Neotropical mammal diversity and the Great American Biotic Interchange: spatial and temporal variation in South America's fossil record

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2 # Interchange: spatial and temporal variation in South America's

3 # fossil record

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18 **Abstract**

19 The vast mammal diversity of the Neotropics is the result of a long evolutionary history.
20 During most of the Cenozoic, South America was an island continent with an endemic
21 mammalian fauna. This isolation ceased during the late Neogene after the formation of the
22 Isthmus of Panama, resulting in an event known as the Great American Biotic Interchange
23 (GABI). In this study, we investigate biogeographic patterns in South America, just before or
24 when the first immigrants are recorded and we review the temporal and geographical
25 distribution of fossil mammals during the GABI. We performed a dissimilarity analysis which
26 grouped the faunal assemblages according to their age and their geographic distribution. Our
27 data supports the differentiation between tropical and temperate assemblages in South
28 America during the middle and late Miocene. The GABI begins during the late Miocene
29 (~10–7 Ma) and the putative oldest migrations are recorded in the temperate region, where the
30 number of GABI participants rapidly increases after ~5 Ma and this trend continues during
31 the Pleistocene. A sampling bias towards higher latitudes and younger records challenges the
32 study of the temporal and geographic patterns of the GABI.

33

34 **Keywords**

35

36 Neotropics, Great American Biotic Interchange, Biogeography, Mammalia, South America

37

1. Introduction

The Neotropics (Neotropical region *sensu lato* of Morrone (2014)) supports an extremely large diversity of living mammals. Currently there are around 1500 recognized species which represent in the order of 30% of the total world mammal diversity. Included are endemic groups such as marsupials (opossums), xenarthrans (sloths, armadillos, and anteaters), caviomorph rodents (capybaras, spiny rats, chinchillas), platyrrhine monkeys, and phyllostomid bats (Patterson and Costa, 2012). The variety of biomes found in the Neotropics (lowland rainforest, savannas, mountain forest, scrublands, and deserts) could provide a partitioned environment enhancing species richness (Tews et. al., 2004).

The current Neotropical mammal fauna is the result of a long evolutionary history. The Cenozoic (66–0 Ma) in South America was characterized by long term geographical isolation with the evolution of an endemic fauna (Simpson, 1980). Sporadic dispersal events from other geographic areas interrupted this isolation introducing novel clades into South America including caviomorph rodents during the middle Eocene (~41 Ma) and platyrrhine monkeys during the late Oligocene (~26 Ma) (Pascual, 2006; Antoine et al., 2012; Croft, 2012; Goin et al., 2012). The isolation of South America's mammal fauna ceased by ~10–7 Ma, when proximity, and then permanent connection was established with Central America. This connection initiated a massive faunal exchange between North America (NA) and South America (SA). This event is known as the Great American Biotic Interchange (GABI) (Simpson, 1980; Webb, 1985). The classic interpretation places the onset of the GABI by ~3.0 Ma, with some early migrations during the late Miocene from SA to NA by ~9 Ma and from NA to SA by ~7 Ma. Other studies using dated molecular phylogenies across a wide range of taxa indicate an important part of the interchange may have predated the permanent land connection by ~3 Ma (Koepfli et al, 2007; Cody et. al, 2010; Eizirik et al, 2010; Eizirik, 2012). The core of the GABI is composed by a series of major migration "waves" during the Pliocene–Pleistocene (2.5–0.012 Ma) (Webb, 2006; Woodburne, 2010). Recently, several NA mammals have been reported from the late Miocene deposits, ~10 Ma, within the Amazon basin. These include a dromomerycine artiodactyl, gomphotheres, peccaries, and tapirs which suggest a more intense earlier connection (Campbell Jr et al., 2000; 2010; Frailey and Campbell, 2012; Prothero et al., 2014). However, the taxonomy and age of some of these fossils have been questioned (Alberdi et al., 2004; Lucas and Alvarado, 2010; Lucas, 2013). In Amazonia, Pleistocene terraces are built from older Cenozoic deposits (Latrubesse et al.,

72   1997), resulting in non-contemporaneous associations (Cozzuol, 2006). Even with these

73   concerns in mind, in the last decades the presence of northern forms in South America is

74   becoming better understood.

75

76   During the late Miocene (11.6–5.3 Ma) and early Pliocene (5.3–3.6 Ma), the GABI was

77   taxonomically balanced, as predicted by the MacArthur-Wilson species equilibrium

78   hypothesis, with similar number of NA and SA families participating in the interchange

79   (Webb, 1976; Marshall et al., 1982). During the Pleistocene, NA mammals appeared to have

80   diversified exponentially in SA, resulting in an overall prevalence of NA over SA–derived

81   mammals. This could be the result of competitive displacement (Webb, 1976; Marshall et al.,

82   1982; Webb, 1991), but this has not been subjected to rigorous analyses. In contrast,

83   ecological replacement has been demonstrated for extinct metatherians and placental

84   carnivores (Prevosti et al., 2013).

85

86   Vrba (1992) analyzed the GABI in the context of the "habitat theory" (i.e. physical

87   environmental changes are the main drivers of "distribution drift") and highlighted the

88   importance of environmental changes over biotic interactions as the major cause of the biotic

89   turnover. Webb (1991) proposed that the Pleistocene glaciations and the widespread

90   development of savannas in the Neotropics facilitated dispersals during the GABI of savanna-

91   adapted mammals. Woodburne (2010) agreed with Webb's model and related the pulses of

92   faunistic movements to the glaciations and sea level changes of the Pliocene and Pleistocene.

93   However, most recent evidence does not support the widespread expansion of savannas in the

94   tropics during glacial times (Behling et al., 2010). The GABI was dynamic with bidirectional

95   migrations (Carlini et al., 2008b; Castro et al., 2014) and with reciprocal exchanges within a

96   single lineage (e.g., procyonids; Baskin, 1989; Forasiepi et al. 2014; and felids; Prevosti,

97   2006).

98

99   Potential biogeographic barriers or corridors along with environmental changes controlled

100   patterns of movements (Webb, 1991; Woodburne, 2010). The Andes are currently an

101   important biogeographic feature in South America extending for about 8000 km from

102   Venezuela to Argentina, reaching average heights of about 4000 masl and maximum

103   elevations up to 7000 masl (Ramos, 1999). The present day elevations of the northern and the

104   north central Andes (north of 20°S) were reached during or soon after the late Miocene (Mora

105 et al., 2009) and may have constituted a colonization corridor during the GABI (Patterson et

106 al., 2012 and references therein).

