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Combined impacts of climate and land use change and the future restructuring of Neotropical bat biodiversity

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51 **Abstract**

52 Forecasting the effects of global change on biodiversity is necessary to anticipate the
 53 threats operating at different scales in space and time. Climate change may create
 54 unsuitable environmental conditions, forcing species to move to persist. However,
 55 land-use changes create barriers that limit the access of some species to future
 56 available habitats. Here, we project the impacts of climate and land-use change on
 57 228 Neotropical bat species by forecasting changes in environmental suitability, while
 58 accounting for the effect of habitat type specialization and simulating dispersal across
 59 suitable patches. We also identify the most vulnerable ecoregions and those that may
 60 offer future stable refugia. We further investigate potential functional changes by
 61 analysing the response of different trophic guilds. We found that the range contraction
 62 of habitat specialists, especially frugivores, was more frequent and stronger under all
 63 simulated scenarios. Projected changes differ markedly across ecoregions. While the
 64 Amazon region is likely to undergo high turnover rates in bat composition, the
 65 Andean grassland, Cerrado and Chaco might experience the greatest losses. The
 66 expansion of habitat generalists, which forage in open areas and commonly establish
 67 large colonies in manmade structures, coupled with the range contraction of habitat
 68 specialists is projected to homogenize bat communities across the Neotropics.
 69 Overall, dispersal will likely be the key for the future of Neotropical bat diversity.
 70 Therefore, safeguarding the refugia highlighted here, by expanding and connecting
 71 the existing network of protected areas, for example, may allow species to move in
 72 response to global change.

73

74 **Keywords:** Chiroptera, dispersal, upward and upslope shifts, functional
 75 homogenization, climate change refugia, landscape connectivity, biodiversity re-
 76 distribution, megadiverse regions

77

78 **Introduction**

79 Climate and land use change are among the main processes driving
80 biodiversity loss in the 21st century (IPCC, 2019). Vulnerability assessments suggest
81 that the Neotropics are where the combined impact of climate change and habitat loss
82 will be the greatest (Colwell et al., 2008). According to these projections, most of the
83 Neotropical region will be subjected to novel climates, while increasing rates of land
84 use change will reduce habitat availability even further (Stauder et al., 2020). Species'
85 responses to global changes depend on extrinsic and intrinsic factors related to the
86 rate and magnitude of change in environments, as well as the species' autecology and
87 climatic tolerances. Exposure to non-analog climates may lead to physiological stress
88 with likely reductions in individual fitness and thus population persistence in the long
89 term (Ribeiro et al., 2016). Furthermore, if species are not able to adapt *in situ* or to
90 track suitable climates, population declines and local extinctions may result in range
91 contractions (Zamora-Gutierrez et al., 2018).

92 Land-use change represents an additional challenge for species dealing with
93 climate change, as human-modified landscapes obstruct species movements by
94 converting habitats into dispersal barriers (Sales et al., 2019). In the Neotropics,
95 where deforestation and climate change pose huge threats to biodiversity, the
96 combination of extrinsic and intrinsic stressors is expected to drive the decline of
97 habitat specialists, which have limited diets and specific environmental requirements
98 to roost and forage (Devictor et al., 2008; Clavel et al., 2011). Conversely, habitat
99 generalists that thrive in a wide variety of environmental conditions and use a variety
100 of resources, may even increase in abundance and geographic distribution in response
101 to changes in the environment (Gonçalves et al., 2017; Farneda et al., 2019). Thus,
102 advancing our understanding of the effects of environmental change on biodiversity
103 requires examining how threats may impact species differently according to their

104 ecological characteristics as well as identifying vulnerable and important conservation
105 areas (Sales et al., 2019).

106 The threats related to the changing climate and habitat loss extend to virtually
107 all clades, and impacts can already be observed, resulting in reduced distribution in
108 invertebrates (Larsen, 2012) and vertebrates (Tingley et al., 2009; Sinervo et al.,
109 2010). Because of their prompt response in terms of richness, abundance and
110 physiology to changes in land use, management intensities and extreme weather
111 events, bats are regarded as bioindicators that help understanding the impacts of
112 environmental change in a broader context, (Sherwin et al., 2013; Gonçalves et al.,
113 2017). Bats can be sensitive to overheating (Crawford and O'keefe, 2021), and
114 changes in distribution of multiple species seem to have happened as a consequence
115 of recent climate change (Wu, 2016). Certain species may even benefit from climate
116 changes, expanding their ranges to regions that are currently unfavourable. For
117 example, in Costa Rica many bat species have recently been documented at higher-
118 than-normal elevations, suggesting range expansions (LaVal, 2004; Arias-Aguilar et
119 al., 2020). Local extinctions and colonization dynamics in response to climate
120 forecasted to the 21st century may redistribute bat species (Pearson and Dawson,
121 2003; Zu 2015). Yet, changes in land use could limit populations in tracking their
122 bioclimatic niches (Mendes et al., 2021) Thus, forecasts of the effects of
123 environmental change on Neotropical bats are important not only to understand how
124 distribution patterns in this diverse group may be altered, but also for a broader
125 assessment of how climate and land use will reorganize biodiversity.

