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## 2 A. TITLE PAGE

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FRESHWATER FISH BIODIVERSITY ESTIMATION

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8 **Title: Quantifying regional biodiversity in the tropics: a case study of freshwater fish in**  
9 **Trinidad and Tobago.**

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33 B. ABSTRACT PAGE (Page 1)

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35 Extinction rates are predicted to accelerate during the Anthropocene. Quantifying and  
36 mitigating these extinctions demands robust data on distributions of species and the diversity  
37 of taxa in regional biotas. However, many assemblages, particularly those in the tropics, are  
38 poorly characterized. Targeted surveys and historical museum collections are increasingly  
39 being used to meet the urgent need for accurate information, but the extent to which these  
40 contrasting data sources support meaningful inferences about biodiversity change in regional  
41 assemblages remains unclear. Here we seek to elucidate uncertainty surrounding regional  
42 biodiversity estimates by evaluating the performance of these alternative methods in  
43 estimating the species richness and assemblage composition of the freshwater fish of Trinidad  
44 and Tobago.

45 We compared estimates of regional species richness derived from two freshwater fish  
46 datasets: a targeted two year survey of Trinidad and Tobago rivers and historical museum  
47 collection records submitted to The University of the West Indies Zoology Museum.

48 Richness was estimated using rarefaction and extrapolation, and assemblage composition was  
49 benchmarked against a recent literature review. Both datasets provided similar estimates of  
50 regional freshwater fish species richness (50 and 46 species, respectively), with a large  
51 overlap (85%) in species identities. Regional species richness estimates based on survey and  
52 museum data are thus comparable, and consistent in the species they include. Our results  
53 suggest that museum collection data are a viable option for setting reliable baselines in many  
54 tropical systems, thereby widening options for meaningful monitoring and evaluation of  
55 temporal trends.

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58 C. KEY WORDS

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60 1. Key words: Provide up to eight key words after the abstract, separated by a semi-  
61 colon (;). Key words should be in English (with the exception of taxonomic information) and  
62 listed alphabetically.

63

64 Assemblage composition; museum collections; species richness; neotropics; rarefaction; extrapolation

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66 ALTHOUGH THERE IS GENERAL AGREEMENT THAT WE HAVE ENTERED THE  
67 ANTHROPOCENE, AN ERA LIKELY TO BE CHARACTERISED BY MASS  
68 EXTINCTIONS (Barnosky et al., 2011; Dirzo & Raven, 2003), there are substantial gaps in  
69 our understanding of biodiversity change, particularly at regional scales (McGill, Dornelas,  
70 Gotelli, & Magurran, 2015), and considerable uncertainty about extinction rates (Ceballos et  
71 al., 2015). Many assemblages, notably those in the tropics, are poorly characterised  
72 (Coddington, Agnarsson, Miller, Kunter, & Hormiga, 2009; Collen, Ram, Zamin, & McRae,  
73 2008). Even in well-sampled areas many species are very rare, and are recorded in surveys  
74 only as singletons or “uniques” (Longino, Coddington, & Colwell, 2002). The presence of  
75 uniques in species accumulation curves is a strong indicator that unseen species are yet to be  
76 detected (Chao, 1984). One solution is to use statistical estimation approaches to deduce the  
77 number of unseen species in survey data (i.e. Chao & Jost, 2012; Gotelli & Colwell, 2001;  
78 Gotelli & Colwell, 2011).

79 Historical natural history museum records and herbarium collections are potential sources of  
80 data for biodiversity estimation, and are increasingly used to address ecological and  
81 conservation questions (Pyke & Ehrlich, 2010; Reznick, Baxter, & Endler, 1994). There are,  
82 though, concerns about possible biases in this type of data, particularly in terms of spatial  
83 representation and sampling bias (Fattorini, 2013; Guralnick & Van Cleve, 2005; Newbold,  
84 2010).

85 The extent to which these different data sources provide meaningful inferences about  
86 biodiversity change in regional assemblages remains unclear. Survey data, on the one hand,  
87 may underestimate species richness to a greater extent than museum records because  
88 sampling is generally targeted at specific areas or habitats, or depends on methods which may  
89 incompletely record certain taxa (Guralnick & Van Cleve, 2005). For example, species that  
90 are known or suspected to be abundant in the sample area but are not easily recorded using

91 the sampling methodology (Longino et al., 2002). On the other hand, while museums  
92 typically seek to maximise the range of specimens in the collection, they rarely set out to  
93 enumerate the species that co-occur in functioning ecosystems. Comprehensive species lists  
94 are accumulated over time, and often include transient taxa and misidentifications, so such  
95 lists are not necessarily an informative guide to the species actually present in an assemblage  
96 during a defined time period (Phillip et al., 2013).

97 Previous assessments of the relative utility of biodiversity quantifications from survey data  
98 and museum collections have focused on species richness rather than species identities  
99 (Guralnick & Van Cleve, 2005; Pyke & Ehrlich, 2010). However, biodiversity change can be  
100 substantially decoupled from species richness change when there is extensive turnover within  
101 assemblages (Dornelas et al., 2014; Hillebrand et al., 2017; Vellend et al., 2013, 2017).

102 Accurate assessment of turnover (beta diversity), both spatial and temporal, is becoming  
103 increasingly important to understanding biodiversity change (Dornelas et al., 2014; McGill et  
104 al., 2015). There is consequently a need to recognize uncertainties and biases not only of  
105 species richness estimates, but also of species identities recorded within these contrasting  
106 datatypes. For example, previous research suggests that while museum records may provide  
107 useful estimates of richness, species identities may be biased towards rare species (Guralnick  
108 & Van Cleve, 2005; Pyke & Ehrlich, 2010). This is of particular concern if species lists  
109 derived from one sampling method will be used as baselines for further assessments using  
110 data collected with other methods.

111 Here we ask how conclusions about the biodiversity of freshwater fish in Trinidad and  
112 Tobago differ when based on a targeted survey versus a museum collection. First, we  
113 evaluate the performance of these alternative data sources when estimating the species  
114 richness of the freshwater fish fauna, and benchmark our results against a recent literature

115 review. Secondly, we analyse the identities of species recorded by both methods to assess  
116 which species are absent, and to pinpoint possible biases in types of species detected.

117 Our initial expectations regarding biases in the datasets are as follows:

- 118 1. The museum data will contain more transient species than the survey data because the  
119 longer period of time covered by the museum data increases the chance of finding a  
120 species that subsequently becomes locally extinct.
- 121 2. There will be more species with specialized habitat requirements or narrow spatial  
122 distributions in the museum collection data than the sampling data. We expect this  
123 because of biases associated with museum collection data, specifically the “rare  
124 representation effect” where collectors target rare species (Guralnick & Van Cleve,  
125 2005; Pyke & Ehrlich, 2010).
- 126 3. The majority of species missing from both datasets will be those that are narrowly  
127 distributed or habitat specialists, because these uncommon species are least likely to  
128 be noticed by collectors or sampled by systematic surveys.