107

108 A full understanding of the GABI is difficult because of the difference in fossil sampling

109 between low and high latitudes (Figure 1). Even with the major recent advances in

110 Neotropical paleontology (Kay et al., 1997; Campbell Jr, 2004; MacFadden, 2006; Sánchez-

111 Villagra et al., 2010; Antoine et al., 2012), our knowledge of this large portion of territory that

112 comprises the neotropics, twice the size of Europe and almost as large as North America is

113 scarce (Croft, 2012).

114

115 In this contribution, we investigate biogeographic patterns for the middle and late Miocene

116 (15.9–5.3 Ma) in SA at the initiation of the GABI. We review the temporal and geographical

117 distribution of fossil mammals during the GABI and discuss the special significance of the

118 fossil record from northern SA to understand the patterns and dynamics of the interchange.

119
120 **2. Materials and methods**

121

122 Species lists from several middle and late Miocene–Pliocene mammal associations (La Venta,

123 Fitzcarrald, Quebrada Honda, Collon Curá, Urumaco, Acre, Mesopotamian, Cerro Azul,

124 Chiquimil, Andalhuala, Monte Hermoso, Inchasi and Uquía) were compiled from several

125 sources (Goin et al., 2000; Cozzuol, 2006; Reguero and Candela, 2011; Brandoni, 2013;

126 Tomassini et al., 2013; Tejada-Lara et al., in press) and other references available in the

127 Paleobiology Database (PBDB) (Alroy, 2013), to which we added 450 references with

128 records of Neogene fossil mammals from the Americas (Figure 2–3; Supplementary Material

129 1–2). We obtained latitude and paleolatitude from each locality from the PBDB (Table 1) and

130 estimated the distance in km among localities using Google Earth. Localities were coded for

131 presence/absence at the generic level (Supplementary Table 1). The biochronology refers to

132 the South American Land Mammal Ages (SALMA) and the calibration of the boundaries of

133 Tomassini et al., (2013, modified from Cione et al., 2007) and Cione and Tonni (1999; 2005).

134 Genera were used as taxonomic unit (including taxonomic identifications with *cf.* and *aff.*

135 qualifiers). Lower taxonomical levels are still unresolved for several localities and data is

136 incomparable.

137

138   We analyzed closely contemporaneous fossil mammal associations from SA using the Bray-

139   Curtis binary dissimilarity index. This reaches a maximum value of 1 when there are no

140   shared taxa between the two compared communities. The Vegan package (Okasanen et al.,

141   2013) was used to perform a cluster analysis with average grouping method and a Nonmetric

142   Multidimensional Scaling (NMDS) set to two dimensions (axes) and 1000 runs. We compared

143   tropical and temperate Miocene localities, and in order to account for differences in the

144   sample size, we set the number of taxa equal to the assemblage with the lowest richness

145   within the subgroup and calculate Bray-Curtis dissimilarity by resampling with replacement

146   1000 times all the localities. The Vegan package was used to obtain genera accumulation

147   curves for tropical assemblages, using the random method. All analyses were performed in R

148   (R Core Team, 2013).

149

150   We obtained records for late Miocene to late Pliocene land mammals for NA and SA from the

151   PBDB. We classified each genus as North or South American if the taxon or its ancestor were

152   in either NA or SA before 10 Ma. We compared the geographic distribution (tropical vs

153   temperate) and time of first appearance datum (FAD) of GABI migrants in the continent

154   (Supplementary Material 3 and Supplementary Table 2). In order to account for the age

155   uncertainty of each FAD, we generate 1000 different random values between the maximal and

156   minimal age estimate and calculate the mean and standard deviation of the age estimate for

157   each record.

158

159   **3.1 Study sites**

160

161   We selected faunal associations from the tropical and temperate regions of South America

162   which all together span from the middle Miocene (~15 Ma) to the late Pliocene (~2 Ma), a

163   critical time period for the GABI. The study sites cover a wide latitudinal gradient across the

164   continent (Table 1).

165

166   **Table 1.** Modern and ancient latitude and elevation of the faunal assemblages used in this

167   study.

168

Faunal association	Latitude	Paleolatitude	Elevation	Paleoelevation	Biome
La Venta	~ 3° N	~ 2.6° N	~380 m	"lowland"	Tropical
Fitzcarrald	~ 10.5° S	~ 12° S	< 300 m	"lowland"	Tropical

Quebrada Honda	~ 22° S	~ 22° S	~ 3500 m	~ 2600 ± 600 m	Temperate
Collón Curá	~ 40° S	~ 41° S	~ 800 m	?	Temperate
Urumaco	~11° N	~ 11° N	< 100 m	"lowland"	Tropical
Acre	~10° S	~ 10.5° S	< 300 m	"lowland"	Tropical
Mesopotamian	~ 32° S	~ 32° S	< 100 m	"lowland"	Temperate
Cerro Azul	~37° S	~ 37° S	~150 m	"lowland"	Temperate
Chiquimil	~27°S	~ 27° S	1000-2500 m	?	Temperate
Andalhuala	~27°S	~ 27° S	1000-2500 m	?	Temperate
Monte Hermoso	~ 38° S	~ 38° S	< 100 m	"lowland"	Temperate
Inchasi	~19° S	~ 20° S	~ 3220 m	?	Temperate
Uquía	~ 23° S	~ 23° S	~ 2800 m	~ 1400-1700 m	Temperate

169

170   **3.1.1. La Venta**

171

172   La Venta is one of the best-studied fossil assemblages from the Neotropics and includes

173   freshwater fishes, crocodiles, turtles and different mammal clades (Kay et al., 1997). These

174   come from the Honda Group in the central Magdalena valley, Colombia (Figure 2). Its age is

175   constrained by radiometric and paleomagnetic data. The assemblage of La Venta served as the

176   basis for defining the Laventan SALMA (middle Miocene, 13.5–11.8 Ma) (Madden et al.,

177   1997).

178

179   **3.1.2. Fitzcarrald**

180

181   The localities of the Fitzcarrald assemblage are found along the Inuya and Mapuya rivers in

182   the Amazon of Peru (Figure 2) from the Ipururo Formation, interpreted as middle Miocene

183   (Laventan Age) (Antoine et al., 2007; Tejada-Lara et. al, in press). The vertebrate assemblage

184   includes fishes, turtles, crocodiles, snakes and 24 mammalian taxa (Negri et al., 2010, Tejada-

185   Lara et.al, in press).

186

187   **3.1.3 Quebrada Honda**

188

189   Quebrada Honda is located in southern Bolivia at ~21°S latitude, 20 km north of the

190   Argentine frontier and at an elevation of about 3500 m (Figure 2). The fossil-bearing deposits

191   crop out in the valley of the Honda River and its tributaries. Paleomagnetic and radioisotopic

192   data provide an extrapolated age of 13–12.7 Ma for the fossil bearing beds (MacFadden et al.,

193   1990). Multiple proxies to estimate paleoelevation of the Central Andean Altiplano have

194 yielded values between 1000-2000m for the middle Miocene (Garzione et. al, 2008);

195 however, a most recent study using clumped isotope thermometry on paleosol carbonates

196 inferred an earlier uplift for the Altiplano, with Quebrada Honda at about 2600 ± 600 m and a

197 mean annual temperature of $\sim 9 \pm 5°$ C (Garzione et. al, 2014). The assemblage includes about

198 30 mammals representing metatherians, xenarthrans, rodents, astrapotheres, litopterns and

199 notoungulates and correspond to the Laventan SALMA (Croft, 2007).

