respectively ($p < 0.0001$ in all cases). Similarly, all pairwise comparisons of completeness values are highly and positively correlated (r values varying from 0.96 between Saturation and Clench adjustments to 0.99 between Rational and Clench). However, exponential and Saturation functions were able to adjust the data provided on a slightly lower number of occasions (179 and 178 countries, respectively) than Clench and Rational adjustments (193 and 189 countries, respectively) (Table 1). Clench function, and even more Rational function, provide higher species richness extrapolations than exponential and Saturation adjusts, thus diminishing the completeness values obtained (Table 1).

The relationship between the ratio of the number of records and the observed species richness (R/S ratio), the slope of the accumulation curve and completeness values based on richness predictions indicates that it is possible to obtain relatively low final slopes and high completeness values with moderate survey efforts (Fig. 2). For the four examined adjustment functions, there is a clear relationship between slope and completeness (Fig. 2); at lower slope values, higher values of completeness were always observed. However, a low slope does not necessarily imply a high completeness, because medium–high completeness values were obtained with slopes lower than 0.01 (Fig. 2 and see Electronic supplementary material 3). If one selects the Clench-derived species richness predictions because it is possible to fit the curve in a high number of countries (Table 1), a completeness value close to 100% is attained with this function when the R/S ratio is around 144 (Fig. 2), and the final slope is then 0.002. Hence, a reasonable basis for identifying relatively good surveyed countries could be a completeness of 90% and a slope value for the accumulation curve of 0.02 or less (two new species added each 100 records), values that can be attained when the R/S ratio is higher than 15 (i.e. when there are 15 times more records than observed species). The relationship between R/S ratio and completeness values (Fig. 2) can be in turn adjusted by a Rational function ($R^2 = 0.962$), indicating that the inflection point of this relationship appears at a completeness value of 78.3% when the R/S ratio is 5.8. In the case of the relationship between R/S ratio and slope ($R^2 = 0.966$), this inflection point occurs when the R/S ratio is 3.5 and the slope is 0.117. Thus, the delimitation of fair surveyed countries could be based on completeness values equal to or higher than 78%, but lower than 90%, slope values equal to or lower than 0.1, but higher than 0.02, and S/R ratios equal to or lower than 6. Therefore, poor surveyed countries are those with a completeness value lower than 78%, a slope higher than 0.1 and/or a S/R ratio lower than 6.

Table 1 Number of administrative areas (countries) for which it was possible to fit the equation (N), mean number of predicted species (S), final slope of the accumulation function (F_s), completeness (C), standard errors (SE) and R^2 values obtained from the four types of functions adjusted to the observed accumulation curve ($\pm 95\%$ confidence values)

	N	S	F_s	C (%)	SE	R^2
Clench	193	252 ± 62	0.18 ± 0.03	66.0 ± 3.4	3.2 ± 1.1	0.99 ± 0.01
Exponential	179	183 ± 38	0.18 ± 0.03	87.9 ± 3.3	5.7 ± 1.5	0.97 ± 0.01
Rational	189	266 ± 67	0.17 ± 0.03	64.4 ± 3.2	2.1 ± 0.7	1.00 ± 0.00
Saturation	178	193 ± 41	0.17 ± 0.03	84.9 ± 3.0	3.4 ± 0.9	0.99 ± 0.01

