Everything you always wanted to know about gene flow in tropical landscapes (but were afraid to ask)

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The bulk of the world's biodiversity is found in tropical regions, which are increasingly threatened by the human-led degradation of natural habitats. Yet, little is known about tropical biodiversity responses to habitat loss and fragmentation. Here we review all available literature assessing landscape effects on gene flow in tropical species, aiming to help unravel the factors underpinning functional connectivity in the tropics. We map and classify studies by focus species, the molecular markers employed, statistical approaches to assess landscape effects on gene flow, and the evaluated landscape and environmental variables. We then compare qualitatively and quantitatively landscape effects on gene flow across species and units of analysis. We found 69 articles assessing landscape effects on gene flow in tropical organisms, most of which were published in the last five years, were concentrated in the Americas, and focused on amphibians or mammals. Most studies employed population-level approaches, microsatellites were the preferred type of markers, and Mantel and partial Mantel tests the most common statistical approaches used. While elevation, land cover and forest cover were the most common gene flow predictors assessed, habitat suitability was found to be a common predictor of gene flow. A third of all surveyed studies explicitly assessed the effect of habitat degradation, but only 14 of these detected a reduced gene flow with increasing habitat loss. Elevation was responsible for most significant microsatellite-based IBR effects and a single study reported significant isolation by non-forested areas in an ant. Our study reveals important knowledge gaps on the study of landscape effects on gene flow in tropical organisms, and provides useful guidelines on how to fill them.

1 **Everything you always wanted to know about gene flow in tropical**

2 **landscapes (but were afraid to ask)**

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17 **Abstract**

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19 threatened by the human-led degradation of natural habitats. Yet, little is known about tropical

20 biodiversity responses to habitat loss and fragmentation. Here we review all available literature

21 assessing landscape effects on gene flow in tropical species, aiming to help unravel the factors

22 underpinning functional connectivity in the tropics. We map and classify studies by focus species,

23 the molecular markers employed, statistical approaches to assess landscape effects on gene flow,

24 and the evaluated landscape and environmental variables. We then compare qualitatively and

25 quantitatively landscape effects on gene flow across species and units of analysis. We found 69

26 articles assessing landscape effects on gene flow in tropical organisms, most of which were

27 published in the last five years, were concentrated in the Americas, and focused on amphibians or

28 mammals. Most studies employed population-level approaches, microsatellites were the preferred

29 type of markers, and Mantel and partial Mantel tests the most common statistical approaches

30 used. While elevation, land cover and forest cover were the most common gene flow predictors

31 assessed, habitat suitability was found to be a common predictor of gene flow. A third of all

32 surveyed studies explicitly assessed the effect of habitat degradation, but only 14 of these

33 detected a reduced gene flow with increasing habitat loss. Elevation was responsible for most

34 significant microsatellite-based IBR effects and a single study reported significant isolation by

35 non-forested areas in an ant. Our study reveals important knowledge gaps on the study of

36 landscape effects on gene flow in tropical organisms, and provides useful guidelines on how to

37 fill them.

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41 **Keywords**: Functional connectivity; isolation by resistance; landscape genetics; matrix

42 permeability; tropical biodiversity.

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46 **Introduction**

47 About two-thirds of all known species occur in tropical forests and the majority of the world's

48 most threatened biodiversity hotspots are in the tropics (Myers et al., 2000; Brown, 2014).

49 Extinction rates from habitat loss and fragmentation are acute in the region, and the degradation

50 of essential ecosystem functions and services are threatening billions of people living in tropical

51 countries (Bradshaw, Sodhi & Brook, 2009). However, the vast majority of studies assessing

52 biodiversity responses to habitat degradation have been undertaken in temperate regions due to a

53 lower investment in research and development in tropical countries (Collen et al., 2008; Barlow

54 et al., 2018). For instance, a recent analysis of 182 studies describing links between biodiversity

55 and ecosystem function (Clarke et al., 2017) found that only 13% were carried in the tropics, and

56 nearly half of these (42%) were conducted in a single country (Costa Rica). There is thus a

57 pressing need to reduce the knowledge gap concerning the impact of the degradation of natural

58 habitats on tropical biodiversity.

59   Community-level approaches assessing biodiversity responses to habitat degradation have

60 focused on measuring changes in species richness, composition, and the abundance of indicator

61 species (Morin, 2009). While these metrics underpin ecosystem function, they may not always be

62 the best proxies to detect rapid responses to habitat loss and fragmentation. Local species

63 extinctions may occur after long periods of time since the onset of disturbance (Jackson & Sax,

64 2009), whereas species abundance can be affected by multiple environmental or demographic

65 factors unrelated to habitat degradation (Ehrlén & Morris, 2015). Moreover, complex inter-

66 specific interactions can make natural communities resilient to environmental change and thus

67 mask the effect of habitat degradation on community composition (Devictor, Julliard & Jiguet,

68 2008). Instead, population-level metrics based on genetic information can offer a higher

69 resolution to detect rapid responses to environmental change (Manel & Holderegger, 2013a). For

70 instance, changes in genetic diversity and gene flow patterns in response to recent landscape

71 modification have been found across several species (Balkenhol et al., 2016; DiLeo & Wagner,

72 2016), although tropical organisms have been rarely assessed (Storfer et al., 2010a).

73   Even though the effects of habitat loss and fragmentation on genetic diversity have been

74 reviewed extensively (Aguilar et al., 2006, 2008; Keyghobadi, 2007; Vranckx et al., 2012; Lino

75 et al., 2018; Schlaepfer et al., 2018), there is an important knowledge gap regarding general

76 landscape effects on gene flow (DiLeo & Wagner, 2016). By influencing the willingness of an

77 organism to cross a particular environment and the physiological or fitness costs of moving

78 through it, the resistance imposed by landscape structure on the dispersal of organisms can

79   ultimately affect genetic differentiation and patterns of gene flow (Zeller, McGarigal & Whiteley,

80   2012; Balkenhol et al., 2016). To understand which landscape features impose a greater resistance

81   on gene flow, landscape geneticists first create resistance surfaces for landscape variables of

82   interest, then use these surfaces to estimate cost or resistance distances between sampling

83   locations, and finally regress measures of gene flow on these resistance distances (Spear,

84   Cushman & McRae, 2016). Significant associations between gene flow metrics and landscape

85   resistance distances are taken for evidence of isolation by resistance (IBR), and effect sizes can

86   be considered proxies of functional connectivity (Manel & Holderegger, 2013b).