## 129 **METHODS**

### 130 **STUDY AREA**

131 The country of Trinidad and Tobago is formed of two main islands lying to the northeast of  
132 Venezuela. Trinidad, the larger island, is 4820 km<sup>2</sup>, and is only 11.3 km from Venezuela.  
133 Tobago is far smaller at 308 km<sup>2</sup>, and sits 30.6 km from the coast of Venezuela. The climate  
134 of both islands is tropical, with a mean annual temperature of around 27°C, and a temperature  
135 range of around 17°C to 33°C. The islands support a variety of freshwater habitats. Streams  
136 in the north of Trinidad and in Tobago contain mostly clear, fast flowing water with firm  
137 substrate ranging from boulders to gravel. The more southern parts of Trinidad contain  
138 slower, more turbid streams, with substrates ranging from sand to mud.

## 139 DATA SOURCES

140 Sampling was designed to provide useful data for conservation and management of the  
141 freshwater fish of Trinidad and Tobago. Ninety-one stream and river sites across the two  
142 islands were selected, representing all major drainages, biogeographic regions and river  
143 types. Each river had between one and three sampling locations. Sampling took place over  
144 two years (1997-1998), and 22 sites were sampled twice. Consistent sampling methods were  
145 used throughout, with small adjustments depending on stream type. Wherever possible, seine  
146 nets were used to block off sections of around 50m of river. A combination of methods  
147 including electrofishing (primarily in clear water), seine netting (in both clear and turbid  
148 water), and gill and trammel nets (particularly in larger rivers), were used to catch as many  
149 fish as possible in the blocked off sections. Species identities and their numerical abundances  
150 at each site were recorded before fish were returned to the stream at the point of capture.

151 The University of the West Indies Zoology Museum (UWIZM) is the de facto zoological  
152 collection for Trinidad & Tobago, and at the time of writing is one of the largest collections  
153 in the Caribbean. There are an estimated 70,000 specimens in the collections, the majority of  
154 which are local in origin. Although there was sporadic collecting of freshwater fish species  
155 from as early as 1936, the first significant fish collecting began in the mid-1960s and  
156 persisted through the rest of the 20<sup>th</sup> century. Few additions were made in the 2000s, but from  
157 2010 onwards there were significant additions from work done by visiting researchers. The  
158 UWIZM data are open access, and available at <https://doi.org/10.15468/m48ug8>.

159 For our analysis, we use collection year as the collection unit of the museum data (Petersen &  
160 Meier, 2003). The nomenclature of the freshwater fish species in both the survey and the  
161 museum collection was also checked using the list of old and new species names provided by  
162 the species list and key of fish species (Phillip et al., 2013), ensuring that all names used in  
163 the final analysis were up to date and comparable.

## 164 ANALYSIS

165 Freshwater fish species lists, particularly those for islands, typically include species that are  
166 mostly restricted to freshwaters, and taxa that are either normally found in estuaries as well as  
167 fish that are predominately marine but occasionally move upstream. In addition these lists  
168 typically include anadromous and catadromous species. Here we follow Phillip et al. (2013)'s  
169 definition of freshwater fish, based on habitat preference and taxonomy. To identify these  
170 freshwater fish, we used a recent literature review that includes a comprehensive species list  
171 and key for fish species (Phillip et al., 2013). From this list, we selected only species that are  
172 considered by Phillip et al. (2013) as truly freshwater, not those that are usually regarded as  
173 marine or coastal species. We included transient species but not species that Phillip et al.  
174 (2013) considered misidentifications. DATP also submitted specimens and records to the  
175 museum between 1997 and 1998 as part of her survey. To avoid any confounding influence  
176 of these records on the museum collection data results, we removed all samples collected by  
177 DATP in 1997 and 1998.

178 To estimate freshwater fish species richness in Trinidad and Tobago, we used rarefaction and  
179 extrapolation curves computed by the 'iNEXT' R package (Chao et al., 2014). Extrapolation  
180 enables the user to estimate the number of species that would be detected if sampling was  
181 increased to include an additional number of individuals or sampling units. In individual  
182 based rarefaction, individuals should be sampled at random (Colwell et al., 2012), an  
183 expectation that museum data (and most ecological surveys) will not satisfy. But sample-  
184 based incidence data need only be representative of the area surveyed, including spatial  
185 heterogeneity (Chao & Colwell, 2017; Colwell, Mao, & Chang, 2004). Nonetheless,  
186 rarefaction and extrapolation has been shown to be a robust and informative method with  
187 different types of data (e.g. phylogenetic diversity (Chao et al., 2015; Hsieh, Ma, & Chao,  
188 2016b) and distributions of stone tools in Pleistocene North America (Buchanan et al., 2017).



189 Also, note that the estimate attained from extrapolation is exactly the same as the non-  
190 parametric Chao2 estimate. For both datasets, we used the “incidence\_freq” datatype option,  
191 that is sample-based rarefaction rather than individual based rarefaction. For sample-based  
192 rarefaction sampling units need only be representative of the sampling area, which is a less  
193 stringent assumption than for individual based rarefaction (Colwell et al., 2004). We  
194 therefore chose sample-based rarefaction rather than individual based rarefaction in both  
195 cases. For the Museum data, we used the year in which an acquisition was recorded as its  
196 sample id. We benchmarked the estimated species richness numbers against the number  
197 provided by a comprehensive species list collated using all available fish records and expert  
198 knowledge of the Trinidad and Tobago freshwater fish fauna (Phillip et al., 2013)

199 To further understand whether the survey dataset and the museum collection dataset differ in  
200 the types of fish they represent, we categorized each fish species by status (i.e. native/non-  
201 native), by habitat specificity, and by how widely it was distributed across Trinidad and  
202 Tobago, using information in Phillip et al. (2013) and FishBase (fishbase.org) - see Table 1  
203 and Table S1. We compared the distribution of characteristics of the species observed in both  
204 the survey and museum datasets against the results of a null model (Fig. S1). The assumption  
205 of the null model was that each species had equal probability of being recorded, as long as it  
206 is found, or has been found, in the rivers of Trinidad and Tobago. For each iteration of the  
207 null model, 39 species (the number of observed species in the Museum data) were randomly  
208 selected from the list of 65 species that are likely to be present in Trinidad and Tobago  
209 according to Phillip et al. (2013). We recorded the native status, distribution, and habitat  
210 specificity of each of the randomly selected species, and then proceeded with the next  
211 iteration. The model had 1000 iterations. We then calculated the quantiles of the observed  
212 numbers of fish in the survey and museum data for each category in relation to the null model  
213 results.

