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1 **Acoustic identification of Mexican bats based on taxonomic and ecological**
2 **constraints on call design**

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31

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38

39 SUMMARY

- 40 1. Monitoring global biodiversity is critical for understanding responses to anthropogenic
41 change, but biodiversity monitoring is often biased away from tropical, megadiverse
42 areas that are experiencing more rapid environmental change. Acoustic surveys are
43 increasingly used to monitor biodiversity change, especially for bats as they are
44 important indicator species and most use sound to detect, localise and classify
45 objects. However, using bat acoustic surveys for monitoring poses several
46 challenges, particularly in mega-diverse regions. Many species lack reference
47 recordings, some species have high call similarity or differ in call detectability, and
48 quantitative classification tools, such as machine learning algorithms, have rarely
49 been applied to data from these areas.
- 50 2. Here, we collate a reference call library for bat species that occur in a megadiverse
51 country, Mexico. We use 4,685 search-phase calls from 1,378 individual sequences
52 of 59 bat species to create automatic species identification tools generated by
53 machine learning algorithms (Random Forest). We evaluate the improvement in
54 species-level classification rates gained by using hierarchical classifications,
55 reflecting either taxonomic or ecological constraints (guilds) on call design, and
56 examine how classification rate accuracy changes at different hierarchical levels
57 (family, genus, and guild).
- 58 3. Species-level classification of calls had a mean accuracy of 66% and the use of
59 hierarchies improved mean species-level classification accuracy by up to 6%
60 (species within families 72%, species within genera 71.2% and species within guilds
61 69.1%). Classification accuracy to family, genus and guild-level was 91.7%, 77.8%
62 and 82.5%, respectively.
- 63 4. The bioacoustic identification tools we have developed are accurate for rapid
64 biodiversity assessments in a megadiverse region and can also be used effectively to
65 classify species at broader taxonomic or ecological levels. This flexibility increases

66 their usefulness when there are incomplete species reference recordings and also
67 offers the opportunity to characterise and track changes in bat community structure.
68 Our results show that bat bioacoustic surveys in megadiverse countries have more
69 potential than previously thought to monitor biodiversity changes and can be used to
70 direct further developments of bioacoustic monitoring programs in Mexico.

71 *Keywords:* acoustic identification, guild, hierarchical classification, random forest, machine
72 learning, Neotropical, whispering bats.

73

74 INTRODUCTION

75 Effective conservation depends on our ability to define, measure and track ecological
76 communities through time and space (Magurran *et al.* 2010). Although biodiversity
77 monitoring programmes are critical to assess the impact of anthropogenic change, many are
78 biased towards high latitude, temperate countries (Collen *et al.* 2009). Megadiverse
79 countries (e.g., Indonesia, Mexico, Zaire) cover only 34% of the Earth surface, yet they
80 harbour 70% of the world's biodiversity and are undergoing rapid environmental degradation
81 (Mittermeier *et al.* 1997). In spite of the great conservation opportunity these hotspot regions
82 offer, biodiversity monitoring programmes are often lacking, causing considerable knowledge
83 gaps.

84 Bioacoustic surveys, especially for bats, are increasingly used to survey and monitor
85 biodiversity responses to anthropogenic change (Jones *et al.* 2013; Amorim *et al.* 2014).
86 Echolocating bats use sound to detect, localise and classify objects (Schnitzler *et al.* 2003)
87 making them detectable both remotely and non-invasively. Bats are also ideal biodiversity
88 indicators since they have a wide range of ecological traits, different tolerances to
89 environmental variables and play key roles in ecosystems (Jones *et al.* 2009; Russo & Jones
90 2015). However, using bat acoustics as a monitoring tool poses several challenges,
91 especially in megadiverse and tropical regions (Walters *et al.* 2013). First, in spite of the
92 growing efforts to create more bat call reference recording libraries, tropical and
93 megadiverse regions have rarely been included in such initiatives. This is compounded by
94 recording method heterogeneity (e.g., full spectrum, frequency division, heterodyne), which
95 makes compiling comprehensive libraries difficult (Walters *et al.* 2013). Such poor and
96 uneven coverage of intra- and inter-specific variation makes Identification of bat calls for
97 these regions challenging

98 Second, although it is possible to identify many bat species based on their calls,
99 phylogenetic relatedness, ecological similarities, and call plasticity have led to overlapping

100 structures and high call similarity among and within species in some groups (Obrist 1995;
101 Jones & Teeling 2006). For example, species may have similar calls within families and
102 genera (Jung *et al.* 2007, 2014), and ecological guild membership may also reflect foraging
103 and echolocation behaviour (e.g., aerial insectivores, gleaners) (Denzinger & Schnitzler
104 2013). An additional challenge is that bat species differ in detectability of their calls. Aerial
105 insectivores typically produce loud calls of high-intensity and low frequency, whereas
106 'whispering' bats (including many bats in the families Phyllostomidae, Natalidae, and
107 Thyropteridae) often produce low-intensity, high frequency calls (Griffin 1958). However,
108 recent findings suggest that some 'whispering' bat calls are more detectable than previously
109 thought. For example, *Macrophyllum macrophyllum* and *Artibeus jamaicensis* can emit calls
110 as loud as those of many aerial insectivores (Brinkløv *et al.* 2009). *Otonycteris hemprichii*, a
111 passive gleaner, can also operate as an aerial hawk and can adjust its call intensity
112 depending on foraging mode even while flying in the same habitat type (Hackett *et al.* 2014).