87   Understanding the factors underpinning functional connectivity across species is essential

88   to design ecological corridors, identify conservation units, assess population threat status,

89   optimize pathogen and invasive species management, assist planning of natural heritage systems,

90   and restore threatened populations (Bowman et al., 2016; Waits LP, Cushman SA, 2016).

91   However, no efforts have yet been made to gather, standardize and compare IBR effects across

92   studies and organisms. For instance, landscape genetics is still a your field of research (Manel &

93   Holderegger, 2013b), and the vast majority of landscape genetic studies have focused in a single

94   species (DiLeo & Wagner, 2016; Waits LP, Cushman SA, 2016). So far, gene flow has been

95   shown to be influenced by various factors, including forest cover, land cover, topography, roads,

96   rivers, and climate, but responses vary greatly across species and units of analysis (populations or

97   individuals; see Balkenhol et al. 2016 and references therein).

98   Aiming to unravel the main drivers of functional connectivity in tropical landscapes, here

99   we compiled all studies that assessed landscape effects on gene flow in tropical species so far. To

100   our knowledge, this work represents the first quantitative comparison of such effects across

101   species and units of analysis. We believe this systematic review can help characterize the current

102   knowledge gap on tropical biodiversity responses to habitat degradation, and thereby highlight

103   future research needs.

104

105   **Survey Methodology**

106   ***Dataset***

107   We employed the following search engines to perform a recursive literature search of landscape

108   effects on gene flow in tropical species published by June 2018: Scielo (http://www.scielo.org),

109   Portal de Periódicos da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior do

110   Ministério da Educação (CAPES/MEC) (http://www.periodicos.capes.gov.br/); Google Scholar

111   (http://www.scholar.google.com.br); Web of Knowledge (http://www.isiknowledge.com), and

112   Scopus (http://www.scopus.com). We used the following combination of keywords and Boolean

113   operators: ("landscape resistance" or landscape or resistance or fragmentation or "land use" or

114   "habitat loss" or deforestation) and (genetic* or "genetic differentiation" or "gene flow" or

115   "genetic distance" or FST or relatedness or kinship). Articles containing at least one of the

116   keywords on each side of the "and" operator were analyzed along with the relevant references

117   therein. Even though this search approach may not be easily replicated (as it involves a

118   substantial effort), it is more likely to minimize omissions than approaches based on the results

119   obtained from search engines alone. We then identified those studies that explicitly related

120   landscape with gene flow metrics in organisms collected between the tropics of Cancer and

121   Capricorn (23.5° north and south of the equator) or within 200km from them. Articles addressing

122   only isolation by geographic distance (IBD) were excluded, as our aim was to survey studies that

123   specifically incorporated landscape effects on gene flow in addition to geographic distance. We

124   then gathered all available information on the study objectives, focus species, study site,

125   ecosystem, the extent of the study area, the unit of analysis employed, sample size, types and

126   number of genetic markers employed, genetic and landscape resistance metrics employed,

127   statistical methods, landscape or environmental predictors assessed, and the effects reported.

128

129   ***Comparing landscape effects on gene flow across studies***

130   We performed both qualitative and quantitative comparisons of landscape effects on gene flow

131   across studies. For the former, we grouped studies by the landscape or environmental factors

132   assessed and the focus taxonomic group, and summarized the reported effects on gene flow. For

133   the quantitative comparison we selected a subset of our dataset containing only studies that: i)

134   Explicitly reported correlation or regression coefficients, calculated from at least three samples,

135   and ii) Employed nuclear microsatellite markers to measure gene flow, given that measures of

136   genetic differentiation obtained with different genetic markers are not directly comparable across

137   studies (Wan et al., 2004; Allendorf, Luikart & Aitken, 2013). We then separated the studies

138   fulfilling these requirements in two groups according to the units of analysis employed: Those

139   using population-level metrics of genetic differentiation (F_{ST} or D_{est}), and those using individual-

140   level metrics of genetic distance (Rousset's a, relatedness and kinship; Dataset S3). We note that

141   these genetic distance metrics should be considered surrogates of actual gene flow, as they reflect

142   the joint influence of genetic drift and dispersal (Prunier et al., 2017). An effect size approach

143   was used to compare isolation by resistance (IBR) within both types of studies (individual and

144   population-level). Correlation coefficients were first normalized using the Fisher's z-

145   transformation (z), and standard errors (se) were calculated as following:

146

147    $z = \frac{1}{2}\ln\left(\frac{1+r}{1-r}\right)$

148    $se = \frac{1}{\sqrt{N-3}}$

149

150   Where r is the correlation coefficient, ln the natural logarithm and N the number of pairwise

151   comparisons (between individuals or populations). Effect sizes were then calculated dividing the

152   normalized correlation coefficients and standard errors (z/se) (Ellis, 2010). Effect sizes of

153   regression coefficients were calculated dividing them by their respective standard errors. To

154   facilitate comparisons between population-level and individual-level metrics of genetic

155   differentiation we inverted the sign of relatedness and kinship estimates, thus representing genetic

156   dissimilarity. We also calculated 95% confidence intervals for all effect sizes and retrieved the

157   statistical significance (p-values) of IBR effects reported in the original studies. We note that

158   effect sizes were only used for comparative purposes, and that as in previous reviews (DiLeo &

159   Wagner, 2016), small sample sizes did not allow performing a formal meta-analysis.

160

161   **Results**

162   We found a total of 69 articles assessing landscape effects on gene flow in tropical organisms

163   (Dataset S1 in Supplemental Information), most of which were undertaken in the Americas (Fig.