214

215 **RESULTS**

## 216 ESTIMATED RICHNESS

217 Visual inspection of the observed species richness accumulation curve for the survey data  
218 (Fig. 1a), suggests an asymptote is close. Although there are far more records overall in the  
219 survey data than the museum data (Table 2), most species are found at only a few sites (under  
220 20) – a typical pattern in ecological surveys (Fig. 1c).

221 In contrast to the survey data results, the museum data accumulation curve does not support  
222 an asymptote close to the 39 species recorded (Fig. 1b). Collection effort is extremely  
223 variable in the museum data, with over 200 records submitted for one year in the 1990s and  
224 fewer than 100 for most other years (Fig. 1d). There is, however, no noticeable increase in  
225 new species during the period of increased specimen submissions (Fig. 1b). In addition, both  
226 data collection methods provide samples that are close to completely representative (Fig. 1e  
227 & 1f).

228 The iNEXT extrapolations estimated were within 10% of each other (50 species for the  
229 survey data (Fig. 1g), 46 for the museum data (Fig. 1h)), and they both lie well within each  
230 other's upper and lower 95% confidence intervals (Table 2). The survey data had higher  
231 uncertainty around this estimate, with the upper 95% richness estimated as 130 species as  
232 opposed to the 68 estimated from the museum data. The range of estimates predicted by both  
233 data types included the 65 species reported by the comprehensive key and species list (Phillip  
234 et al., 2013) (note the 66 quoted in the text of (Phillip et al., 2013) is a miscount of the true  
235 number listed in the table of species).

## 236 ASSEMBLAGE COMPOSITION

237 Fewer species are missing from the museum data but recorded in the survey data (4) than  
238 recorded in the survey but missing from the museum data (6) (Fig.2). No transient species  
239 were recorded in either dataset (Table 3), and the majority of species in both datasets were  
240 native. A high proportion of species missed by both data collection methods either were data  
241 deficient, transient, narrowly distributed or habitat specialists (Table 3).

242 Contrary to our expectation, there were no biases evident between types of fish recorded in  
243 the survey and museum data (Table 3; Fig. 3). Both underestimated the number of species  
244 thought to be present in Trinidad and Tobago, but the fraction of native species was higher in  
245 both cases than in the overall list provided by Phillip *et al.* (2013). Both datasets also included  
246 more intermediately or widely distributed species than this overall list, although the  
247 difference was more marked in the museum data than the survey data. There are also more  
248 habitat generalists in the observed data (both methods) than expected if they were a random  
249 draw from the overall list. This difference, however, is less pronounced because the number  
250 of habitat generalists in both surveys fall within the 95% quantiles of the null model.

251 **DISCUSSION**

252 Despite the two orders of magnitude fewer records contained in the museum data than the  
253 targeted survey data, both datasets provided comparable estimates of regional freshwater fish  
254 species richness in Trinidad and Tobago. The richness estimates of the museum and survey  
255 data were within 10% of each other (50 species and 46 species, respectively), and there was a  
256 large overlap (85%) of species identified. Both estimates fall 20% below the maximum  
257 number (65) of species potentially present according to the exhaustive list (Phillip *et al.*,  
258 2013; Table 2), but the upper confidence intervals of the estimates are inclusive of this  
259 maximum number of potential species.

260 We expected differences in the composition of species observed in the two contrasting  
261 datasets because of biases in the collection methods of the museum data. For example,  
262 sampling in historical museum collections generally occurs *ad hoc* by a variety of  
263 uncoordinated collectors, typically leading to an overrepresentation of easily accessible areas  
264 and centres of population (Engemann et al., 2015; Guralnick & Van Cleve, 2005; Soberón,  
265 Llorente, & Oñate, 2000; Tobler, Honorio, Janovec, & Reynel, 2007). Another bias is the  
266 “rare representation” effect: the tendency for collectors to favour unusual species, combined  
267 with longer collection times, giving a greater likelihood of finding species outside of their  
268 usual ranges (Guralnick & Van Cleve, 2005; Pyke & Ehrlich, 2010). The rare representation  
269 effect could cause overestimations of species richness, which in turn might inflate the  
270 importance of transient species that do not contribute to ecosystem processes. Contrary to our  
271 expectations, we found a striking similarity between the identities of the species recorded in  
272 the survey and museum data (Figs 1 & 3), suggesting these biases do not strongly influence  
273 regional species richness estimates in these data. The majority (85%) of species were  
274 recorded in both datasets. In addition, there was no indication of biases in types of species  
275 recorded; the museum collection data did not contain more transient species, nor habitat  
276 specialists or narrowly distributed species, than the survey data.

277 Our results suggest that, although collection methods differ considerably between datasets,  
278 survey and museum data can provide comparable estimations of the regional assemblage  
279 species composition. The substantial overlap in species present in both datasets is particularly  
280 notable because the dissimilarity between samples is inflated by incomplete species lists  
281 (Chao, Chazdon, Colwell, & Shen, 2005). Consequently, historical museum collection data  
282 are potentially useful for analysing other aspects of biodiversity change in addition to  
283 richness. Rates of turnover of species identity within assemblages, for instance, could be  
284 assessed with species lists. Rates of turnover are variable and driven by a complex collection

285 of biotic and abiotic factors (Korhonen, Soininen, & Hillebrand, 2010), and warrant more  
286 analysis. Datasets such as the collections held at The University of the West Indies Zoology  
287 Museum, Trinidad, could serve as a baseline for furthering our understanding of turnover  
288 within communities. Within the Caribbean region, for instance, collections similar to those  
289 held by The University of the West Indies Zoology Museum, Trinidad, include those held at  
290 The National Zoological Collection of Suriname (NZCS) and The Museo Nacional de  
291 Historia Natural “prof. Eugenio de Jesus Marcano” in Santo Domingo, Dominican Republic.  
292 More widely, there are similar museums with extensive collections that could be used to form  
293 the basis of species lists in Costa Rica, Cuba, Venezuela, Colombia, Panama and Nicaragua.  
294 There are also increasing possibilities for searching for and combining collections from  
295 multiple sources as more museum collection data are uploaded onto online repositories like  
296 the Global Biodiversity Information Facility (GBIF), meaning collections held outside of  
297 tropical regions can also be harnessed for creating baseline species lists.

