- Sampbias, a method to evaluate geographic
- sampling bias in species distribution data
- Alexander Zizka^{1,2,3}, Alexandre Antonelli^{3,4,5}, Daniele Silvestro^{3,4}
- 1. German Center for Integrative Biodiversity Research, University of Leipzig, Leipzig,
- 5 Germany
- 2. Naturalis Biodiversity Center, Leiden University, Leiden, The Netherlands
- 3. Gothenburg Global Biodiversity Centre, University of Gothenburg, Gothenburg, Sweden
- 4. Department of Biological and Environmental Sciences, University of Gothenburg,
- 9 Gothenburg, Sweden
- 5. Royal Botanical Gardens Kew, Richmond, Surrey, United Kingdom

1 Abstract

Georeferenced species occurrences from public databases have become essential to biodiversity research and conservation, but have limitations. Geographically biased sampling is a widely 13 recognized issue that might severely affect analyses. Especially "roadside bias", i.e. differences in sampling intensity among localities caused by differences in accessibility for humans is 15 ubiquitous and might differ in strength among taxonomic groups and datasets. Yet, no general 16 methodology exists to quantify the effect of roadside or other sources of bias on a dataset 17 level. Here we present sampbias, a novel algorithm and software to estimate the biasing effect 18 of accessibility (by roads, rivers, airports, cities, or any user-defined structures) in species 19 occurrence datasets. Sampbias is based on a null model of even sampling and assesses whether instead sampling probability decays exponentially with distance. The results are comparable 21 among biasing factors and datasets. Sampbias is implemented as a user-friendly R package, and Shiny app. We exemplify the use of sampbias on a dataset of mammal occurrences from the Indonesian island of Borneo, downloaded from www.gbif.org. Sampbias offers an efficient and largely automated means for biodiversity scientists and non-specialists alike to explore 25 bias in species occurrence data. The output of sampbias may be used to identify priorities for further collection or digitalization efforts, provide bias surfaces for species distribution 27 modelling, or assess the reliability of scientific results based on publicly available species distribution data.

30 Keywords

- ³¹ Collection effort, Global biodiversity Information Facility (GBIF), Presence only data, Road-
- 32 side bias, Sampling intensity

33 Introduction

Publicly available datasets of geo-referenced species occurrences, such as provided by the Global Biodiversity Information Facility (www.gbif.org) have become a fundamental resource 35 in biological sciences, especially in biogeography, conservation, macroecology, and systematics. However, because these datasets are "presence-only" data, they rarely include information on collection effort. Instead they are typically not collected systematically and often compiled from a variety of sources (e.g. scientific expeditions, census counts, genetic barcoding studies, and citizen-science observations), thus becoming subject to collection biases (Meyer, Weigelt, and Kreft 2016). That is the number of data points available is biased by factors other than species' presence or abundance, including the under-sampling of specific taxa ("taxonomic bias", e.g., birds vs. nematodes), specific geographic regions ("geographic bias", i.e. easily accessible vs. remote areas), and specific temporal periods ("temporal bias", i.e. wet season vs. dry season, Isaac and Pocock 2015; Boakes et al. 2010). While these biases are broadly recognized, and approaches exist to account for them in some analyses (for instance for species-richness estimation (Engemann et al. 2015) species distribution modelling (Stolar and Nielsen 2015; Beck et al. 2014; Fithian et al. 2014; Warren et al. 2014; Boria et al. 2014; Varela et al. 2014; Fourcade et al. 2014), occupancy modelling (Kery and Royle 2016), or abundance estimations (Shimadzu and Darnell 2015)), few attempts have been made to discern among different sources of bias or to compare the strength of bias among datasets 51 (but see Ruete 2015). 52