113 Third, although acoustic species identification tools for different species are developing
114 rapidly (e.g., European bats Walters *et al.* 2012; birds Stowell & Plumley 2014), they
115 remain rare for megadiverse regions. The immense amount of data obtained from acoustic
116 monitoring can be daunting and automatic analytical tools are extremely useful in analysing
117 such data (Walters *et al.* 2013). Bat call identification tools have been mainly developed
118 using multivariate statistical techniques such as discriminant function analysis (e.g.,
119 Vaughan *et al.* 1997; Russo & Jones 2002; Avila-Flores & Fenton 2005; MacSwiney *et al.*
120 2008) or machine learning algorithms (e.g., Skowronski & Harris 2006, Walters *et al.* 2012),
121 the latter generally providing higher species-level classification accuracy (Armitage & Ober
122 2010; Britzke *et al.* 2011; Keen *et al.* 2014). Machine learning algorithms have mostly been
123 applied to classify data at one level of categorisation (e.g., species) and have rarely
124 incorporated hierarchical information to aid classification accuracy (e.g., species within
125 families or orders). Hierarchical classification approaches have been shown to improve
126 general species classification accuracy for European bat calls up to 13% (Parsons & Jones

127 2000; Walters *et al.* 2012). Assigning taxa to classes within a hierarchy may reduce model
128 complexity and minimise misclassifications outside their hierarchy (Vens *et al.* 2008).
129 However, if an erroneous hierarchy is applied, then classification errors are added
130 cumulatively across different levels, leading to a reduction in classification accuracy.

131 A hierarchical classification approach may be useful to classify calls to broader classes (e.g.,
132 genera, families or guilds) when reference material is missing for species, or where
133 discrimination at species-level is difficult. For example, where there is high call variability
134 within species, or a high overlap of call parameters between species. Although identification
135 to species is most desirable, monitoring the status of the same recognizable signal over time
136 without specific identification may be sufficient in some situations (Redgwell *et al.* 2009;
137 Armitage & Ober 2010). Finding alternatives to species-level studies is needed in
138 megadiverse areas, which usually face considerable financial and data constraints but are a
139 priority for rapid conservation assessments.

140 Here, we collate a reference call library for bat species that occur in a megadiverse country
141 to create acoustic identification tools using machine learning algorithms. We focus on
142 Mexico because it contains one of the highest number of species in the world and has one of
143 the highest rates of species extinction and habitat loss (Myers *et al.* 2000; Brooks *et al.*
144 2002). We also evaluate the improvement in species-level classification rates gained by
145 using hierarchical classifications reflecting either taxonomic or ecological constraints on call
146 design. Our results show that accurate bioacoustic identification tools can be developed for
147 rapid biodiversity assessments in megadiverse regions where hierarchies generally improve
148 species-level classifications. These tools can also be used effectively to classify calls at
149 broader levels, so increasing the usefulness of the tool when there are incomplete species
150 reference recordings.

151

152 MATERIALS AND METHODS

153 Reference call library

154 We collated reference search-phase echolocation calls for bat species that occur in Mexico
155 through a combination of field work and donated material. Field work was conducted in
156 central and northern Mexico from June 2012 to May 2013 at 35 sites (Fig. 1a). Bats were
157 caught with mist nets and identified to species level using field keys (Reid 1997; Medellín *et*
158 *al.* 2008), before being released. Full spectrum, real time recordings were made from all
159 individuals in the habitat in which they were captured using a Pettersson D1000x detector,
160 sampling rate 500kHz, high pass filter off (Pettersson Elektronik AB, Uppsala, Sweden).
161 Files were saved in WAV format on a flash card. We obtained 907 recordings of 39 species
162 from 6 families (see Table S1 in Supporting Information). Additionally, 1,403 full spectrum
163 recordings of bat calls from 87 species that occur in Mexico were donated by colleagues,
164 giving a total of 2,310 recordings (each recording was assumed to contain one individual call
165 sequence) from 92 species in 8 families (68% of species and 100% of families of bats
166 occurring in Mexico). These recordings were obtained from bats released in different ways
167 using several different real time or time-expanded full spectrum detectors, and in a range of
168 habitats across species' distributions (including localities outside Mexico) (Table S2). The
169 inclusion of call variation in the dataset avoids generating biases for any particular recording
170 situation or method (Walters *et al.* 2013), and provides the acoustic identification tools with
171 more flexibility and generality (see Walters *et al.* 2012).

172 Taxonomy followed Simmons (2005), but because of taxonomic changes since 2005 we
173 assume that Natalidae contains only one species, *Natalus stramineus* (López-Wilchis *et al.*
174 2012). Data from *Molossus sinaloae* and the new species *M. alvarezi* (González-Ruiz *et al.*
175 2011) were analysed together as *M. sinaloae* because most of the material was recorded
176 prior to the description of the new species. As some species are hard to identify in the field,
177 we only used the material which were confidently identified. To examine the taxonomic and
178 geographic coverage of the reference call library within Mexico, distribution maps were
179 downloaded from the IUCN mammal assessments (IUCN 2012) and species richness within

180 each 50 km² grid cell was estimated by overlaying and counting how many of those range
181 maps overlap in each grid cell (Hawths Tools, Beyer, 2004). We then calculated the
182 proportion of species both recorded and used in our classifiers from out of those potentially
183 distributed in each cell.

184 Acoustic Identification Tools

185 We visually inspected all recorded sequences using the sound analysis software BatSound
186 Pro v.3.31b (Pettersson Elektronik AB, Uppsala Sweden) to remove non search-phase calls.
187 We distinguished search-phase calls from approach-phase and terminal-phase calls as
188 these phase shifts are characterized by a decrease in call duration and interval, and
189 increase in repetition rate (Schnitzler & Kalko 2001). Social calls were distinguished from
190 echolocation calls by their duration, frequency and pattern of change over time, with social
191 calls being more sporadic and often of a lower frequency range (Fenton 2003). In addition,
192 bats were recorded in situations that significantly minimized the presence of social calls and
193 approach and end-phase echolocation calls (e.g., recorded in open spaces upon release).
194 We then automatically extracted and parameterised search-phase calls using the in-built
195 algorithms in Sonobat v.3 (Szewczak 2010) (following methods in Walters *et al.* 2012). For
196 species which used harmonics, we used measurements from the call used as the main
197 harmonic. We measured a total of 21,064 search-phase echolocation calls from 1,692
198 sequences and 85 species in 8 families, with each sequence assumed to be from a different
199 individual. Material recorded in Mexico contained 16,344 calls, 1,187 sequences from 65
200 species in 7 families across 91 different localities (Fig. 1a).