200

201 **3.1.4 Collon Curá**

202

203 The Collón Curá Formation is largely exposed at the west of Nord-Patagonian Massif

204 (Neuquén and Río Negro provinces, and Norwest Chubut Province). The rich vertebrate

205 association is represented by reptiles, birds, and principally mammals: metatherians,

206 xenarthrans, rodents, notoungulates, litopterns, and astrapotheres (Kramarz et al., 2011). The

207 fossil mammals collected in the vicinities of the Collón Curá river by Santiago Roth in the

208 late 19th Century are the basis for the definition of the Colloncuran SALMA, although a

209 critical review of most of the findings is still pending. Several radiometric dates for the Collón

210 Curá Formation indicate ages between 15.5 and 10 Ma for the vertebrate association (e.g.

211 (Rabassa, 1974; Marshall et al., 1977; Rabassa, 1978; Bondesio et al., 1980; Mazzoni and

212 Benvenuto, 1990; Madden et al., 1997).

213

214 **3.1.5 Urumaco**

215

216 The Urumaco sequence is found in the Falcón State in northwestern Venezuela (Figure 2). It

217 includes the Querales, Socorro, Urumaco, Codore and San Gregorio formations, which

218 together span from the middle Miocene to late Pliocene (Quiroz and Jaramillo, 2010). The

219 Urumaco sequence shows a high diversity of crocodilians (Scheyer et al., 2013) and

220 xenarthrans (Carlini et al., 2006 a,b; 2008 a,c). We focus our analysis on the Urumaco

221 Formation. Linares (2004), on the basis of a mammal list of undescribed material suggested a

222 middle to late Miocene age. However until a detail taxonomic revision is conducted, the

223 biostratigraphic correlation of the Urumaco association remains tentative.

224

225 **3.1.6 Acre**

226

227 The Acre region in the southwestern Amazonia includes several fossiliferous localities which

228 would represent different time intervals considering the geological and palinological evidence

229 (Cozzuol, 2006). Fossil vertebrates come from the Solimões Formation of the state of Acre,

230 Brazil and Peruvian and Bolivian localities from the Madre de Dios Formation (Negri et al.,

231 2010) (Figure 2). The vertebrate assemblage is very diverse and includes fishes, snakes,

232 lizards, birds, turtles, crocodiles, and mammals including whales, dolphins, manatees and a

233 diverse assemblage of terrestrial forms. The Acre mammal assemblage has been referred to

234 late Miocene, Huayquerian SALMA (Cozzuol, 2006; Ribeiro et al., 2013) or included also in

235 the Pliocene, Montehermosan SALMA (Cozzuol, 2006). Campbell Jr et al. (2001) reported

236 $^{40}A /^{39}A$ dates of 9.01 ± 0.28 Ma for the base of the Madre de Dios Formation and 3.12 ± 0.02

237 Ma near the top.

238

239 **3.1.7 Mesopotamian**

240

241 The continental mammals of the Mesopotamian assemblage come from the lower levels of the

242 Ituzaingó Formation, which crops out along the cliffs of the Paraná River in Corrientes and

243 Entre Ríos provinces, north-east Argentina (Figure 2). The vertebrate assemblage is rich and

244 includes fishes, crocodiles, birds and mammals (Cione et al., 2000; Brandoni and Noriega,

245 2013). It differs taxonomically from other associations in Argentina at the same latitudes and

246 this was explained by a southern extension of the northern realm (Cozzuol, 2006). The age of

247 the Mesopotamian assemblage has been largely debated (Cione et al 2000 and references

248 therein); it is currently assigned to the late Miocene, Huayquerian SALMA (Cione et al.,

249 2000) or also extended into the Chasicoan SALMA (Brandoni, 2013; Brunetto et al., 2013).

250 The dating of 9.47 Ma for the upper levels of the lower Paraná Formation (Pérez, 2013)

251 represents a maximum limit for the Mesopotamian assemblage.

252

253 **3.1.8 Cerro Azul**

254

255 Several localities in central east Argentina (La Pampa and Buenos Aires provinces) have

256 provided abundant fossil vertebrates from the Cerro Azul and Epecuén formations which are

257 considered geologically correlated (Goin et al., 2000). This assemblage includes reptiles, birds

258 and a rich mammal association. These units are assigned to the late Miocene, Huayquerian

259 SALMA (Goin et al., 2000; Montalvo et al., 2008; Verzi and Montalvo, 2008; Verzi et al.,

260 2011) on the basis of mammal biostratigraphy. This association is currently the most complete

261 list for this age (Goin et al., 2000). The possibility of extension into the late Pliocene cannot

262 be discarded for some localities assigned to the Cerro Azul Formation (Prevosti and Pardiñas,

263 2009).

264

265 **3.1.9 Chiquimil**

266

267 The Chiquimil Formation is exposed in north-west Argentina (Catamarca Province) and is

268 divided in three members. The Chiquimil A (Riggs and Patterson, 1939; Marshall and

269 Patterson, 1981) or El Jarillal Member (Herbst et al., 2000; Reguero and Candela, 2011)

270 provided a rich fossil record. The mammalian association has been assigned to the late

271 Miocene, Huayquerian SALMA (Reguero and Candela, 2011). A dating in the middle section

272 of the Chiquimil Formation indicated ~ 6.68 Ma (Marshall and Patterson, 1981).