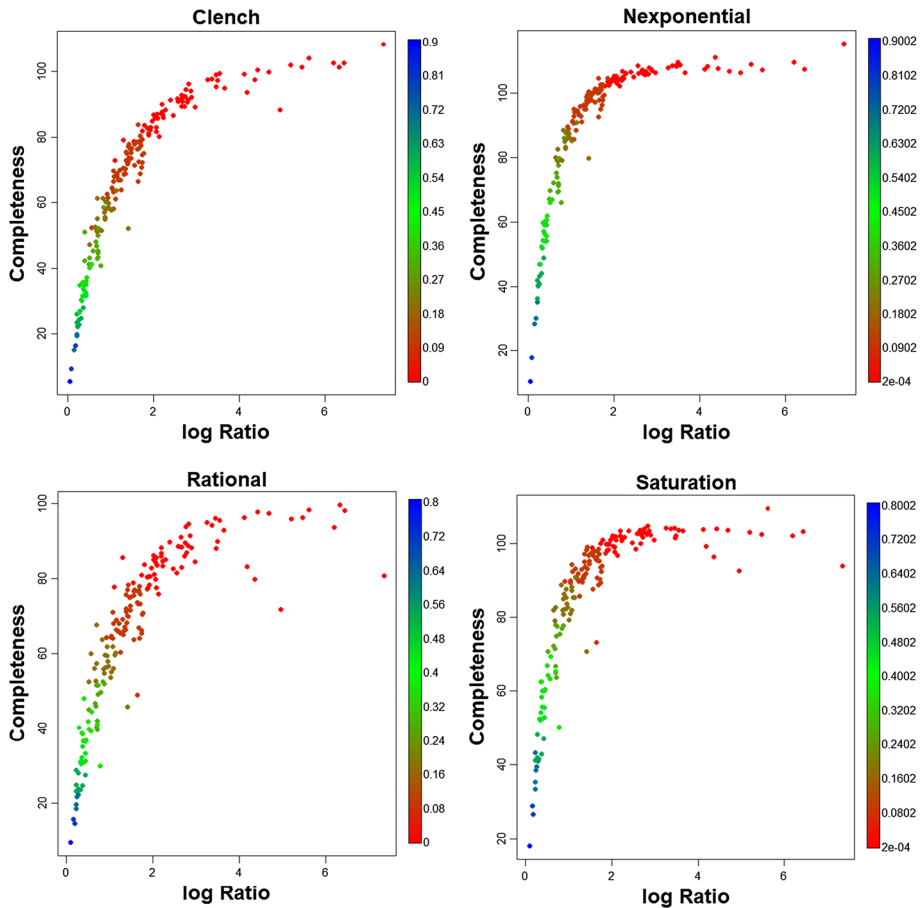


Fig. 2 Relationships between the ratio of number of records/observed richness and the completeness obtained with all four considered functions used to adjust the observed accumulation curve. The colour scale indicates the slope of the curve

Completeness ranged between 5.3% (Guinea-Bissau) and 108.4% (United Kingdom in which the predicted number of species is even lower than the observed number), with a pooled mean of 66.0% (Table 1). Twenty-six nations (12.2% of the total) meet the requirements for consideration as having good inventories (Figs. 3, 4 and 5; see also Electronic supplementary material 3), ranging from Brazil (S/R ratio=16.2, Clench completeness=90.7%, and final slope=0.014) to UK (S/R ratio=1557.8, Clench completeness=108%, and final slope=0). As expected, the countries that can be considered as having good inventories of freshwater fish are mainly located in Europe and North America (Fig. 5). The inventories of 35 countries can be considered as having fair inventories (16.4% of total), in this case mainly distributed in South America and Africa. However, most of the countries have freshwater fish inventories that can be considered as poor (62.0% of total; 132 countries) or with such a low number of records that it is impossible to generate any predictions (20 countries; 9.4% of total) (see Electronic supplementary material 3).