Geographic sampling bias, the fact that sampling effort is spatially biased, rather than equally distributed over a given study area is prevalent in all non-systematically collected datasets

of species distributions. Many factors can affect sampling effort, such as socio-economic factors (i.e. national research spending, history of scientific research; Meyer et al. 2015, @Daru2018) and political factors (armed conflict, democratic rights; Rydén et al. 2019) or physical accessibility (i.e. distance to a road or river, terrain conditions, slope; Yang, Ma, and Kreft 2014; Botts, Erasmus, and Alexander 2011). Especially physical accessibility is omnipresent as a biasing factor (e.g. Lin et al. 2015; Engemann et al. 2015), across spatial scales, and the term "roadside bias" has been coined for it. In practice, this means that most species observations (occurrence points) are made in or near cities, along roads and rivers, and near other human settlements (such as airports). Less observations come from the middle of a tropical rainforest or from a mountain top. Interestingly, since the observation of different taxonomic groups has different challenges, geographic sampling bias and the effect of accessibility may differ among taxonomic groups (Vale and Jenkins 2012).

The implications of not considering spatial collection bias in biodiversity research are likely to be substantial (Meyer, Weigelt, and Kreft 2016; Rocchini et al. 2011; Shimadzu and Darnell 2015; Yang, Ma, and Kreft 2013; Kramer-Schadt et al. 2013; Barbosa, Pautasso, and Figueiredo 2013). While it is unrealistic to expect that spatial biases in biodiversity data will ever disappear, it is crucial that researchers realise the intrinsic biases associated with the biodiversity data they are dealing with. This is the first step towards estimating to which extent these biases may affect their analyses, results, and conclusions drawn from such data. Therefore, it is advisable for any study dealing with species occurrence data to assess the strength of accessibility bias in the underlaying data.

Here, we present sampbias, a novel method to quantify accessibility bias in individual datasets

- of species occurrences, in a way that is comparable across datasets. *Sampbias* is implemented as an R-package. Specifically, *sampbias* uses a null-model of random sampling to address two questions:
- 1) How strong is the accessibility bias in a given dataset?
- 2) How important are different means of human accessibility, such as to airport, cities, rivers or roads, in causing this bias?
- 3) How is sampling bias distributed in space, i.e. which areas are a priority for targeted sampling?

$_{85}$ Description

86 General concept

Under the assumption that organisms exist across the entire area of interest, we can expect
the number of sampled occurrences to be distributed uniformly in space (even though, of
course, the density of individuals and the species composition may be heterogeneous). [[I
think we should acknowledge here that this assumption is valid when looking at a geographically
restricted area, eg within a tropical forest. Of course different biomes eg forest, alpine, oceanic
will result in different carrying capacity]] With sampbias we assess if a set of occurrences
significantly departs from a null uniform distribution and whether these discrepancies between
expected and observed distributions can be explained by distance from factors that potentially
bias their sampling probability (e.g. distance from cities or roads).

Sampbias works on a user-defined scale, and any dataset of multi-species occurrence records
can be tested against any geographic gazetteer (reliability increases with increasing dataset
size). Default large-scale gazetteers for airports, cities, rivers and roads are provided with
sampbias. Species occurrence data as downloaded from the data portal of GBIF can be
directly used as input data for sampbias. The output of the package includes measures of
bias effect, which are comparable between different gazetteers (e.g. comparing biasing effect
of roads and rivers), different taxa (e.g. birds vs. flowering plants) and different data sets
(e.g. specimens vs. human observations).

CoordinateCleaner is implemented in R (R Core Team 2019) based on standard tools for spatial statistics: ggplot2 (Wickham 2009), geosphere (Hijmans 2019), maptools (Bivand and Rundel 2019), raster (Hijmans 2019), sp (Pebesma and Bivand 2005; Bivand, Pebesma, and Gomez-Rubio 2013), and viridis (Garnier 2018).

Distance calculation

Sampbias uses gazetteers of the geographic location of bias sources (e.g. roads) to generate a 100 grid across the study area (the geographic extent of the dataset) for each gazetteer and then 110 calculates the distance ("as the crow flies") [[meaning?]] of the midpoint of each grid cell 111 to the closest cell containing an instance of the gazetteer. We then use these distance grids 112 to sample the distribution of distances in the observed dataset and the null distribution in 113 a reference dataset of equal size with randomly distributed records (the null model). The 114 resolution of the grid defined the precision of the distance estimates, for instance a 1x1 degree 115 raster will yield approximately a 100km precision at the equator. 116

