1 Ecological niches and their evolution among Neotropical manakins

2 (Aves: Pipridae)

3

4

5 **Marina Anciães[1] and A. Townsend Peterson**

6 Natural History Museum and Biodiversity Research Center, 1345 Jayhawk Blvd., University of

7 Kansas, Lawrence, KS 66045-7561 USA

8

9

10 Corresponding author:

11 Marina Anciães

12 [2] Coordenação de Pesquisa em Ecologia e Programa de Coleções e Acervos, Instituto Nacional

13 de Pesquisas da Amazônia (INPA), Av. André Araújo 2936, Aleixo, CEP 69060-001, Manaus –

14 AM, Brasil.

15 Email: marina.anciaes@gmail.com

16

17

18

19

20

21

---

[1] Research conducted in part at Peabody Museum of Natural History, Yale University, New Haven, CT.
[2] Current address.

22   Study of the evolution of ecological characteristics using phylogenetic information is only

23   beginning, but several new tools and approaches open fascinating possibilities. The Pipridae is a

24   diverse and well-known family of frugivorous birds that are easily sampled and that are broadly

25   distributed across many Neotropical environments, and as such are appropriate for studies of

26   ecological niche evolution. Using known occurrences and climate and topography data sets, we

27   modeled ecological niches for each species in the family, and carried out analyses aimed at

28   describing ecological niches of manakins and understanding historical patterns of ecological

29   change in the family. Most species' ecological niches were characterized by warm and relatively

30   humid conditions, reflecting the great diversification of the family in lowland and montane

31   forests of western South America. Ecological niche evolution was in general conservative, with

32   most sister species pairs being closely similar ecologically, indicating that isolation rather than

33   adaptation to new ecological conditions has dominated the diversification in this family.

34   Exceptions to this pattern represent interesting foci for future research, whereas studies of

35   ecological niches focusing on past distributions of manakins will allow further biogeographic

36   inferences.

37

38   *Key-words:* manakin, evolution, ecological niche, geographic distribution, speciation.

39

40

41

42

43

44

45   Ecological niches have long been the subject of intense interest in biogeography and evolution,

46   given their early formulation as the key tie between species' physiology and natural history and

47   their geographic potential (Grinnell 1917, Grinnell 1924). Although the concept of ecological

48   niches has itself evolved since its original formulation, with addition of consideration of species'

49   roles in ecological communities (Hutchinson 1957, MacArthur 1972), its usefulness in

50   understanding why species are where they are, and why they are not where they are not,

51   continues. Answering this question for sets of species provides a first-level view of the ecology

52   and history of distributional phenomena affecting the group (Soberón and Peterson 2005,

53   Soberón 2007).

54   Recent studies have focused on conservatism of ecological niche characteristics, asking

55   whether these features are evolutionary labile or not, over different evolutionary time periods

56   (e.g. Peterson et al. 1999, Prinzig et al. 2001, Webb et al. 2002, Losos et al. 2003, Rice et al.

57   2003, Graham et al. 2004, Knouft et al. 2006, Wiens et al. 2006, Wellenreuther et al. 2007). Most

58   of these studies do not consider biotic factors, such as competition or the role of species in

59   communities, in describing ecological niches of species, and thus are based on pioneering

60   concepts of ecological niches (review in Chase and Leibold 2003). At the shallowest level,

61   species invasions have been used to investigate whether the ecological 'niche' (at coarse spatial

62   scales) of a species depends on the community makeup in which they are distributed, with the

63   general result that they appear quite insensitive (Peterson 2003a). This result indicates that

64   abiotic factors are frequently suitable for describing ecological niches of species, and also

65   corroborates expectations from neutral theory concerning niche differentiation in ecological

66   communities (Hubbel 2001). Second, a few studies have assessed the predictivity between

67   present-day and Pleistocene geographic distributions (over time periods of 10^3-10^4 yr) and their

68 ecological characteristics, again concluding conservative niche evolution (Martínez-Meyer et al.

69 2004, Martínez-Meyer et al. 2006). Finally, studies comparing ecological niche characteristics

70 between sister species pairs, and deeper into phylogenetic history, have revealed ecological niche

71 conservatism over time periods of at least 10^4-10^6 yr, and breakdown of that conservatism over

72 longer time periods (Huntley et al. 1989, Martínez-Meyer 2002, Peterson et al. 1999, Rice et al.

73 2003). Overall, the picture is one of ecological niche conservatism over short-to-medium periods

74 of evolutionary time, coinciding with recent theoretical results (Holt and Gaines 1992, Holt and

75 Gomulkiewicz 1996, review in Wiens 2004) and providing a fascinating context for a predictive

76 understanding of ecological and geographic phenomena in biodiversity (Soberón and Peterson

77 2004, 2005, Wiens and Graham 2005). This result, nonetheless, is based on a relatively small

78 sample of studies, placing a premium on additional analyses addressing evolutionary

79 conservatism of ecological niche characteristics and consequences for speciation and

80 biogeography.

81   Tests of niche conservativism are also relevant to conservation questions, indicating areas

82 holding unique sets of species, both taxonomically and ecologically (Kremen et al. 2008). Such

83 studies are also important for assessing habitat suitability and risks for species reintroductions

84 (Martínez-Meyer et al. 2006), and of particular interest for understanding the adaptive potential

85 of species facing habitat change (Peterson 2003b, Anciães and Peterson 2006, Araújo et al. 2006,

86 Graham et al. 2006, Nunes et al. 2007, Seavy et al. 2008).

87   The manakins (Aves: Pipridae) are a diverse clade of small frugivorous birds distributed

88 across the Neotropics (Ridgely and Tudor 1994, Snow 2004). All told, the family includes ~45

89 species, depending on the taxonomic treatment followed, and several clades broadly distributed

90 across diverse habitats, including lowland rain forest, other lowland forests, and some montane

91   forests. Moreover, they are easily collected, and so are well-represented in collections, and a

92   molecular phylogeny is in the final stages of completion (S. Hackett, pers. comm.). As such,

93   manakins represent an ideal basis for examination of the evolutionary stability of ecological

94   niche characteristics over phylogenetic history, allowing insights into modes of speciation and

95   differentiation. This study aims to describe ecological niches of manakins, based on the coarse

96   grain abiotic characteristics of their geographic distributions; map their potential distributions;

97   and evaluate historical patterns of ecological change in the family. Additional studies, including

98   outlining the likely Pleistocene geography of the group, will complement these analyses

99   (Anciães and Peterson, in prep.).

100

101   **Methods**

102   *Input data.*— Ecological niche modeling (hereafter "ENM") requires two data inputs: occurrence

103   information for the species of interest, and electronic GIS coverages summarizing features of the

104   ecological landscape. For this study, occurrence information in the form of unique geographic

105   localities at which specimens of a particular species have been collected were accumulated from

106   data associated with natural history museum specimens for all manakin species and for 10

107   species in closely related families (genera *Neopelma*, *Neopipo*, *Piprites*, and *Tyranneutes*) for

108   comparison (Table 1). Records drawn from the literature and field observations complemented

109   the data set; lists of sources are available on request from the senior author.

110   We used 13 GIS layers to summarize aspects of the ecological landscape, including aspects

111   of topography (elevation, slope, aspect, topographic index; from the U.S. Geological Survey's

112   Hydro-1K data set, http://edcdaac.usgs.gov/gtopo30/hydro/, spatial resolution, 1 km^2) and

113   aspects of climate (annual means) including diurnal temperature range; precipitation; maximum,

114   minimum, and mean temperatures; solar radiation; wet days; frost frequency; and vapor pressure,

115   interpolated from weather station data from 1961-1990 and resampled to 30′ resolution (from the

116   Intergovernmental Panel on Climate Change, http://www.ipcc.ch/). All environmental data sets

117   were generalized to a final pixel resolution of 0.1 x 0.1°, or about 10 x 10 km, for an area

118   including all of tropical America (34° N to 40° S latitude).

119   *Ecological niche modeling.*— The ecological niche of a species can be defined as the

120   conjunction of ecological conditions within which it is able to maintain populations without

121   immigration (Grinnell 1917, Holt and Gaines 1992); as such, it is defined in multidimensional

122   ecological and environmental space (MacArthur 1972). Several approaches have been used to

123   approximate species' ecological niches (Nix 1986, Austin et al. 1990, Carpenter et al. 1993, Elith

124   et al. 2006); that which has seen broadest application to questions of ecological niche evolution

125   is the Genetic Algorithm for Rule-set Prediction (GARP), which includes several inferential

126   methods in an iterative optimization approach (Stockwell 1999, Stockwell and Noble 1992,

127   Stockwell and Peters 1999).

128   All modeling in this study was carried out on a desktop implementation of GARP (Pereira

129   2002). In GARP, available occurrence points are divided evenly into data sets for model building

130   (25% for model training and 25% for intrinsic testing and tuning of models) and extrinsic test

131   data sets (50%) for model evaluation. GARP is designed to work based on presence-only data;

132   absence information is included in the modeling via sampling of pseudo-absence points from the

133   set of pixels where the species has not been detected, and thus its probability of presence is

134   decidedly below unity. Models were generated through intrinsic data sets alone when sample

135   sizes were <20 known locality points. GARP works in an iterative process of rule selection,

136   evaluation, testing, and incorporation or rejection: first, a method is chosen from a set of

137   possibilities (e.g., logistic regression, bioclimatic rules), and then is applied to the training data

138   and a rule is developed. Rules may evolve by a number of means (e.g., truncation, point changes,

139   crossing-over among rules) to maximize predictivity. The accuracy of rules in predicting

140   intrinsic test points is evaluated for model refinement, based on 1250 points resampled from the

141   intrinsic test data and 1250 points sampled randomly from the study region as a whole, by

142   comparing the proportion of test points correctly predicted in relation to random expectations.

143   The change in predictive accuracy from one iteration to the next is used to evaluate whether a

144   particular rule should be incorporated into the model, and the algorithm runs either 1000

145   iterations or until convergence.