201 We used Random Forest (RF) models (randomForest package, Liaw & Wiener 2002) to train
202 the classifiers, rejecting species that had less than five sequences. RF models consist of a
203 collection or ensemble of decision tree classifiers where each classifier is randomly built
204 using a bootstrapped sample of the training dataset (Breiman 2001). Each classifier is
205 estimated using a selection of the predictor variables (in our case call parameters) that best
206 separate the classes of interest (e.g., species, families) at different branching splits or nodes

207 in the tree. RF model classifications are then derived from averages of the tree ensembles.
208 RF models possess several advantages over other machine learning algorithms as they are
209 not affected by heteroscedasticity or distributional errors in the data, are not sensitive to
210 outliers or irrelevant variables, can deal with mixed data and missing variables, and are
211 relatively simple to train using reasonable computational resources (Olden *et al.* 2008). We
212 selected 27 of the relevant call parameter variables (following methods in Walters *et al.*
213 2012) extracted and parameterised by Sonobat (Table S3), and ran a grid search to find the
214 mtry value (optimal number of variables to be randomly sampled at each node). This value
215 was allowed to range from 2-10, in steps of one. Each forest was grown to 2,000 trees and
216 the final mtry value and number of trees were selected for their highest accuracy. The final
217 set of parameters used was 1,000 trees and an mtry value of three. We used the coefficient
218 of the Gini impurity index (used by the RF models to select the most informative variables at
219 nodes during training), as an indicator of call parameter variable importance (Breiman 2001).

220 We trained four different RF model classifiers: Classifier 1 - Species-level without a
221 hierarchy; Classifier 2 - Species-level within a family hierarchy (see call examples in Fig.
222 S1a-f); Classifier 3 - Species-level within a genus hierarchy (see call examples in Fig. S1g);
223 and Classifier 4 - Species-level within a guild hierarchy, following definitions of guilds from
224 Denzinger & Schnitzler (2013) (see call examples in Fig. S2a-e): Guild 1 represented Open
225 space aerial foragers; Guild 2 - Edge space aerial foragers; Guild 3 - Edge space trawling
226 foragers; Guild 4 - Narrow space flutter detecting foragers; and Guild 5 - Narrow space
227 passive gleaning foragers and Guild 6 - Narrow space passive/active gleaning foragers.
228 Guild 7 - Narrow space active gleaning foragers was not included in the study because of
229 the lack of reference material.

230 We used five-fold cross-validation to assess the accuracy of all four RF classifiers and
231 assigned the individual calls into the five folds by sequence rather than individual calls
232 (Stathopoulos *et al.* 2014). This procedure ensured that calls from the same individual (i.e.,
233 sequence) were not used in the same training and testing run of the cross-validation to avoid

234 over-fitting. We set a maximum of 100 calls per species for Classifier 1 and a minimum of 20
235 calls per species for Classifiers 2, 3 and 4, as a compromise between maximising the
236 number of calls and balancing the datasets, since RF classifiers tend to be biased towards
237 the majority class (species, genus, family or guild with the highest number of training calls)
238 (Chen *et al.* 2004). Only the highest quality calls were selected from each sequence
239 (determined by the signal to noise ratio given by Sonobat), until the selected number of calls
240 was reached. However, for some species with smaller sample sizes, we continued selecting
241 calls from sequences in descending order of quality until we had used all available data or
242 reached the number of calls allowed (Table S4). The number of calls selected per sequence
243 was a compromise between maximising the number of calls and avoiding over-fitting the RF
244 models. Sample sizes after this selection process were 4,685 calls and 1,378 sequences
245 from 8 families, 32 genera, and 59 species that occur in Mexico. See Figure S3 for an outline
246 of the analytical procedure.

247 As we used recordings from locations from both inside and outside of Mexico, we checked
248 that the variation in call parameters recorded in locations outside of Mexico did not impact
249 species classification accuracy. To investigate this, we compared model accuracy using the
250 four classifiers of two datasets consisting of 47 species recorded from locations inside
251 Mexico and the same species recorded from all locations. We found very little difference in
252 classification accuracy between the two datasets. Classifier 1 had the biggest difference in
253 classification accuracy, albeit with only 1.5% reduction in correct classification rates (67.1%
254 and 65.6% for inside Mexico and for all locations, respectively). We therefore used
255 recordings from outside Mexico to complement species with less than five Mexican
256 sequences. All analyses were performed in R version 3.0.2 (R Development Core Team
257 2013).

258

259 RESULTS

260 Database coverage

261 Our collated library of echolocation call recordings covered 69% of the species, 79% of the
262 genera, and 100% of the families occurring in Mexico. Data of high enough quality to build
263 the automatic identification tools covered 43% of the species, 51% of the genera, and 100%
264 of the families (Table S5). There was generally a good representation of species for the
265 identification tools within genera and families (>50%), except for Phyllostomidae, where only
266 19% of the species were represented. Species coverage was more comprehensive within
267 the central and northern parts of Mexico for both the library and identification tools (Fig. 1b-
268 c).