126 Here, we infer the combined impacts of climate and land use change on
127 Neotropical bats focusing on potential changes in spatial patterns of bat richness.
128 Using species distribution models we generate projections of changes in

129 environmental suitability for a representative sample of the Neotropical bat biota (ca.
130 80% of all species) under two (Mitigation A1B and Business-as-usual A2) climate
131 and land use socio-economic development scenarios for the end of the 21st century.
132 We also investigate three different dispersal scenarios to test how important natural
133 and anthropogenic barriers can be in determining future spatial distribution patterns.
134 Based on the resulting projections we examine how differences in habitat use and diet
135 may affect distribution patterns and, thus, reshape the configuration of bat diversity
136 across Neotropical ecoregions.

137

138 **Methods**

139 **Study system**

140 To assess the effects of climate and land use change on Neotropical bat distributions
141 we studied the distribution of 228 Neotropical bat species, which corresponds to ca.
142 80% of documented species in the region. The species not included in the study are
143 species for which there is limited information on distribution or habitat use or those
144 whose distribution is too restricted (see Appendix S1 for further details on the
145 Methods and Appendix S2 for more information on the studied species). We focused
146 our analyses on the Neotropics, ranging from northern Mexico to central Argentina
147 and including the whole Caribbean (Morrone 2014). We also investigated differences
148 across Neotropical ecoregions by adopting the Neotropical division into 10
149 ecoregions proposed by Antonelli et al. (2018): Amazonia, Atlantic Forest, Andean
150 Grassland, Cerrado and Chaco, Caatinga, Dry Western, Dry Northern, West Indies
151 and Mesoamerica (Fig. 1).

152

153 **Ecological niche models**

154 To assess potential changes in species distribution patterns, we fitted ecological niche
155 models calibrated with climate data from locations within which species are known to
156 occur. Ecological niche models are correlational procedures aimed at assessing the
157 environmental conditions associated to the occurrence of species in order to estimate
158 their potential distribution, i.e. the locations where the environment is similar to that
159 within the species' known distribution. We used the species ranges available in the
160 IUCN database (www.iucnredlist.org, date of access: August 08th, 2020) as the
161 source for distribution information. For each species, we sampled a number of
162 random points within the species inferred range that was proportional to its range size
163 and used species distribution models to generate potential distribution maps. To do so,
164 we first rasterized the IUCN range maps into a gridded file of 10' resolution
165 (approximately 0.17 degree of lat/long) and, to be conservative and avoid
166 overestimation, we restricted our analysis to species whose range size was larger than
167 30 cells. For species whose range size was larger than 1000 cells, we sampled 12.5%
168 of these cells, thus considered "presences" in the rasterized map. For species with
169 range size varying from 501 to 1000 and 101 to 500 we sampled 25% and 50% of the
170 cells within species ranges. Finally, for species with less than 100 cells within the
171 total range we used all cells as occurrences to calibrate distribution models. Because
172 we used IUCN range maps as a source of distribution information, the outcome of our
173 ecological niche models represents the environmental conditions most frequently
174 observed across species' known distributional limits. Therefore, our results should not
175 be interpreted in terms of probability of occurrence *per se*, neither can be directly
176 translated in any abundance-related metric. Such broadly defined climate envelopes
177 are meant to provide an initial assessment of species climatic suitability at the
178 continental scale and are useful to investigate macroecological relationships between

179 biotas and environments (Sales et al., 2020; Sales et al., 2020a, Sales et al., 2020b).
 180 Therefore, we stress that our results should not be considered at face value in
 181 conservation assessments at local spatial scale.

182 We acknowledge that using information from range maps to assess species
 183 climatic niches is not the “gold-standard” choice in ecological niche modelling, and
 184 that a comprehensive and non-autocorrelated dataset taken from confirmed on-ground
 185 presences and absences would be ideal (Araújo et al., 2019). However, this scenario is
 186 impractical for multispecies studies at continental scale, especially for large
 187 extensions of biodiversity-rich yet remote and under-sampled locations, such as most
 188 of the Neotropics (Etard et al., 2020; Zizka et al., 2021). Moreover, capture rates of
 189 bats are subjected to the complexity of the environment, being generally higher in
 190 open environment than in habitat with a more complex vegetation structure like
 191 forests. Although this source of bias may also affect range maps, the impact is much
 192 greater for the distribution of occurrence points. Data gaps (e.g. tropical rainforest
 193 and mountain top regions) in the distribution of Neotropical bats limit our ability to
 194 conduct large-scale analyses based on occurrence points, whereas biases can impact
 195 the validity of extrapolations (Aguiar et al., 2020; Delgado-Jaramillo et al., 2020).
 196 Furthermore, the sub-setting of realized niches due to defaunation and other non-
 197 climatic stressors creates truncated relationships between environmental suitability
 198 and environmental variables, underestimating biodiversity predictions (Faurby and
 199 Araújo, 2018) and overestimating the impact of future stressors (Lima-Ribeiro et al.,
 200 2017). Thus, by using species’ range maps the basis for distribution models instead of
 201 occurrence points with critical gaps and biases, we produce a conservative assessment
 202 and our analyses should be interpreted as a baseline of the potential effects of climate
 203 change on bat distribution.