146   To optimize model quality, we developed 100 replicate models for each species, and selected

147   the 10 best models using a best-practices procedure for identifying optimal models (Anderson et

148   al. 2003). This procedure is based on the observation that (i) models vary in quality; (ii) variation

149   among models involves an inverse relationship between errors of omission (leaving out true

150   distributional area) and errors of commission (including areas not actually inhabited); and (iii)

151   best models (as judged by experts blind to error statistics) are clustered in a region of minimum

152   omission of independent test points and moderate commission error. Specifically, we used a soft

153   omission threshold, focusing on the extreme 20% of the distribution of omission values across

154   models. We then chose models presenting intermediate levels of commission (i.e., the central

155   50% of the commission index distribution). The 10 best models were summed in ArcView 3.2,

156   and we took as a best and most conservative distributional estimate the areas predicted present

157   by all of these models.

158   Because the focus of this study was on ecological niche characterization rather than on

159   distributional prediction, and given both the small sample sizes available and prior experience

160   with modeling such species in these regions (e.g., Peterson et al. 2002), we did not subset data

161   for independent model validations. We used the raw GARP output (i.e., maps of species'

162   *potential* distributions, rather than actual distributions) for estimating levels of interpredictivity

163   between species pairs (see below). For 8 species for which locality data were insufficient for

164   generating models accurately, known distributional limits were used in order to complete the

165   following analyses. This procedure likely did not biased the results considerably because of the

166   reduced known ranges of these species - which is believed to represent their regional rarity rather

167   than sampling effort – and the broad scale of the analyses. Finally, for a few analyses that

168   required species' actual distributions, and because species are often prevented from inhabiting

169   the entire spatial extent of their appropriate ecological niche conditions by barriers to dispersal or

170   the presence of competitors, we reduced the raw maps to those areas within or contiguous to

171   known distributional limits (Hellmayr 1924, Peters 1931, Hilty and Brown 1986, Sick 1993,

172   Ridgely and Tudor 1994, Ridgely and Greenfield 2001, Hilty 2003).

173   *Analyses*.— The overall diversity of manakins was estimated by summing final distributional

174   models (i.e., *actual* distributional estimates) across all species. We divided the study region into

175   6 ecoregions, based on known distributional limits of the main biomes and biogeographic regions

176   in the Neotropics (Amazon, Andes, Guianas, Atlantic Forest, Central America - Chocó,

177   Cerrado), and estimated numbers of species predicted to occur in each region based on presences

178   and absences in the final distributional models. To control for area effects, we standardized

179   numbers of species by the total area of each region.

180   To visualize niches of species in ecological space, we used the COMBINE option of the Grid

181   Tools extension of ArcView 3.2 to identify all unique environmental combinations across the

182   region (i.e., unique combinations of values of the environmental variables). Variables were *z*-

183   standardized (mean = 0, s.d. = 1) by subtracting the mean and dividing by the standard deviation.

184   Centroids of ecological niches of species were estimated as the multivariate means of variables

185   across all pixels predicted present for a given species. Niche breadth of each species was

186   estimated as the number of unique environmental combinations in its modeled distribution.

187   Unique environmental combinations and centroids of ecological niches were estimated in a 4-

188   dimensional space, given computational limitations and previous knowledge about the relevance

189   of selected variables (mean temperature, precipitation, wet days, and topographic index) to

190   distributions of Neotropical birds (e.g. Peterson et al. 2002). We estimated proportional

191   occupancy of potential distributions as the proportion of the entire spatial extent of appropriate

192   ecological niche conditions (i.e., potential distribution) that was likely inhabited (i.e., actual

193   distribution).

194   Similarity or difference of ecological niches among species was measured in two ways,

195   following Martínez-Meyer (2002). (1) We used pairwise Euclidean distances between centroids

196   of ecological niches, given by: $D = \sqrt{\sum(v_{iA}-v_{iB})^2}$, where v_{iA} is the mean of the ith variable within

197   the distribution of species A, and likewise v_{iB} for species B. (2) We also measured ecological

198   similarity via interpredictivity between the model for one species and the distribution for the

199   other (Peterson et al. 1999). Here, we overlaid the potential distribution estimates for a particular

200   species on the occurrence points of another species, and interpredictivity was measured as the

201   proportion of points successfully predicted. We tested for spatial autocorrelation effects on

202   ecological similarity among taxa by calculating geographic centroids of species' predicted

203   distributions using the Centroid option in ArcGis 8.0, and computing pairwise Euclidean

204   distances between distributions of species in geographic space. Associations between pairwise

205   ecological and geographic distances were tested using Mantel's tests within major clades in the

206   family.

207   To provide a view of the phylogenetic history of the family, we used a molecular phylogeny

208   based on 1067 bp of the mitochondrial cytochrome *b*, ND2 and ND3 genes, kindly provided by

209   S. Hackett (unpubl. data). Using this historical framework, we overlaid pairwise ecological

210   distance measures on the tree topology using the Fitch optimization option in PHYLIP

211   (http://evolution.gs.washington.edu/phylip.html). The result was a diagram summarizing

212   ecological change along each evolutionary lineage, assuming that the topology is correct (Rice et

213   al. 2003). Considering the similarity between the two measures of ecological distance (Martínez-

214   Meyer 2002, Rice et al. 2003, this study), we used only the Euclidean distances between

215   centroids in ecological space in this analysis.

216

217   **Results**

218   Our survey of natural history museum collections and other data sources regarding species'

219   occurrences resulted in 2045 unique locality records for 47 manakin species and 10 outgroup

220   species. Ecological niches varied among species in spatial extent from ~15,000 km^2 (*Corapipo*

221   *heteroleuca, Manacus milleri*) up to ~5,000,000 km^2 (*M. manacus, Dixiphia pipra, Chiroxiphia*

222   *pareola*). Ecological niches varied in breadth from 13 combinations (*Corapipo heteroleuca*) up

223   to ~5000 environmental combinations (*M. manacus*; Table 1).

224   As a whole, manakin species were predicted to be distributed across about two-thirds of the

225   Neotropics, with up to 18 species predicted to occur (potentially) in sympatry (note that the

226   coarse grain in our analysis admits some spatial and ecological diversity into the definition of

227   'sympatry'). Areas of highest expected species diversity (e.g., ≥13 species) were in the Amazon

228   Basin and Guianan Shield (Fig. 1), particularly from the Rio Negro and Rio Amazonas north to

229   the Guianas, and from the Rio Tapajós and Rio Madeira south along the slopes of the Peruvian

230   Andes in the west. Regional diversity calculations yielded similar results: the Amazon presented

231   highest regional diversity (32 species, 68% predicted to be present); on a per-area basis,

232   however, regions such as the Andes, Central America, and Guianan Shield were emphasized.

233   The Atlantic Forest and the Cerrado had low species:area ratios. Overall, our results point clearly

234   to a northwestern center of diversity in the Neotropics, with fewer species inhabiting forested

235   environments farther to the east.

236   Visualizing these predicted geographic distributions in ecological dimensions (Fig. 2)

237   revealed that manakin species generally have ecological niches characterized by high

238   temperature and precipitation, although a few species occur under cooler or more arid conditions.

239   In extreme cases, species occupy cold dry areas in the southern Andes (*Chiroxiphia boliviana*),

240   and hot humid areas of the western Amazon and Choco (e.g. *Heterocercus aurantiivertex*,

241   *Manacus vittellinus*). Arid open areas are mostly unoccupied by manakins.

242   Most species had relatively small geographic distributional areas. In general, niche breadth

243   and distributional area were closely and positively related ($r^2 = 0.986$; Fig. 3). Species inhabited

244   on average $39 \pm 26\%$ (range 2–90%) of their potential distributions, and only one-third of species

245   inhabited >50% of their potential distributions.

246   In general, sister species pairs were separated by smaller distances in ecological space than

247   non-sister species within or among major clades in the family (Fig. 4). Interpredictivity-based

248   approaches to measuring ecological similarity and distance yielded a similar picture—

249   interpredictivity was higher among sister species pairs than among non-sister taxa. *Lepidothrix*,

250   for example, shows similar niches among sister species (*L. iris* and *L. nattereri*), but

251   differentiation from close relatives above the sister species level; *Corapipo-Masius*, on the other

252   hand, shows broader niche conservativism, including above sister species to include much of

253   *Corapipo* (Fig. 5). These findings indicate niche conservativism among closely related species;

254   ecological niche characteristics among more distantly related species are often more divergent.

255   Ecological similarity measured by Euclidean and interpredictivity distances provided similar

256   results, but the interpredictivity measures are bounded, so we used Euclidean distances in the

257   remainder of our analyses (Martínez-Meyer 2002).

258   Pairwise ecological similarity between species was significantly related to geographic

259   proximity (Mantel's $r = 0.293$; $t = 4.144$; $P = 0.004$). Results were different, however, across

260   species within genera—here, in most cases, ecological similarity was not related to geographic

261   distances between species' range centroids (Table 2). Hence, within clades, levels of niche

262   similarity are not a function of geographic proximity, but of niche conservativism over time.

263   Phylogenetic reconstructions of change in ecological parameters show relatively little

264   variation in total amount of evolutionary change reconstructed along different lineages (Fig. 6).

265   That is to say, most manakin lineages show similar overall total differentiation from the manakin

266   ancestor, which suggests that evolution of ecological niche characteristics is not wildly variable

267   over evolutionary time periods. The few long branches observed—most notably *Chiroxiphia*

268   *boliviana*—appear to represent taxa reinvading higher-elevation, cooler climates from the hot

269   and humid lowlands characteristic of the genus (Fig. 2). Most sister species pairs again were

270   closely similar (e.g., *Manacus candei* and *M. aurantiacus*, *Corapipo altera* and *C. leucorrhoa*)—

271   on the other hand, some pairs showed substantial ecological distances (e.g., *Pipra chloromeros*

272   and *P. rubrocapilla*, *Machaeropterus regulus* and *M. striolatus*, *Chiroxiphia lanceolata* and *C.*

273   *linearis*).

274

Discussion

276   Ecological niches of most manakin species are characterized by warm and humid climates,

277   typical of lowland forests in the Neotropics. Although greatest diversity was predicted in the

278   Amazon Basin, some montane forests also presented high diversity, particularly on a per-area

279   basis. The full geographic extent of species' potential distributions, however, was only partially

280   occupied in most species, suggesting that manakin distributions are frequently constrained by

281   barriers to dispersal, or possibly by competitors. Although barriers to dispersal and interespecific

282   competition represent two distinct processes, acting on different time scales and with different

283   predictions regarding adaptation to local environments, both may explain absence of a species

284   from otherwise suitable areas. Additional studies would provide interesting tests for the role of

285   competitive exclusion, as well as other interactions (e.g., Anderson et al. 2002), in limiting

286   species' distributions and circumscribing ecological niches within manakins. Absence of species

287   from parts of their predicted ranges is unlikely to be explained by human-driven habitat change:.