269

270 Acoustic Identification Tools

271 Overall 16 out of the 27 parameters used to train the models contributed most to all classifiers
272 (based on a score >30 for the Gini Coefficient from the RF models) (Table S6, Fig 2a-d).
273 Although different parameters were important for each hierarchy, the most important overall
274 were Fc Characteristic call frequency (kHz), Fctr Frequency at the center of the call duration
275 (kHz), FLed Frequency of the ledge (kHz), StartF Frequency at the start of a call (kHz),
276 HFreq Highest call frequency (kHz), and FMPwr Frequency of the maximum call amplitude
277 (kHz) (Fig. 2a-d, see Table S3 for further variable definitions).

278

279 Overall mean species-level classification accuracies for Mexican bat species varied across
280 the four classifiers between 66.0% (Classifier 1: Species-level without a hierarchy) and
281 72.0% (Classifier 2: Species-level within a family hierarchy), with Classifiers 3 (Species-level
282 with a genus hierarchy) and 4 (Species-level with a guild hierarchy) having accuracies of
283 71.2% and 69.1%, respectively (Table 1). Across all classifiers, on average the highest
284 classification accuracies were found for species within families Natalidae (100%),
285 Mormoopidae (94.6%), Thyropteridae (81.5%), and Emballonuridae (77.7%), with the lowest
286 found within Noctilionidae (70.4%), Molossidae (67%), Vespertilionidae (51.5%), and
287 Phyllostomidae (51.4%) (Fig. 3). Phyllostomid species were mostly misclassified with other
288 phyllostomids or with vespertilionids, whereas vespertilionids were commonly misclassified

289 with other vespertilionids or with molossids (Table 1). For the ecological classifier, species
290 within Guild 4 (narrow space flutter detecting foragers) (100%), Guild 3 (edge space trawling
291 foragers) (74.6%), and Guild 1 (open space aerial foragers) (63.8%) had on average the
292 highest classification rates. The lowest average classification rates for species were found
293 within in the gleaners (Guild 5 58.5% and Guild 6 57.7%) Guild 2 (edge space aerial
294 foragers) (54.5%) (Fig. 4).

295

296 Classification accuracy at different hierarchical levels was highest at family-level with a mean
297 of 91.7% across all families (Table 1, Fig. 3), where Natalidae and Mormoopidae had the
298 highest classification accuracies (100% and 97.3%, respectively). Noctilionidae had the
299 lowest classification accuracy (72.8%) and was frequently misclassified as Molossidae (17%
300 of the calls). Genus-level mean classification accuracy was 77.8% across all genera (Table
301 1), *Natalus* (Natalidae) and *Rhynchonycteris* (Emballonuridae) had the highest classification
302 accuracies (100%), and 18 genera had accuracies >80% (Fig. 3). The genus *Myotis* yielded
303 a classification accuracy of 73.8%, with two species over >80% (*Myotis thysanodes* and
304 *Myotis keaysi*) and only 4 with <50%. Genera with the lowest classification accuracies
305 (<50%) were in the Phyllostomidae and Vespertilionidae (Fig. 3). Phyllostomids were mostly
306 misclassified as other phyllostomids, while vespertilionids were misclassified as other
307 vespertilionids and molossids. Mean guild-level classification accuracy was 82.5% across all
308 guilds (Table 1, Fig. 4). Guild 4 (narrow space flutter detecting foragers) had the highest
309 classification accuracy (100%), followed by Guild 6 (88.3%) although 6% of these calls were
310 misclassified with Guild 5. Guild 5 had the worst classification accuracy (68%), and 18% of
311 calls were misclassified as Guild 6 (Fig. 4).

312

313 DISCUSSION

314 We have collated the most extensive bat acoustic library for a megadiverse region (all
315 families and over half of the species occurring in Mexico) and developed the most

316 comprehensive bat acoustic automated species-level classifiers to date. The mean species-
317 level classification accuracy rate of 66-72% (depending on which hierarchy is chosen) is
318 reasonable given the high level of call similarity of the bat species in this area (Walters *et al.*
319 2013). The species-level classifiers also contain a large variation in accuracy rates, where
320 some species are classified to >80% accuracy (species of Emballonuridae, Mormoopidae,
321 Natalidae and Thyropteridae), with the poorest results overall from species of
322 Vespertilionidae and Phyllostomidae. This suggests that acoustic monitoring may be more
323 feasible focusing on a few species whose calls can be reliably classified.

324 The bat call library and classifiers incorporate both extensive geographic (from 9 countries
325 within the species range of Mexican bats) and intra-specific variation in call types (e.g., the
326 classifiers were trained on the different search-phase echolocation call types found within
327 molossid species, Jung *et al.* 2014). However, the species-level classifiers have a very low
328 coverage of Phyllostomidae and results should be interpreted with caution. It has been
329 traditionally assumed that whispering bats, which include all phyllostomids, echolocate at
330 intensities that were too low for the inclusion of these species in acoustic studies. However,
331 recent field studies of their echolocation behaviour challenged these assumptions about their
332 echolocation characteristics (Brinkløv *et al.* 2009; Hackett *et al.* 2014). Future work should
333 focus on collecting more reference material for the family, to better assess its potential for
334 acoustic monitoring programmes.

335 Our classifiers will be the most accurate in regions where there is a higher coverage of the
336 species present, such as the less species-rich arid and semi-arid regions of Mexico. These
337 ecosystems (e.g., xerophytic scrubland and grasslands) cover at least 40% of the territory
338 (Rzedowski 2006), and together with other North American drylands, support some of the
339 biggest concentrations of mammalian abundance, because bats can form colonies of several
340 millions of individuals (O'Shea & Bogan 2003). These bat populations can provide important
341 ecosystem services such as pollination and control of insect populations (Cleveland *et al.*
342 2006; Munguía-Rosas *et al.* 2009). These important arid and semi-arid environments are

343 increasingly threatened by environmental changes (Villers-Ruiz & Trejo-Vázquez 2003;
344 Rodríguez-Estrella 2007) and future efforts should focus on these arid areas where there are
345 considerable information gaps.