204 To build distribution models we obtained climate information as 10'
 205 resolution gridded raster files for land areas, derived from interpolation of worldwide
 206 ground weather stations, available in CliMond (<https://www.climond.org/>). Date
 207 referred to “present-day” conditions encompass averages of measurements between
 208 years 1961 – 1990. Although CliMond data includes 35 bioclimatic predictors, we
 209 only used a subset of predictors when calibrating ecological niche models. Before
 210 selecting among predictors, we built species-specific study areas, limiting the
 211 background extent of each species to regions likely accessible via migration (Barve et
 212 al., 2011). To do so, we defined a bounding box to extreme latitude/longitude
 213 coordinates, plus an additional 10 degrees to each bound and cropped climatic layers
 214 to adjust to the study extent. Then, we extracted the climatic information related to
 215 each species background extent. To select among predictors, we used a hybrid
 216 approach that combines pairwise correlations with variance inflation factor (VIF)
 217 (Marquardt, 1970), implemented in *usdm* R package (Naimi et al., 2014; R Core
 218 Team, 2021). After measuring the correlation between pairs of climatic variables, the
 219 pair with highest correlation value (threshold = 0.6) was identified and the variable
 220 with higher VIF was excluded from the pair. This procedure was repeated until all the
 221 strongly correlated variables were excluded.

222 After defining a proper set of uncorrelated predictors for each species models,
 223 we used an ensemble-based ecological niche modelling approach, using the *usdm* R
 224 package (Naimi et al., 2014). To accommodate the sensitivity of our predictions to
 225 method variation, we used two algorithms: boosted regression trees (BRT) and
 226 maximum likelihood (MaxLike). While boosted regression trees join recursing binary
 227 to adaptive boosting, combining several models in an ensembled prediction with
 228 higher performance (Elith and Leathwick, 2009), MaxLike is a method based on

maximum likelihood, whose parameter output is formally related with the widely-used Maxent software (Merow and Silander, 2014). Both methods rely on machine-learning approaches, which are known to accurately predict simulated response curves (Elith and Leathwick, 2009), notably in cases of small sample size (Pearson et al., 2007).

The outcome of our ecological niche models was, then, evaluated for their accuracy using a repeated sub-sampling procedure where 25% of the records were regarded as the “test” sub-set, used to measure the performance of the models that were fitted using the remaining 75% of the records, the “training” sub-set. This procedure was repeated 100 times for each modelling method *per* species. We used the area under the receiver operating characteristic curve (AUC), a threshold-independent metric (Fielding and Bell, 1997), to evaluate the accuracy of our predictions (Appendix S2). AUC values of model performance vary from 0 to 1, where a value of 0.5 indicates accuracy similar to that of a random model a value of 1 indicates a perfect discrimination by both metrics. Because binary predictions were required as input in our simulation of dispersal via cellular automata (see below), we also calculated the true skill statistic (TSS) of the models to determine proper thresholds for each species and then created binary maps of suitable/unsuitable cells.

Climate change forecasts

To generate projections of the potential effects of climate change on the potential distribution of Neotropical bats, we projected ecological niche models according to forecasts of climate dated to years 2030, 2050, 2070 and 2090. The fact that we project changes for every 20 years allowed us to track climatic niche bridges between successive timesteps (Littlefield et al., 2017). Accommodating the inherent

uncertainty of climate change forecasts, we used two possible future scenarios, based on different expectations of human population growth, socioeconomic development, and associated emissions of greenhouse gases. The *Mitigation* scenario, A1B, estimates a temperature increase of 1.7 – 4.4°C by the end of the 21st century, whereas the *Business-as-usual*, A2, forecasts a 2.0 – 5.5°C temperature increase. Those forecasts roughly correspond to the representative concentration pathways *RCP6.0* and *RCP8.5* from the IPCC-AR5 (IPCC, 2014) and project temperature increases above the 1.5°C threshold recommended to avoid the deleterious effects of climate change on ecosystems and human well-being (IPCC, 2019) but are congruent with observed changes from years 2000-2010 (IPCC, 2014) (see Appendix S1 climate data for details).