17 Quantifying accessibility bias using maximum likelihood

Given the placement of a particular bias sources in the area of interest and assuming a 118 uniform distribution of samples, the probability of a sampled occurrence located at a distance 119 d from the closest bias source is a function of the amount of available area at that distance. 120 That is, the larger the area located at distance d from a bias source the more samples we 121 expect. For simplicity we discretize the area of interest in a number of grid cells and indicate 122 with f(x) the function describing the number of available grid cells at any distance x, for 123 $0 < x < \max(x)$, where $\max(x)$ is the maximum observed distance between a cell and the 124 clostest bias source. The function f(x) is therefore calculated based on the distances of each 125 grid cell from its closest bias source. 126 The distribution of samples, in the absence of bias, should therefore represent a random 127

The distribution of samples, in the absence of bias, should therefore represent a random sample from f(x) and reflect its shape, i.e. d f(x) (Fig. 1). However, in the presence of a bias, we expect the probability of finding occurrences to decrease with increasing distance from a bias source. This in turn will alter the resulting distribution of samples that no longer match the expected distribution. Here, we model the effect of sampling bias by assuming that the probability of sampling an occurrence decreases exponentially with increasing distance (Fig. 1), following the function $b(x, l) = l \exp(-lx)$, where l is the rate parameter. Under these assumption the expected distribution of samples is given by $g(x, l) \propto f(x)b(x, l)$.

[[I wonder if we shouldn't use " $b(x,l) = \exp(-lx)$ " so the Y-value is always 1 at a distance of 0. That would require normalizing the likelihood based on the integral of the curve though, as it will be different from 1.]

144

get the distribution from all grid cells and normalize by the number of all available grid cells, 138 not downsampled to the same number of points ignore the starting at 1/intercept

a possion likelihood where the rate i two paramters, 1. speed of decae 2. how high is the bias 140 at distance zero 141

$$b(x,l) = \exp(-lx) \ q * exp(-lambdax) / \int_0^\infty (q * exp(-lambdax))$$

Average the bias by Akaike wheights, or likelihood

The rate parameter l describes the strength of the bias effect. When l is large the expected probability of sampling occurrences decreases very quickly as you move away from a bias 145 source (Fig. 1). In contrast, when the l parameter is small, the resulting exponential 146 distribution effectively becomes more and more similar to a uniform distribution (Fig. 1), 147 indicating that increasing distance from e.g. a city does not affect the sampling probability. 148 We treat l as an unknown variable and estimate it using maximum likelihood from the data 149 based on the probability density function described by q(x,l). This essentially means finding 150 the value of l that best explains any discrepancies between the expected distribution (f(x))151 and the observed occurrences. [I think this is in fact a posterior probability where f(x) is the 152 empirical prior and b(x,l) the likelihood and we do a maximum a posteriori optimization. Once we have an estimated value of l, we can infer the expected accessibility bias as a function 154 of distance using b(x,l). Since the function b(x,l) describes the exponentially decreasing 155 sampling probability in relation to distance, we can define a standardized bias function as: 156 B(x,l) = 1 - b(x,l)/b(0,l), [[Actually I think this is effectively equivalent to what I wrote 157

above $b(x, l) = \exp(-lx)$ where the level of bias is set to 0 at distance 0 from the bias 158 source. The standardized bias function tends asymptotically to 1 as the distance tends to infinity. However, since in any area $max(x) << \infty$, for small values of l (i.e. little or no bias), 160 B(x,l) will look essentially like a uniform distribution with values very close to 0. Large 161 values of l (i.e. strong bias) will instead result in a curve that quickly approaches 1 with increasing distance. The values provided by the standardized bias function can be interpreted 163 as the proportion of occurrences that are missing from the sample, compared to the observed 164 samples at distance 0. Thus, if for a given estimated l we have B(50, l) = 0.20, we can expect 165 that at 50 Km from e.g. a road the number of occurrences per grid cell will be about 80% of 166 the occurrences sampled at distance 0 from the road, with 20\% missing due to sampling bias. 167 When running sampbias, we typically test different sources of biases, such as roads, cities, airports, etc. For each factor an independent expected distribution (f(x)) is computed and a 169 parameter l is estimated from q(x,l). These estimates can be use to produce maps showing 170 the intensity of potential biases across the area based on the standardized bias function. The 171 bias values obtained from different sources can then be averaged in each grid cell to produce 172 a map showing the combined effects of all sources. [[yeah this part is still weird. Basically, if 173 rivers are not explaining anything they should count nothing toward the combined estimate, 174 whereas they do now. I think we could try to see if the max likelihoods are comparable and 175 weight the average by that.]] 176