164   1). We recorded 154 target species belonging to eight major taxonomic groups, from which

165   amphibians contained the largest number of species and mammals the highest number of papers

166   (Fig. 2). Most focus species were terrestrial and only three exclusively aquatic species were

167   evaluated. The majority of studies analyzed a single species, but nine publications evaluated two

168   or more. Three studies contributed with more than 40% of all recorded species (Wang, Glor &

169   Losos, 2013; Paz et al., 2015; Jaffé et al., 2016). The oldest study found in our literature search

170   (Trénel et al., 2008) investigated the impact of contemporary Andean landscape features on the

171   spatial genetic structure of a palm tree. After this work, we observed a jump in the number of

172   publications from 2013 onward (Fig. 3).

173   The surveyed studies often had overlapping objectives, which comprised assessing

174   contemporary and historical effects of climate on gene flow (Trénel et al., 2008; Ramírez-

175   Barahona & Eguiarte, 2014); predicting gene flow with habitat suitability models (Poelchau &

176   Hamrick, 2012; Guarnizo & Cannatella, 2013; Paz et al., 2015); assessing landscape and climatic

177   effects on gene flow (Hohnen et al., 2016; Lanes et al., 2018); identifying dispersal routes

178   (Andraca-Gómez et al., 2015; Cleary, Waits & Finegan, 2017; Thatte et al., 2018) and barriers to

179   gene flow (Robertson, Duryea & Zamudio, 2009; Boff et al., 2014; Oliveira et al., 2017); and

180   evaluating the impact of habitat fragmentation on gene flow (Balkenhol et al., 2013; Joshi et al.,

181   2013; de Campos Telles et al., 2014; Carvalho et al., 2015; Ruiz-Lopez et al., 2015).

182   Five types of molecular markers were found across all studies (Fig. 4), and only five

183   publications used more than one type of marker (usually microsatellites and mtDNA).

184   Microsatellites were the most frequently used markers, with more studies using them than

185   publications using all other markers combined. More than 70% of all studies were performed at

186   the population-level and only five studies used both population and individual-level approaches

187   (Dataset S1). Electrical resistance (ER) was the most common resistance metric employed

188   (McRae, 2006), and Mantel and partial Mantel test the most common statistical methods used to

189   relate genetic with resistance distances (Fig. 5).

190   Landscape and environmental predictors of gene flow included elevation (altitude, terrain

191   ruggedness and slope), land cover, forest cover, habitat suitability (derived from species

192   distribution models), water (rivers, streams and the ocean), precipitation, roads and temperature

193   (Fig. 6, Dataset S1). Only six out of 22 studies considering elevation, four out of 22 studies

194   evaluating land cover, four out of 21 studies assessing forest cover, and 14 out of 17 studies

195   relying on habitat suitability models reported an effect on gene flow (Table S1). Most plant and

196   amphibian studies used habitat suitability models to generate resistance surfaces, but no

197   amphibian study analyzed forest cover, precipitation, roads or temperature independently; no bird

198   study used habitat suitability models; no plant study assessed the effect of water bodies; no reptile

199   or plant study addressed the effect of roads; and no mammal study considered temperature (Fig.

200   6).

201   The effect of habitat loss on gene flow was assessed in 25 studies and 39 species (Dataset

202   S2). From these, only 14 studies detected a reduction of gene flow with increasing habitat loss in

203   three plants, five mammals, one amphibian, two birds and one insect. Remarkably, most insects

204   were unaffected by habitat loss. Only 11 articles reported microsatellite-based IBR effects,

205   comprising 25 species (Dataset S3). Whereas IBD drove most significant effects across this group

206   of studies, individual-level studies (N = 14 effects; Fig. 7) showed larger effect sizes than

207   population-level ones (N = 78 effects; Fig. 8). Two individual-level IBR effects were significant

208 (revealing isolation by elevation in a bird and an ant, Fig. 7), and three significant IBR effects

209 were identified in population-level studies (revealing isolation by elevation in a plant and a bee,

210 and isolation by non-forested areas in an ant, Fig. 8).

211

212 **Discussion**

213 Despite the extraordinary levels of biological diversity comprised in the tropics, the study of

214 landscape effects on gene flow in tropical organisms only began to gain general attention in the

215 past five years. Still, published studies are mainly concentrated in the Americas and most of them

216 have focused on amphibians or mammals. The majority of studies were performed at the

217 population-level, electrical resistance was the most common resistance metric employed,

218 microsatellites were the most frequently employed type of molecular marker, and Mantel and

219 partial Mantel tests the most common statistical approaches used. While elevation, land cover and

220 forest cover were the most common gene flow predictors assessed, habitat suitability was found

221 to be a common predictor of gene flow. A third of all surveyed studies explicitly assessed the

222 effect of habitat degradation on gene flow, and only 14 studies detected a reduced gene flow with

223 increasing habitat loss. Finally, individual-level microsatellite-based IBR effects showed higher

224 effect sizes than population-level ones, elevation was responsible for most significant effects and

225 a single study reported significant isolation by non-forested areas in an ant.

226 One of the main aims of the field of landscape genetics has been to understand how landscape

227 characteristics shape patterns of functional connectivity (Manel & Holderegger, 2013b), a subject

228 that has been addressed by many studies undertaken in temperate regions (Balkenhol et al.,

229 2016). Here we show that the study of landscape effects on gene flow in tropical organisms has

230 lagged behind, and that published studies are concentrated in the Americas, as are general

231 research effort on biodiversity in human-modified tropical forests (Gardner et al., 2009;

232 Schlaepfer et al., 2018). Moreover, we found that amphibians and mammals were over

233 represented in our surveyed studies, and most studies outside the Americas focused on mammals

234 (Figs. 1 and 2), reflecting taxonomic biases in biodiversity data and societal preferences (Troudet

235 et al., 2017). Our results thus highlight how little we still understand about landscape effects on

236 gene flow in the tropics, and call for more studies on unrepresented taxonomic groups, tropical

237 areas outside the Americas, and exclusively aquatic organisms.