273

274 **3.1.10 Andalhuala**

275

276 The Andalhuala Formation is exposed in the Santa María Valley in north-west Argentina

277 (Catamarca Province). This is a classical fossiliferous unit of the South American Neogene

278 with abundant and diverse fossil remains, including plants, invertebrates, and vertebrates

279 (Riggs and Patterson, 1939; Marshall and Patterson, 1981). Basal levels of the Andalhuala

280 Formation have been dated to ~ 7.14 Ma (Latorre et al., 1997) and ~ 6.02 Ma (Marshall and

281 Patterson, 1981) while a tuff sample close to the upper part of the sequence was dated to

282 ~3.53 Ma (Bossi et al., 1993). The mammal association has been referred to the

283 Montehermosan–Chapadmalalan SALMAs (Reguero and Candela, 2011).

284

285 **3.1.11 Monte Hermoso**

286

287 The Monte Hermoso Formation is exposed in the Atlantic coast at the south west of Buenos

288 Aires Province, Argentina. This unit has provided fishes, anurans, reptiles, birds, and a

289 diverse mammal association. Recent biostratigraphic and biochronological analyses

290 (Tomassini and Montalvo, 2013; Tomassini et al., 2013) have recognized a single biozone

291 (the *Eumysops laeviplicatus* Range Zone) in the Montehermosan Formation which is the base

292 for the Montehermosan SALMA. The Montehermosan was restricted to the early Pliocene

293 between <5.28 and 4.5/5.0 Ma by considering the dating of 5.28 Ma in levels with

294   Huayquerian mammals and paleomagnetic correlations in the upper Chapadmalal Formation

295   (Tomassini et al., 2013).

296

297   **3.1.12 Inchasi**

298

299   The locality of Inchasi is found in the eastern cordillera in the department of Potosí, Bolivia at

300   an elevation of about 3220 masl and ~19°S latitude (Figure 2). The mammal assemblage

301   includes 10 mammals, representing xenarthra, rodentia, and native ungulates (Litopterna and

302   Notoungulata) (Anaya and MacFadden, 1995). Paleomagnetic analysis indicates an age of

303   about 4–3.3 Ma. The analysis of the mammal association first suggested Montehermosan

304   and/or Chapadmalalan ages (MacFadden et al., 1993). A later revision (Cione and Tonni,

305   1996) correlated Inchasi with the Chapadmalalan, although probably older than the classical

306   Chapalmalalan sections at the Atlantic coast.

307

308   **3.1.13 Uquía**

309

310   The Uquía Formation crops out in the Quebrada de Humahuaca, Jujuy province, north

311   western Argentina at an elevation of ~2800 masl and ~23ºS latitude (Figure 2). The Uquía

312   Formation is divided in three units: the Lower Unit was assigned to the late Chapadmalalan,

313   the Middle Unit to the Marplatan (Vorhuean, Sanandresian), and the Upper Unit to the

314   Ensenadan (Reguero et al., 2007; Reguero and Candela, 2011).^{40}K -^{40}Ar data from a volcanic

315   tuff ("Dacitic tuff") in the Lower Unit provided ~3.0 Ma. Another tuff (U1) dated as 2.5 Ma is

316   the boundary between the Middle and Upper Unit. The geological and paleontological

317   evidence suggested that during the late Pliocene the area was a wide intermountain valley at

318   about 1700–1400 masl (Reguero et al., 2007).

319

320   **4. Results**

321

322   **4.1 Middle and late Miocene–Pliocene mammal faunas from SA**

323

324   In the NMDS analysis (stress value = 0.083), the analyzed South American localities are

325   primarily grouped by age and secondarily by geographic position (Figure 4A). The NMDS1

326   clearly separates middle Miocene, late Miocene and Pliocene localities and for the middle and

327   late Miocene assemblages, the NMDS2 separates tropical from temperate localities. For the

328   middle Miocene (Colloncuran, Laventan), the cluster analysis separates the tropical

329   assemblages of La Venta (~2.6°N paleolatitude) and Fitzcarrald (~12.5°S paleolatitude) from

330   the southern Collon Curá (~41.3°S paleolatitude) and Quebrada Honda (~22.3°S

331   paleolatitude). For the late Miocene (Huayquerian–Montehermosan), Urumaco (~10.9°N

332   paleolatitude) appears outside the groups formed by Acre (~10.5°S paleolatitude) and

333   Mesopotamian (~32.5°S paleolatitude), another cluster includes the Argentinean assemblages

334   of Andalhuala (~26.8°S paleolatitude), Chiquimil (~27.0°S paleolatitude), Cerro Azul

335   (~37.0°S paleolatitude), and Monte Hermoso (~38.9°S paleolatitude). Finally, the early

336   Pliocene (Chapadmalalan– Marplatan) temperate associations from Inchasi (~19.9°S

337   paleolatitude) and Uquía (~23.4°S paleolatitude) cluster together, although there are no

338   tropical assemblages to compare with. If we compare only faunal assemblages from the same

339   time period (middle Miocene, late Miocene and Pliocene), there is a positive relationship

340   between the Bray-Curtis dissimilarity and the distance of each pair of assemblages studied

341   (Figure 4B).

342

343   The Bray-Curtis dissimilarity values with resampling calculated for the tropical, temperate

344   and tropical vs. temperate assemblages for the middle and late Miocene shows that all the

345   assemblages are very different (Figure 4C). The Bray-Curtis dissimilarity between middle

346   Miocene tropical (La Venta and Fitzcarrald) and temperate (Quebrada Honda and Collon

347   Curá) assemblages compared to the dissimilarity between tropical vs temperate are found to

348   be statistically significant. Dissimilarity values of middle Miocene tropical (mean=0.830) are

349   lower than middle Miocene tropical vs temperate (mean=0.956) (Mann-Whitney U, p <2.2 e-

350   16); whereas middle Miocene temperate dissimilarity (mean=0.964) is higher than middle

351   Miocene tropical vs. temperate dissimilarity (Mann-Whitney U, p=<2.87e-15). For the late

352   Miocene, dissimilarity of tropical assemblages (Acre and Urumaco) is lower (mean=0.873)

353   than tropical vs temperate (mean=0.969) (Mann-Whitney U, p<2.2e-16). We also found

354   difference between temperate assemblages (Mesopotamian, Chiquimil, Andalhuala, Cerro

355   Azul, and Monte Hermoso; mean=0.899) and tropical vs. temperate dissimilarity (Mann

356   Whitney U, p<2.2e-16).

357

358   The number of PBDB collections was used to generate accumulation curves for the tropical

359   assemblage (Figure 5). Each collection represents a geographic and stratigraphic point where

360   the fossils have been found and provide a good proxy for sampling effort. We excluded from

361   the analysis the Acre collection with unknown stratigraphic provenance. The accumulation

362 curves show that generic richness for tropical assemblages is underestimated, even for the

363 better known assemblage of La Venta.