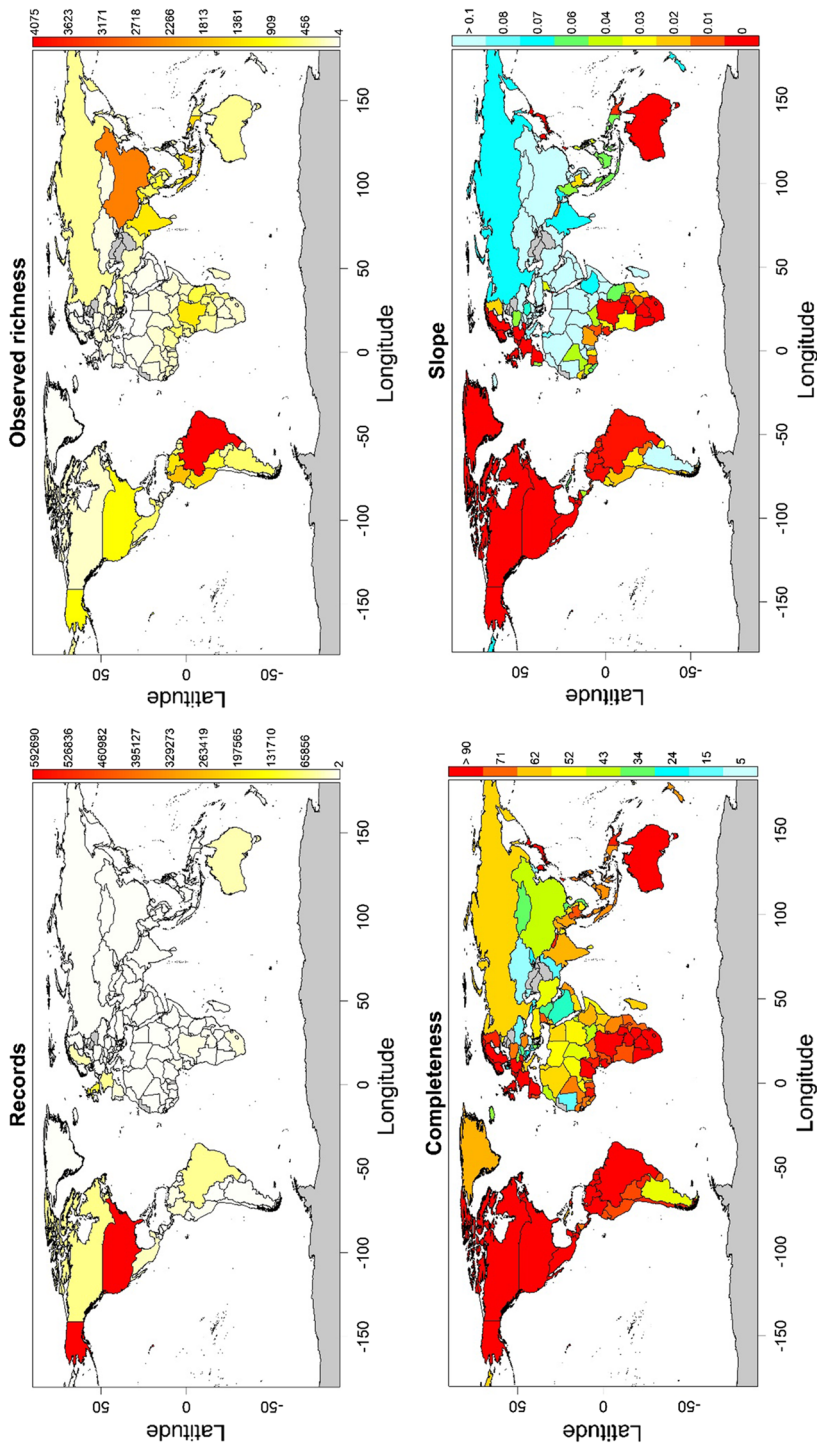
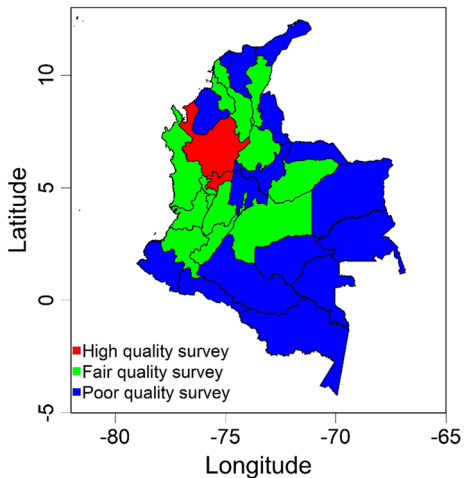


Fig. 3 Number of records, observed richness, final slope of the accumulation curve obtained with the *exact* analytical formula of Ugland et al. (2003), and completeness values after adjusting this accumulation curve to a Rational function for all countries worldwide. The countries with a grey background had no records, no species and/or it was not possible to estimate the slope and/or completeness

Fig. 6 Departments in Colombia with good, fair and poor quality surveys obtained from the function *Survey Quality*, using at the same time the ratio between the number of records and the observed species richness, the slope of the accumulation curve, and completeness values based on richness predictions



Discussion

There are very few global-scale datasets available of animal taxa, such as birds, mammals, amphibians and fish, that can be used in biogeographical, macroecological, macroevolutionary and conservation studies (Tedesco et al. 2017). As far as we know, ours is the first study that examines the quality of inventories of animal taxa on a global scale.

The obtained results are highly dependent on the structure of the data used (the distribution of records between species) and the quality and extent of public databases to reflect the taxonomic and biogeographic knowledge available in each country. Despite that, they show a global overview that it is far from being representative and complete, even at a country spatial resolution, probably mainly due to low scientific investment, lack of expertise and topographic/geographical difficulty in survey. Only North American countries, some countries of Europe, Central America and southern Africa, Brazil, Australia, Japan and Korea appear to have relatively complete inventories of freshwater fish. Of course, this incompleteness will be even greater if the considered resolution diminishes; only 1.4% of total world terrestrial one-degree grid cells would show complete inventories (Pelayo-Villamil et al. 2015).

The biases and shortcomings of the available information for freshwater fish can also be observed within countries with an important taxonomical and biogeographical task force, such as the United States (Troia and McManamay 2016), because when you look at a finer spatial resolution there are areas that can be considered insufficiently surveyed. Thus, the number of catchment areas in the United States that can be considered as well-surveyed dramatically diminished at higher resolutions (Troia and McManamay 2017).