77 Running sampbias

A default sampbias analysis can be run with few lines of code in R. The main function

SamplingBias creates an object of the class "sampbias", for which the package provides

a plotting and summary method. Based on a data.frame including species identity and

geographic coordinates, sampbias provides a bias effect estimate for each gazetteer and an

average bias. Additionally some options exist to provide custom gazetteers, custom distances

for the bias estimation, a custom grain size of the analysis, as well as some operators for the

calculation of the bias distances. A tutorial on how to use sampbias is available with the

package and in the electronic supplement of this publication (Appendix S1).

```
library(sampbias)

# a data table with species identify, longitude, and latitude

example.in <- read.csv(system.file("extdata", "mammals_borneo.csv", package = "sampbias"

sep = "\t")

# running sampbias

example.out <- SamplingBias(x = example.in, res = 0.1)

# summarizing the results

summary(example.out)

plot(example.out)</pre>
```

For data exploration we implemented the basic functionalities in a shiny app as graphical user interface (Fig. 2). Analyses can be run based on a tab separated .txt file with occurrence information including the column headers "species", "decimallongitude" and "decimallatitude", as for instance files downloaded from www.gbif.org, using custom gazetteers. A tutorial on how to use the *sampbias* GUI is available online (https://ropensci.github.io/sampbias/) and in the electronic supplement of this publication (Appendix S2).

Empirical example

To exemplify the use and output of sampbias, we downloaded the occurrence records of all mammals available from the Indonesian island of Borneo (???), and quantify the biasing effect of airports, cities and roads in the dataset. Something on the results, also add a table (Fig. 3)

Assumptions and future prospective

Two assumptions of *sampbias* are a equal sampling of occurrence records across the study
area as null model and an exponential increase of the biasing effect with distance from the
gazetteers. We considered both acceptable approximations for the purpose of the package,
but future expansions of *sampbias* could relax these assumptions, for instance by allowing
other distance decay functions, such as gamma or Weibull distributions, and by changing the
sampling scheme of the background points. The first steps towards these goals are already
implemented in the current version of *sampbias* with the option to limit background points

to a convex hull around the dataset or limiting background points to terrestrial surface. [[Idon't understand this part]]

A practical limitation of sampbias is the trade-off between the resolution of the grid for the distance calculation and the geographic extent of the dataset. For instance, a 100m resolution for a global dataset would lead to the generation of grid for which distance calculation will become computationally prohibitive in most practical cases, Hence, sampbias is best suited for local or regional datasets at high resolution (c. 100 - 10,000m) or continental datasets at low resolution (c. 10 - 100km).

\mathbf{Todo}

214 re-run empirical analysis

215 test units

Data accessibility

The software presented here is available under a GPL-3 license. The *sampbias* R package and the source code for the shiny app are available via https://github.com/azizka/sampbias, the shiny app can be accessed at https://azizka.shinyapps.io/sampbias/. The R package includes an example dataset as well as vignettes detailing the use of the R package, the use of the shiny app and possibly warnings produced by the package (Appendix S3).

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- this research. We thank all data collectors and contributors to GBIF for their effort.

225 Author contributions

- 226 All authors conceived of this study, AZ and DS developed the statistical algorithm, AZ and
- DS wrote the R-package and AZ the Shiny app, AZ and DS wrote the manuscript with
- contributions from AA.