265

266 **Habitat filter masks**

Ecological niche models calibrated with IUCN range maps are based on the assumption that any species can occupy all of the habitat within its extent of occurrence, which turns predictions overly “optimistic” and, thus, subjected to commission error (Lobo et al., 2010). To minimize these erroneous relationships in our maps of potential distribution, we created species-specific land cover masks, based on the IUCN habitat classification scheme, the most comprehensive effort available to characterize species habitat affiliations (<https://www.iucnredlist.org/resources/habitat-classification-scheme>). The major habitat types according to this scheme are forest, savanna, shrubland, grassland, wetlands (inland), rocky areas (e.g., inland cliffs, mountain peaks), caves and subterranean (non-aquatic), arid or semi-arid (desert), artificial-terrestrial (e.g. Pastureland, Plantations, Urban areas and heavily degraded forest). We considered

279 habitat specialist species all those species whose occurrence was restricted to a single
 280 major land cover type (e.g. forest), regardless the specific category of land cover (88
 281 species). Accordingly, we consider a habitat generalist species any species whose
 282 occurrence is not restricted to a single major land cover type (140 species). Species
 283 were, assumed to be unable to occupy major habitat types where they had not been
 284 recorded before. As these habitat types can be matched with terrestrial land cover,
 285 known as the area of habitat (Brooks et al., 2019), we grouped the habitat data into six
 286 major land cover classes (forest, savanna, grassland, farmland, urban, and barren). By
 287 doing so, we were able to reconcile the information on species-habitat associations to
 288 a global model that project changes on land-use and land-cover (LULC) (Li et al.
 289 2017, described in Appendix S1 land-use and land-cover section).

290

291 **Dispersal assumptions**

292 In heterogeneous landscapes, the quality and permeability of the matrix act as
 293 environmental filters that affect species' persistence and ability to colonize newly
 294 suitable areas (Gonçalves et al., 2017; Farneda et al., 2019). Here, we explicitly
 295 incorporate dispersal into the future estimates of potential distribution assuming that
 296 expansion of a species distribution depends on the availability of habitat that allows
 297 dispersal across space. Specifically, we consider that dispersal is more likely across
 298 land cover types corresponding to habitat types where a species is known to occur,
 299 whereas land cover types that are not listed as major habitat types or habitats used for
 300 that species are considered barriers to movement across suitable climatic pockets.
 301 Therefore, we assume that dispersal limitation can prevent a species to access and
 302 occupy suitable environments in the future (see Appendix S3). To simulate dispersal
 303 we used the R package MigClim (Engler et al., 2012), a cellular automata model

where dispersal depends on landscape barriers and species-specific dispersal limitations contingent on environmental suitability. We used the following parameterization of function “MigClim.migrate” for all dispersal simulations. The function argument hsMap included the habitat suitability models for intermediate timesteps (years 2030, 2050 and 2070); envChgSteps and dispSteps, i.e. the number of environmental change steps and the number of dispersal steps were set to three (the number of intermediate timesteps). The argument barrier included a raster file with the land-use and land-cover types listed as unsuitable for each species, and barrierType was defined as “weak” or “strong”, depending on habitat generalization or specialization, respectively. Finally, replicate NB was set to three full simulations of dispersal per species. For the remaining arguments we used the function default values (for further details on the dispersal simulation see the section modelling occupancy dynamics and dispersal in Appendix S1). To understand how dispersal constraints may affect future climate-driven range dynamics, we examined future patterns of potential distribution considering three different assumptions on dispersal ability. The 1) *Unlimited Dispersal* scenario, where bat species are assumed to have the ability to disperse across any type of land cover and fragmented landscape. The 2) *No Dispersal* scenario, where species are not allowed to move outside current distribution limits and estimates of change in climatically suitable areas are restricted to grids within present-day extent of occurrence. The (3) *Limited Dispersal* scenario, which is more realistic than the previous scenarios and assumes that bat species have the ability to disperse across areas where land cover is analogue to that where it occurs in the present, whereas no-analog environment is considered a barrier to dispersal. By performing simulations under these three different scenarios, we

intended to infer the roles of environmental suitability and accessibility on the projected outcomes

For each combination of climate change, land use change and dispersal limitation scenarios we registered whether the potential range of each species would decrease or increase in the future. Based on the projected ranges we estimated the number of species that could potentially occupy each cell for the Neotropics as a whole and for each ecoregion (see Appendix S1 - modelling occupancy dynamics and dispersal). To understand how the reorganization of bat assemblages may translate into shifts in ecological functions, we also classify species according to trophic guilds and analyse the changes in spatial patterns for each guild. For the analysis of which trophic guild might be affected, we classified bats based on their main food items (feeding habit) according to Simmons (2005): Phytophagous bats: (1) frugivore and (2) nectarivore; Animalivorous bats: (3) carnivores, (4) sanguivores, (5) insectivores and (6) piscivores; and species that feeding on both animal and plant: (7) Omnivore (for further details about models and dispersal scenarios, see Appendix S1- modelling occupancy dynamics and dispersal).