288   in the first place, many manakins are reasonably tolerant of fine-scale habitat degradation (e.g.,

289   secondary forests and fragmentation), and in the second place, the coarse resolution of the

290   climate parameters used in this study largely ignore human-driven change.

291   ENMs are well-documented to demonstrate excellent predictivity of species' distributions

292   (Panetta and Dodd 1987, Hoffmann 2001, Peterson et al. 2002, Nakazawa et al. 2004, Graham et

293   al. 2004, Soberón and Peterson 2005, Araújo et al. 2006, Elith et al. 2006). Ecological niche

294   models did show areas of overprediction that resulted from the large region considered in this

295   analysis, which includes considerable historical and geographic heterogeneity—as such, this

296   overprediction does not represent low predictive power (Peterson et al. 2007). Overpredictions

297   occur when suitable conditions exist in regions not occupied by a species because of interactions

298   with other species (e.g. Anderson et al. 2002) or because of barriers that prevent colonization

299   (Brown and Lomolino 1998, Patterson 1999, Peterson et al. 1999).

300   The comparative approach used here required a large, inclusive region for model

301   development for all species, as models had to be developed based on the same environmental

302   data. The geographic heterogeneity of this broad region made it necessary to trim species'

303   potential distributions to be able to estimate their *actual* distributions. ENM estimates of

304   potential distributions are roughly equivalent to fundamental niches (sensu Hutchinson 1957),

305   except for consideration of geographic and historical factors as well (Soberón and Peterson

306   2005). The 'overpredictions' that are the difference between potential and actual distributions

307   (Anderson et al. 2003, Phillips et al. 2006) actually make possible synthetic evolutionary and

308   ecological applications (Peterson et al. 1999, Peterson and Vieglais 2001, Anderson et al. 2002,

309   Peterson et al. 2007). Considering overall niche similarity among closely related manakins, for

310   example, and predictivity of parapatric distributions between closely related species within the

311   Amazon Basin (Haffer 1974), low occupancy of potential distributions suggests that rivers

312   represent barriers to dispersal that may be involved in the speaciation process (Wallace 1852,

313   Haffer 1992). Wiens (2004) discussed the idea that ecological similarity is expected to be

314   frequent across barriers to dispersal among closely-related taxa. Nevertheless, studies of

315   ecological niches focusing on narrower geographic scales and conducted on a per species basis,

316   or species complexes, will be able to depict more accurately the level of ecological similarity

317   among closely related taxa, which was not within the scope of this study.

318   Ecological similarity as measured by Euclidean and interpredictivity distances provided

319   similar results. However, as others have noted (Martínez-Meyer 2002), interpredictivity

320   measures are bounded, so we used Euclidean distances principally in describing ecological

321   niches. Interpredictivity measures may fail to characterize ecological distances accurately when

322   differences are in only one or a few dimensions (Rice et al. 2003), which may explain some of

323   the disagreements in results between the two distance measures (Martínez-Meyer 2002, Rice et

324   al. 2003, Nakazawa et al. 2004). Species predicted to inhabit larger distributional areas also had

325   broader ecological niches, indicating area effects on environmental heterogeneity used by

326   manakins. Although this result could be indicative of reduced vulnerability to habitat alteration

327   by more generalist manakins species, these species are found mainly in lowland forests, and so

328   likely face higher rate of area loss than species with more restricted ranges, typically found in

329   montane forests (Anciães and Peterson 2006). Further, the weak associations between ecological

330   similarity and geographic proximity indicate that ecological characteristics of species in such

331   areas were potentially constrained by phylogeny. Hence, although the overall pattern is of a

332   positive ecology-geography relationship, the most relevant relationships—those *within* genera—

333   are generally not significant and are not strongly positive, suggesting that ecological similarity

334   among species is not simply a consequence of geographic proximity.

335   Our findings indicate niche conservativism in general among closely related manakins

336   species. Levels of niche similarity among sister taxa observed here suggest that ecological

337   diversification accompanies speciation events only infrequently, and therefore that species

338   diverged in allopatry without adaptation to new environments being evoked. This result is

339   consistent with theoretical results that suggest that ecological innovation should be relatively rare

340   (Holt and Gaines 1992, Holt and Gomulkiewicz 1996, Wiens 2004). These findings are similar

341   to those from other studies (Peterson et al. 1999, Prinzig et al. 2001, Webb et al. 2002, Martínez-

342   Meyer 2004, Wiens et al. 2006), whereas other studies have indicated niche plasticity (Johnson

343   and Cicero 2002, Rice et al. 2003, Losos et al. 2003, Graham et al. 2004, Kruft et al. 2006,

344   Wellenreuther et al. 2007), suggesting variation among taxonomic groups and across

345   phylogenetic scales in the relative importance of ecological diversification over evolutionary

346   time. A relevant point is that the null hypothesis tested herein is whether niches are more similar

347   than would be expected by chance (rather than whether they are identical; Warren et al. 2008),

348   which also explains some of the contrast in results.

349   The directionality of change in ecological space occupied by manakins during their

350   evolutionary history is of particular interest, as it can inform about general evolutionary

351   tendencies in the family. The instances of fast ecological change observed herein suggest that

352   new ecological potential may occasionally arise, which may in turn open opportunities for

353   invasion of new geographic ranges. Clearly, more studies of taxonomic divergence (speciation)

354   as it relates to ecological differentiation are needed, as evidence exists for both niche

355   conservativism and rapid differentiation (Peterson and Holt 2003).

356   Although the preliminary nature of the phylogenetic topology (S. Hackett, pers. comm.) in

357   Figure 6 limits our inferences, evidence from morphological and molecular data supports most

358   inter- and intra-clade relationships presented (Lanyon 1985, Prum 1990, 1992, Brumfield and

359   Braun 2001, Snow 2004, Cheviron et al. 2005, 2006, Rêgo et al. 2007). Therefore, we expect

360   error from mistaken taxonomic affinities to be minor, specially considering that results present

361   higher niche conservativism for cases of closest taxonomic relationships – those best known to

362   date.

363   Estimating times of divergence among lineages is difficult, as it demands accuracy of a

364   molecular clock and measuring variation in rates of evolution among lineages, genetic markers,

365   and time periods. In the present case, the challenge is even greater, as we did not have branch-

366   length information available to us regarding the manakins—as such, we present ecological

367   characters on the simple branching topology for the family, and are unable to calculate rates of

368   change per unit of real time. Nevertheless, our results indicate conservativism of ecological

369   niches over long evolutionary time periods, among manakin species. Estimating age of manakin

370   species will allow analyses addressing variation in rates of ecological change among lineages

371   and across time.

372   This study is intended as a first pass of analyses of ecological niche evolution in manakins,

373   and as such leaves many details untapped. Among outstanding issues, larger sample sizes of

374   occurrence localities are needed for some key clades (e.g., *Machaeropterus*) to allow more

375   rigorous modeling and testing of model accuracy. We are extending this work via projecting

376   models back onto Pleistocene climates to reconstruct past potential distributions and test

377   biogeographic hypotheses (Bonaccorso et al. 2006, Peterson and Nyári 2008), and via comparing

378   ecological niches of populations within species to investigate exceptions to the general picture of

379   conservative ecological change observed here. Applications of these results are relevant to

380   conservation and management plans: for example, projecting models onto future climates has

381   indicated that manakin species inhabiting flatland areas will be under increasing threat by

382   climate change predicted for the coming decades, whereas montane species will be a

383   conservation concern more owing to deforestation ongoing in these habitats (Anciães and

384   Peterson 2006). Additional work remains, but this paper presents basic results—demonstrating

385   general ecological conservatism in the manakins over their evolutionary history.

386

402

403   References

404   Anciães, M. and Peterson, A. T. 2006. Climate change effects on Neotropical manakin diversity

405   based on ecological niche modeling. – Condor 108: 778–791.

406   Anderson, R. P., Gómez–Laverde, M. and Peterson, A. T. 2002. Geographical distributions of

407   spiny pocket mice in South America: Insights from predictive models. – Glob. Ecol.

408   Biogeogr. 11: 131–141.

409   Anderson, R. P., Peterson, A. T. and Gómez-Laverde, M. 2002. Using niche-based GIS

410   modeling to test geographic predictions of competitive exclusion and competitive release in

411   South American pocket mice. - Oikos 98: 3-16.

412   Anderson, R. P., Lew, D. and Peterson, A. T. 2003. Evaluating predictive models of species'

413   distributions: Criteria for selecting optimal models. – Ecol. Model. 162: 211–232.

414   Araújo, M. B., Thuiller, W. and Pearson R. G. 2006. Climate warming and the decline of

415   amphibians and reptiles in Europe. – J. Biogeogr. 33: 1712-1728.

416   Austin, M. P., Nicholls, A. O. and Margules, C. R. 1990. Measurement of the realized qualitative

417   niche: environmental niches of five *Eucalyptus* species. – Ecol. Monogr. 60: 161–177.

418   Bonaccorso, E., Koch, I. and Peterson, A. T. 2006. Pleistocene fragmentation of Amazon

419   species' ranges. – Diver. Distrib. 12: 157–164.

420   Brumfield, R. T. and Braun, M. J. 2001. Phylogenetic relationships in Bearded Manakins

421   (Pipridae: *Manacus*) indicate that male plumage color is a misleading taxonomic character. -

422   Condor 103: 248-258.

423   Carpenter, G., Gillison, A. N. and Winter, J. 1993. DOMAIN: A flexible modeling procedure for

424   mapping potential distributions of animals and plants. – Biodiv. Conserv. 2: 667–680.

425   Chase, J. M. and Leibold, M. A. 2003. Ecological Niches: Linking Classical and Contemporary

426   Approaches, University of Chicago Press, Chicago, IL.

427   Cheviron, Z. A., Hackett, S. J. and Capparella, A. P. 2005. Complex evolutionary history of a

428   Neotropical lowland forest bird (*Lepidothrix coronata*) and its implications for historical

429   hypotheses of the origin of Neotropical avian diversity. - Mol. Phyl. Evol. 36: 338-357.