364

365 **4.2 Temporal and spatial distribution patterns of GABI**

366

367 The cumulative first appearance datum (FAD) of non-native taxa for both NA and SA

368 continents (Figure 6A, Supplementary Table 2) shows that first migrations are recorded in the

369 temperate region (cumulative FAD mean=2 by 10 Ma), represented by the ground sloths

370 *Thinobadistes* (Mylodontidae) and *Pliometanastes* (Megalonychidae) recorded at McGehee

371 Farm, Florida (Hirschfeld and Webb, 1968;Webb, 1989). During the late Miocene (12–5

372 Ma), the number of FAD is similar between the tropics (cumulative FAD mean = 6 by 5 Ma)

373 and temperate (cumulative FAD mean= 7 by 5 Ma). In the tropics, the oldest records of

374 migrants are those from the Acre region in Peru (Campbell Jr et al., 2010; Prothero et al.,

375 2014) of disputable age (Alberdi et al., 2004; Lucas and Alvarado, 2010; Lucas, 2013).

376 During the Pliocene (between 3 to 4 Ma) there is an increase in the number of FAD at higher

377 latitudes (cumulative FAD mean=21), but this is not recorded in the tropics (cumulative FAD

378 mean=9). Finally, during the Pleistocene (2–1 Ma) a higher number of FADs are recorded in

379 tropical and temperate regions. Most of the collections in the PBDB with records of land

380 mammals in the Americas are in the temperate region and are younger than 4 Ma (Figure 6B).

381

382 **5. Discussion**

383

384 **5.1. Middle and late Miocene–Pliocene mammal faunas from SA**

385

386 The NMDS1 shows that a strong temporal component establishes the dissimilarity

387 relationships among the faunas. In addition, an important influence of the geographic position

388 is reflected in the distribution of the faunas along the NMDS2 axis. There is a positive

389 relationship between the Bray-Curtis dissimilarity values and the distance between faunas

390 (Figure 4 A-B).

391

392 For the middle Miocene, Colloncuran–Laventan faunal associations, a differentiation between

393 the tropical assemblages of La Venta and Fitzcarrald, and the southern Quebrada Honda and

394 Collon Curá was observed (Figure 4A). The middle latitude fauna Quebrada Honda appears

395 unique, although it is closer to the slightly older and temperate Collon Curá than to the

396   contemporaneous tropical faunas of La Venta and Fitzcarrald (Croft, 2007; Tejada-Lara et al,

397   in press). The reconstructed paleoenvironment for the middle Miocene Monkey Beds

398   assemblage at La Venta considered an estimated annual rainfall between 1500 and 2000 mm

399   using diet, locomotion and body size indices of the mammal community (Kay and Madden,

400   1997a;b).

401

402   For the late Miocene assemblages, the NMDS indicates a high dissimilarity between the

403   tropical faunas of Urumaco and Acre. For the Urumaco mammal assemblage, xenarthrans and

404   rodents are the most conspicuous elements, but further studies on other clades promise to

405   document a higher diversity than currently recognized. The temperate assemblages of

406   Chiquimil, Andalhuala, Cerro Azul, and Monte Hermoso cluster together and the

407   Mesopotamian is between this group and Acre (Figure 4A).

408

409   After taking into account the differences in sample size, we found that the dissimilarity values

410   of tropical assemblages (mean=0.830 for middle Miocene, and mean=0.879 for late Miocene)

411   and late Miocene temperate assemblages (mean=0.899 for late Miocene) are lower than the

412   values for tropical vs. temperate assemblages (mean=0. 956 for middle Miocene and mean=0.

413   969 for late Miocene) (Figure 4C). Consequently, the Bray-Curtis dissimilarity between

414   faunas of the same age and biome is lower than between faunas of different biomes (tropical

415   vs. temperate); although, the mean dissimilarity values in all cases are high (> 0.8).

416

417   As shown by the accumulation curves (Figure 5), the generic richness of the tropical

418   assemblages studied are underestimated. A more comprehensive knowledge of tropical faunas

419   is needed to better understand the paleodiversity patterns and paleobiogeography in the new

420   world.

421

422   **5.2. Temporal and spatial distribution patterns of GABI**

423

424   The cumulative FAD across time of GABI participants in each continent shows that the GABI

425   was a gradual process that began in the late Miocene (~10 ma) (Figure 6A). The early phase

426   of GABI (pre GABI *sensu* Woodburne (2010)) is characterized by a small number of

427   migrants, with a mean cumulative FAD =6 between 4–5 Ma in the tropics and a cumulative

428   FAD=7 in the temperate region. The land connection between the two continents occurred at

429   the Isthmus of Panama, located within the tropical zone. Therefore, it would be expected that

13

430 the Neotropics record the earliest GABI immigrants, but older immigrants have been found at

431 higher latitudes.

432

433 The findings reported by Campbell and colleagues (Campbell Jr et al., 2010; Frailey and

434 Campbell, 2012; Prothero et al., 2014) in the Acre region of the Amazon basin, assigned to

435 late Miocene (~9 Ma) sediments would represent the oldest NA immigrants. However, the

436 dromomerycine artiodactyl, peccaries, tapirs, and gomphotheres have not been found in other

437 late Miocene localities in SA and these findings await further clarifications. In SA, the most

438 frequent pre-GABI elements are procyonids recorded in several late Miocene–Pliocene

439 (Huayquerian–Chapadmalalan) SA localities since ~7.3 Ma (Cione et al., 2007; Reguero and

440 Candela, 2011; Forasiepi et.al, 2014). The evidence of the fossil record combined with the

441 living species distribution suggests that much of the evolutionary history of procyonids

442 occurred in the Neotropics, possibly in SA (Eizirik, 2012). Molecular studies have predicted

443 that the diversification of the group occurred in the early Miocene (~20 Ma), with most of the

444 major genus-level lineages occurring in the Miocene (Koepfli et al. 2007, Eizirik et al. 2010;

445 Eizirik, 2012). This scenario requires a bias in the fossil record, claims an evolutionary history

446 for procyonids in SA that largely precedes the GABI, and suggests an arrival into SA long

447 before previously thought as for several other mammalian clades (Almendra and Rogers, 2012

448 and references therein).

449

450 Since 4 Ma, the number of FAD at higher latitudes rapidly increases and this trend continues

451 during the Pleistocene. In contrast, the number of FAD in the tropics remains low during the

452 Pliocene (cumulative FAD mean=9 by 2–3 Ma), but rapidly increases during the Pleistocene.

453 A large difference in the number of PBDB collections across time and latitude is observed for

454 land mammals for the last 12 Ma (Figure 6B). Most records come from higher latitudes and

455 are younger than 4 Ma, by the time the FAD increases; this suggest that temporal and

456 geographic patterns of GABI are influenced by the sampling bias towards high latitudes and

457 the higher number of Pliocene–Pleistocene records.