Figures 5

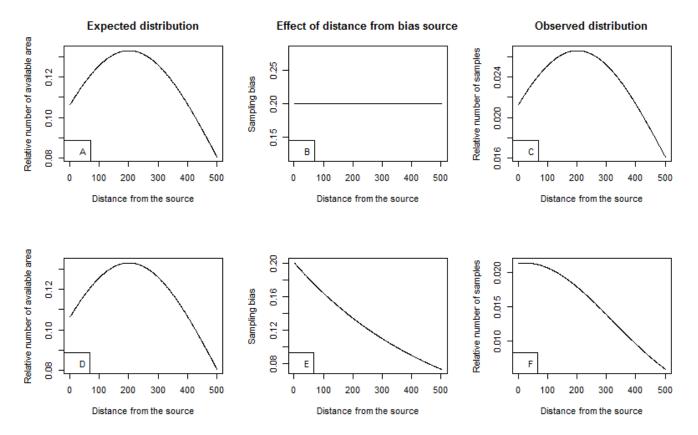


Figure 1: Schematic representation of the *sampbias* algorithm. The upper panel (A-C) shows a case without accessibility bias: the observed distribution of distances from the geographic feature of interest matches the expected distribution and hence the bias function is flat. The lower panel (D-F) shows a case with bias: the expected and observed distribution differ and the bias is best represented by an exponential function.

Sampling bias in species distribution records

Occurence File Choose File ...160822134323880.csv Occurrence number Bias Type None Species Cities Airports Rivers Roads 114 Longitude Combined Raster resolution [deg] 0.1 Bias effect 0.0 -2.5 114 Longitude 117

Figure 2: The interface of the sampbias shiny app. With a navigation panel on the left and visualization of the results on the right.

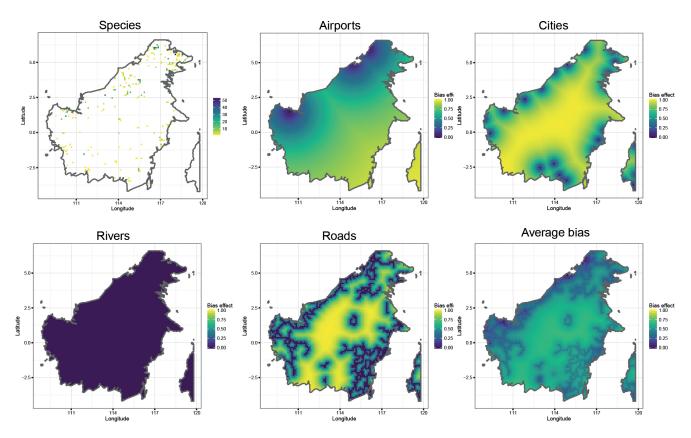


Figure 3: The spatial projection of the accessibility bias in an empirical example dataset of mammal occurrences on the Indonesian island of Borneo from www.gbif.org. *Sampbias* finds a strong biasing effect by roads, cities and lower by airports, but, surprisingly, no effect of rivers.

230 Supplementary material

- 231 Appendix S1 Tutorial running sampbias in R
- 232 Appendix S2 Tutorial running the samplias shiny app
- Appendix S3 Possible warnings and their solutions

References

- Barbosa, A. Márcia, Marco Pautasso, and Diogo Figueiredo. 2013. "Species-people corre-
- 236 lations and the need to account for survey effort in biodiversity analyses." Diversity and
- 237 Distributions 19 (9): 1188–97. https://doi.org/10.1111/ddi.12106.
- Beck, Jan, Marianne Böller, Andreas Erhardt, and Wolfgang Schwanghart. 2014. "Spatial
- bias in the GBIF database and its effect on modeling species' geographic distributions."
- 240 Ecological Informatics 19: 10–15. https://doi.org/10.1016/j.ecoinf.2013.11.002.
- ²⁴¹ Bivand, Roger, and Colin Rundel. 2019. "rgeos: Interface to Geometry Engine Open Source
- 242 ('GEOS')." https://cran.r-project.org/package=rgeos.
- ²⁴³ Bivand, Roger S., Edzer J. Pebesma, and Virgilio Gomez-Rubio. 2013. Applied spatial data
- 244 analysis with R, Second edition. New York, USA: Springer.
- Boakes, Elizabeth H., Philip J K Mcgowan, Richard A Fuller, Ding Chang-Qing, Natalie
- E Clark, Kim O Connor, and Georgina M. Mace. 2010. "Distorted views of biodiversity:
- Spatial and temporal bias in species occurrence data." PLoS Biology 8 (6): e1000385.
- 248 https://doi.org/10.1371/journal.pbio.1000385.
- Boria, Robert A., Link E. Olson, Steven M. Goodman, and Robert P. Anderson. 2014. "Spatial
- 250 filtering to reduce sampling bias can improve the performance of ecological niche models."
- 251 Ecological Modelling 275 (March): 73–77. https://doi.org/10.1016/j.ecolmodel.2013.12.012.
- 252 Botts, Emily A., Barend F N Erasmus, and Graham J. Alexander. 2011. "Geographic