346

347 Our species-level classifier mean accuracy was similar to that of previous studies of bats for
348 species shared with this study (Mexico - MacSwiney *et al.* 2008; Stathopoulos *et al.* 2014;
349 West Indies - Pio *et al.* 2010; United States - Skowronski & Harris 2006; Britzke *et al.* 2011).
350 However, our classification accuracies were slightly lower for some species compared with
351 previous work. This is a consequence of the higher number of classes (species) included in
352 our classifiers compared to all previous studies. Higher numbers of species increases the
353 similarity in the call parameters of several species. For example, we included 26
354 vespertilionids and 8 *Myotis* species, compared to 6 vespertilionids and one *Myotis* in
355 MacSwiney *et al.* (2008) and 9 vespertilionids and two *Myotis* in Stathopoulos *et al.* (2014).
356 Our study nearly triples the number of species used compared to any other quantitative bat
357 call classification study in the Americas or any other megadiverse tropical region in the
358 world. We also included a wide range of ecological, technological and methodological
359 variation in the training dataset, which on one hand increases the classification challenge,
360 but on the other makes the classifiers more robust to real-world recording situations. In spite
361 of the great difference in the number of species used here, we also obtained higher
362 classification accuracies to species level and better mean accuracies than previous studies
363 (e.g., Pio *et al.* 2010; Stathopoulos *et al.* 2014).

364

365 Our use of taxonomic and ecological guild hierarchies improved mean species-level
366 classification rates. By using hierarchical classification approaches the number of final
367 classes is considerably reduced and misclassifications are limited to classes within the
368 respective hierarchy (Vens *et al.* 2008). Mean species-level classification accuracies were
369 most improved using a family hierarchy, closely followed by genera (72% and 71%,
370 respectively), although not all species improved their accuracies (contrary to other studies -

371 Parsons & Jones 2000; Walters *et al.* 2012). The genus-level hierarchy produced the highest
372 number of species-level classifications with >80% accuracy but for many genera not all
373 species were included in the analysis and genus-level taxonomic names can be subject to
374 rapid changes (Simmons 2005). This may suggest that using a genus-level hierarchy may
375 be more problematic than a family hierarchy, especially with incomplete reference material.
376 For example, accuracy may decrease as more species are included, whereas variation
377 within a family may be already adequately represented. In contrast, classification to genus
378 level may be more helpful to reduce the number of options of possible misclassifications
379 inside the hierarchy and further methods for call identification could then be applied (e.g.,
380 visual inspection).

381 Although we found species-level classification rates within an ecological guild-level hierarchy
382 were worse than species-level classification rates within either taxonomic hierarchy,
383 classification of calls to guild-level performed well and could provide a useful alternative to
384 taxonomic-level classifiers. Gleaners, in particular the speciose family Phyllostomidae, are
385 the most abundant and diverse in bat communities in the Americas, yet poorly represented
386 in acoustic libraries. Our results at family and guild-level suggest that there is a good
387 potential for accurate acoustic identification of gleaners. As more sensitive microphones with
388 better signal/noise ratios become available, the detectability of these species will improve, as
389 will the potential for monitoring them acoustically. Guilds 5 and 6, representing gleaning
390 foragers, were frequently confused with each other, so these should be grouped into one
391 class, since the main difference among them is how they use other non-echolocation cues to
392 forage (Denzinger & Schnitzler 2013).

393 Acoustic analysis techniques are evolving rapidly and there is a growing tendency to replace
394 classifications based on parameters extraction with those of whole signal analysis. However,
395 applications of these approaches have mainly focused on bird and marine mammal
396 acoustics (e.g., Ren *et al.* 2009; Damoulas *et al.* 2010) and most bat acoustic classification
397 tasks still represent classifications with a few parameters and further classify them using

398 manual or non-parametric techniques. Such whole signal analyses in bat acoustics are
399 growing (Obrist *et al.* 2004; Skowronski & Harris 2006; Stathopoulos *et al.* 2014) but should
400 be further explored. However, exploration of new approaches requires adequate reference
401 material collected in a systematic way, controlling for variation introduced by the use of
402 different methods, and we strongly encourage further efforts to collect comprehensive
403 reference bat call libraries.

404

405 Applications

406 Standardized identification tools such as these, offer the opportunity for objective and
407 repeatable identifications of monitoring 'units' to identify changes in populations, distributions
408 or community structures through time and space. Furthermore, hierarchical approaches offer
409 the flexibility to adapt the identification tools to the purpose of the study or monitoring
410 programme and the geographic and taxonomic coverage of the reference material available.
411 Although the accuracy reached for some groups might not be sufficient for studies targeting
412 their particular species (e.g., *Myotis* spp.), the hierarchical classifiers can act as filters for
413 large amounts of data. The use of hierarchies considerably reduces the list of species to
414 which an unknown call could belong, thus making detailed inspections and further
415 validations more feasible.

416 Hierarchical classifications, in particular at family-level, could help reduce the costs of
417 monitoring tropical bat communities, which is crucial due to the limited funding these regions
418 often devote to conservation efforts. Despite the relatively poor classification accuracies to
419 species-level within the guild-level hierarchy, classification to guild-level could be used to
420 rapidly characterize ensemble/environment associations or to track changes in community
421 structure. The hierarchical approach may be improved through the use of regional classifiers
422 which allow the reduction of the number of classes and the improvement of classification
423 accuracy. However, such an approach should be used with caution as least known species
424 or those with expanding ranges could be ignored.