298 Surveys provide robust data on species distributions and abundance, and are generally  
299 suitable for a wider variety of analyses than museum data. For example, the combination of  
300 species identity and relative abundance values of systematic survey data mean diversity  
301 metrics such as Hill numbers (which include forms of Shannon and Simpson diversity  
302 measures) can be calculated (Hill, 1973). These estimates allow the almost unbiased  
303 “effective” number of frequent species within assemblages to be estimated (Hsieh, Ma, &  
304 Chao, 2016a). However, surveys are not practical in many cases. Undertaking surveys can be  
305 expensive and requires good access to expertise and sites. The survey we used in this analysis  
306 took place over two years, and involved many hours of preparation and field work. Even in  
307 relatively well sampled sites, a short period of sampling activity does not often come close to  
308 the actual number of species in an area (Fattorini, 2013). This is a particular problem in  
309 tropical regions, where there is a substantial need for data. Alternative data gathering

310 exercises, namely intensive local sampling areas (i.e. Bouchet, Lozouet, Maestrati, & Heros,  
311 2002; Brown et al., 2018; Longino et al., 2002) could also be useful, but these sampling  
312 endeavours also require extremely high levels of expertise and investment, which are often  
313 unavailable, and are not practical on a regional scale. In these cases, museum and other  
314 historical natural history collections provide a useful resource for estimating regional species  
315 richness. This is not to say that historical museum data can or should replace systematic  
316 survey. For instance, an aspect of biodiversity change that may strongly affect ecosystem  
317 functioning is reordering of species abundances with assemblages (Jones, Ripplinger, &  
318 Collins, 2017). To what extent such reordering of community structure, in particularly  
319 whether dominant species are changing identity, requires representative relative abundance  
320 data, which cannot be extracted from *ad hoc* museum collections.

321 While both datasets investigated in this study gave similar estimates of species richness and  
322 assemblage compositions, there was substantial divergence between their estimates and that  
323 of a recent literature review and key (Phillip et al., 2013; Table 3). The species missed from  
324 both datasets tended to be narrowly distributed habitat specialists or recent additions to the  
325 Trinidad and Tobago freshwater fauna, and may include some species that were presumed  
326 native but may not be currently present in the region. Such biases are extremely common in  
327 ecological assemblage data (Longino et al., 2002), with most undescribed species believed to  
328 be narrowly distributed and uncommon within their home ranges (Pimm et al., 2014). These  
329 biases raise the question of whether both our empirical datasets underestimate species  
330 richness, or whether the exhaustive list compiled from a literature search is an overestimate.  
331 This is an important consideration, because how much emphasis is given to the most difficult  
332 to detect species in an assemblage heavily influences estimated extinction and turnover rates.  
333 Recently detected species may go extinct before or just after their discovery (Barnosky et al.,

334 2011; Lees & Pimm, 2015), particularly if they are transient species (Magurran & Henderson,  
335 2003) or have restricted distributions (Pimm et al., 2014).

336 CONCLUDING REMARKS

337 Uncertainty around biodiversity levels and distribution hinders our understanding of key  
338 biodiversity statistics and consequently our ability to make informed conservation decisions  
339 (Pimm et al., 2014). Understanding the information gaps around biodiversity knowledge is  
340 essential for progression of the field (Hortal et al., 2015). In our analysis we demonstrated  
341 that both historical museum collection data and survey data can provide useful regional  
342 species richness estimates to use as baselines for assessing biodiversity change. Both datasets  
343 also provided comparable estimates of the identities of species within the assemblage, as they  
344 detected all but the transient or very difficult to detect species. Most assemblages display  
345 similar species abundance distributions, characterised by both common and rare species  
346 (McGill et al., 2007) and often include both “core” and “transient” species (Magurran &  
347 Henderson, 2003; Taylor, Evans, White, & Hurlbert, 2018). Our results suggest that the  
348 majority of a region’s “core” species are detected by both museum data and survey data to  
349 similar extents. Consequently, species lists for assessing turnover within tropical regions, and  
350 amongst these “core taxa”, could be compiled from existing historical museum collections  
351 where suitable systematic survey data are unavailable. This would provide opportunities for  
352 monitoring and understanding biodiversity change within tropical regions that otherwise lack  
353 appropriate baseline data.

354 Then again, it is difficult to verify which of the fish species potentially in Trinidad and  
355 Tobago are actually present in the region at a given time. This uncertainty needs to be taken  
356 into account in baseline estimates of regional species richness and turnover/extinction  
357 analyses.

358 Based on our results, and with appropriate caveats, we therefore recommend increased use of  
359 historical museum collections, particularly those containing tropical data, in assessments of  
360 regional biodiversity. These data are more readily available than intensive systematic survey  
361 data in many parts of the world, and assemblage composition within such collections can be  
362 sufficiently unbiased as to serve as useful baselines for assessing temporal turnover of species  
363 identities. By harnessing their full potential, we can provide a useful source of biodiversity  
364 information to help bridge the knowledge gap between temperate and tropical systems.

365



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## 376 **F. DATA ACCESSIBILITY**

377 The Phillip survey data are available at [https://doi.org/10.17630/e60bce64-2926-42d4-a69f-](https://doi.org/10.17630/e60bce64-2926-42d4-a69f-91e36ade4629)  
378 [91e36ade4629](https://doi.org/10.17630/e60bce64-2926-42d4-a69f-91e36ade4629). The UWIZM data are open access, and available at  
379 <https://doi.org/10.15468/m48ug8>

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384 **G. LITERATURE CITED**

- 385 BARNOSKY, A. D., MATZKE, N., TOMIYA, S., WOGAN, G. O. U., SWARTZ, B., QUENTAL, T.  
 386 B., ... FERRER, E. A. (2011). Has the Earth's sixth mass extinction already arrived?  
 387 *Nature*, 471(7336), 51–57. <https://doi.org/10.1038/nature09678>
- 388 BOUCHET, P., LOZOUET, P., MAESTRATI, P., & HEROS, V. (2002). Assessing the magnitude of  
 389 species richness in tropical marine environments : exceptionally high numbers of  
 390 molluscs at a New Caledonia. *Biological Journal of the Linnean Society*, 75, 421–436.  
 391 <https://doi.org/10.1046/j.1095-8312.2002.00052.x>
- 392 BROWN, B. V., BORKENT, A., ADLER, P. H., AMORIM, D. DE S., BARBER, K., BICKEL, D., ...  
 393 ZUMBADO, M. A. (2018). Comprehensive inventory of true flies (Diptera) at a tropical  
 394 site. *Communications Biology*, 1(1), 21. <https://doi.org/10.1038/s42003-018-0022-x>
- 395 BUCHANAN, B., CHAO, A., CHIU, C. H., COLWELL, R. K., O'BRIEN, M. J., WERNER, A., &  
 396 EREN, M. I. (2017). Environment-induced changes in selective constraints on social  
 397 learning during the peopling of the Americas. *Scientific Reports*, 7(March), 1–12.  
 398 <https://doi.org/10.1038/srep44431>
- 399 CEBALLOS, G., EHRLICH, P. R., BARNOSKY, A. D., GARCÍA, A., PRINGLE, R. M., & PALMER, T.  
 400 M. (2015). Accelerated modern human-induced species losses: entering the sixth mass  
 401 extinction. *Sciences Advances*, 1(e1400253), 1–5.  
 402 <https://doi.org/10.1126/sciadv.1400253>
- 403 CHAO, A. (1984). Nonparametric Estimation of the Number of Classes in a Population.  
 404 *Scandinavian Journal of Statistics*, 11(4), 265–270.
- 405 CHAO, A., CHAZDON, R. L., COLWELL, R. K., & SHEN, T.-J. (2005). A new statistical approach  
 406 for assessing similarity of species composition with incidence and abundance data.