430   Cheviron, Z. A., Hackett, S. J. and Brumfield, R. T. 2006. Sequence variation in the coding

431   region of the melanocortin-1 receptor gene (MC1R) is not associated with plumage variation

432   in the blue-crowned manakin (*Lepidothrix coronata*). - Proc. R. Soc. Lon. B 273: 1613-1618.

433   Elith, J., Graham, C. H. anderson, R. P., Dudı´k, M., Ferrier, S., Guisan, A., Hijmans, R. J.,

434   Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A.

435   Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. McC., Peterson, A. T.,

436   Phillips, S. J., Richardson, K., Scachetti–Pereira, R., Schapire, R. E., Soberón, J., Williams,

437   S., Wisz, M. S. and Zimmermann, N. E. 2006. Novel methods improve prediction of

438   species'distributions from occurrence data. – Ecography 29: 129–151.

439   Graham, C. H., Ron, S. R., Santos, J. C., Schneider, C. J. and Moritz, C. 2004. Integrating

440   phylogenetics and environmental niche models to explore speciation mechanisms in

441   dendrobatid frogs. – Evolution 58: 1781–1793.

442   Graham, C. H., Moritz, C. and Williams, S. E. 2006. Habitat history improves prediction of

443   biodiversity in rainforest fauna. Proc. Natl. A. Sci. 103: 632-636.

444   Grinnell, J. 1917. Field tests of theories concerning distributional control. – Am. Nat. 51: 115–

445   128.

446   Grinnell, J. 1924. Geography and evolution. – Ecology 5: 225–229.

447   Haffer, J. 1974. Avian speciation in tropical South America. – Nut. Orn. Club, Cambridge, MA.

448   Haffer, J. 1992. On the "river effect" in some forest birds of southern Amazonia. – Bol. Mus. P.

449   E. Goeldi S. Zool. 8: 217–245.

450   Hellmayr, C. E. 1924. Catalogue of birds of the Americas. – Field Mus. Nat. Hist. Publ. Zool. 6.

451   Hilty, S. L. 2003. Birds of Venezuela. Princeton University Press, Princeton, NJ.

452   Hilty, S. L. and Brown, W. L. 1986. A guide to the birds of Colombia. Princeton University

453   Press, Princeton, NJ.

454   Hoffmann, M. H. 2001. The distribution of *Senecio vulgaris*: capacity of climatic range models

455   for predicting adventitious ranges. – Flora 196:395–403.

456   Holt, R. D. and Gaines, M. S. 1992. Analysis of adaptation in heterogeneous landscapes:

457   implications for the evolution of fundamental niches. – Evol. Ecol. 6: 433–447.

458   Holt, R. D. and Gomulkiewicz, R. 1997. The evolution of species' niches: a population dynamic

459   perspective. Pages 25–50 in H. G. Othmer, F. R. Adler, M. A. Lewis and J. C. Dallon, eds.

460   Case studies in mathematical modeling: ecology, physiology and cell biology. Prentice–Hall,

461   Saddle River, N.J.

462   Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton

463   University Press, Princeton, NJ

464   Huntley, B., Bartlein, P. J. and Prentice, I. C. 1989. Climatic control of the distribution and

465   abundance of beech (*Fagus* L.) in Europe and North America. – J. Biogeogr. 16: 551–560.

466   Hutchinson, G. E. 1957. Concluding remarks. – Cold Spr. Harb. Symp. Quant. Biol. 22: 415–

467   427.

468   Johnson, N. K. and Cicero, C. 2002. The role of ecologic diversification in sibling speciation of

469   *Empidonax* flycatchers (Tyrannidae): multigene evidence from mtDNA. – Mol. Ecol. 11:

470   2065–2081.

471   Knouft, J. H., Losos, J. B., Glor, R. E. and Kolbe J. J. 2006. Phylogenetic analysis of the

472   evolution of the niche in lizards of the *Anolis sagrei* group. – Ecology 87:S29–S38.

473   Kremen, C., Cameron, A., Moilanen, A., Phillips, S. J., Thomas, C. D., Beentje, H., Dransfield,

474   J., Fisher, B. L., Glaw, F., Good, T. C. Harper, G. J., Hijmans, R. J., Lees, D. C., Louis Jr.,

475   E., Nussbaum, R. A., Raxworthy, C. J., Razafimpahanana, A. Schatz, G. E., Vences, M.,

476   Vieites, D. R., Wright, P. C., Zjhra M. L. 2008. Aligning conservation priorities across taxa

477   in Madagascar with high-resolution planning tools. – Science 320: 222-225.

478   Lanyon, S. M. 1985. Molecular perspective on higher-level relationships in the Tyrannidae

479   (Aves). - Syst. Zool. 34: 404-418.

480   Losos, J. B., Leal, M., Glor, R. E., de Queiroz, K., Hertz, P. E., Schettino, L. R., Lara, A. C.,

481   Jackman, T. R. and Larson, A. 2003. Niche lability in the evolution of a Caribbean lizard

482   community. – Nature 424: 542–545.

483   MacArthur, R. 1972. Geographical Ecology. Princeton University Press, Princeton, N.J.

484   Martínez–Meyer, E. 2002. Evolutionary Trends in Ecological Niches of Species. Ph.D.

485   dissertation, University of Kansas, Lawrence, Kansas.

486   Martínez–Meyer, E., Peterson, A. T. and Hargrove, W. W. 2004. Ecological niches as stable

487   distributional constraints on mammal species, with implications for Pleistocene extinctions

488   and climate change projections for biodiversity. – Glob. Ecol. Biogeogr. 13: 305–314.

489   Martínez-Meyers, E., Peterson, A. T., Sevín, J. I. and Kiff, L. F. 2006. Ecological niche

490   modeling and prioritizing areas for species reintroductions. – Oryx 40: 411-418.

491   Nakazawa, Y., Peterson, A. T., Martínez–Meyer, E. and Navarro–Sigüenza, A. G.. 2004.

492   Seasonal niches of Nearctic–Neotropical migratory birds: implications for the evolution of

493   migration. – Auk 121: 610–618.

494   Nix, H. A. 1986. A biogeographic analysis of Australian elapid snakes. Pages 4–15 in Atlas of

495   elapid snakes of Australia (R. Longmore, Ed.). Australian Government Publishing Service,

496   Canberra.

497   Nunes, M. F. C., Galetti, M., Marsden, S., Scachetti-Pereira, R. and Peterson, A. T. 2007. Are

498   large-scale distributional shifts of the blue-winged macaw (*Primolius maracana*) related to

499   climate change? J. Biogeogr. 34: 816-827.

500   Panetta, F. D. and Dodd, J. 1987. Bioclimatic prediction of the potential distribution of skeleton

501   weed *Chondrilla juncea* L. in western Australia. – J. Austr. Inst. Agr. Sci. 53:11–16.

502   Patterson, B. D. 1999. Contingency and determinism in mammalian biogeography: the role of

503   history. – J. Mamm. 80: 345–360.

504   Peters, J. L. 1931. Checklist of Birds of the World. Harvard University Press. Vol. 9.

505   Peterson, A. T. 2003a. Predicting the geography of species' invasions via ecological niche

506   modeling. – Q. Rev. Biol. 78: 419–433.

507   Peterson, A. T. 2003b. Projected climate change effects on Rocky Mountain and Great Plains

508   birds: generalities of biodiversity consequences. – Glob. Chang. Biol. 9: 47-655.

509   Peterson, A. T., Ball, L. G. and Cohoon, K. C. 2002. Predicting distributions of Mexican birds

510   using ecological niche modelling methods. – Ibis 144: e27–e32.

511   Peterson, A. T. and Nyari, A. S. 2008. Ecological niche conservatism and Pleistocene Refugia in

512   the Thrush–like Mourner, *Schiffornis* sp., in the Neotropics. – Evolution 62: 173–183.

513   Peterson, A. T., Papeş, M. and Eaton, M. 2007. Transferability and model evaluation in

514   ecological niche modeling: A comparison of GARP and Maxent. – Ecography 30: 550–560.

515   Peterson, A. T., Soberón, J. and Sánchez–Cordero, V. 1999. Conservatism of ecological niches

516   in evolutionary time. – Science 285: 1265–1267.

517   Prum, R. O. 1990. Phylogenetic analysis of the evolution of display behavior in the Neotropical

518   manakins (Aves: Pipridae). - Ethology 84: 202-231.

519   Prum, R. O. 1992. Syringeal morphology, phylogeny, and evolution of the Neotropical manakins

520   (Aves: Pipridae). - Am. Mus. Nat. Hist. Novit. 3043: 1-65.

521   Phillips, S. J. Anderson, R. P. and Schapire, R. E. 2006. Maximun entropy modeling of species

522   geographical distributions. – Ecol. Model. 190: 231–259.

523   Prinzig, A., Durka, W., Klotz, S. and Brandl, F. 2001. The niche of higher plants: evidence for

524   phylogenetic conservativism. – Proc. R. Soc. Lond. B 268: 2383–2389.

525   Rêgo, P. S., Araripe, J., Marceliano, M. L.V., Sampaio, I. and Schneider, H. 2007. Phylogenetic

526   analyses of the genera *Pipra, Lepidothrix and Dixiphia* (Pipridae, Passeriformes) using

527   partial cytochrome b and 16S mtDNA genes. Zool. Scripta 36: 1-11.

528   Rice, N. H., Martínez–Meyer, E. and Peterson, A. T. 2003. Ecological niche differentiation in the

529   *Aphelocoma* jays: a phylogenetic perspective. – Biol. J. Linn. Soc. 80: 369–383.

530   Ridgely, R. S. and Greenfield, P. 2001. The Birds of Ecuador Vols. 1–2. Cornell University

531   Press, Ithaca, NY.

532   Ridgely, R. S. and Tudor, G. 1994. The Birds of South America. Vol. 2. University of Texas

533   Press, Austin, TX.

534   Scachetti-Pereira, R.. 2002. Desktop GARP. http://www.lifemapper.org/desktopgarp/.

535   Seavy, N. E., Dybala, K. E. and Snyder, M. A. 2008. Climate models and ornithology. –Auk

536   125: 1-10.