425

426 CONCLUSIONS

427 Our study shows that there is more potential for bat acoustic monitoring in megadiverse
428 countries than previously considered. Hierarchies considerably reduced the complexity of
429 call identification at different levels and provided sufficient confidence in the classification of
430 unknown calls into higher taxonomic levels and ecological guilds. While the classifiers did
431 not provide high classification accuracies for several species, they did offer the opportunity
432 to have objective and repeatable identification of monitoring 'units' to implement in national
433 acoustic monitoring programmes.

434

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443 permit was granted by SEMARNAT, Mexico (No. 03374).

444

445 DATA ACCESSIBILITY

446 Complete call measurements for each of the 4,685 search-phase calls from 1,378 individual
447 sequences of 59 bat species used to create the identification tools, and R scripts will be
448 uploaded to DataDyrad if accepted for publication.

449

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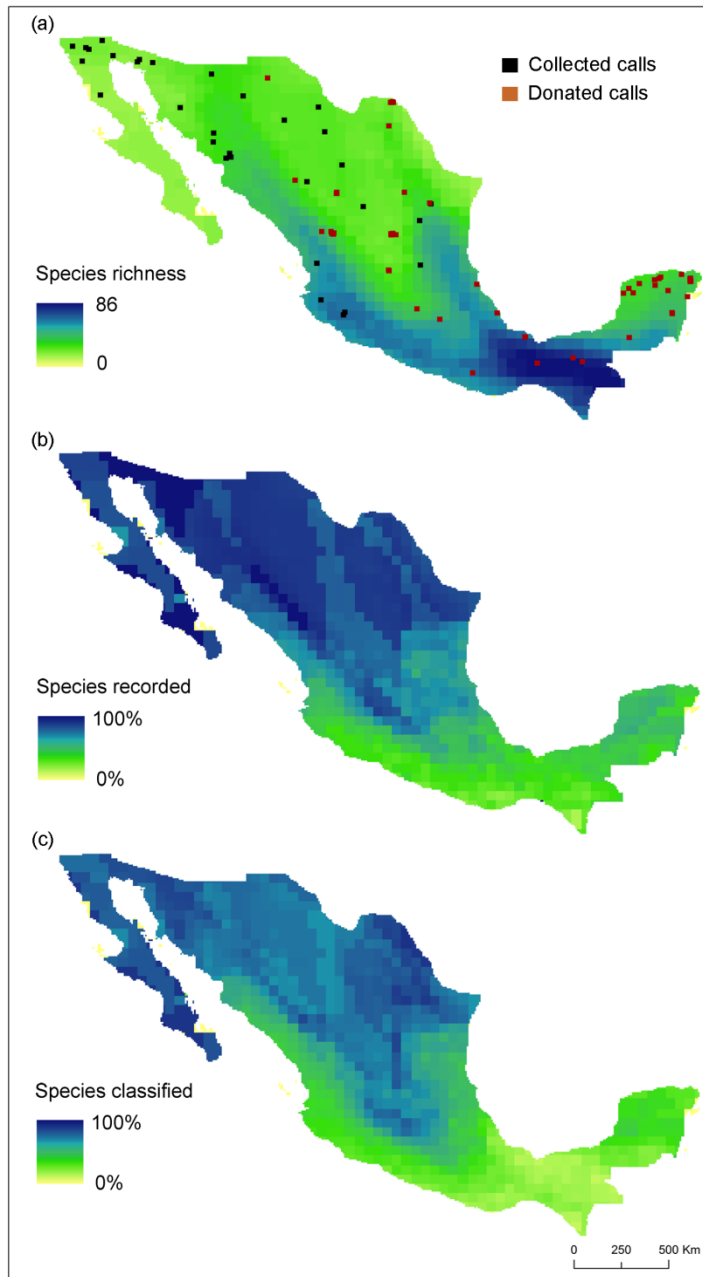
610 **Table 1.** Comparison of classification accuracies of four acoustic classifiers for Mexican bat
 611 species (n=59 species). Where Classifier 1 represents species-level without a hierarchy;
 612 Classifier 2: species-level within families; Classifier 3: species-level within genera; Classifier
 613 4: species-level within guild. Misclassification represents those classes having the most
 614 misclassifications with each other for each classifier and level, where Phyllo Phyllostomidae;
 615 Vesp Vespertilionidae; Molo Molossidae; and Noct Noctilionidae.

616

Classifier	Level	Accuracy (range) %	% of classes $\geq 80\%$ accuracy	% of classes $\leq 60\%$ accuracy	Misclassifications
1	Species	66 (4.2-100)	29	41	Species of Phyllo with themselves or Vesp; Vesp with themselves or Molo
2	Species	72 (0-100)	32	44	Species within families
	Family	91.7 (72.8-100)	88	0	Noct with Molo
3	Species	71.2 (0-100)	36	37	Species within genera
	Genus	77.8 (0-100)	56	16	Phylo with other Phylo and Vesp genera; and Vesp with Phylo and Molo genera
4	Species	69.1 (4.5-100)	25	44	Species within guilds
	Guild	82.5 (68-100)	50	0	Guild 5 with Guild 6; Guild 6 with Guild 5