Results

The magnitude of range shift

The magnitude of range shift in response to climate and land use change varied considerably according to different scenarios of climate change and dispersal limitation (Fig. 2). Simulating a realistic dispersal scenario, in which dispersal across space is limited by barriers of non-analog environment, most of the habitat-generalist species could expand their ranges in both (A1B) the Mitigation ($A1B_LD_G_{median} = 26 \pm 1374\%$) and (A2) B.A.U. scenario ($A2_LD_G_{median} = 4 \pm 1148\%$), but most

habitat-specialist species are projected to experience major reductions in their ranges in the A2 scenario ($A1B_LD_S_{median} = 32 \pm 347\%$ and $A2_LD_S_{median} = -47 \pm 217\%$) (Fig. 2 and Appendix S2).

Next, we simulated two dispersal scenarios representing opposite extremes regarding dispersal to test how accessibility changes the outcomes of environmental changes for Neotropical bats. Assuming that bats are confined to their current distribution limits, even the generalist species regarding land cover would be expected to lose a large proportion of their potential distribution ($A1B_ND_G_{mean} = -14 \pm 18\%$ and $A2_ND_G_{mean} = -27 \pm 22\%$). Again, habitat-specialist species would be more impacted showing largest range reductions ($A1B_ND_S_{mean} = -27 \pm 19\%$ and $A2_ND_S_{mean} = -71 \pm 19\%$; Fig. 2). This suggests that the area that is climatically suitable within the distributions of all species will reduce in the future.

Under the *Unlimited Dispersal* scenario, in which bat species have ability to disperse through any type of matrix, most of the habitat-generalist species could expand their ranges in both climate change scenarios ($A1B_UD_G_{median} = 34 \pm 2437\%$ and $A2_UD_G_{median} = 16\% \pm 2236\%$), but most habitat-specialist species are still projected to undergo range contraction in the A2 scenario ($A1B_UD_S_{median} = 122 \pm 559\%$ and $A2_UD_S_{median} = -11\% \pm 217\%$) (Fig. 2). This suggests that although within current ranges suitability will decrease, the total area of suitable climate will increase for most species.

Neotropical ecoregions with higher projected impact

Despite projected losses in richness in many areas (Table 1), the overall outcome of projected range shifts was an increase in the mean richness at the local (cell) scale across most ecoregions (Fig. 3; Table 2), owing to the range expansion of habitat-

378 generalist species (Fig. 4). However, at the regional scale, most ecoregions are
 379 projected to undergo a net loss in species richness (Table 1; Fig. 4). The Amazon was
 380 the region projected to experience the largest gains in richness at the local (cell) scale
 381 (Fig. 3; Table 2), especially nearby Andean mountains and Guiana Highlands (Fig. 4).
 382 Yet, these range shifts resulted in no net gains or losses in richness at the regional
 383 scale (Table 1). The Dry Western South America is the region projected to experience
 384 the greatest proportional gains, with richness increasing more than 2.5 times at the
 385 local scale (from 4 to 11 species; Fig. 3; Table 2) and 61 new species at the regional
 386 level (Table 1). Despite little change in local richness, Mesoamerica and the
 387 Patagonian steppe are also projected to gain species, with 28 and 10 novel species,
 388 respectively (Table 1). In contrast, the Andean grassland is projected to lose 22
 389 species at the regional level in spite of a substantial increase in local richness (from 3
 390 to 10 species) (Table 1). All remaining ecoregions are projected to suffer more losses
 391 than gains with the Caatinga, the Cerrado/Chaco, and the West Indies losing more
 392 than 15% of their current species (Table 1).

393 Our projections indicate different trophic guilds will be impacted differently
 394 by climate and land use change (Fig. 5). Within most ecoregions, the number of
 395 frugivorous bats projected to undergo range reductions is more than twice as large as
 396 the number of species projected to undergo expansions (Appendix S4-S13). For other
 397 guilds, patterns are less consistent. For instance, in the Caatinga (Appendix S6) and
 398 Cerrado/Chaco (Appendix S8) regions more insectivores are projected to undergo
 399 range reduction than expansion, while in the Dry Western (Appendix S10) and
 400 Patagonian steppe (Appendix S13) most insectivores are projected to expand in range.
 401 Two sanguivorous bats (*Diaemus youngi* and *Diphylla ecaudata*) are projected to
 402 expand their ranges into Dry Western and Patagonian steppe respectively (Appendix

403 S10 and S13) and five Neotropical endemic bat species *Phyllostomus latifolius*
 404 (omnivore, Dry Northern South America), *Dryadonycteris capixaba* and
 405 *Lonchophylla mordax* (nectarivore, Atlantic Forest), *Chilonatalus micropus*
 406 (insectivore, West Indies) and *Eptesicus innoxius* (insectivore, Dry Western South
 407 America) are predicted to become globally extinct by the combined effects of climate
 408 and land use changes (Table 1).