537   Sick, H. 1993. Birds in Brazil: a natural history. Princeton University Press, Princeton, NJ.

538   Snow, D. W. 2004. Family Pipridae (Manakins). Pages 110-169 in Handbook of the Birds of the

539   World. Vol. 9. Cotingas to Pipits and Wagtails. (J. del Hoyo, A. Elliott and D. A. Christie,

540   Eds.). Lynx Editions, Barcelona.

541   Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. - Ecol.

542   Letters 10: 1-9.

543   Soberón, J. and Peterson, A. T. 2004. Biodiversity informatics: managing and applying primary

544   biodiversity data. – Phil. Trans. R. Soc. Lon. B 359: 689–698.

545   Soberón, J. and Peterson, A. T. 2005. Interpretation of models of fundamental ecological niches

546   and species' distributional areas. – Biod. Inf. 2: 1–10.

547   Stockwell, D. R. B. 1999. Genetic algorithms II. Pages 123–144 in Machine learning methods

548   for ecological applications (A. H. Fielding, Ed.). Kluwer Academic Publishers, Boston.

549   Stockwell, D. R. B. and Peters, D. P. 1999. The GARP modelling system: problems and

550   solutions to automated spatial prediction. – Int. J. Geogr. Inf. Syst. 13: 143–158.

551   Stockwell, D. R. B. and Noble, I. R. 1992. Induction of sets of rules from animal distribution

552   data: a robust and informative method of analysis. – Math. Comp. Sim. 33: 385–390.

553   Warren, D. Glor, R. E., and Turelli, M. 2008. Environmental niche equivalency versus

554   conservatism: Quantitative approaches to niche evolution. - Evolution 62: 2868-2883.

555   Webb, C. O., Ackerly, D. D., McPeek, M. A. and Donoghue, M. J. 2002. Phylogenies and

556   community ecology. – Ann. Rev. Ecol. Syst. 33: 475–505.

557   Wellenreuther, M., Barrett, P. T. and Clements, K. D. 2007. Ecological diversification in habitat

558   use by subtidal triplefin fishes (Tripterygiidae). – Mar. Ecol. Prog. S. 330: 235–246.

559   Wiens, J. J. 2004. Speciation and ecology revisited: Phylogenetic niche conservativism and the

560   origin of species. - Evolution 58: 193-197.

561   Wiens, J. J. and Graham, C. H. 2005. Niche conservativism: integrating evolution, ecology, and

562   conservation biology. – Ann. Rev. Ecol. Syst. 36: 519–539.

563   Wiens, J.J., Graham, C.H., Smith, S., Moen, D. and Reeder, T. 2006. Evolutionary and

564   ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the

565   roots of high tropical diversity. – Am. Nat. 168:579–596.

566   **Figure Legends**

567   Fig. 1. Species diversity of manakins across the Neotropics according to species' modeled geographic

568   distributions.

569   Fig. 2. Two-dimensional centroids of ecological niches for manakins and outgroup species.

570   Small black dots represent available combinations of mean temperature and precipitation in

571   the study region; symbols represent species' means for the two variables.

572   Fig. 3. a) Area of modeled geographic distribution among the studied species; b) Relationship

573   between area of predicted distribution and niche breadth, measured as the number of unique

574   combinations of ecological variables observed in the modeled distributions, for each species.

575   Fig. 4. Frequency of P-values from pairwise interpredictivity tests, for the ability of modeled potential

576   distribution of species A in predicting the actual localities of species B, and mean ($\pm$ 1 se) pairwise

577   distance among centroids of ecological niches, n is indicated above bars. Inter-family values are

578   pairwise comparisons of manakins to species in the outgroup.

579   Fig. 5. Interpredictivity between modeled distributions from known localities of species A (dotted circles) and

580   known localities of species B: Upper panels - Model for *Lepidothrix nattereri* predicting localities of (a) its

581   sister species, *L. iris* (black squares) and (b) other *Lepidothrix* species (*L. coronata*, diamonds; *L.*

582   *caeruleocapilla,*open circles; *L. isidorei*, open squares*; L. serena*, black circles, *L. suavissima*, triangles.

583   Botton panels – Model for *Corapipo altera* predicting localities of (c) its sister species, *C. leucorrhoa*

584   (black squares) and (d) *C. gutturalis* (black circles) and *Masius chrysopterus* (triangles).

585   Fig. 6. Evolution of ecological niches among manakins. Branch lengths represent the amount of

586   ecological change between nodes and terminal taxa, estimated by the Fitch algorithm of

587   character evolution, based on the molecular phylogeny proposed by Hackett (in prep).
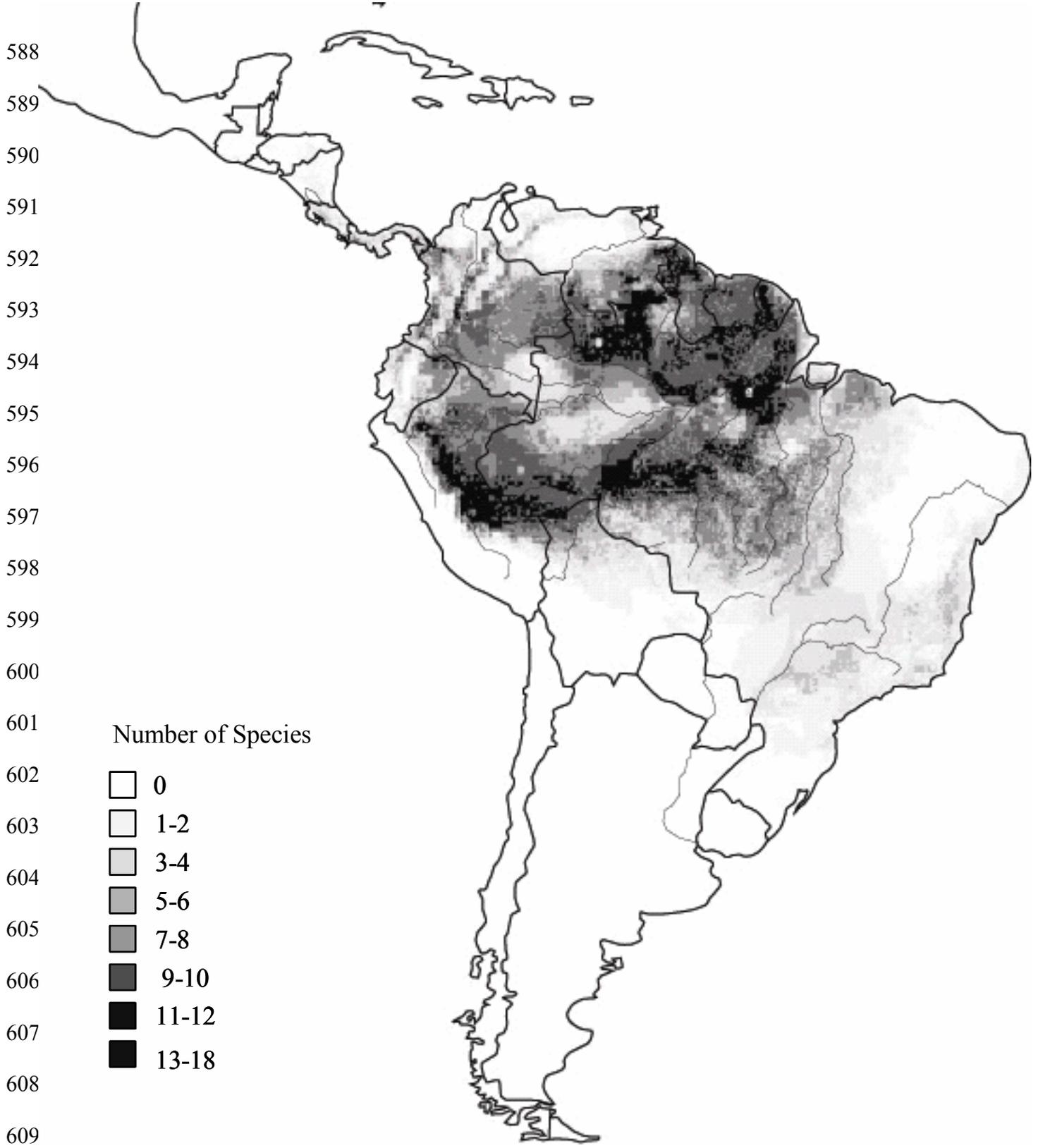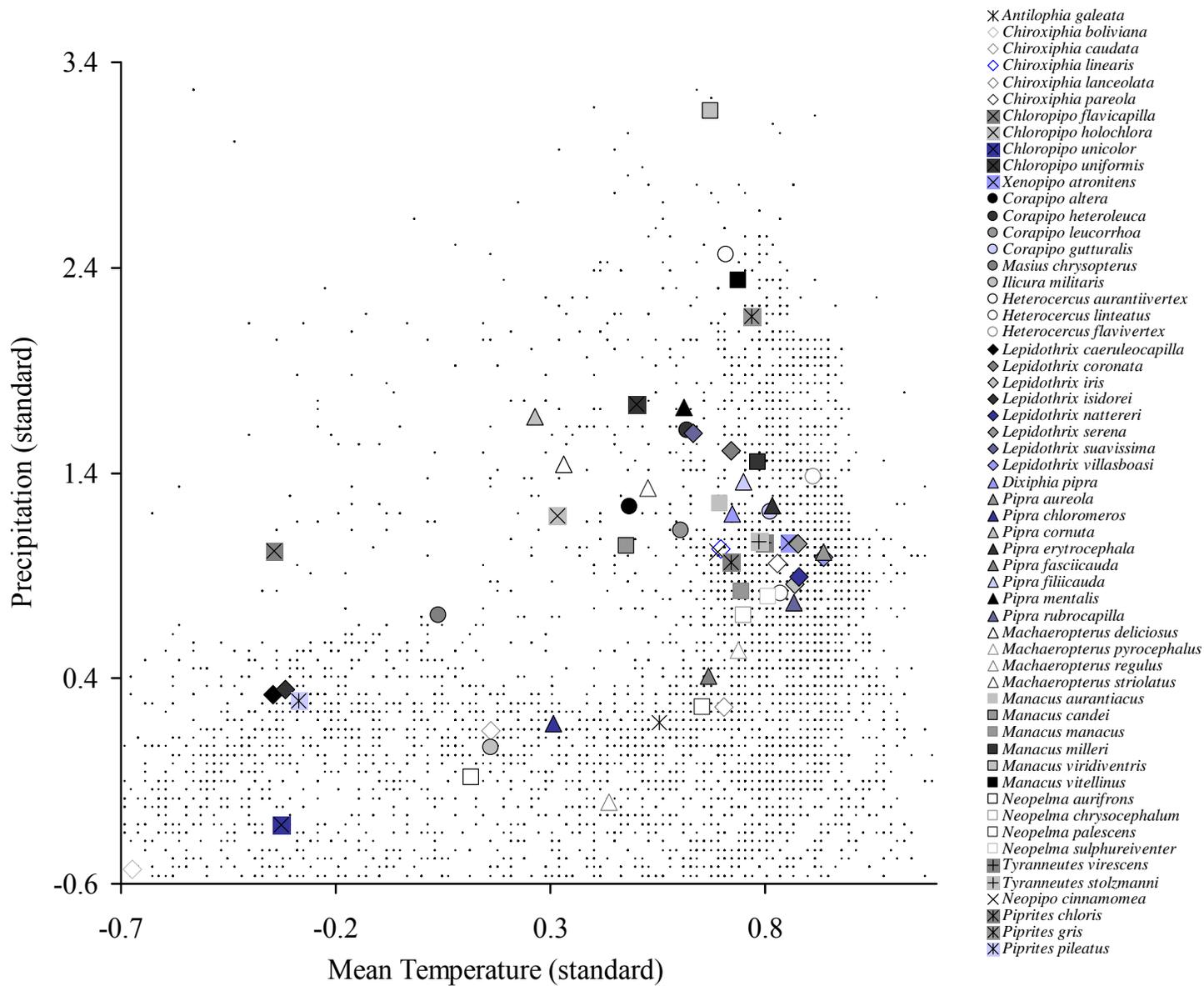
588

