

# 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 70 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.

Microsatellites were the preferred type of markers, Mantel and partial Mantel tests the most common statistical approaches, and forest cover and elevation the most frequent gene flow predictors assessed. A third of all surveyed studies explicitly assessed the effect of habitat degradation, and only 12 of these detected a reduced gene flow with increasing habitat loss. Finally, elevation was found to be a key mediator of functional connectivity in tropical landscapes, as it was responsible for most significant isolation by resistance effects. 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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16

17 **Abstract**

18 The bulk of the world's biodiversity is found in tropical regions, which are increasingly  
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 70  
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. Microsatellites were the preferred type of markers, Mantel and partial Mantel tests the  
29 most common statistical approaches, and forest cover and elevation the most frequent gene flow  
30 predictors assessed. A third of all surveyed studies explicitly assessed the effect of habitat  
31 degradation, and only 12 of these detected a reduced gene flow with increasing habitat loss.  
32 Finally, elevation was found to be a key mediator of functional connectivity in tropical  
33 landscapes, as it was responsible for most significant isolation by resistance effects. Our study  
34 reveals important knowledge gaps on the study of landscape effects on gene flow in tropical  
35 organisms, and provides useful guidelines on how to fill them.

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37 **Keywords:** Functional connectivity; isolation by resistance; landscape genetics; matrix  
38 permeability; tropical biodiversity.

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## 42 **Introduction**

43 About two-thirds of all known species occur in tropical forests and the majority of the world's  
44 most threatened biodiversity hotspots are in the tropics (Myers et al., 2000; Brown, 2014).  
45 Extinction rates from habitat loss and fragmentation are acute in the region, and the degradation  
46 of essential ecosystem functions and services are threatening billions of people living in tropical  
47 countries (Bradshaw, Sodhi & Brook, 2009). However, the vast majority of studies assessing  
48 biodiversity responses to habitat degradation have been undertaken in temperate regions due to a  
49 lower investment in research and development in tropical countries (Collen et al., 2008; Barlow  
50 et al., 2018). For instance, a recent analysis of 182 studies describing links between biodiversity  
51 and ecosystem function (Clarke et al., 2017), found that only 13% were carried in the tropics, and  
52 nearly half of these (42%) were conducted in a single country (Costa Rica). There is thus a  
53 pressing need to reduce the knowledge gap concerning the impact of habitat loss and  
54 fragmentation on tropical biodiversity.

55 Community-level approaches assessing biodiversity responses to habitat degradation have  
56 focused on measuring changes in species richness, composition, and the abundance of indicator  
57 species (Morin, 2009). While these metrics underpin ecosystem function, they are not always be  
58 the best proxies to detect rapid responses to environmental changes. Local species extinctions  
59 may occur after long periods of time since the onset of disturbance (Jackson & Sax, 2009),  
60 whereas species abundance can be affected by multiple environmental or demographic factors  
61 unrelated to habitat degradation (Ehrlén & Morris, 2015). Moreover, complex inter-specific  
62 interactions can make natural communities resilient to environmental change and thus mask the  
63 effect of habitat degradation on community composition (Devictor, Julliard & Jiguet, 2008).  
64 Instead, population-level metrics based on genetic information can offer a higher resolution to  
65 detect rapid responses to environmental change (Manel & Holderegger, 2013a). For instance,  
66 changes in genetic diversity and gene flow patterns in response to recent landscape modification  
67 have been found across several species (Balkenhol et al., 2016a), although tropical organisms  
68 have been rarely assessed (Storfer et al., 2010a).

69 Even though the effect of habitat fragmentation on genetic variation has been reviewed  
70 extensively (Aguilar et al., 2006, 2008; Keyghobadi, 2007; Vranckx et al., 2012), there is an  
71 important knowledge gap regarding general landscape effects on gene flow. This is because the  
72 vast majority of landscape genetic studies have focused in a single species (but see (Waits LP,  
73 Cushman SA, 2016), and no efforts have yet been made to gather, standardize and compare  
74 isolation by landscape resistance (IBR) effects across studies and organisms. So far, gene flow

75 has been shown to be influenced by forest cover, land cover, topography, roads, rivers, and  
76 climate, but responses vary greatly across species and units of analysis (population or individual-  
77 level studies; see Balkenhol et al. 2016a and references therein). Understanding the factors  
78 underpinning functional connectivity across species is nevertheless essential to design ecological  
79 corridors, identify conservation units, assess population threat status, optimize pathogen and  
80 invasive specie's management, assist planning of natural heritage systems, and restore threatened  
81 populations (Keller et al., 2014; Bowman et al., 2016).