238 Most of the surveyed studies used microsatellite markers, despite the not so recent shift

239 towards genotyping by sequencing (GBS) triggered by next generation sequencing technologies

240 (Allendorf, Hohenlohe & Luikart, 2010; Benestan et al., 2016). For instance, microsatellite

241 genotyping is still cheaper than GBS, and cross-amplification of SSR markers in related species

242 often reduces the cost of developing species-specific markers (Storfer et al., 2010b). However,

243 SNPs are rapidly becoming the new standard in population and landscape genomic studies, due to

244 their genome-wide coverage and analytical simplicity (Morin, Luikart & Wayne, 2004).

245 Moreover, sequencing costs have fallen dramatically (Shendure et al., 2017), and GBS

246 approaches (such as RAD-sequencing) allow an affordable high-coverage sequencing of a

247 representation of the genome and the discovery of thousands of SNPs in organisms lacking a

248 reference genome (Rowe, Renaut & Guggisberg, 2011; Hohenlohe, Catchen & Cresko, 2012).

249 Perhaps the most important obstacle preventing the widespread adoption of GBS is the

250 complexity of bioinformatic processing (pre-processing of sequence data) and working with very

251 large datasets (Johnson, 2009), but we believe that a much higher resolution coupled with the

252 possibility to study both neutral and adaptive genetic variation are worth the effort (Rodriguez et

253 al., 2015; Lanes et al., 2018).

254   Electrical resistance was the most common resistance metric employed, revealing its ample

255 adoption as a general predictor of animal and plant gene flow (McRae & Beier, 2007).

256 Additionally, we found that Mantel and partial Mantel tests were the most widely used statistical

257 approaches to relate landscape and environmental characteristics with gene flow, even though

258 better methods are available (Prunier et al., 2015; Richardson et al., 2016). The limitations of

259 Mantel tests have been thoroughly discussed (Guillot & Rousset, 2013; Zeller et al., 2016), and

260 include high type-I error rates (i.e. false positives), the inability to model the effect of multiple

261 covariates simultaneously (as in a multiple regression), and the absence of a maximum-likelihood

262 framework that allows for model selection (Shirk et al., 2010; Shirk, Landguth & Cushman,

263 2018). Maximum likelihood population effects (MLPE) are particularly appealing mixed-effects

264 models for use landscape genetic studies because they allow implementing multiple regressions

265 that account for the non-independence of pairwise distances within a likelihood framework

266 (Clarke, Rothery & Raybould, 2002) compatible with model selection based on information

267 criteria such as AIC (Jaffé et al., 2016; Row et al., 2017; Shirk, Landguth & Cushman, 2018).

268   Most surveyed studies assessed gene flow responses to few landscape and environmental

269 variables, from which elevation, land cover and forest cover were the most common. For

270 instance, no plant study assessed the effect of water bodies; no reptile or plant study addressed

271 the effect of roads; and no mammal study considered temperature. Again, these finding suggest

272 data and societal preferences (Troudet et al., 2017), although the more limited availability of

273 environmental layers in tropical compared with temperate regions must be highlighted too.

274   Making available more spatially explicit environmental data in the tropics could certainly help

275   broaden the scope of future efforts to capture landscape effects on gene flow (Collen et al., 2008;

276   Barlow et al., 2018). The surveyed studies were nevertheless able to quantify functional

277   connectivity (Balkenhol et al., 2013; Carvalho et al., 2015; Ruiz-Lopez et al., 2015), propose

278   ecological corridors (Atickem et al., 2013; Yumnam et al., 2014), assess threat status (Lanes et

279   al., 2018), evaluate restoration effectiveness (Moraes et al., 2018), and forecast the impact of

280   future climate and environmental changes on gene flow (Thomassen et al., 2009; Velo-Antõn et

281   al., 2013; Thatte et al., 2018). Interestingly, several studies found an effect of habitat suitability

282   on gene flow, suggesting that habitat suitability models are useful when proposing ecological

283   corridors or forecasting the impact of future climate on gene flow (Franklin & Miller, 2009),

284   although habitat suitability does not always reflect permeability for dispersal (Mateo-Sánchez et

285   al., 2015). Additionally, elevation was responsible for most significant microsatellite-based IBR

286   effects (Figs. 7 and 8), a result that suggests elevation is an important mediator of functional

287   connectivity in tropical landscapes (Worboys, Francis & Lockwood, 2010).

288   Despite global concerns with the negative effects of habitat degradation on tropical

289   biodiversity (Barlow et al., 2018), only 25 studies have so far explicitly assessed the effect of

290   habitat degradation on gene flow. From these, only 14 found reduced gene flow with increasing

291   habitat loss, and a single microsatellite-based study reported a significant isolation by non-

292   forested areas in an army ant (Fig. 8). In contrast to other flying insects where both females and

293   males disperse, army ant queens are permanently wingless, so gene flow is restricted and mainly

294   driven by male dispersal (Jaffé, Moritz & Kraus, 2009; Pérez-Espona, McLeod & Franks, 2012).

295   These findings suggest that the effect of habitat loss on gene flow is difficult to detect, as species

296   with extremely restricted dispersal are more likely to show large effect sizes and thus be less

297   susceptible to type-II errors (false negatives).

298   Many sources of variation could have influenced the detection of landscape effects on gene

299   flow, including species-specific differences in dispersal ability and reproductive systems,

300   historical processes underpinning genetic differentiation, different sample sizes, the resolution of

301   the spatial data (grain size), the extent of the study area, sampling design, and time-lags in the

302   responses to landscape changes (Anderson et al., 2010; Balkenhol et al., 2016; Schlaepfer et al.,

303   2018). However, small sample sizes, limited information on the natural history of most studied

304   species and inconsistencies in the way data was reported across studies preclude a quantitative

305   assessment of the impact of these factors on our observed effect sizes (Dataset S3). Even though

306   the majority of the surveyed studies employed population-level approaches, individual-level

307 studies showed higher effect sizes, a finding that reinforces that individual-level analyses based
308 on continuously distributed samples are more powerful and appropriate for landscape genetic
309 studies (Landguth et al., 2010; Balkenhol et al., 2016). Additionally, studies that account for the
310 underlying population structure or inter-population variations in effective population size (Ne) are
311 more likely disentangle landscape from drift effects on gene flow (Prunier et al., 2017). This is
312 because population-level metrics of genetic connectivity like the frequently used F_{ST} actually
313 measures the balance between genetic drift on the one hand, and migration on the other. To the
314 best of our knowledge, none of the analyzed studies accounted for variations in Ne between
315 sample units when modeling IBR. This can be done by employing different distance metrics
316 [such as conditional genetic distance (Dyer, Nason & Garrick, 2010)], by restricting IBR models
317 to sample units belonging to the same genetic cluster (i.e. with the same Ne), by including a
318 random effect specifying the nature of pairwise genetic distances (from sample units belonging to
319 the same or different genetic clusters), or through gravity models that explicitly incorporate Ne or
320 other node-level proxy of population size (DiLeo & Wagner, 2016; Zero et al., 2017).