458

459 The migration of northern taxa into SA after the completion of the land bridge by ~3 Ma was

460 correlated with supposed expansion of savannas and grasslands in the Neotropics during

461 glacial periods (Webb, 1991; Webb 2006; Leigh et. al, 2013). The expansion of savannas

462 during glacial times has been questioned (Behling et al., 2010). If this is the case, the Andes

463 could have served as route of migration of northern taxa towards temperate environments in

464 SA (Webb, 1991), as NA taxa seem to have been more successful in temperate biomes

465 whereas SA taxa dominate in the tropics (Webb, 1991; Webb, 2006; Leigh et. al, 2014).

466

467 **6. Conclusions**

468

469 The dissimilarity analysis primarily grouped the faunal assemblages by age and secondarily

470 by geographic distribution. The dissimilarity values among the fossil faunal assemblages

471 analyzed support the differentiation between tropical and temperate assemblages in SA during

472 the middle Miocene (Colloncuran–Laventan) and late Miocene (Huayquerian–

473 Montehermosan). The mid-latitude, middle Miocene assemblage of Quebrada Honda has

474 higher affinities with the slightly older and temperate Collon Curá than with the tropical

475 assemblages of La Venta and Fitzcarrald. For the late Miocene, the temperate assemblages of

476 Chiquimil, Andalhuala, Cerro Azul, and Monte Hermoso cluster together, while the

477 Mesopotamian is between this group and the tropical assemblages of Acre and Urumaco.

478

479 The cumulative FAD across time and latitude shows that faunisitc movements related to

480 GABI began during the late Miocene (~10 Ma) with the oldest records found at higher

481 latitudes. The number of FAD remained relatively low until 4–5 Ma when FAD starts to

482 increase, peaking during the Pleistocene.

483

484 The study of paleodiversity patterns and paleobiogeography in the Americas is challenged by

485 the sampling bias towards higher latitudes and the still scarce data from tropical faunas. The

486 interpretation of the temporal and geographic patterns of GABI is likely influenced by these

487 sampling issues.

488

489 **Conflict of interest statement**

490

491 The authors declare that the research was conducted in the absence of any commercial or

492 financial relationships that could be construed as a potential conflict of interest.

493

494 **Author and contributors**

495

514

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845

846   Figure 1. Number of collections in the Paleobiology database (PBDB) across latitude for land
847   mammals in North America (gray boxes) and South America (white boxes) for each 1 ma
848   period in the last 12 ma. The boxplot shows the mean and standard deviation of the latitude of
849   the PBDB collections for each time interval.

850

851   Figure 2. Middle and late Miocene – Pliocene main fossil sites for land mammals in South
852   America. Triangles = middle Miocene; circles = late Miocene; squares = Pliocene.

853

854   Figure 3. Chronostratigraphy, South American Land Mammal Ages (SALMAs) and temporal
855   distribution of the faunal assemblages discussed in the text. Colloncuran:15.7 – 14 Ma
856   (Madden et al., 1997) Laventan: 13.5–11.8 Ma. (Madden et al., 1997); Mayoan: 11.8 – 10
857   Ma. (Flynn and Swisher III, 1995); Chasicoan: 10– ~8.5 (Flynn and Swisher III, 1995) ;
858   Huayquerian = ~8.5 – 5.28 Ma. (lower age following (Cione and Tonni, 2001;Reguero and
859   Candela, 2011) and upper age following (Tomassini et al., 2013); Montehermosan = 5.28 –
860   4.5/5.0 Ma. (Tomassini et al., 2013); Chapadmalalan = 4.5/5.0 –3.3 (Tomassini et al., 2013);
861   Marplatan = 3.3 – ~2.0 Ma (lower age following (Tomassini et al., 2013) and upper age
862   following (Cione and Tonni, 1999;Cione et al., 2007); Ensenadan = ~2.0 – <0.78(0.5?) Ma.
863   (Cione and Tonni, 1999;Cione et al., 2007); Bonaerian = <0.78(0.5?) – 0.13 Ma. (Cione and
864   Tonni, 1999); Lujanian =0.13–0.08 Ma (Cione and Tonni, 1999).

865

866   Figure 4. A, NMDS plot of the faunal associations using Bray-Curtis dissimilarity; triangles =
867   middle Miocene; circles = late Miocene; squares = Pliocene. The grey lines show the
868   clustering result. B, Bray-Curtis dissimilarity relationship with distance in km, between each
869   locality pair. We include only localities pairs which are within the same time interval (middle
870   Miocene, late Miocene, Pliocene), red= tropical-tropical pair; blue = temperate-temperate
871   pair; black = tropical–temperate pair. C, Density histograms of the Bray-Curtis dissimilarity
872   values among the different faunal associations analyzed for the middle and late Miocene,
873   red=only tropical faunas, blue= only temperate faunas, black= tropical vs. temperate faunas.

874

875   Figure 5. Accumulation curves estimated with random method for the tropical faunal
876   associations, shaded areas represent the 95% confidence interval.