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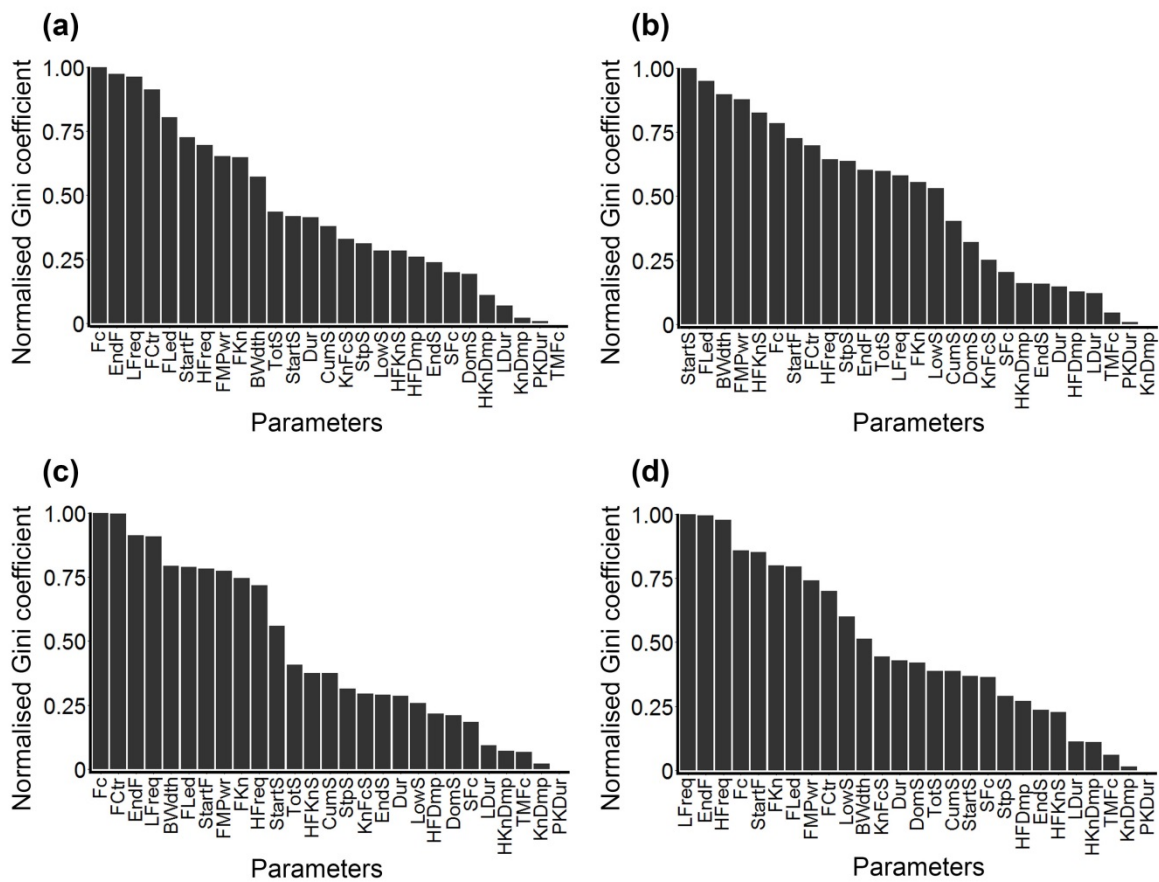


619

620 Figure 1. Spatial coverage of the number of species recorded in Mexico using a grid size of
621 50 km², where (a) shows recording locations in solid squares (n = 91) overlaid with bat
622 species richness, (b) proportion of species recorded compared to potential species richness
623 in each grid, and (c) proportion of species used in the classifiers compared to potential
624 species richness in each grid. A gradient of light green to dark blue indicate higher number
625 of species and higher percentages. Black solid squares represent collection sites which were
626 sampled in this study and red solid squares represent collection sites of donated material.

627

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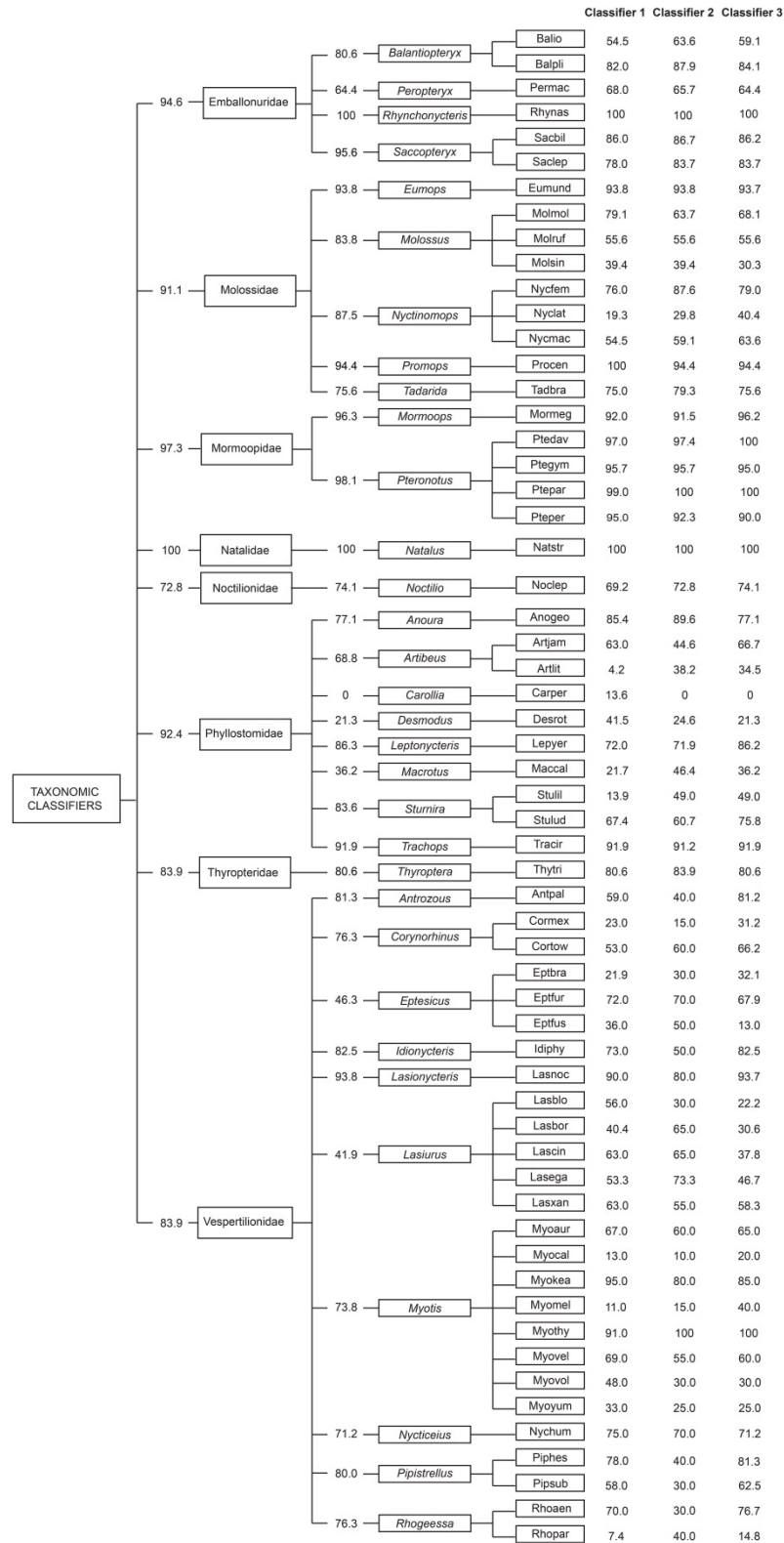