321

322 **Conclusions**

323 Our study reveals important knowledge gaps regarding landscape effects on gene flow in tropical
324 organisms, which prevent making cross-species generalizations. However, general patterns of
325 genetic connectivity provide important insights into common barriers to gene flow or responses
326 to land use changes (Poelchau & Hamrick, 2012; Wang, Glor & Losos, 2013; Paz et al., 2015;
327 Jaffé et al., 2016; Lanes et al., 2018). Such knowledge is particularly important to inform
328 conservation actions seeking to safeguard ecosystem function, and not only target species (Manel
329 & Holderegger, 2013b). Our work nevertheless provides some useful guidelines to help fill these
330 knowledge gaps: 1) Increased efforts are needed to study unrepresented taxonomic groups and
331 tropical areas outside the Americas, as well as generate more spatially explicit environmental data
332 in the tropics; 2) The adoption of genotyping by sequencing and individual-level approaches
333 could substantially increase statistical power and shed light into both neutral and adaptive
334 patterns of genetic variation; 3) Using mixed effect MLPE models to relate genetic and spatial
335 data, could minimize type-I errors, result in more accurate parameter estimates (which account
336 for multiple landscape and environmental predictors), and help establish a common model-
337 selection framework across landscape genetic studies (Row et al., 2017; Shirk, Landguth &
338 Cushman, 2018); 4) Explicitly modeling the impact of historical processes underpinning genetic
339 differentiation, the resolution of the spatial data, and possible time-lags (DiLeo & Wagner, 2016;

340   Waits LP, Cushman SA, 2016), could help provide more confidence in landscape effects on gene

341   flow and make IBR estimates comparable across studies.

342

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346

347   **Supplemental Information**

348   Supplemental Datasets.

349

350   **References**

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Figure 1

Sampling locations of the surveyed studies.

Taxonomic groups are indicated by colors and the unit of analysis by shapes (triangles indicate individual-level studies and circles population-level ones). Horizontal dotted lines represent the Tropic of Cancer, the Equator and the Tropic of Capricorn respectively, from North to South.
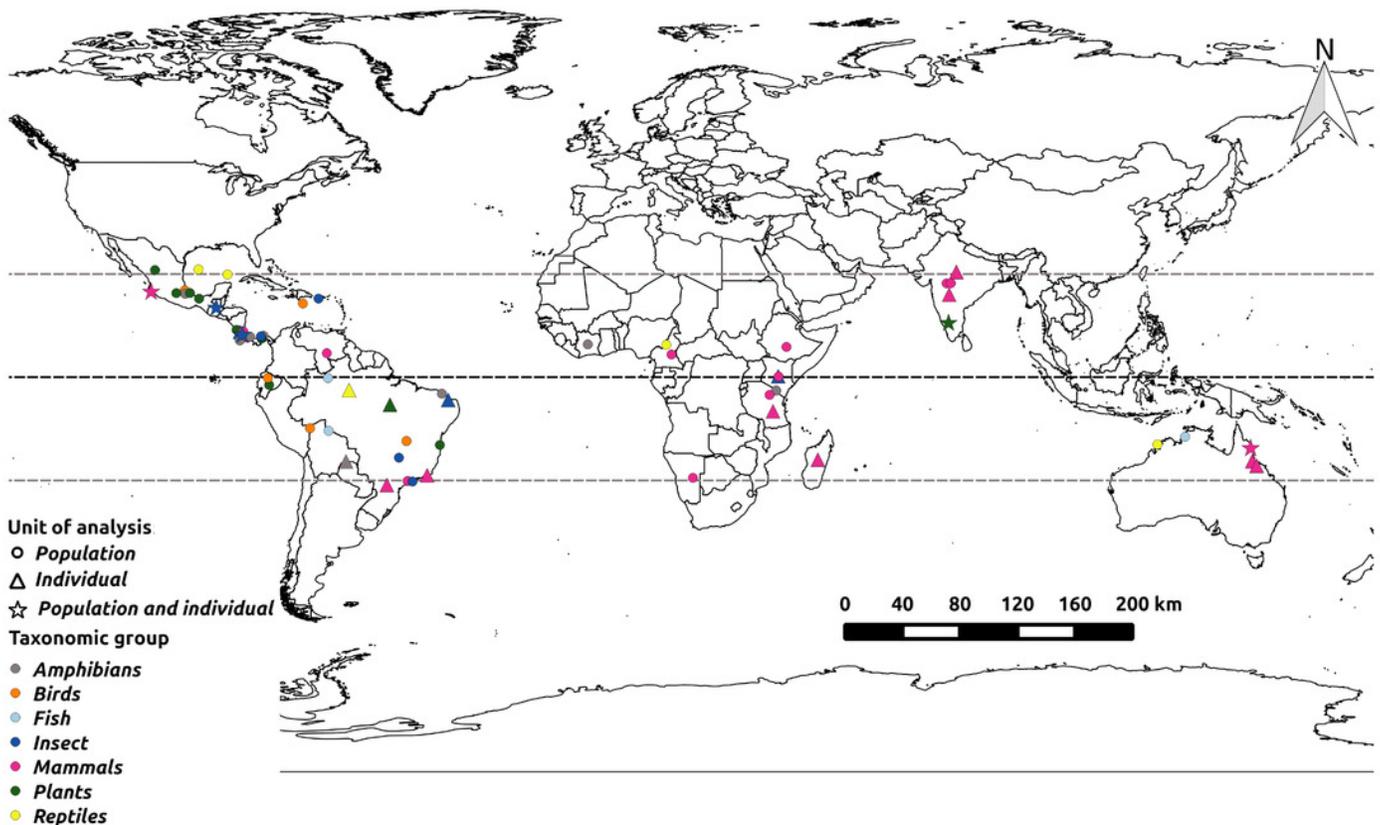
Figure 2