409

410 **Discussion**

411 **The magnitude of range shift**

412 This is the first effort to evaluate the possible future consequences of two of the most
 413 important drivers of current global environmental change - land use and climate
 414 change - on Neotropical bats. Focusing on the more realistic scenario of socio-
 415 economic development (B.A.U), our projections suggest substantial future declines in
 416 environmental suitability for the Neotropical bat fauna, especially for bat species that
 417 have specialised on a specific type of environment. The widespread loss of specialised
 418 species in our projections was compensated by the expansion of generalised species
 419 that forage in open areas and commonly establish large colonies in manmade
 420 structures (Gonçalves et al., 2017). The balance between the loss of habitat specialists
 421 and expansion of generalists may lead to little net change of species richness at the
 422 local level, but greater homogeneity in species composition. Functional
 423 homogenisation is considered a global prominent forms of biodiversity
 424 impoverishment induced by recent environmental change (Devictor et al., 2008;
 425 Clavel et al., 2011). Species that exhibit morphological and functional specialization
 426 on specific conditions are more sensitive to changes because unique traits restrict
 427 them to only a narrow set of environments and resources (Clavel et al., 2011;

Newbold et al., 2018; Staude et al., 2020). In addition, the use of a restricted range of habitats implies that habitat-specialist bat species are unable or unlikely to cross-gaps of unsuitable environment to colonize isolated suitable patches. Therefore, habitat specialists are not only threatened by changes in their current habitat, but also by the inability to access novel suitable habitat.

Neotropical ecoregions with higher projected impacts

Several Neotropical bat species may be forced to shift their range to refuges that are less vulnerable climate change, venturing into regions of different elevation and/or latitudes while facing new environmental challenges in response to the land use and climate change. Our projections showed that areas nearby the Andean mountains (Northern Andean) and the Guiana Highlands would be considered climate change refugia for several Neotropical bat species (Fig. 4; Fig. 5). Yet, Climate-driven migrations will only allow occupancy of newly suitable climates if permeable migratory routes allow dispersal across landscapes (Engler et al., 2012). When we considered dispersal barriers, our analyses revealed no net gains of species in Amazonia although this region is projected to harbour suitable conditions for many species. Reduced accessibility due to the ‘Arch of Deforestation’ (Sales et al., 2019), a region of high agricultural pressure from cattle-ranching and soy plantations, restricts climate-driven movements of forest specialist species from the regions south of the Amazon basin and vice-versa.

Our models predicted higher gains of species in the Dry Western South America (61 species, increasing potential richness in 60%) located in the Andes foothills at mid-elevation (1000-2500m). This means that there is a great potential for Neotropical bat species immigration at these elevations. The major factors driving this

453 trend are the upslope dispersal of lowland species in response to global changes
 454 combined with projections of low changes in land use in the region. Such upslope
 455 movements are predicted by the hypothesis of upward and upslope shifts in species
 456 ranges due to elevated temperatures (Colwell et al., 2008) and have been reported for
 457 birds (Bender et al., 2019) and dung beetles (Larsen, 2012) in the same region and for
 458 bats in the Mountains of northern Costa Rica (LaVal 2004, Arias-Aguilar et al.,
 459 2020). . Our findings thus highlight the potential of mountains and highlands to act as
 460 refugia for bats occurring in low elevation over time.

461 Conversely, our models predicted high losses of species from the regional
 462 species pool in the Andean Grassland (22 species, representing 13% of total richness)
 463 located at high-elevation (3200-3500m). Yet, all species currently occurring in this
 464 region were projected to persist at the continental scale, as long as they can disperse
 465 to suitable environment (Table 1). This could be a consequence of the wide
 466 elevational ranges of species at such altitude which is consistent with Rapoport's rule
 467 that species at high elevations tend to have wider elevational ranges, covering several
 468 elevational levels, whereas species in the lowlands tend to have narrow elevational
 469 ranges (Stevens, 1992). The greatest proportional loss in species richness was found
 470 for the West Indies, 27% of the species (7 out of the 26) and the Caatinga, 22% (17
 471 out of 79 species). Species in these regions are projected to be subjected to non-
 472 analogue climates and habitat loss, which combined with dispersal limitation, will
 473 prevent occupancy of neighbouring suitable environment. These species are thus
 474 expected to undergo severe range contractions because of their inability to colonize
 475 the novel suitable environments that may surround their current ranges. Our
 476 projections also showed high species turnover in Cerrado and Chaco (Table 1), where
 477 losses may be partially compensated by gains.