- 407 *Ecology Letters*, 8, 148–159. <https://doi.org/10.1111/j.1461-0248.2004.00707.x>
- 408 CHAO, A., CHIU, C. H., HSIEH, T. C., DAVIS, T., NIPPERESS, D. A., & FAITH, D. P. (2015).  
409 Rarefaction and extrapolation of phylogenetic diversity. *Methods in Ecology and*  
410 *Evolution*, 6(4), 380–388. <https://doi.org/10.1111/2041-210X.12247>
- 411 CHAO, A., & COLWELL, R. K. (2017). Thirty years of progeny from Chao’s inequality:  
412 Estimating and comparing richness with incidence data and incomplete sampling. *Sort*,  
413 41(1), 3–54.
- 414 CHAO, A., GOTELLI, N. J., HSIEH, T. C., SANDER, E. L., MA, K. H., COLWELL, R. K., &  
415 ELLISON, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework  
416 for sampling and estimation in species diversity studies. *Ecological Monographs*, 84(1),  
417 45–67. <https://doi.org/10.1890/13-0133.1>
- 418 CHAO, A., & JOST, L. (2012). Coverage-based rarefaction and extrapolation: standardizing  
419 samples by completeness rather than size. *Ecology*, 93(12), 93–95.  
420 <https://doi.org/10.1890/11-1952.1>
- 421 CODDINGTON, J. A., AGNARSSON, I., MILLER, J. A., KUNTER, M., & HORMIGA, G. (2009).  
422 Undersampling bias: the null hypothesis for singleton species in tropical arthropod  
423 surveys. *Journal of Animal Ecology*, 78, 573–584. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2656.2007.0)  
424 [2656.2007.0](https://doi.org/10.1111/j.1365-2656.2007.0)
- 425 COLLEN, B., RAM, M., ZAMIN, T., & MCRAE, L. (2008). The Tropical Biodiversity Data Gap:  
426 Addressing Disparity in Global Monitoring. *Tropical Conservation Science*, 1(2), 75–  
427 88. <https://doi.org/10.1177/194008290800100202>
- 428 COLWELL, R. K., CHAO, A., GOTELLI, N. J., LIN, S. Y., MAO, C. X., CHAZDON, R. L., &  
429 LONGINO, J. T. (2012). Models and estimators linking individual-based and sample-

- 430 based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant*  
431 *Ecology*, 5(1), 3–21. <https://doi.org/10.1093/jpe/rtr044>
- 432 COLWELL, R. K., MAO, C. X., & CHANG, J. (2004). Interpolating, Extrapolating, and  
433 Comparing Incidence-Based Species Accumulation Curves. *Ecology*, 85(10), 2717–  
434 2727. <https://doi.org/10.1890/03-0557>
- 435 DIRZO, R., & RAVEN, P. H. (2003). Global State of Biodiversity and Loss. *Annual Review of*  
436 *Environment and Resources*, 28(1), 137–167.  
437 <https://doi.org/10.1146/annurev.energy.28.050302.105532>
- 438 DORNELAS, M., GOTELLI, N. J., MCGILL, B., SHIMADZU, H., MOYES, F., SIEVERS, C., &  
439 MAGURRAN, A. E. (2014). Assemblage time series reveal biodiversity change but not  
440 systematic loss. *Science*, 344(6181), 296–299. <https://doi.org/10.1126/science.1248484>
- 441 ENGEMANN, K., ENQUIST, B. J., SANDEL, B., BOYLE, B., JØRGENSEN, P. M., MORUETA-  
442 HOLME, N., ... SVENNING, J. C. (2015). Limited sampling hampers “big data” estimation  
443 of species richness in a tropical biodiversity hotspot. *Ecology and Evolution*, 5(3), 807–  
444 820. <https://doi.org/10.1002/ece3.1405>
- 445 FATTORINI, S. (2013). Regional Insect Inventories Require Long Time, Extensive Spatial  
446 Sampling and Good Will. *PLoS ONE*, 8(4).  
447 <https://doi.org/10.1371/journal.pone.0062118>
- 448 GOTELLI, N. J., & COLWELL, R. K. (2001). Quantifying biodiversity: procedures and pitfalls in  
449 the measurement and comparison of species richness. *Ecology Letters*, 4, 379–391.  
450 <https://doi.org/10.1046/j.1461-0248.2001.00230.x>
- 451 GOTELLI, N. J., & COLWELL, R. K. (2011). Estimating species richness. In A. E. Magurran &  
452 B. J. McGill (Eds.), *Biological diversity; frontiers in measurement and assessment* (pp.

- 453 39–54). Oxford University Press. <https://doi.org/10.2307/3547060>
- 454 GURALNICK, R., & VAN CLEVE, J. (2005). Strengths and weaknesses of museum and national  
455 survey data sets for predicting regional species richness: Comparative and combined  
456 approaches. *Diversity and Distributions*, 11(4), 349–359. [https://doi.org/10.1111/j.1366-](https://doi.org/10.1111/j.1366-9516.2005.00164.x)  
457 [9516.2005.00164.x](https://doi.org/10.1111/j.1366-9516.2005.00164.x)
- 458 HILL, M. O. (1973). Diversity and evenness: a unifying notation and its consequences.  
459 *Ecology*, 54(2), 427–432. <https://doi.org/10.2307/1934352>
- 460 HILLEBRAND, H., BLASIUS, B., BORER, E. T., CHASE, J. M., DOWNING, J., ERIKSSON, B. K., ...  
461 RYABOV, A. B. (2017). Biodiversity change is uncoupled from species richness trends.  
462 *Journal of Applied Ecology*, 55(March), 1–16. <https://doi.org/10.1111/ijlh.12426>
- 463 HORTAL, J., DE BELLO, F., DINIZ-FILHO, J. A. F., LEWINSOHN, T. M., LOBO, J. M., & LADLE, R.  
464 J. (2015). Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. *Annual*  
465 *Review of Ecology, Evolution, and Systematics*, 46(1), 523–549.  
466 <https://doi.org/10.1146/annurev-ecolsys-112414-054400>
- 467 HSIEH, T. C., MA, K. H., & CHAO, A. (2016a). iNEXT: an R package for rarefaction and  
468 extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*,  
469 7(12), 1451–1456. <https://doi.org/10.1111/2041-210X.12613>
- 470 HSIEH, T. C., MA, K. H., & CHAO, A. (2016b). iNEXT: iNterpolation and EXTrapolation for  
471 species diversity. Retrieved from url:%0A [http://chao.stat.nthu.edu.tw/blog/software-](http://chao.stat.nthu.edu.tw/blog/software-download/)  
472 [download/](http://chao.stat.nthu.edu.tw/blog/software-download/).
- 473 JONES, S. K., RIPLINGER, J., & COLLINS, S. L. (2017). Species reordering, not changes in  
474 richness, drives long-term dynamics in grassland communities. *Ecology Letters*, 20(12),  
475 1556–1565. <https://doi.org/10.1111/ele.12864>