- 253 sampling bias in the South African Frog Atlas Project: Implications for conservation planning."
- $Biodiversity \ and \ Conservation \ 20 \ (1): \ 119-39. \ https://doi.org/10.1007/s10531-010-9950-6.$
- Daru, Barnabas H, Daniel S Park, Richard B Primack, Charles G Willis, David S Barrington,
- ²⁵⁶ Timothy J S Whitfeld, Tristram G Seidler, et al. 2018. "Widespread sampling biases in
- herbaria revealed from large-scale digitization." New Phytologist 217 (2): 939–55. https:
- ²⁵⁸ //doi.org/10.1111/nph.14855.
- Engemann, Kristine, Brian J Enquist, Brody Sandel, Brad Boyle, Peter M Jørgensen, Naia
- Morueta-Holme, Robert K Peet, Cyrille Violle, and Jens-Christian Svenning. 2015. "Limited
- sampling hampers 'big data' estimation of species richness in a tropical biodiversity hotspot."
- 262 Ecology and Evolution 5 (3): 807–20. https://doi.org/10.1002/ece3.1405.
- Fithian, William, Jane Elith, Trevor Hastie, and David a. Keith. 2014. "Bias correction in
- species distribution models: pooling survey and collection data for multiple species." Methods
- 265 in Ecology and Evolution 6 (4): 424–38. https://doi.org/10.1111/2041-210X.12242.
- Fourcade, Yoan, Jan O. Engler, Dennis Rödder, and Jean Secondi. 2014. "Mapping Species
- 267 Distributions with MAXENT Using a Geographically Biased Sample of Presence Data: A
- Performance Assessment of Methods for Correcting Sampling Bias." PLoS ONE 9 (5): e97122.
- 269 https://doi.org/10.1371/journal.pone.0097122.
- Garnier, Simon. 2018. viridis: Default Color Maps from 'matplotlib'. https://cran.r-project.
- 271 org/package=viridis.
- Hijmans, Robert J. 2019. "geosphere: Spherical Trigonometry." https://cran.r-project.org/

- 273 package=geosphere.
- ²⁷⁴ Isaac, Nick J B, and Michael J O Pocock. 2015. "Bias and information in biological records."
- 275 Biological Journal of the Linnean Society 115 (3): 522–31. https://doi.org/10.1111/bij.12532.
- Kery, Marc, and J Andrew Royle. 2016. Applied Hierarchical Modeling in Ecology Analysis
- of distribution, abundance and species richness in R and BUGS: Volume 1: Prelude and
- 278 Static Models. Amsterdam: Academic Press, Elsevier.
- 279 Kramer-Schadt, Stephanie, Jürgen Niedballa, John D. Pilgrim, Boris Schröder, Jana Linden-
- born, Vanessa Reinfelder, Milena Stillfried, et al. 2013. "The importance of correcting for
- sampling bias in MaxEnt species distribution models." Diversity and Distributions 19 (11):
- 282 1366–79. https://doi.org/10.1111/ddi.12096.
- Lin, Yu-pin, Dongpo Deng, Wei-chih Lin, Rob Lemmens, Neville D Crossman, Klaus Henle,
- and Dirk S Schmeller. 2015. "Uncertainty analysis of crowd-sourced and professionally
- collected field data used in species distribution models of Taiwanese moths." Biological
- 286 Conservation 181: 102–10. https://doi.org/10.1016/j.biocon.2014.11.012.
- Meyer, Carsten, Holger Kreft, Robert P Guralnick, and Walter Jetz. 2015. "Global priorities
- for an effective information basis of biodiversity distributions." Nature Communications 6
- 289 (e1057): 8221. https://doi.org/10.1038/ncomms9221.
- Meyer, Carsten, Patrick Weigelt, and Holger Kreft. 2016. "Multidimensional biases, gaps
- 291 and uncertainties in global plant occurrence information." Ecology Letters 19: 992–1006.
- ²⁹² https://doi.org/10.1111/ele.12624.