877

878   Figure 6. A, Cumulative first appearance datum (FAD) of GABI participants in North and
879   South America for each million year since 12 Ma; red= FADs record in the tropics, blue=
880   FADs record in the temperate regions. Solid circles represent the mean and dashed lines the
881   standard deviation. B, Number of collections with records of land mammals in the
882   Paleobiology database (PBDB) for each million year since 12 Ma; red = collections in the
883   tropics, blue= collections in the temperate region.
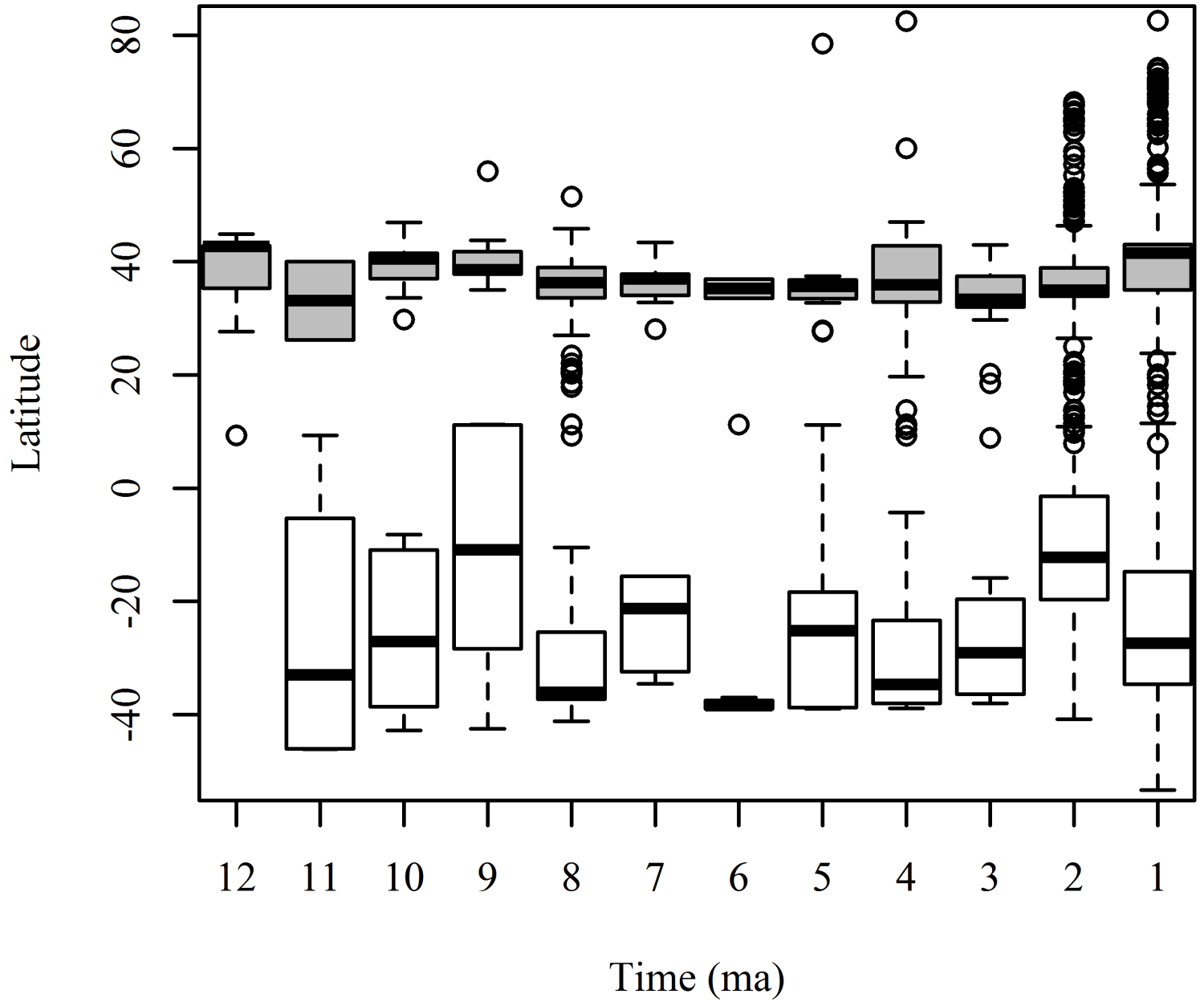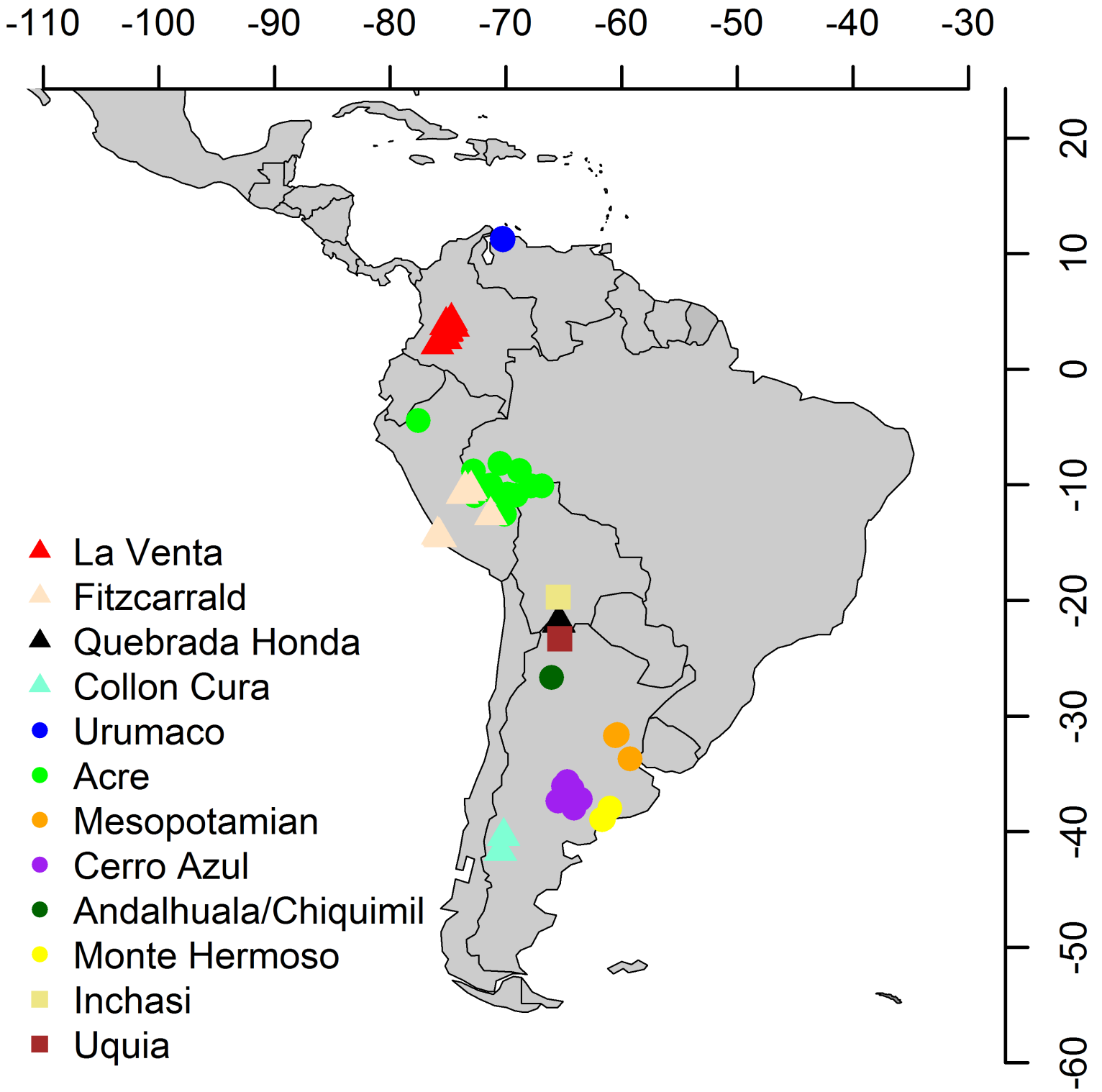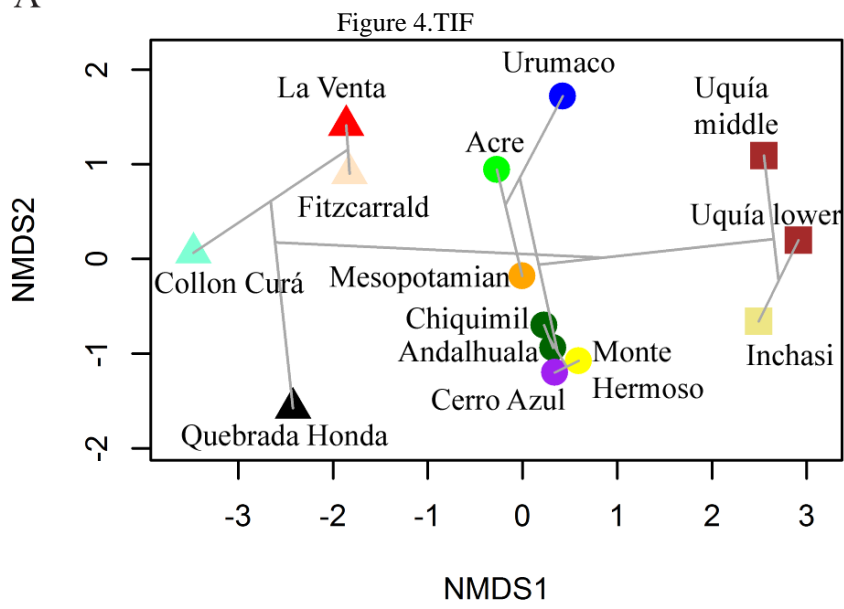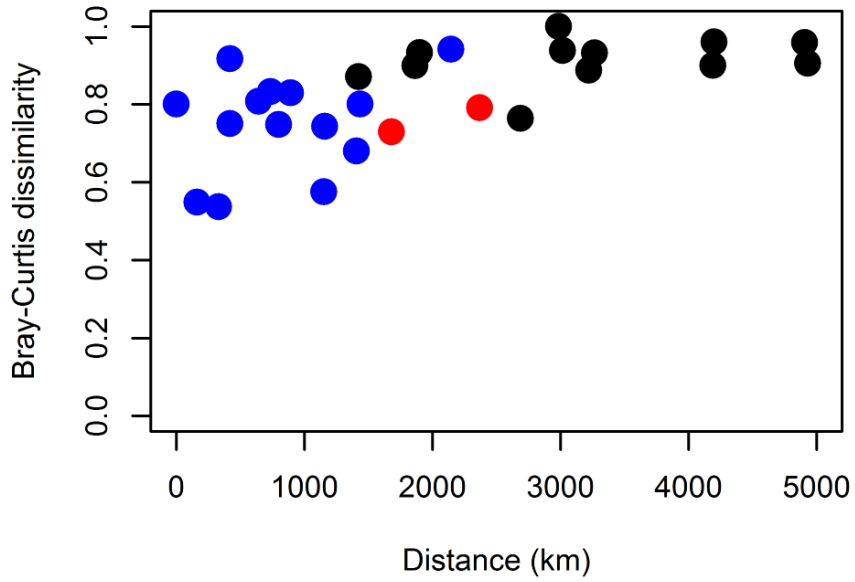
884