Number of species assessed and number of publications for each taxonomic group.
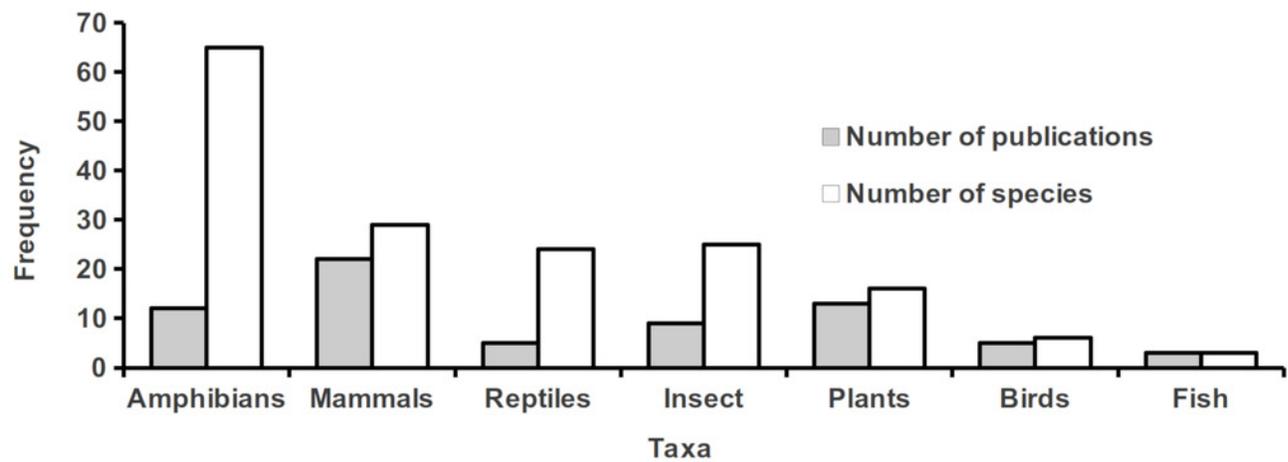
Figure 3

Number of studies assessing landscape effects on gene flow in tropical organisms, published between 2008 and 2018.
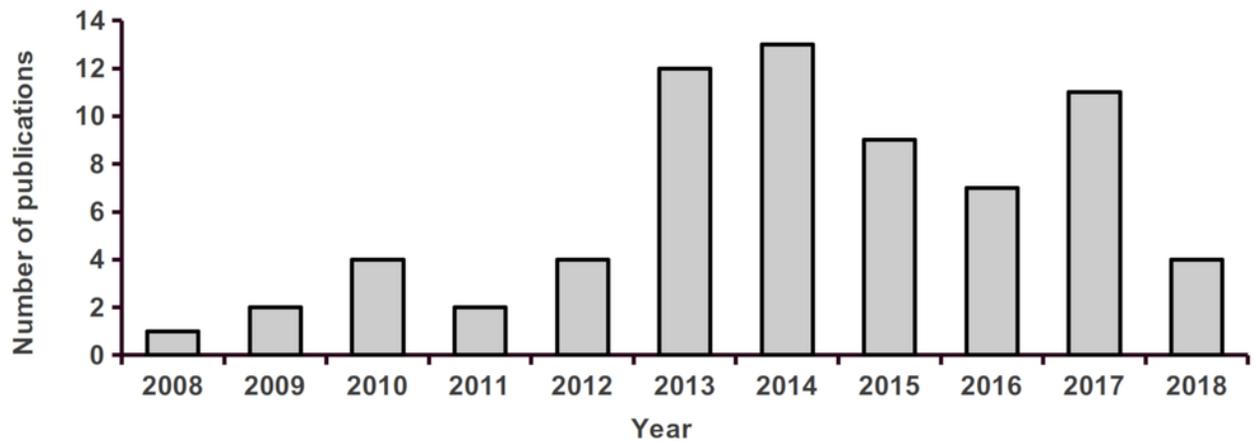
Figure 4

Proportion of studies using different types of genetic markers to assess landscape effects on gene flow in tropical organisms.

Microsatellites, AFLPs and SNPs refer to nuclear DNA. Mitochondrial DNA (mtDNA) and Chloroplast DNA (cpDNA) are specified as such.
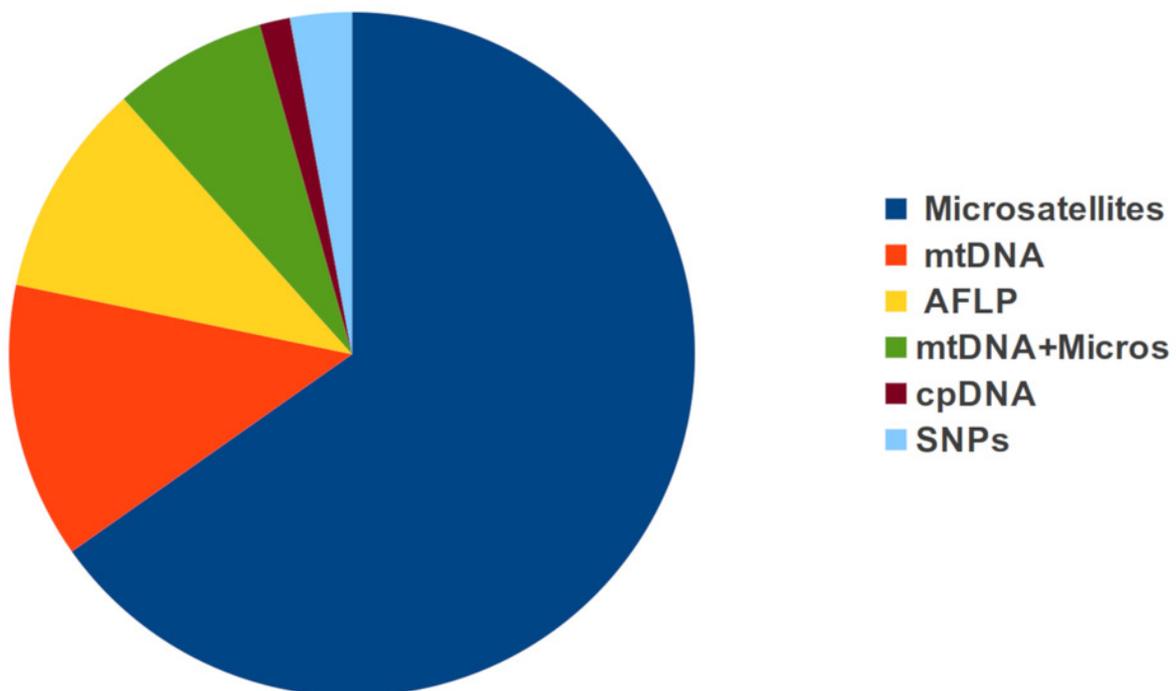
Figure 5