- Pebesma, Edzer J., and Roger S. Bivand. 2005. "Classes and methods for spatial data in R."
- 294 R News 5 (2). https://cran.r-project.org/doc/Rnews/.
- R Core Team. 2019. "R: A Language and Environment for Statistical Computing." Austria,
- ²⁹⁶ Vienna: R Foundation for Statistical Computing. https://www.r-project.org/.
- Rocchini, Duccio, Joaquín Hortal, Szabolcs Lengyel, Jorge M Lobo, Alberto Jiménez-Valverde,
- ²⁹⁸ Carlo Ricotta, Giovanni Bacaro, and Alessandro Chiarucci. 2011. "Accounting for uncertainty
- when mapping species distributions: The need for maps of ignorance." Progress in Physical Ge-
- ography: Earth and Environment 35 (2): 211–26. https://doi.org/10.1177/0309133311399491.
- Ruete, Alejandro. 2015. "Displaying bias in sampling effort of data accessed from biodiversity
- databases using ignorance maps." Biodiversity Data Journal 3 (1): e5361. https://doi.org/10.
- 303 3897/BDJ.3.e5361.
- Rydén, Oskar, Alexander Zizka, Sverker C Jagers, Staffan I Lindberg, and Alexandre Antonelli.
- ³⁰⁵ 2019. "Linking democracy and biodiversity conservation: Empirical evidence and research
- gaps." Ambio, June. https://doi.org/10.1007/s13280-019-01210-0.
- Shimadzu, Hideyasu, and Ross Darnell. 2015. "Attenuation of species abundance distributions
- 308 by sampling." Royal Society Open Science 2 (4): 140219. https://doi.org/10.1098/rsos.140219.
- Stolar, Jessica, and Scott E. Nielsen. 2015. "Accounting for spatially biased sampling effort
- in presence-only species distribution modelling." Diversity and Distributions 21 (5): 595–608.
- 311 https://doi.org/10.1111/ddi.12279.

- Vale, Mariana M., and Clinton N. Jenkins. 2012. "Across-taxa incongruence in patterns of collecting bias." *Journal of Biogeography* 39 (9): 1744–4. https://doi.org/10.1111/j.1365-2699.

 2012.02759.x.
- Varela, Sara, Robert P. Anderson, Raúl García-Valdés, and Federico Fernández-González.

 2014. "Environmental filters reduce the effects of sampling bias and improve predictions of
 ecological niche models." *Ecography*, no. September 2013: 1084–91. https://doi.org/10.1111/
 j.1600-0587.2013.00441.x.
- Warren, Dan L., Amber N. Wright, Stephanie N. Seifert, and H. Bradley Shaffer. 2014.

 "Incorporating model complexity and spatial sampling bias into ecological niche models of
 climate change risks faced by 90 California vertebrate species of concern." Diversity and
 Distributions 20 (3): 334–43. https://doi.org/10.1111/ddi.12160.
- Wickham, Hadley. 2009. ggplot2 Elegant Graphics for Data Analysis. New York: Springer.

 https://doi.org/10.1007/978-0-387-98141-3.
- Yang, Wenjing, Keping Ma, and Holger Kreft. 2013. "Geographical sampling bias in a large distributional database and its effects on species richness-environment models." *Journal of Biogeography* 40 (8): 1415–26. https://doi.org/10.1111/jbi.12108.
- 2014. "Environmental and socio-economic factors shaping the geography of floristic collections in China." Global Ecology and Biogeography 23 (11): 1284–92. https://doi.org/10. 1111/geb.12225.