- 476 KORHONEN, J. J., SOININEN, J., & HILLEBRAND, H. (2010). A quantitative analysis of temporal  
477 turnover in aquatic species assemblages across ecosystems. *Ecology*, *91*(2), 508–517.  
478 <https://doi.org/10.1890/09-0392.1>
- 479 LEES, A. C., & PIMM, S. L. (2015). Species, extinct before we know them? *Current Biology*,  
480 *25*(5), R177–R180. <https://doi.org/10.1016/j.cub.2014.12.017>
- 481 LONGINO, J. T., CODDINGTON, J., & COLWELL, R. K. (2002). The Ant Fauna of a Tropical  
482 Rain Forest : Estimating Species Richness Three Different Ways. *Ecology*, *83*(3), 689–  
483 702. <https://doi.org/10.2307/3071874>
- 484 MAGURRAN, A. E., & HENDERSON, P. A. (2003). Explaining the excess of rare species in  
485 natural species abundance distributions. *Nature*, *422*(6933), 714–716.  
486 <https://doi.org/10.1038/nature01547>
- 487 MCGILL, B. J., DORNELAS, M., GOTELLI, N. J., & MAGURRAN, A. E. (2015). Fifteen forms of  
488 biodiversity trend in the anthropocene. *Trends in Ecology and Evolution*, *30*(2), 104.  
489 <https://doi.org/10.1016/j.tree.2014.11.006>
- 490 MCGILL, B. J., ETIENNE, R. S., GRAY, J. S., ALONSO, D., ANDERSON, M. J., BENECHA, H.  
491 K., ... WHITE, E. P. (2007). Species abundance distributions: Moving beyond single  
492 prediction theories to integration within an ecological framework. *Ecology Letters*,  
493 *10*(10), 995–1015. <https://doi.org/10.1111/j.1461-0248.2007.01094.x>
- 494 NEWBOLD, T. (2010). Applications and limitations of museum data for conservation and  
495 ecology, with particular attention to species distribution models. *Progress in Physical  
496 Geography*, *34*(1), 3–22. <https://doi.org/10.1177/0309133309355630>
- 497 PETERSEN, F. T., & MEIER, R. (2003). Testing species richness estimation methods on single  
498 sample collection data using the Danish Diptera. *Biodiversity and Conservation*, 687–

- 499           702.
- 500   PHILLIP, D. A. T. (1998). *Biodiversity of the freshwater fishes of Trinidad and Tobago*.  
501           University of St Andrews, Scotland, UK. Retrieved from [http://research-repository.st-](http://research-repository.st-andrews.ac.uk/handle/10023/2832)  
502           andrews.ac.uk/handle/10023/2832
- 503   PHILLIP, D. A. T., TAPHORN, D. C., HOLM, E., GILLIAM, J. F., LAMPHERE, B. A., & LÓPEZ-  
504           FERNÁNDEZ, H. (2013). *Annotated list and key to the stream fishes of Trinidad &*  
505           *Tobago*. *Zootaxa* (Vol. 3711). <https://doi.org/10.11646/zootaxa.3711.1.1>
- 506   PIMM, S. L., JENKINS, C. N., ABELL, R., BROOKS, T. M., GITTLEMAN, J. L., JOPPA, L. N., ...  
507           SEXTON, J. O. (2014). The biodiversity of species and their rates of extinction,  
508           distribution, and protection. *Science*, *344*(6187).  
509           <https://doi.org/10.1126/science.1246752>
- 510   PYKE, G. H., & EHRLICH, P. R. (2010). Biological collections and ecological/environmental  
511           research: A review, some observations and a look to the future. *Biological Reviews*,  
512           *85*(2), 247–266. <https://doi.org/10.1111/j.1469-185X.2009.00098.x>
- 513   REZNICK, D., BAXTER, R. J., & ENDLER, J. (1994). Long-Term Studies of Tropical Stream  
514           Fish Communities : The Use of Field Notes and Museum Collections to Reconstruct  
515           Communities of the Past. *American Zoologist*, *34*(3), 452–462.
- 516   SOBERÓN, J. M., LLORENTE, J. B., & OÑATE, L. (2000). The use of specimen-label databases  
517           for conservation purposes: an example using Mexican Papilionid and Pierid butterflies.  
518           *Biodiversity and Conservation*, *9*, 1441–1466.
- 519   TAYLOR, S. S., EVANS, B. S., WHITE, E. P., & HURLBERT, A. H. (2018). The prevalence and  
520           impact of transient species in ecological communities. *Ecology*, *0*(0), 1–11.  
521           <https://doi.org/10.1002/ecy.2398>

- 522 TOBLER, M., HONORIO, E., JANOVEC, J., & REYNEL, C. (2007). Implications of collection  
523 patterns of botanical specimens on their usefulness for conservation planning: An  
524 example of two neotropical plant families (Moraceae and Myristicaceae) in Peru.  
525 *Biodiversity and Conservation*, 16(3), 659–677. [https://doi.org/10.1007/s10531-005-](https://doi.org/10.1007/s10531-005-3373-9)  
526 3373-9
- 527 VELLEND, M., BAETEN, L., MYERS-SMITH, I. H., ELMENDORF, S. C., BEAUSÉJOUR, R., BROWN,  
528 C. D., ... WIPF, S. (2013). Global meta-analysis reveals no net change in local-scale  
529 plant biodiversity over time. *Proceedings of the National Academy of Sciences of the*  
530 *United States of America*, 110(48), 19456–19459.  
531 <https://doi.org/10.1073/pnas.1312779110>
- 532 VELLEND, M., DORNELAS, M., BAETEN, L., BEAUSEJOUR, R., BROWN, C., DE FRENNE, P., ...  
533 SIEVERS, C. (2017). Estimates of local biodiversity change over time stand up to  
534 scrutiny. *Ecology*, 98, 583–590. <https://doi.org/10.1101/062133>
- 535
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538 Tables

539 *Table 1. Category descriptions for assigning species characteristics. Information was*  
 540 *extracted from (Phillip et al., 2013). Any fish described as “mistake” were removed from the*  
 541 *analysis during data preparation.*