589

590

591

592

593

594

595

596

597

598

599

600

601

602

603

604

605

606

607

608

609

610

Number of Species

- [ ] 0
- [ ] 1-2
- [ ] 3-4
- [ ] 5-6
- [ ] 7-8
- [ ] 9-10
- [ ] 11-12
- [ ] 13-18

Fig. 1

Fig. 2

611

612

Fig. 3

636

637

638

639

640

641

642

643

644

645

646

647

648

649

650

651

652

Fig. 4

a)

b)
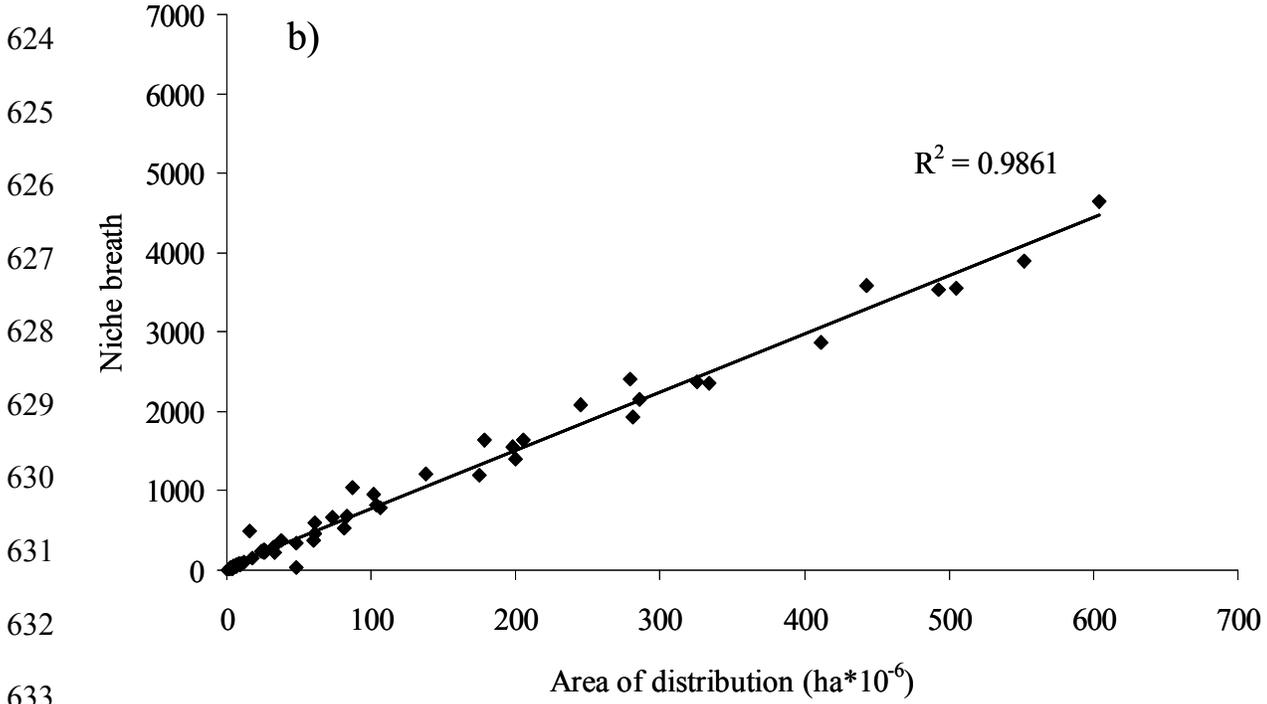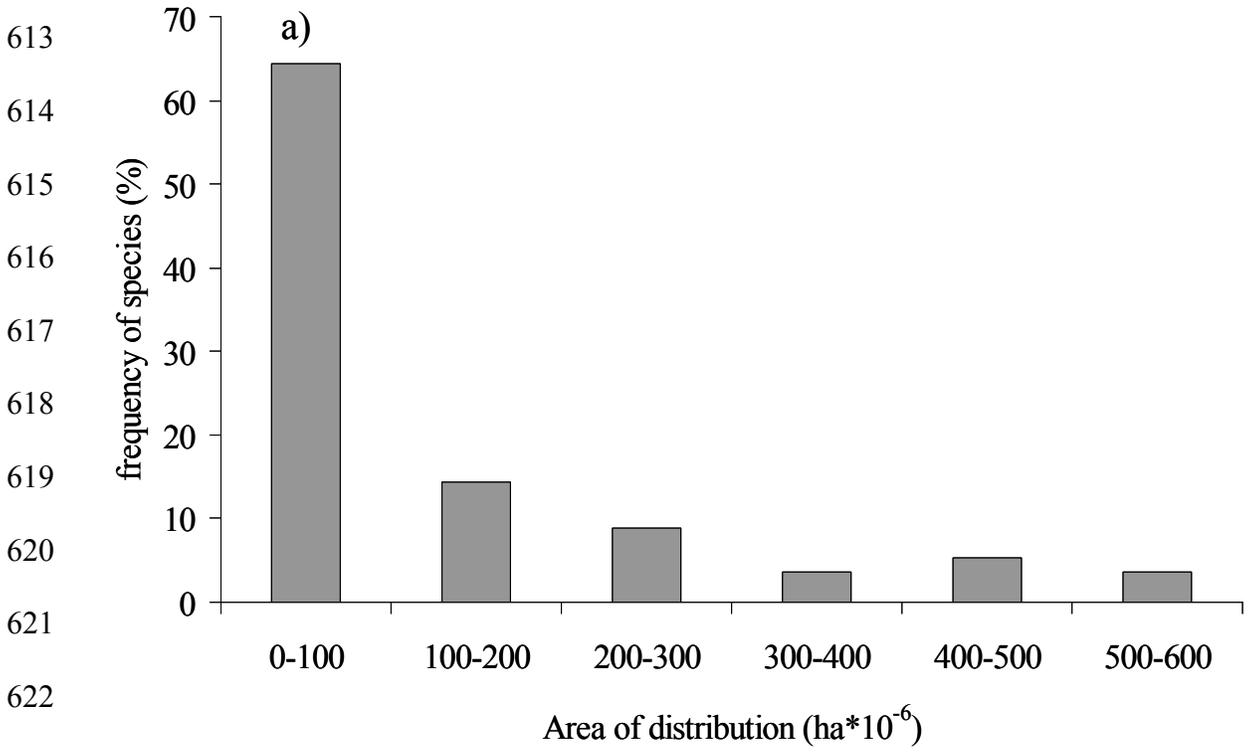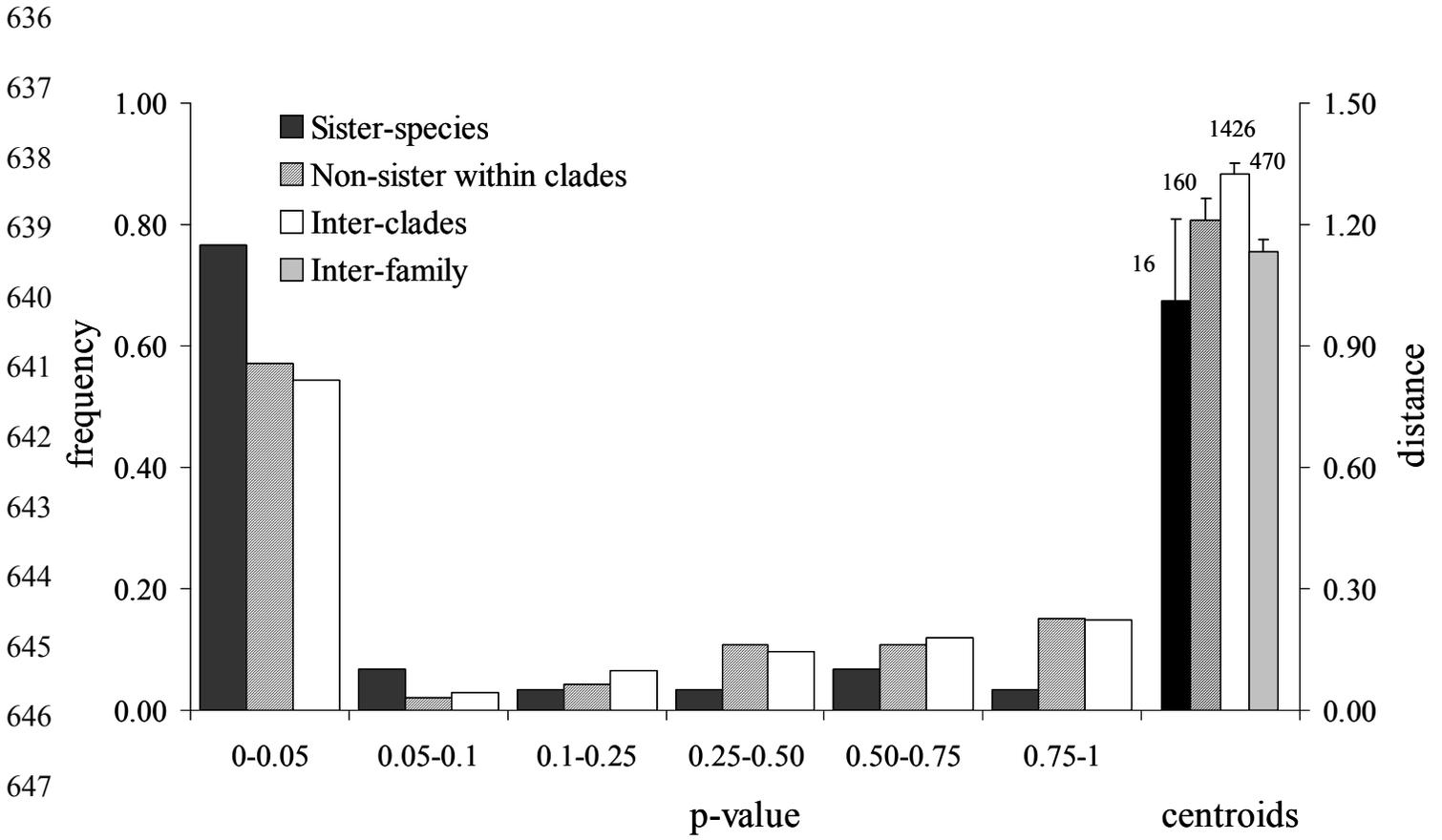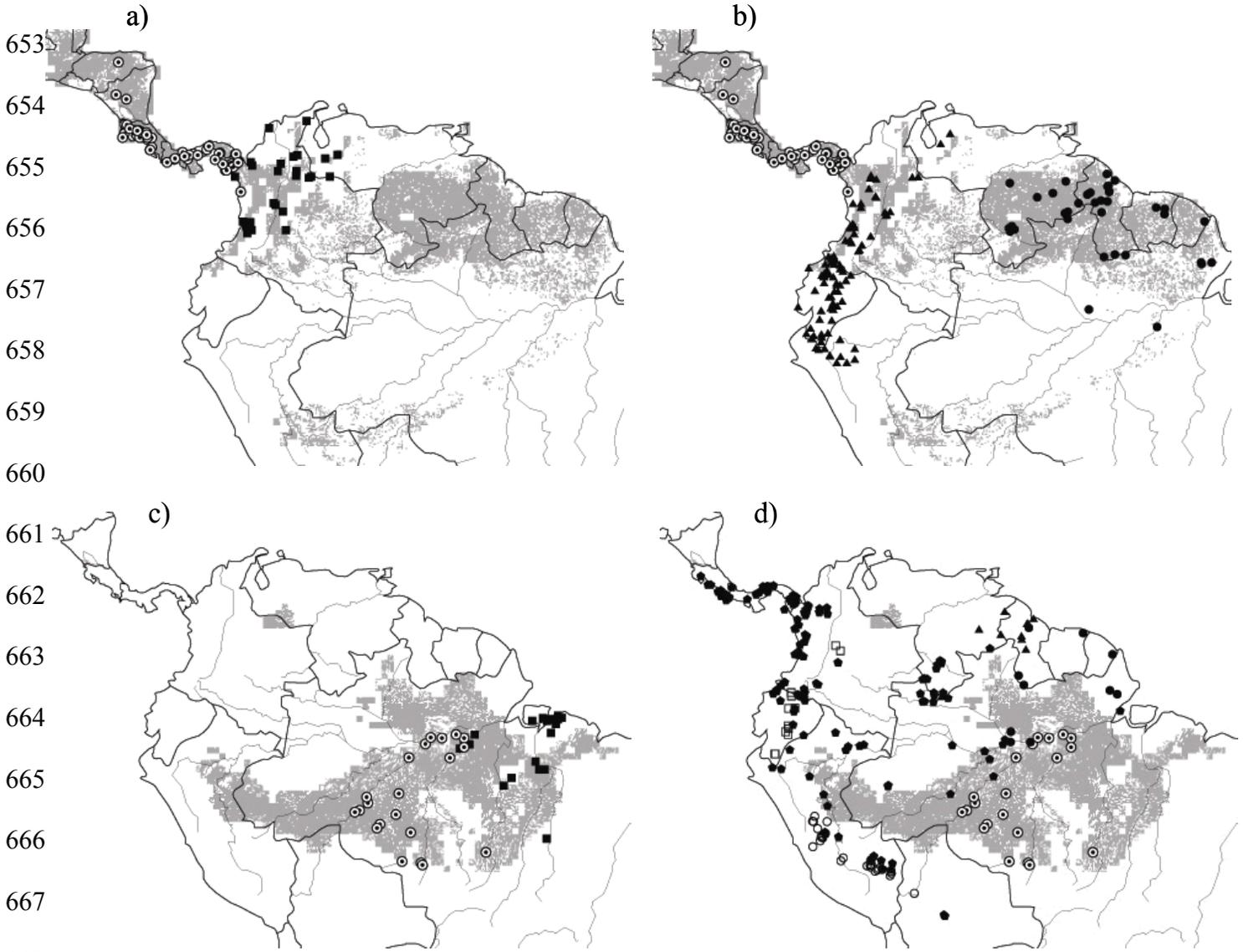
653