Number of studies using different statistical approaches to assess landscape effects on gene flow in tropical organisms.

Full methods names, by order of appearance on the figure are: Mantel and Partial Mantel tests, Maximum likelihood population effects (MLPE) models, generalized dissimilarity models (GDM), redundancy analyses (RDA), multiple regression on distance matrices (MRDM), generalized linear models (GLM), linear mixed-effect models (LMM), Monte Carlo permutation matrix regression technique (MCPMRT), matrix regression approach (MRA), Random Forest Analysis (RFA), Structural equation modelling (SEM), and Linear Model with Permutation (LMP).
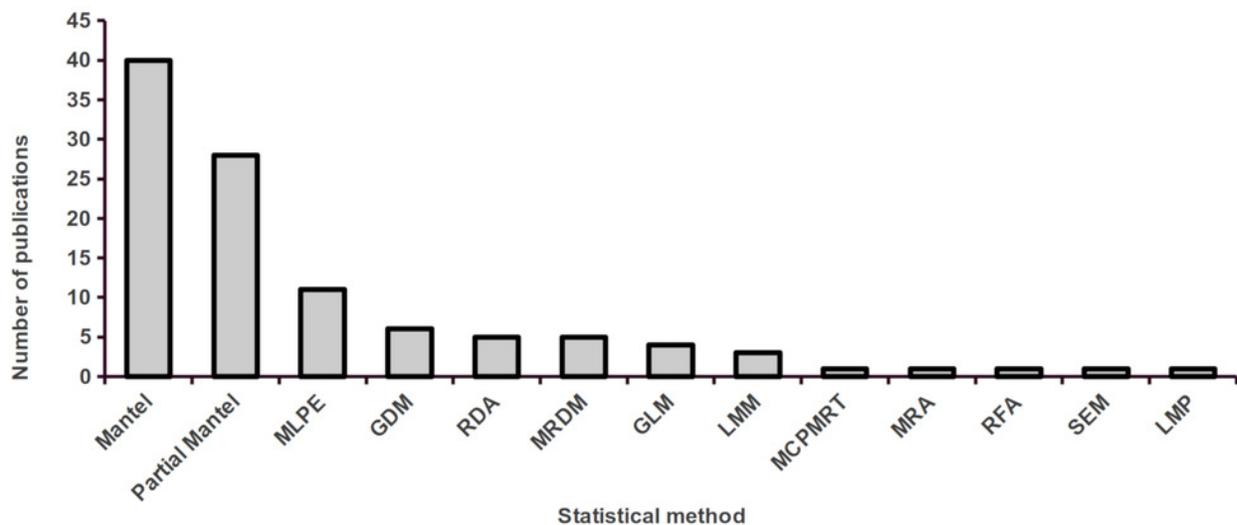
Figure 6

Number of studies focusing on different landscape effects on gene flow for each taxonomic group.

See Dataset S1 for details on the reported effects.
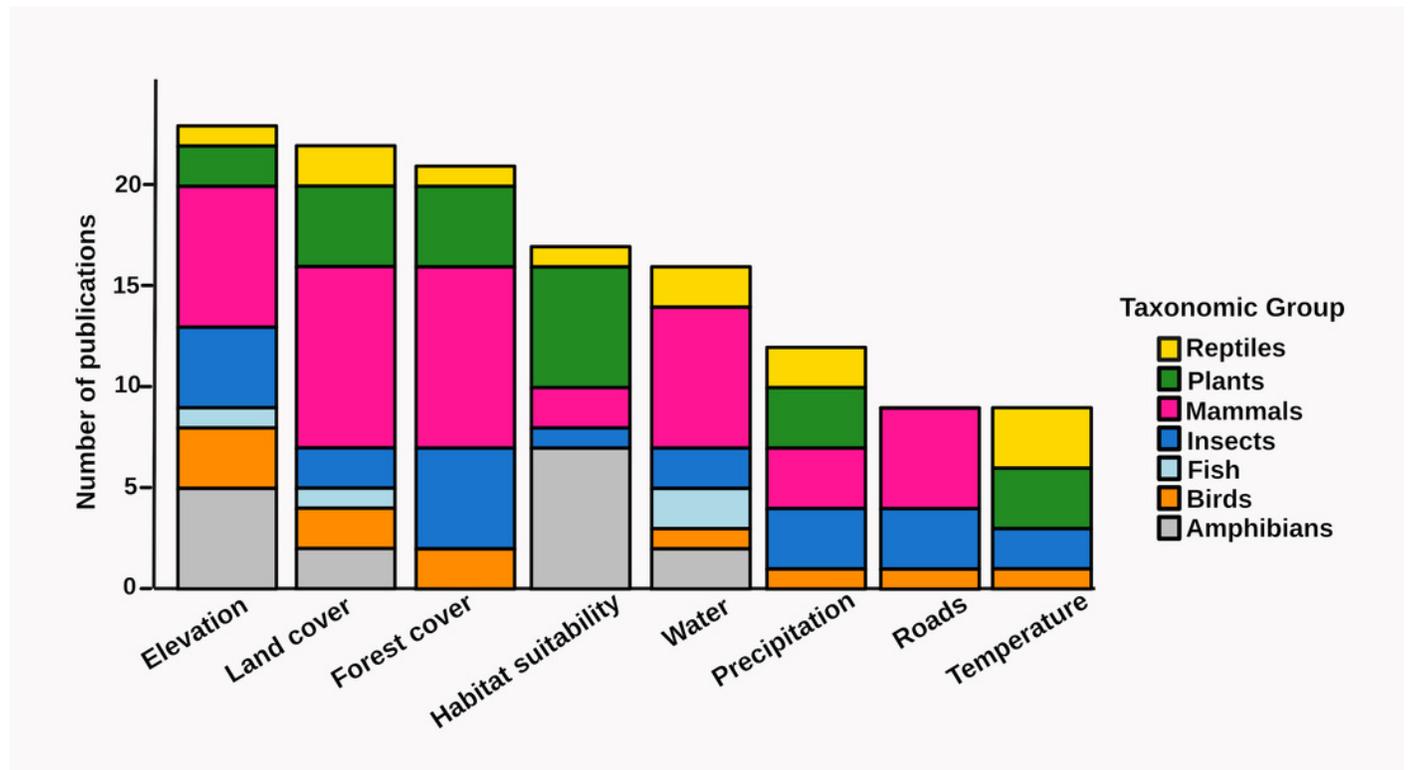
Figure 7