<b>Designation</b>	<b>Description</b>
<b>Status</b>	
No data	No data on this characteristic in the fish key
Introduced	Species colonised from a human introduction
Mistake	Misidentifications
Presumed native	Presumed native to Trinidad and Tobago
Recent Colonist	Natural colonists from the Orinoco River
Transient	Species not recorded in the last 2 to 3 surveys. They are natural colonists from the Orinoco River that did not become established
<b>Habitat</b>	
<b>Specificity</b>	
No data	No data on this characteristic in the fish key
Specialist	Lives in only one water type, i.e. clear and fast flowing
Generalist	Can live in different water types, i.e. clear fast flowing water and turbid water
<b>Distribution</b>	
No data	No data on this characteristic in the fish key
Narrow	Only found in a few sites

Intermediate	Either found in a subsection of Trinidad that is more than a few streams or fish described as “widely distributed” in a subsection of Trinidad
Wide	Found in most of Trinidad, or found in both Trinidad and Tobago, or described as "widely distributed"

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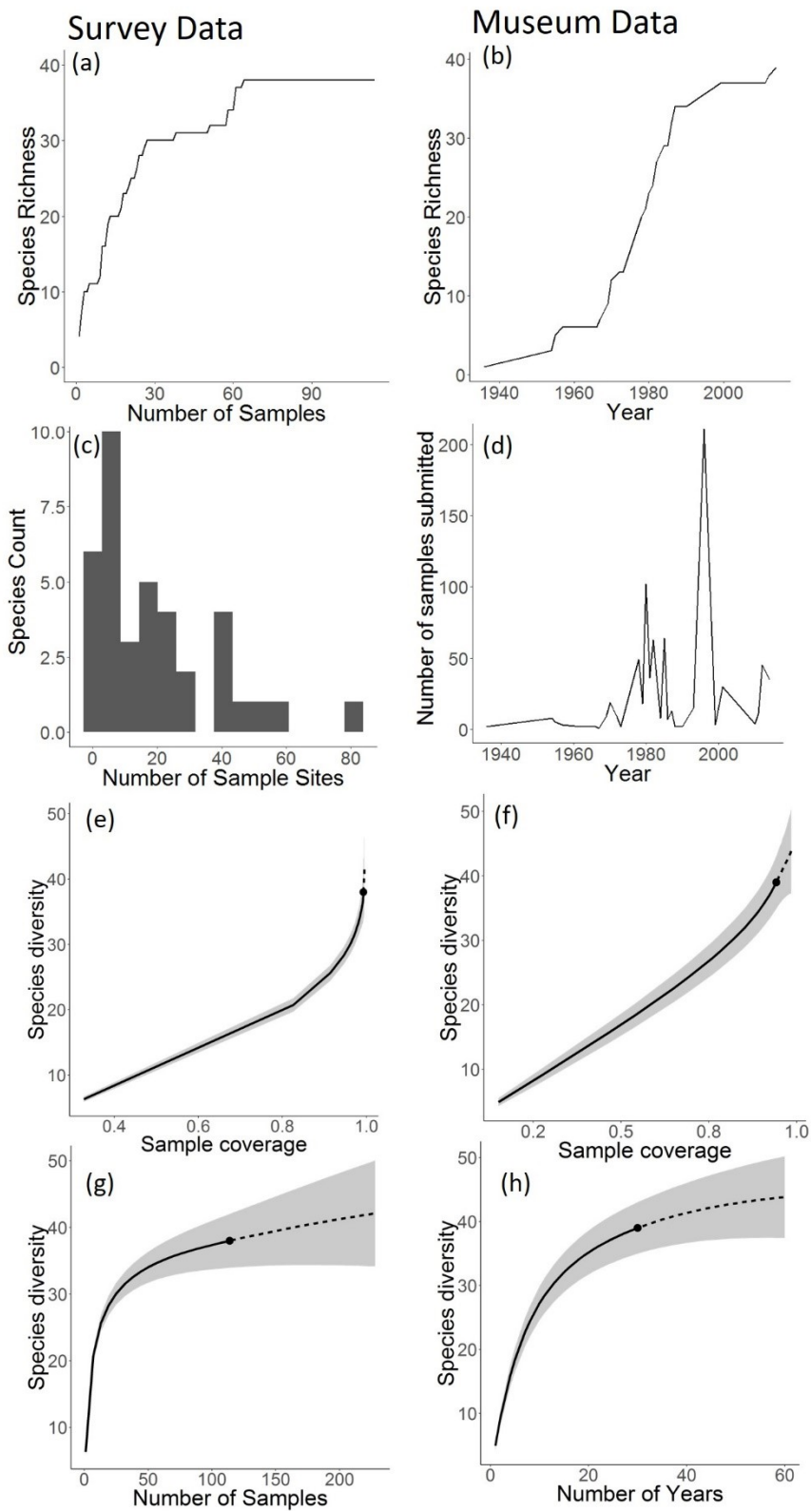
*Table 2. A breakdown of the numbers of acquisition records uniques (species only recorded once), duplicates (species recorded twice), and the observed number of species in the sampling and museum freshwater fish, as well as the number of freshwater fish estimated to be extant in Trinidad and Tobago according to rarefaction and extrapolation using iNEXT. These species richness estimate are exactly that of the non-parametric Chao 2 estimate.*

<b>Dataset type</b>	<b>Acquisitions</b>	<b>Sampling Units</b>	<b>Uniques</b>	<b>Duplicates</b>	<b>Species Observed</b>	<b>Species Richness estimate</b>	<b>Lower bound</b>	<b>Upper bound</b>
Survey	21153	56	4	3	38	50 (+/- 17)	40	131
Museum	785	30	2	3	39	46(+/- 6)	40	68