654

655

656

657

658

659

660

c)

d)

661

662

663

664

665

666

667

668

669

670

Fig. 5

671

672

673

674

675

676
677
678
679
680
681
682
683
684
685
686
687
688
689
690
691
692
693
694
695
696
697
698

0.26 Neopelma aurifrons
0.12 Tyranneutes stolzmanni 0.02
Tyranneutes virescens 0.01
0.43 Neopelma palescens
0.34 Neopelma sulphureiventer
Neopelma chrysocephalum 0.09
0.16 Ilicura militaris
Corapipo gutturalis 0.09
0.72 Masius chrysopterus
0.11 0.12 Corapipo leucorrhoa
0.12 Corapipo altera
0.12 Antilophia galeata
0.03 0.33 Chiroxiphia caudata
0.27 Chiroxiphia linearis
0.10 0.66 Chiroxiphia lanceolata
Chiroxiphia pareola 0.07
1.95 Chiroxiphia boliviana
1.05 Chloropipo unicolor
0.50 Chloropipo uniformis
0.03 Xenopipo atronitens 0.04
0.42 Chloropipo holochlora
Lepidothrix serena 0.04
0.23 Lepidothrix suavissima
0.22 Lepidothrix coronata
0.01 0.13 Lepidothrix nattereri
0.23 Lepidothrix iris
0.63 0.42 Lepidothrix isidorei
0.50 Lepidothrix caeruleocapilla
1.27 Heterocercus aurantiivertex
0.12 Heterocercus linteatus
0.10 Pipra filiicauda
0.26 Pipra aureola
0.01 0.27 Pipra fasciicauda
0.29 Machaeropterus pyrocephalus
0.54 Machaeropterus deliciosus
0.72 Machaeropterus regulus
0.31 Machaeropterus striolatus
0.10 Dixiphia pipra
0.49 Pipra cornuta
0.78 Pipra chloromeros
0.19 Pipra rubrocapilla
0.37 Pipra mentalis
Pipra erytrocephala 0.09
0.21 Manacus manacus
0.91 Manacus vitellinus
0.07 0.15 Manacus candei
0.17 Manacus aurantiacus
0.22 Neopipo cinnamomea

Fig. 6

32

699 Table I. Known occurrences, spatial and ecological dimensions of modeled distributions for each species. Model fit and ecological variables describing

700 species' niches are summarized. Unique localities are at least 5 km apart from other localities, and were used for model generation; niche breath was

701 re-scaled to 1-10. Chi-square and p-values refer to accuracy tests for models with n localities >20. *species with estimated distribution maps. OG =

702 species from the outgroup.