478 Five endemic bat species that occupy small areas in the Neotropics are
 479 predicted to become globally extinct (Table 1), but this number may be higher since
 480 our conservative analysis is restricted to species whose range size was larger than 30
 481 cells (Appendix S1). Neotropical endemic bat species and/or species that occupy such
 482 a small area, may have entire populations exposed to physiological stress or resource
 483 shortage even under small environmental variation (Newbold et al., 2018; Staude et
 484 al., 2020). Those narrow-ranged species are also vulnerable to non-climatic stressors,
 485 such as population stochasticity, low variability and Allee effect, that impact small
 486 populations (Newbold et al., 2018).

487

488 **Shifts in ecological functions**

489 Our analyses revealed that combined effects of land use and climate change
 490 are likely to favour many animalivorous bat species that forage in unobstructed areas
 491 outside or above forested sites and easily establish high-densities colonies in
 492 manmade structures (Gonçalves et. al. 2017; Farneda et al., 2019). Those are typical
 493 attributes of molossid and some phyllostomid bats (Simmons, 2005), which may
 494 allow species to increase their ranges by colonizing other ecoregions in response to
 495 changes. Bat species with these characteristics are usually evaluated with a lower risk
 496 of extinction (IUCN, 2020), which is consistent with their success to persist within
 497 modified landscapes and under variable climatic conditions. However, several
 498 phytophagous bats (nectarivores and frugivores) are projected to experience major
 499 reductions in their ranges. Species that rely on the vegetation as food sources and
 500 natural roosting places are more likely to be impacted by land use change (Popa-
 501 Lisseanu and Voigt, 2009; Moussy et al., 2013; Sherwin et al., 2013; Gonçalves et al.,
 502 2017; Farneda et al., 2019). The interplay between species dispersal abilities and its

503 ecological requirements will shape the species-specific responses to environmental
504 change.

505 These uneven outcomes for different trophic guilds may impact ecosystem
506 functions locally. As species expand or retract, their interactions are also
507 redistributed. The replacement of phytophagous bats by insectivore species may result
508 in local declines in pollination and seed dispersal of many plants. Likewise, range
509 reduction of carnivorous and piscivorous bats forecasted for some regions may impair
510 the control of prey populations and transport of nutrients across the landscape
511 (Gonçalves et al., 2017). Range expansions of a species may also result in the
512 expansion of its pathogens, including those associated with zoonotic diseases
513 (Gonçalves et al., 2020). The projected range expansion of two sanguivorous bats into
514 Dry Western and Patagonian steppe for instance, could increase the probability of
515 transmission of rabies and other saliva-borne viruses (Olival et al., 2017).

516

517 Implications for species extinction risk and conservation biogeography

518 Based on the expected changes in climatic conditions in the Neotropics, we
519 argue that the most effective way to protect these species will be by increasing
520 landscape connectivity through habitat restoration, connecting native vegetation
521 fragments and forest patches with broad corridors (Arroyo-Rodríguez et al., 2020).
522 Despite the potential of bats for large-scale species migration, reserves should also
523 remain as a component of conservation strategy under land use and climate changes.
524 Creating new protected areas, especially surrounding climate change refugia, and
525 preserving existing ones will also act to protect high quality habitat, reducing
526 extinction risk as well as providing suitable regions for colonizing species or stepping
527 stones for species on the move. A mosaic of land uses and less damaging landscape

practices, such as low intensity forestry, may also provide some opportunity for persistence or migration (Arroyo-Rodríguez et al., 2020). Enhancing existing linear habitat features, such as river banks, hedgerows and embankments may improve connectedness without actively creating new corridors (Sales et al., 2019).

Proactive conservation can be applied in all ecoregions but should especially focus in the Northern Andean mountains, Guiana highlands and Mesoamerica mountains as these regions still retain a high percentage of natural habitat where the biota is relatively intact (Antonelli et al., 2018; Ribeiro et al., 2017; Sales et al., 2019; Fragoso et al., 2019). In these regions, large-scale conservation, such as the protection of a large extension of land, might be achieved with relatively low investment. Due to the highest losses of bat species projected for the West Indies (specially the Caribbean dry forest), Andean grassland, and for the Caatinga and Cerrado/Chaco regions we stress the need for efficient measures to halt habitat loss and fragmentation and continued monitoring of species responses to climate change.

Fine-scale reactive conservation should be applied for long-term monitoring of climate change responses by five endemic bat species that are predicted to become extinct and also species that occupy small areas and in the Neotropics. Monitoring would also be important to help detecting the functional shifts related to expansion/retraction of bats from different guilds projected here, and is especially important considering the projected range expansion of two vampire bats into new ecoregions (Gonçalves et al., 2021), which might be of public health concern (Olival et al., 2017). We caution that our projections considering multiple species simultaneously have been designed for large scale assessment of broad distribution patterns and did not account for species-specific physiological or behavioural responses to small scale environmental and landscape properties. Thus, conservation

planning focused at individual species should not rely exclusively on such models, which can be used as a starting point, but should be combined with fine-grained field data as well as a more in-depth analysis of how different climate variables and biotic contexts affect fitness (Mawdsley et al., 2009).