82 Here we compiled all studies that assessed landscape effects on gene flow in tropical  
83 species so far. To our knowledge, this work represents the first quantitative comparison of such  
84 effects across species and units of analysis. We believe this systematic review can help  
85 characterize the current knowledge gap on tropical biodiversity responses to habitat degradation,  
86 and thereby highlight future research needs.

87

## 88 **Survey Methodology**

### 89 ***Dataset***

90 We employed the following search engines to perform a recursive literature search of landscape  
91 effects on gene flow in tropical species published by June 2018: Scielo (<http://www.scielo.org>),  
92 Portal de Periódicos da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior do  
93 Ministério da Educação (CAPES/MEC) (<http://www.periodicos.capes.gov.br/>); Google Scholar  
94 (<http://www.scholar.google.com.br>); Web of Knowledge (<http://www.isiknowledge.com>), and  
95 Scopus (<http://www.scopus.com>). We used the following combination of keywords and Boolean  
96 operators: ("landscape resistance" or landscape or resistance or fragmentation or "land use" or  
97 "habitat loss" or deforestation) and (genetic\* or "genetic differentiation" or "gene flow" or  
98 "genetic distance" or FST or relatedness or kinship). Articles containing at least one of the  
99 keywords on each side of the "and" operator were analyzed along with the relevant references  
100 therein. Even though this search approach may not be easily replicated (as it involves a  
101 substantial effort), it is more likely to minimize omissions than approaches based on the results  
102 obtained from search engines alone. We then identified those studies that explicitly related  
103 landscape with gene flow metrics in organisms collected between the tropics of Cancer and  
104 Capricorn (23.5° north and south of the equator) or within 200km from them. Articles addressing  
105 only isolation by distance (IBD) were excluded, as our aim was to survey studies that specifically  
106 incorporated landscape effects on gene flow in addition to geographic distance. We then gathered  
107 all available information on the focus species, study site, types and number of genetic markers

108 employed, genetic distance metrics, landscape or environmental factors assessed, and the  
109 statistical methods employed to evaluate landscape effects on gene flow.

110

### 111 *Comparing landscape effects on gene flow across studies*

112 We performed both qualitative and quantitative comparisons of landscape effects on gene flow  
113 across studies. For the former, we grouped studies by the landscape or environmental factors  
114 assessed and the focus taxonomic group, and summarized all reported effects of habitat loss and  
115 fragmentation on gene flow. For the quantitative comparison we selected a subset of our dataset  
116 containing only studies that: i) Explicitly reported correlation or regression coefficients,  
117 calculated from at least three samples, and ii) Employed nuclear microsatellite markers to  
118 measure gene flow, given that measures of genetic differentiation obtained with other genetic  
119 markers are not directly comparable across studies (Wan et al., 2004; Balkenhol et al., 2016b).  
120 We then separated the studies fulfilling these requirements in two groups according to the units of  
121 analysis employed: Those using population-level metrics of genetic differentiation (Jost's D,  
122 Lynch, Euclidian Distance, FST or GST), and studies using individual-level metrics of genetic  
123 distance (Rousset's  $a$ , relatedness and kinship; Fig. 1). An effect size approach was used to  
124 compare isolation by resistance (IBR) within both types of studies (individual and population-  
125 level). Correlation coefficients were first normalized using the Fisher's z-transformation (z), and  
126 standard errors (se) were calculated as following:

127

$$128 \quad z = \frac{1}{2} \ln \left( \frac{1+r}{1-r} \right)$$

$$129 \quad se = \frac{1}{\sqrt{N-3}}$$

130

131 Where r is the correlation coefficient, ln the natural logarithm and N the number of pairwise  
132 comparisons (between individuals or populations). Effect sizes were then calculated dividing the  
133 normalized correlation coefficients and standard errors (z/se) (Ellis, 2010). Effect sizes of  
134 regression coefficients were calculated dividing them by their respective standard errors. To  
135 facilitate comparisons between population-level and individual-level metrics of genetic  
136 differentiation we inverted the sign of relatedness and kinship estimates, thus representing genetic  
137 dissimilarity. The statistical significance ( $p$ -values) of IBR effects reported in the original studies

138 were also retrieved. We note that effect sizes were only used for comparative purposes, and that  
139 no formal meta-analysis was performed.

140

## 141 **Results**

142 We found a total of 70 articles assessing landscape effects on gene flow in tropical organisms  
143 (Dataset S1 in Supplemental Information), most of which were undertaken in The Americas (Fig.  
144 1). We recorded 157 target species belonging to eight major taxonomic groups, from which  
145 amphibians and mammals were the best represented (Fig. 2). Most studies analyzed a single  
146 species, but nine publications evaluated two or more. Some of these multi-species studies (Wang,  
147 Glor & Losos, 2013; Paz et al., 2015; Jaffé et al., 2016) contributed with more than 40% of all  
148 recorded species. The oldest study found in our literature search (Trénel et al., 2008) investigated  
149 the impact of contemporary Andean landscape features on the spatial genetic structure of a palm  
150 tree. After this work, we observed a jump in the number of publications from 2013 onwards (Fig.  
151 3).

152 Five types of molecular markers were found across all studies (Fig. 4), and only five  
153 publications used more than one type of marker. Microsatellites were the most frequently used  
154 markers, with more studies using them than publications using all other markers combined. We  
155 found eleven statistical methods employed to relate landscape variables with gene flow, from  
156 which Mantel and partial Mantel test were the most common (Fig. 5). Landscape and  
157 environmental predictors of gene flow included forest cover, habitat suitability (derived from  
158 species distribution models), land cover, elevation, precipitation, temperature, roads and water  
159 (rivers, streams and the ocean; Fig. 6, Dataset S1). From these, elevation and forest cover were  
160 the most frequent predictors across all studies.

161 The effect of habitat loss on gene flow was assessed in 25 studies and 39 species (Dataset  
162 S2). From these, only 12 studies detected a reduction of gene flow with increasing habitat loss in  
163 three plants, five mammals, one amphibian, two birds and one insect. Remarkably, most insects  
164 were unaffected by habitat loss. Only 11 articles reported microsatellite-based IBR effects,  
165 comprising 26 species (Dataset S3). Whereas IBD drove most significant effects across this group  
166 of studies, individual-level studies (N = 13 effects; Fig. 7) showed higher effect sizes than  
167 population-level ones (N = 81 effects; Fig. 8). Two individual-level IBR effects were significant  
168 (revealing isolation by elevation in a bird and an ant, Fig. 7), and four significant IBR effects  
169 were identified in population-level studies (revealing isolation by elevation in a frog, a plant and  
170 a bee, and isolation by deforestation in an ant, Fig. 8).

171

172 **Discussion**

173 Despite the extraordinary levels of biological diversity comprised in the tropics, the study of  
174 landscape effects on gene flow in tropical organisms only began to gain general attention in the  
175 past five years. Still, published studies are mainly concentrated in the Americas and most of them  
176 have focused on amphibians or mammals. Microsatellites were by far the most frequently  
177 employed type of molecular marker, and Mantel and partial Mantel tests the most common  
178 statistical approaches used. Forest cover and elevation were the most common gene flow  
179 predictors assessed, and only 12 studies detected a reduced gene flow with increasing habitat  
180 loss. Finally, elevation was responsible for most significant microsatellite-based IBR effects.