| Species	Sampled distribution		Modeled distribution			Model fit				Mean (±1 se) of ecological variables							
	# known localities	# unique localities	regions	area ha*10^{-6}	niche breadth	X^2	p	Comm.	Omiss.	temperature Mean	±1 se	precipitation Mean	±1 se	wetdays Mean	±1 se	top. index Mean	±1 se
Antilophia galeata	41	40	CE; AM; AF	138.23	2.41	104.63	0.00	14.02	0.00	241.38	6.49	40.73	0.46	153.11	0.13	525.18	0.55
Chiroxiphia boliviana	6	6	AD	6.23	0.11	-	-	3.61	0.00	165.02	99.34	23.80	2.47	72.20	1.73	2099.96	1.22
Chiroxiphia caudata	192	186	AF; CE	178.38	3.29	345.78	0.00	3.78	0.00	216.98	6.86	39.83	0.50	149.11	0.15	565.61	0.65
Chiroxiphia lanceolata	70	59	CC; AD; AM	24.04	0.47	97.23	0.00	12.38	0.00	250.77	45.80	42.58	1.60	102.53	1.16	508.89	2.35
Chiroxiphia linearis	27	26	CC	6.06	0.09	49.77	0.00	38.46	8.33	250.36	54.49	60.91	1.70	132.29	3.30	423.84	1.92
Chiroxiphia pareola	84	79	AF; GU; AD; AM	493.16	7.06	39.22	0.00	39.50	2.33	258.49	3.87	59.26	0.18	183.11	0.25	228.03	0.40
*Chloropipo flavicapilla**	4	4	AD	4.20	0.11	-	-	-	-	185.63	142.70	60.70	5.77	160.41	3.59	1752.54	2.45
Chloropipo holochlora	50	48	CC; AD; AM	72.91	1.33	15.95	0.00	31.87	0.00	226.73	34.29	64.72	1.46	162.26	1.09	829.76	1.40
Chloropipo unicolor	6	6	AD; AM	8.32	0.18	-	-	7.21	0.00	186.61	67.28	28.94	3.08	127.68	1.20	1604.74	2.31
Chloropipo uniformis	9	6	GU	10.14	0.18	-	-	3.71	0.00	238.16	48.86	77.65	0.92	167.82	0.83	884.79	1.52
Corapipo altera	48	44	CC; AD	11.84	0.22	40.23	0.00	22.00	0.00	237.07	45.22	65.76	1.81	152.47	2.37	512.75	1.95
Corapipo gutturalis	37	36	GU; AM	103.73	1.65	41.55	0.00	22.72	5.26	257.52	9.79	65.22	0.33	179.69	0.40	254.24	0.43
Corapipo heteroleuca	21	19	CC	1.46	0.03	415.32	0.00	3.09	0.00	245.46	150.37	74.62	4.68	158.00	3.64	647.85	2.06
Corapipo leucorrhoa	28	27	CC; AD; AM	26.80	0.47	11.95	0.00	47.71	7.14	244.60	50.15	62.98	1.68	145.29	1.39	630.00	2.38
Dixiphia pipra	130	118	AF; GU; CC; AD; AM	505.19	7.11	55.79	0.00	22.20	1.49	252.11	8.71	65.01	0.40	177.83	0.29	354.90	0.51
*Heterocercus aurantiivertex**	0	0	AD; AM	48.41	0.06	-	-	-	-	251.13	3.19	95.00	0.48	217.52	0.25	293.94	0.50
Heterocercus flavivertex	14	13	GU; AM	33.61	0.45	-	-	17.05	0.00	263.70	13.40	69.28	0.37	192.04	0.65	140.32	1.13
Heterocercus linteatus	15	15	CE; AM	175.14	2.38	-	-	30.05	0.00	258.94	4.13	55.80	0.18	174.21	0.18	220.76	0.73
Ilicura militaris	90	85	AF; CE	101.47	1.90	240.18	0.00	9.43	0.00	217.03	8.35	37.92	0.60	160.62	0.20	650.99	0.54
Lepidothrix caeruleocapilla	28	26	AD	8.94	0.15	127.28	0.00	9.27	7.14	185.49	104.16	43.99	4.63	102.53	2.36	1465.53	1.40
Lepidothrix coronata	131	115	GU; CC; AD; AM	281.24	3.87	27.57	0.00	28.37	3.13	251.93	12.30	72.29	0.40	179.80	0.45	404.22	0.78
Lepidothrix iris	26	23	AM	61.25	0.93	52.79	0.00	12.21	0.00	261.06	4.79	56.78	0.23	195.42	0.27	165.15	0.66
Lepidothrix isidorei	12	11	AD	25.69	0.53	-	-	42.95	0.00	187.22	61.80	44.56	2.54	154.83	1.33	1648.22	1.54
Lepidothrix nattereri	23	21	AM	60.43	0.75	68.41	0.00	5.54	0.00	261.74	5.51	57.63	0.28	174.87	0.21	157.98	1.04
Lepidothrix serena	10	10	GU; AM	47.78	0.69	-	-	13.46	0.00	261.52	5.95	61.49	0.33	184.70	0.55	175.94	0.64
Lepidothrix suavissima	11	11	GU; AM	25.83	0.45	-	-	13.05	0.00	246.30	26.56	74.32	0.83	172.98	0.70	485.51	0.77
*Lepidothrix villasboasi**	2	2	AM	0.53	0.02	-	-	-	-	265.25	27.92	59.88	1.18	187.50	1.23	114.63	0.42
Machaeropterus deliciosus	20	20	AD	2.75	0.07	102.93	0.00	11.37	10.00	227.57	196.19	70.65	3.10	171.35	3.28	1404.62	3.65

703

Species			Region															
Machaeropterus pyrocephalus	41	39	CE; AD; AM	198.33	3.12	28.45	0.00	19.87	4.76	252.92	5.75	49.14	0.35	142.98	0.28	347.69	0.79
Machaeropterus regulus	20	19	AF	17.26	0.31	321.84	0.00	5.56	0.00	234.14	16.07	31.62	0.61	174.68	0.44	275.62	1.91
Machaeropterus striolatus	39	38	AD; AM	204.91	3.29	10.93	0.00	31.46	5.26	239.81	18.91	67.95	0.80	174.93	0.51	643.73	0.86
Manacus aurantiacus	19	17	CC	3.87	0.06	434.69	0.00	7.56	0.00	250.23	113.13	66.20	3.19	153.40	3.23	552.30	2.63
Manacus candei	23	22	CC	26.20	0.47	23.44	0.00	43.39	0.00	236.69	31.04	61.26	1.14	148.11	1.33	521.25	1.22
Manacus manacus	189	171	AF; CE; AM; GU; AD; CC	604.03	9.30	38.81	0.00	32.94	7.61	253.28	5.19	56.01	0.25	167.23	0.23	312.22	0.50
Manacus milleri	9	8	CC; AD	1.46	0.04	-	-	15.08	0.00	255.72	10.73	70.89	3.16	140.61	8.62	138.44	12.22
Manacus viridiventris	7	6	CC; AD	6.46	0.13	-	-	8.01	0.00	248.94	47.24	111.65	1.66	190.30	5.00	397.05	2.49
Manacus vitellinus	18	17	CC; AD	7.99	0.17	17.72	0.00	47.14	10.00	252.83	31.00	91.94	1.22	170.88	4.13	253.40	3.26
Masius chrysopterus	100	91	AD; AM	60.59	1.19	46.28	0.00	21.24	0.00	209.51	41.88	53.28	1.78	153.82	1.15	1235.76	1.52
Pipra aureola	42	37	GU; AM	81.65	1.05	79.18	0.00	48.80	5.26	265.32	1.54	60.47	0.17	194.22	0.34	63.76	0.78
Pipra chloromeros	54	47	CE; AD; AM	83.18	1.38	22.90	0.00	11.16	3.57	226.08	30.63	40.70	1.51	99.83	0.74	765.02	1.10
Pipra cornuta	6	5	GU; AD; CC	378.00	0.03	-	-	35.19	0.00	223.47	101.52	76.18	3.90	167.59	1.67	1259.76	2.58
Pipra erytrocephala	164	152	GU; CC; AD; AM	411.91	5.74	38.63	0.00	35.11	7.41	257.86	6.05	65.87	0.23	174.43	0.30	256.74	0.62
Pipra fascicauda	62	57	AF; CE; AD; AM	443.12	7.18	19.81	0.00	16.80	6.06	248.55	4.02	46.17	0.29	152.29	0.18	379.46	0.56
Pipra filicauda	50	46	GU; AD; AM	199.43	2.81	18.59	0.00	18.68	12.00	253.66	9.98	68.65	0.43	175.84	0.37	337.58	0.74
Pipra mentalis	49	49	CC; AD	32.41	0.60	21.22	0.00	25.70	4.76	245.05	26.61	77.21	0.88	160.33	1.68	431.04	1.54
Pipra rubrocapilla	76	69	AF; AM	334.09	4.72	69.85	0.00	42.06	2.70	260.98	2.34	54.70	0.13	184.65	0.25	189.13	0.44
Xenopipo atronitens	29	28	GU; AM	285.53	4.29	35.54	0.00	14.62	6.67	260.24	3.66	61.58	0.14	185.85	0.23	204.99	0.34
Neopelma aurifrons [OG]	8	8	AF	38.20	0.74	-	-	54.26	0.00	214.14	13.64	34.48	0.80	162.97	0.35	655.98	0.75
Neopelma chrysocephalum [OG*]	1	1	GU; AM	86.46	2.08	-	-	-	-	253.70	12.73	66.97	0.45	172.59	0.44	373.79	0.55
Neopelma palescens [OG]	15	15	AF; CE; AM	279.19	4.81	-	-	48.11	0.00	247.76	4.86	42.53	0.30	170.83	0.24	427.62	0.35
Neopelma sulphureiventer [OG*]	1	1	AM	15.54	0.98	-	-	-	-	257.15	8.42	55.41	0.50	145.41	0.46	265.61	1.71
Neopipo cinnamomea [OG]	12	11	AD; GU; AM	244.76	4.15	-	-	44.63	0.00	249.98	9.55	60.58	0.41	161.87	0.32	404.87	0.59
Piprites chloris [OG]	17	16	AF; CE; GU; AM; AD	325.72	4.76	-	-	-	0.00	251.78	6.74	59.28	0.44	171.35	0.17	281.16	0.69
Piprites gris [OG*]	0	0	CC	3.46	0.08	-	-	-	-	254.87	9.37	87.79	1.48	166.59	2.37	54.92	3.63
Piprites pileatus [OG*]	2	2	AF	24.69	0.48	-	-	-	-	189.22	20.80	43.25	0.96	170.46	0.29	707.37	1.24
Tyranneutes stoltzmanni [OG]	17	16	GU; AD; AM	552.10	7.78	6.83	0.01	36.52	9.09	255.87	5.16	61.76	0.24	175.00	0.22	276.59	0.52
Tyranneutes virescens [OG*]	1	1	GU; AM	106.12	1.58	-	-	-	-	256.69	10.24	61.60	0.45	175.79	0.44	262.19	0.55

704

705   AF = Atlantic Forest; CE = Cerrado; AM = Amazon; AD = Andes; GU = Guiana; CC = Central America-Choco.

706   Table II. Summary of Mantel statistics testing the associations between the geographic and ecological distance matrices.

707   For positive correlations ($r > 0$), the null hypothesis of no significant correlation is rejected if the probability of random

708   values of Z being greater than the observed Z is smaller than 0.05. Significant results are highlighted. OG = Outgroup

709   species.

710
711
712

Genera	r^2	Matrix Correlation r	*Mantel-t*	*P*	*P* Zo > Zr	*P* Zr > Zo	*n* points
Chiroxiphia	0.087	-0.296	-0.909	0.182	0.182	0.797	10
Chloropipo - Xenopipo	0.160	0.221	0.482	0.283	0.482	0.283	6
Corapipo - Masius	0.414	0.643	1.296	0.207	0.903	0.207	6
Heterocercus	0.972	0.986	0.000	0.167	0.500	0.167	3
Lepidothrix	0.518	0.720	3.395	**0.004**	1.000	0.004	28
Manacus	0.016	-0.128	-0.371	0.355	0.355	0.458	15
Pipra-Machaeropterus	0.265	0.545	0.834	0.151	0.798	0.151	28
Neopelma-Tyranneutes[OG]	0.805	0.897	2.808	**0.044**	0.998	0.044	10