629

630 **Figure 2.** Echolocation call parameters (n = 27) selected to build each Random Forest
 631 classifier ranked by Gini Coefficient where (a) Classifier 1: Species-level without a hierarchy;
 632 (b) Classifier 2: Species-level within a family hierarchy; (c) Classifier 3: Species-level within a
 633 genus hierarchy; and (d) Classifier 4: Species-level within a guild hierarchy. See Table S3
 634 for parameter definitions.

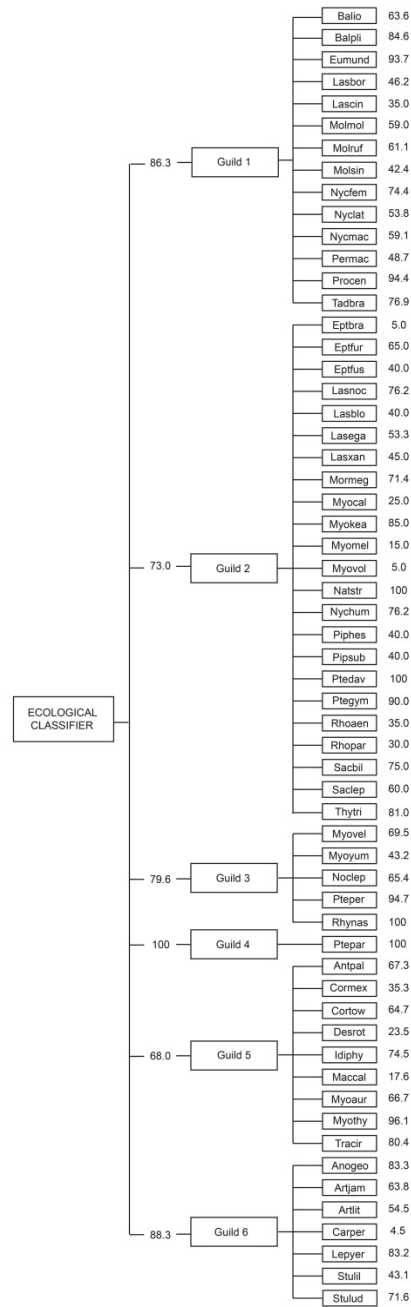
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636

637 **Figure 3.** Random Forest percentage classification accuracies obtained for the taxonomic
 638 classifiers (Classifiers 1-3). Species-level accuracies are shown at the end of each branch
 639 for Classifier 1, 2 and 3. Classification accuracies per family and genus are shown in the
 640 middle of each branch (n = 59 species).



641

642 **Figure 4.** Random Forest percentage classification accuracies obtained for the ecological
 643 guild classifier (Classifier 4). Species-level accuracies are shown at the end of each branch.
 644 Classification accuracies per guild are shown in the middle of each branch (n = 59 species).
 645 Guild 1 - Open space aerial foragers; Guild 2 – Edge space aerial foragers; Guild 3 – Edge
 646 space trawling foragers; Guild 4 – Narrow space flutter detecting foragers; Guild 5 - Narrow
 647 space passive gleaning foragers and Guild 6- Narrow space passive/active gleaning
 648 foragers.

649 **Supporting Information**

650 Additional Supporting Information may be found in the online version of this article:

651 **Table S1.** Metadata for the search-phase echolocation calls collected during field work in
652 Mexico from June 2012 to May 2013.

653 **Table S2.** Metadata for the search-phase echolocation calls donated for this study.

654 **Table S3.** Definitions of the 27 call parameters extracted by Sonobat v.3 used for training
655 the Random Forest classifiers.

656 **Table S4.** Number of classes included in each hierarchy of the four classifiers and number of
657 calls used in the training process.

658 **Table S5.** Taxonomic coverage of the bat call library within each family for the number of
659 genera and species recorded / used in the classifiers.

660 **Table S6.** Descriptive statistics (mean and standard deviation) for the 16 most important call
661 parameters ranked by Random Forest Gini Coefficient measured by Sonobat for the 59
662 species.

663 **Figure S1.** Spectrograms showing the inter-specific variability of representative search-
664 phase echolocation calls within taxonomic groups used for the classifiers.

665 **Figure S2.** Spectrograms showing inter-specific variability of representative search-phase
666 echolocation calls within ecological guilds used for the classifiers.

667 **Figure S3.** Schematic representation of the protocol used to build the classifiers.

668

669