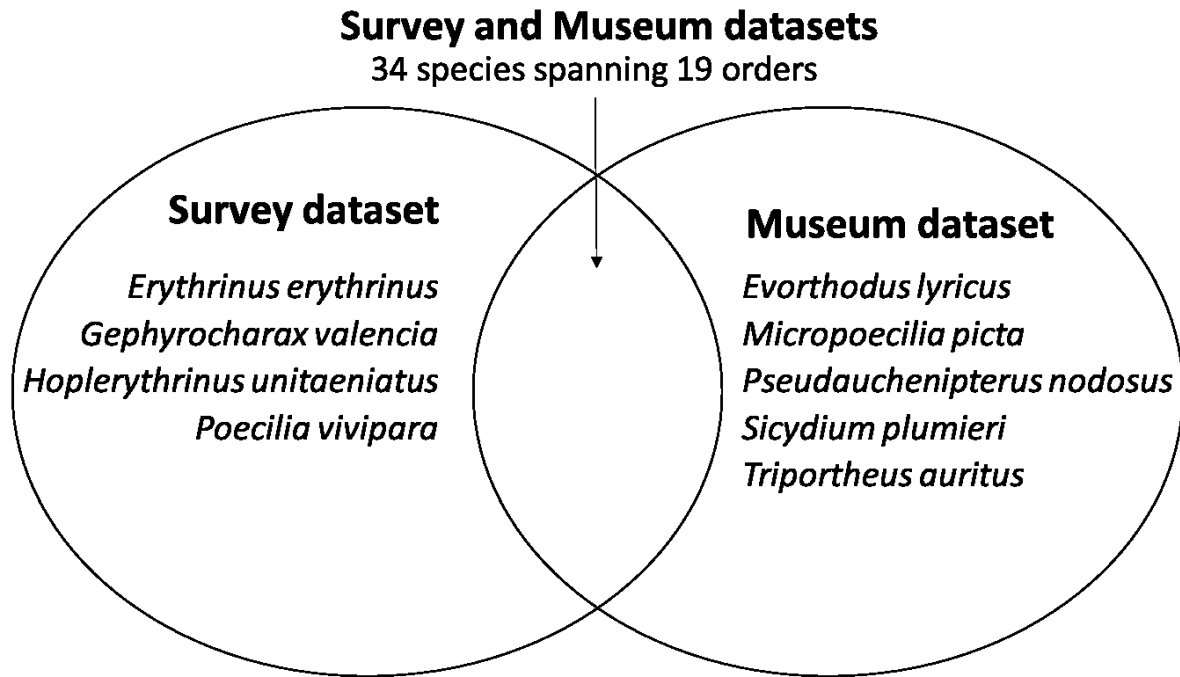
Table 3. A breakdown of the status, distribution and habitat preference characteristics of all freshwater fish species in Trinidad and Tobago as stated in (Phillip et al., 2013). A further breakdown of the characteristics of the fish found in the survey and museum datasets is also included, and the quantiles of these values in relation to the null model results. Finally, we include a breakdown of the characteristics of the fish found in neither the Survey nor the Museum data.

		<b>All</b>	<b>Survey</b>	<b>Museum</b>	<b>Survey</b>	<b>Museum</b>	<b>Not</b>
		<b>Species</b>			<b>Quantile</b>	<b>Quantile</b>	<b>found</b>
<b>Status</b>	No data	3	0	0	0.18	0.18	3
	Introduced	5	2	2	0.42	0.42	3
	Native	53	33	34	1.00	1.00	16
	Recent Colonist	4	3	3	0.92	0.92	0
<b>Distribution</b>	No data	11	0	0	0.00	0.00	11
	Narrow	13	6	4	0.34	0.05	6
	Intermediate	24	19	22	1.00	1.00	2
	Wide	17	13	13	0.99	0.99	3
<b>Habitat</b>	No data	2	0	0	0.00	0.00	2
	Specialist	23	14	14	0.84	0.84	7
	Generalist	40	24	25	0.94	1.00	13

## Figures



*Figure 1. Plots of the Trinidad and Tobago freshwater fish targeted survey data and museum collection data. Plot (a) is the accumulation of species richness as new sites were added to the survey data in terms of the actual temporal sequence of data collection. Plot (b) shows the accumulation of species richness in the museum collections through time. Plot (c) shows the frequency of species found in multiple sites, and plot (d) shows the unequal distribution of sample submissions to the museum collection over time. Plots (e) and (f) show the coverage-based extrapolation for the survey and museum data respectively, and (g) and (h) show the estimated species richness of the survey and museum data, respectively, using the iNEXT sample-based extrapolation. The grey ribbon represents the 95% Confidence Intervals of the estimates.*



*Figure 2. A breakdown of which species were recorded only in the survey data and only in the museum data. The majority (34) species were recorded in both datasets. For a complete list of which species were found in each dataset see Table S1.*

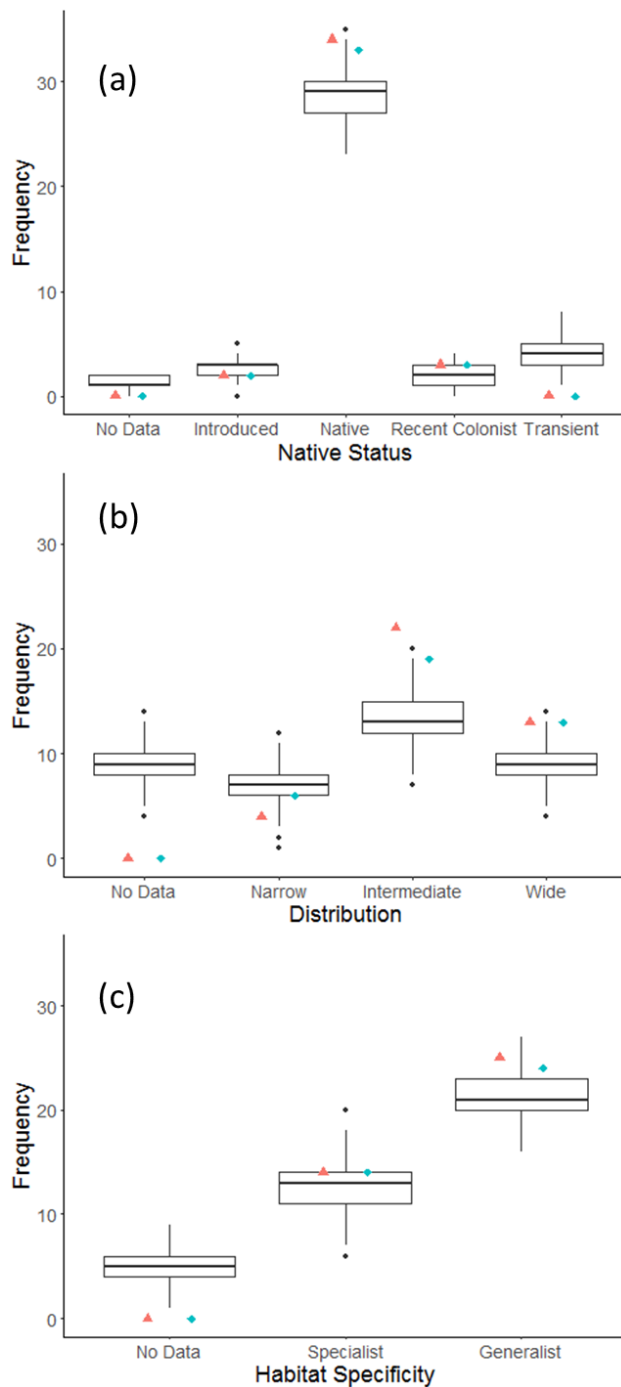


Figure 3. The native status (a), distribution (b) and habitat specificity (c) of 39 fish randomly selected by a null model with 1000 iterations (black boxplots), compared to the observed habitat specificity of species found in the survey data (red triangles) and museum data (blue diamonds). Box plots show medians, upper and lower quantiles and outliers. A violin plot showing the observed values and the sampling distribution of the model can be found in Fig. S2.