Individual-level effect sizes for isolation by geographic distance (a), isolation by elevation (b) and isolation by forest cover (c).

Dots represent effect sizes and colors indicate taxonomic groups. Significance of the effects reported in the original articles is also highlighted.
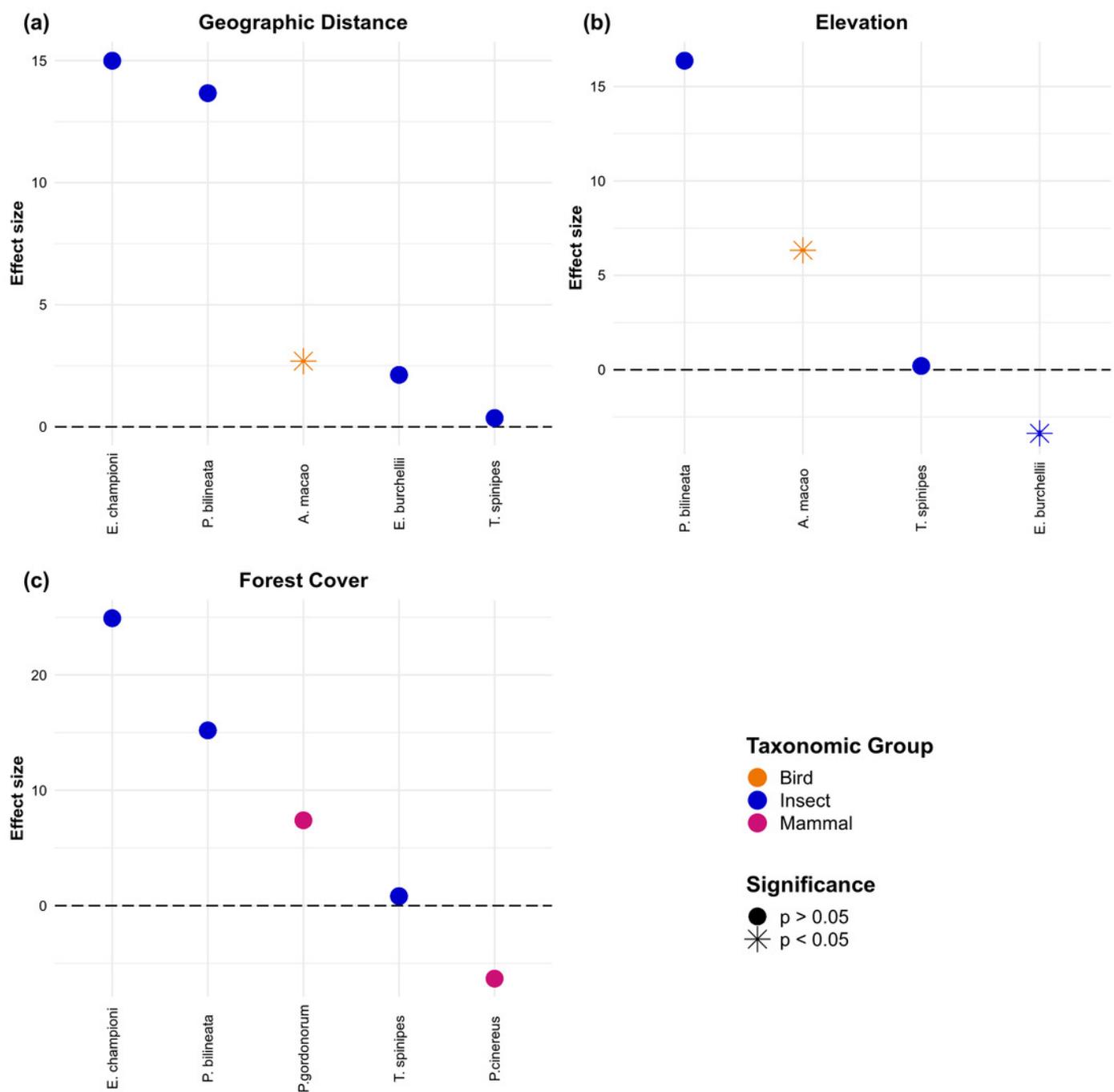
Figure 8

Population-level effect sizes for isolation by geographic distance (a), elevation (b), precipitation (c), temperature (d) and forest cover (e).

Dots represent effect sizes and colors indicate taxonomic groups. Significance of the effects reported in the original articles is also highlighted.