Figure 1.TIFF

Figure 2.TIFF

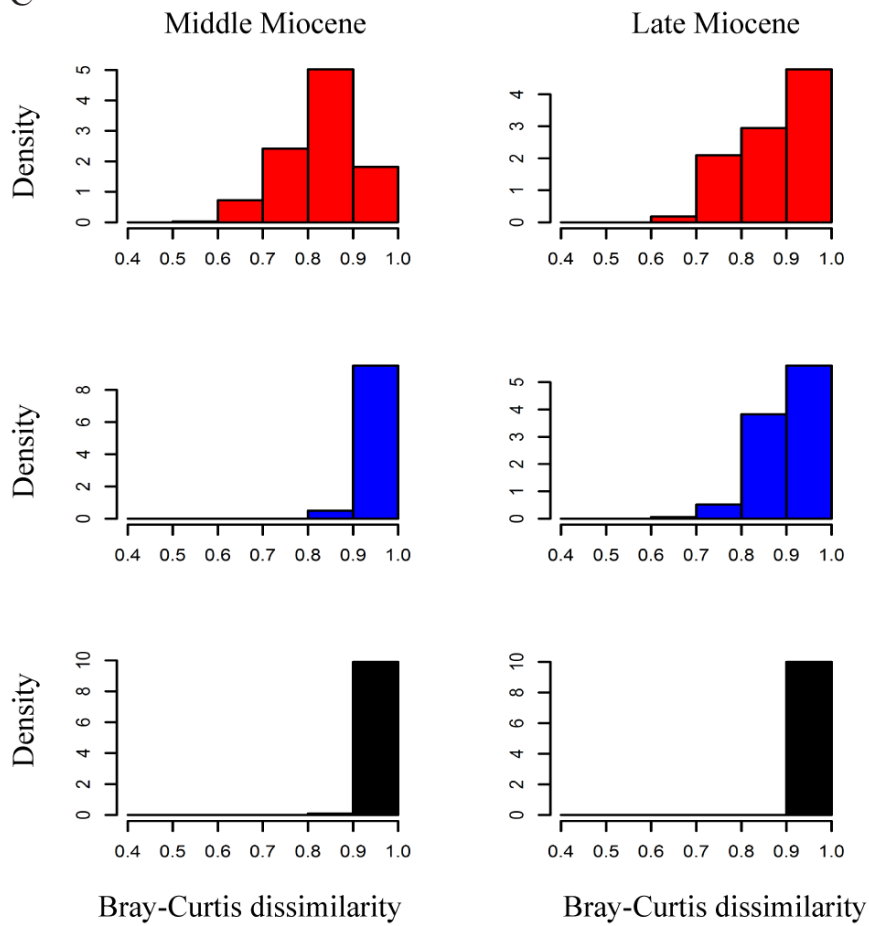| Ma	Period	Epoch	Stage/Age	SALMA	Faunal assemblages		
0.12	Quaternary	Pleistocene	Middle	Lujanian			
				Bonaerian			
0.5			Calabrian	Ensenadan			
1							
2						Uquía	
			Gelasian	Marplatan			
3	Neogene	Pliocene					
			Messinian	Chapadmalalan	Inchasi		
4							Urumaco - Cerro Azul - Andalhuala - Chiquimil
5				Monte hermosan	Monte Hermoso		
6				Huayquerian			
7						Acre	
8		Miocene	Tortonian				
9					Mesopotamian		
10				Chasicoan			
11				Mayoan			
12			Servallian	Laventan	La Venta Fitzcarrald Quebrada Honda		
13							
14			Langhian	Colloncuran	Collon Curá		
15							

Figure TS

Figure 5.TIFF

Figure 6.TIF