Conclusions

Overall, our results provide new insights to guide landscape management, policy and practice to maintain or enhance bat diversity and their ecological functions in the Neotropics. A main highlight of our projections is that, despite the low number of habitat specialist species observed in land use/climate change-influenced area, increasing landscape connectivity and maintenance of old-growth forests is crucial for Neotropical bat ecosystem services conservation in the future. Long-term monitoring programs will be important to track the combined impacts of climate and land use changes on Neotropical bats and provide conservationist with information to evaluate the effectiveness of conservation plans (Sherwin et al., 2013). Furthermore, better determining the dispersal abilities, realized niche width and physiological tolerances at the species level will be particularly important for understanding the vulnerability of Neotropical bats to climate and land use change and their ability to persist or redistribute in response to the changing environment (Mawdsley et al., 2009; Zamora-Gutierrez et al., 2018).

Supplementary Material

Additional information (Appendix S1-S13) and R code are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding

579 author. Supplementary Information is also available on GitHub
580 (github.com/fhmgoncalves).

581

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Tables

Table 1: Potential richness variation of Neotropical bat species at regional scale under the business-as-usual (B.A.U) scenario of climate and land-use changes and assuming limited dispersal (bat species have the ability to disperse only over analog environment).

Ecoregions	Present	Future			
	Species richness	Species gains	Regional extinction	Global extinction	Species richness
<u>Forested Wet</u>					
Amazonia	212	0	0	0	212
Atlantic forests	98	3	13	<i>D. capixaba/L. mordax</i>	86
<u>Open Dry</u>					
Andean Grassland	160	8	21	0	147
Caatinga	79	6	17	0	68
Cerrado and Chaco	140	14	21	0	133
Dry Northern	172	3	14	<i>Phyllostomus latifolius</i>	161
Dry Western	103	61	7	<i>Eptesicus innoxius</i>	157
Patagonian steppe	30	10	7	0	33
<u>Mixed</u>					
Mesoamerica	105	28	0	0	133
West indies	27	0	6	<i>Chilonatalus micropus</i>	21

Table 2: Potential change in species richness of Neotropical bats for ecoregions at the local scale. Numbers represent the mode of species richness for all cells in each ecoregion in the present and projected under the business-as-usual (B.A.U) scenario of climate and land-use changes and assuming limited dispersal (bat species have the ability to disperse only over analog environment).

Ecoregions	Present	Future	
	Cell richness	Cell richness	Gain (+) Loss (-)
<u>Forested Wet</u>			
Amazonia	85	59	-26
Atlantic Forests	16	17	1
<u>Open Dry</u>			
Andean Grasslands	3	10	+7
Caatinga	18	18	
Cerrado and Chaco	15	17	+2
Dry Northern South America	27	26	-1
Dry Western South America	4	11	+7
Patagonian Steppe	2	4	+2
<u>Mixed</u>			
Mesoamerica	15	16	+1
West Indies	6	5	-1

Figure legends

FIG. 1: Neotropical region limits (sensu Olson et al., 2001) and ecoregion classification (sensu Antonelli et al., 2018) adopted in the analyses.

FIG. 2 Proportional change in potential distribution for 140 habitat-generalist bat species and 88 habitat-specialist bat species in response to combined effects of climate and land use change. Projections correspond to two different scenarios for climate/land-use changes and different levels of dispersal limitation. A1B and A2 refer to Mitigation and B.A.U., i.e. more optimistic and less optimistic climate and land use change scenarios. Unlimited Dispersal assumes that bat species have ability to disperse across any type of environment and across fragmented landscape. Limited dispersal assumes that bat species have the ability to disperse only across analog environment, whereas non-analog environment is considered a dispersal barrier. In the No Dispersal scenario species are restricted to their current range.

FIG. 3 Current (Present) and projected (future) richness of bat species per cell in the Neotropical regions under the business-as-usual (B.A.U) scenario of climate and land-use changes and assuming limited dispersal (bat species can disperse only across analog environment).

FIG. 4 Projected change in richness of (A) environment-specialist and (B) environment-generalist bat species under the business-as-usual scenario of climate and land use changes (B.A.U). Dispersal is assumed to be limited so that bat species have the ability to disperse only across analog environment.

FIG. 5 Projected change in richness of bat species according to feeding habits and under the business-as-usual scenario of climate and land use changes (B.A.U). Dispersal is assumed to be constrained so that bat species have ability to disperse only over land cover analog to current occurrence patterns. (A) Insectivores, (B) Frugivores, (C) Piscivores, (D) Omnivores, (E) Nectarivore, (F) Sanguivores and (G) Carnivores.

Insectívoros **Frugívoros** **Piscívoros** **Omnívoros** **Nectarívoros** **Sanguívoros** **Carnívoros**