Our results present a picture in which obvious biases appear and most tropical and sub-tropical countries possess a lack of knowledge about their inventory of freshwater fish. In addition to the potential effect of low investment in science per head of population, the lack of well-trained researchers in fish taxonomy in some countries may be also a limiting factor for the preparation of taxonomic inventories of pre-existing species and the description of new ones. The large size of some countries and difficulties in accessing some areas may be among the factors that explain the low quality of inventories for some countries and regions.


Finally, these results outline the need for extra and well-planned survey efforts aimed at increasing the current level of taxonomical and geographical knowledge of freshwater fishes in many countries of the world. However, the lack of exhaustive information should not be an obstacle to designing conservation measures, which could be based on the combined use of existing data and distribution models and estimations.

References

- Anderson RP (2003) Real vs. artefactual absences in species distributions: tests for *Oryzomys albigularis* (Rodentia: Muridae) in Venezuela. *J Biogeogr* 30:591–605
- Anderson RP, Araújo M, Guisan A, Lobo JM, Martínez-Meyer E, Peterson AT, Soberón J (2016) Final report of the task group on GBIF data fitness for use in distribution modelling. GBIF, Geneva. <http://www.gbif.org/resource/82612>
- Clench H (1979) How to make regional lists of butterflies: some thoughts. *J Lepid Soc* 33:216–231
- Flather CH (1996) Fitting species-accumulation functions and assessing regional land use impacts on avian diversity. *J Biogeogr* 23:155–168
- Franklin J (2010) Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge
- García-Roselló E, Guisan C, González-Dacosta J, Heine J, Pelayo-Villamil P, Manjarrés-Hernández A, Vaamonde A, Granado-Lorencio C (2013) ModestR: a software tool for managing and analyzing species distribution map databases. *Ecography* 36:102–1207
- García-Roselló E, Guisan C, Heine J, Pelayo-Villamil P, Manjarrés-Hernández A, González-Vilas L, González-Dacosta J, Vaamonde A, Granado-Lorencio C (2014) Using ModestR to download, import and clean species distribution records. *Methods Ecol Evol* 5:703–713
- García-Roselló E, Guisan C, Manjarrés-Hernández A, González-Dacosta J, Heine J, Pelayo-Villamil P, Vari RP, Vaamonde A, Granado-Lorencio C, Lobo JM (2015) Can we derive macroecological patterns from primary GBIF data? *Global Ecol Biogeogr* 24:335–347
- Guisan C, Lobo JM (2018) Discriminating well surveyed spatial units from exhaustive biodiversity databases. R package version. 1.3. <http://cran.r-project.org/web/packages/KnowBR>
- Guisan C, Manjarrés-Hernández A, Pelayo-Villamil P, Granado-Lorencio C, Riveiro I, Acuña A, Prieto-Piraquive E, Janeiro E, Matías JM, Patti C, Patti B, Mazzola S, Jiménez S, Duque V, Salmerón F (2010) Ipez: an expert system for the taxonomic identification of fishes based on machine learning techniques. *Fish Res* 102:240–247
- Guisan C, Heine J, González-DaCosta J, García-Roselló E (2014) RWizard Software. University of Vigo, Vigo
- Hortal J, Lobo JM (2005) An ED-based protocol for the optimal sampling of biodiversity. *Biodivers Conserv* 14:2913–2947
- Hortal J, Jiménez-Valverde A, Gómez JF, Lobo JM, Baselga A (2008) Historical bias in biodiversity inventories affects the observed environmental niche of the species. *Oikos* 117:847–858
- Hortal J, Bello Fd, Diniz-Filho JAF, Lewinsohn TM, Lobo JM, Ladle RJ (2015) Seven shortfalls that beset large-scale knowledge of biodiversity. *Annu Rev Ecol Evol Syst* 46:523–549
- Lobo JM (2008) Database records as a surrogate for sampling effort provide higher species richness estimations. *Biodiv Conserv* 17:873–881
- Lobo JM, Martín-Piera F (2002) Searching for a predictive model for species richness of iberian dung beetle based on spatial and environmental variable. *Conserv Biol* 16:158–173
- Lobo JM, Lumaret JP, Jay-Robert P (1997) Les atlas faunistiques comme outils d'analyse spatiale de la biodiversité. *Ann Soc Entomol Fr* 33:129–138
- Lobo JM, Hortal J, Yela JL, Millán A, Sánchez-Fernández D, García-Roselló E, González-Dacosta J, Heine J, González-Vilas L, Guisan C (2018) KnowBR: an application to map the geographical variation of survey effort and identify well-surveyed areas from biodiversity databases. *Ecol Ind* 91:241–248
- Meyer C, Jetz W, Guralnick RP, Fritz SA, Kreft H (2015a) Global drivers of species variation in mobilized point-occurrence information. *PeerJ PrePrints* 3:e1493
- Meyer C, Kreft H, Guralnick RP, Jetz W (2015b) Global priorities for an effective information basis of biodiversity distributions. *PeerJ PrePrints* 3:e1057
- Mora C, Tittensor DP, Myers RA (2008) The completeness of taxonomic inventories for describing the global diversity and distribution of marine fishes. *Proc R Soc B* 275:149–155

- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H (2017) *Community Ecology Package*. R package version 2.4-3. <http://cran.r-project.org/web/packages/vegan>
- Pelayo-Villamil P, Guisande C, Vari RP, Manjarrés-Hernández A, García-Roselló E, González-Dacosta J, Heine J, González-Vilas L, Patti B, Quinci EM, Jiménez LF, Granado-Lorencio C, Tedesco PA, Lobo JM (2015) Global diversity patterns of freshwater fishes—Potential victims of their own success. *Divers Distrib* 21:345–356
- Rocchini D, Hortal J, Lengyel S, Lobo JM, Jiménez-Valverde A, Ricotta C, Bacaro G, Chiarucci A (2011) Accounting for uncertainty when mapping species distributions: the need for maps of ignorance. *Prog Phys Geogr* 35:211–226
- Ruete A (2015) Displaying bias in sampling effort of data accessed from biodiversity databases using ignorance maps. *Biodivers Data J* 3:e5361
- Sainge MN, Onana JM, Nchu F, Kenfack D, Peterson AT (2017) Botanical sampling gaps across the cameroon mountains. *Biodivers Inform* 12:76–83
- Soberón J, Llorente BJ (1993) The use of species accumulation functions for the prediction of species richness. *Conserv Biol* 7:480–488
- Soberón J, Jimenez R, Golubov J, Koleff P (2007) Assessing completeness of biodiversity databases at different spatial scales. *Ecography* 30:152–160
- Sousa-Baena MS, Garcia LC, Peterson AT (2014) Completeness of digital accessible knowledge of the plants of Brazil and priorities for survey and inventory. *Divers Distrib* 20:369–381
- Swanson B (2015) Moore's Law at 50. The performance and prospects of the exponential economy. American Enterprise Institute for Public Policy Research, Washington, D.C
- Tedesco PA, Beauchard O, Bigorne R, Blanchet S, Buisson L, Conti L, Cornu JF, Dias MS, Grenouillet G, Hugueny B, Jézéquel C, Leprieur F, Brosse S, Oberdorff T (2017) A global database on freshwater fish species occurrence in drainage basins. *Sci Data* 4:170141. <https://doi.org/10.1038/sdata.2017.141>
- Track E, Forbes N, Strawn G (2017) The end of Moore's law. *Comput Sci Eng* 19:4–6
- Troia MJ, McManamay RA (2016) Filling in the gaps: evaluating completeness and coverage of open-access biodiversity databases in the United States. *Ecol Evol* 6:4654–4669
- Troia MJ, McManamay RA (2017) Completeness and coverage of open-access freshwater fish distribution data in the United States. *Divers Distrib* 23:1482–1498
- Ugland KI, Gray JS, Ellingsen KE (2003) The species-accumulation curve and estimation of species richness. *J Anim Ecol* 72:888–897
- Van Sickle J (2010) Basic GIS coordinates, 2nd edn. CRC Press, Boca Raton

Affiliations

Patricia Pelayo-Villamil¹ · Cástor Guisande²  · Ana Manjarrés-Hernández³ · Luz Fernanda Jiménez¹ · Carlos Granado-Lorencio⁴ · Emilio García-Roselló⁵ · Jacinto González-Dacosta⁵ · Juergen Heine⁵ · Luis González-Vilas² · Jorge M. Lobo⁶

¹ Grupo de Ictiología, Universidad de Antioquia, A.A. 1226, Medellín, Colombia

² Facultad de Ciencias, Universidad de Vigo, Lagoas-Marcosende, 36200 Vigo, Spain

³ Instituto Amazónico de Investigaciones-IMANI, Universidad Nacional de Colombia, A.A. 215, Leticia, Colombia

⁴ Departamento de Biología Vegetal y Ecología, Facultad de Biología, Universidad de Sevilla, Seville, Spain

⁵ Departamento de Informática, Edificio Fundición, Universidad de Vigo, Campus Lagoas-Marcosende, 36310 Vigo, Spain

⁶ Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales (CSIC), c/José Gutiérrez Abascal 2, 28006 Madrid, Spain