181         Although landscape genetics is still a relatively new field of research (Manel et al., 2003),  
182 it has now become an independent interdisciplinary discipline (Dyer, 2015). One of its main aims  
183 is to understand how landscape characteristics shape patterns of functional connectivity, a subject  
184 that has been addressed by many studies undertaken in temperate regions (Balkenhol et al.,  
185 2016a). Here we show that the study of landscape effects on gene flow in tropical organisms has  
186 lagged behind, and that published studies are concentrated in the Americas, as are general  
187 research effort on biodiversity in human-modified tropical forests (Gardner et al., 2009).  
188 Moreover, we found that amphibians and mammals were over represented in our surveyed  
189 studies,  
190 reflecting taxonomic biases in biodiversity data and societal preferences (Troudet et al., 2017).  
191 Our results thus highlight how little we still understand about landscape effects on gene flow in  
192 the tropics, and call for more studies on unrepresented taxonomic groups and tropical areas  
193 outside the Americas.

194         Most of the surveyed studies used microsatellite markers, despite the not so recent shift  
195 towards genotyping by sequencing (GBS) triggered by next generation sequencing technologies  
196 (Allendorf, Hohenlohe & Luikart, 2010; Benestan et al., 2016). For instance, microsatellite  
197 genotyping is still cheaper than GBS, and cross-amplification of SSR markers in related species  
198 often reduces the cost of developing species-specific markers (Storfer et al., 2010b). However,  
199 SNPs are rapidly becoming the new standard in population and landscape genomic studies, due to  
200 their genome-wide coverage and analytical simplicity (Morin, Luikart & Wayne, 2004).  
201 Moreover, sequencing costs have fallen dramatically (Shendure et al., 2017), and GBS  
202 approaches (such as RAD-sequencing) allow an affordable high-coverage sequencing of a  
203 representation of the genome and the discovery of thousands of SNPs in organisms lacking a

204 reference genome (Rowe, Renaut & Guggisberg, 2011; Hohenlohe, Catchen & Cresko, 2012).  
205 Perhaps the most important obstacle preventing the widespread adoption of GBS is the  
206 complexity of bioinformatic processing and working with very big datasets (Johnson, 2009), but  
207 we believe that a much higher resolution coupled with the possibility to study both neutral and  
208 adaptive genetic variation are worth the effort (Rodriguez et al., 2015; Lanes et al., 2018).

209 We found that Mantel and partial Mantel tests were the most widely used statistical  
210 approaches to relate landscape and environmental characteristics with gene flow, even though  
211 better methods are already available (Richardson et al., 2016). The limitations of Mantel tests  
212 have been thoroughly discussed (Guillot & Rousset, 2013; Zeller et al., 2016), and include high  
213 type-I error rates (i.e. false positives), a maximum of two predictor variables that can be  
214 simultaneously analyzed, and the absence of a maximum-likelihood framework that allows for  
215 model selection (Shirk et al., 2010; Shirk, Landguth & Cushman, 2017). Maximum likelihood  
216 population effects (MLPE) are particularly appealing for landscape genetic studies because they  
217 allow implementing multiple regressions that account for the non-independence of pairwise  
218 distances within a likelihood framework (Clarke, Rothery & Raybould, 2002; Row et al., 2017),  
219 compatible with model selection (Jaffé et al., 2016; Shirk, Landguth & Cushman, 2017).

220 Most surveyed studies assessed gene flow responses to few landscape and environmental  
221 variables, from which forest cover and elevation were the most common. This finding seems to  
222 reflect the more limited availability of environmental layers in tropical compared with temperate  
223 regions (Balkenhol et al., 2016b), and highlights the need to generate more spatially explicit  
224 environmental data in the tropics (Collen et al., 2008; Barlow et al., 2018). Nonetheless, the  
225 surveyed studies were able to quantify functional connectivity (Balkenhol et al., 2013; Da Silva  
226 Carvalho et al., 2015; Ruiz-Lopez et al., 2015), propose ecological corridors (Atickem et al.,  
227 2013; Yumnam et al., 2014), assess threat status (Lanes et al., 2018), evaluate restoration  
228 effectiveness (Moraes et al., 2018), and forecast the impact of future climate and environmental  
229 changes on gene flow (Thomassen et al., 2009; Velo-Antón et al., 2013; Thatte et al., 2018).  
230 Interestingly, elevation was responsible for most significant microsatellite-based IBR effects  
231 (Figs. 7 and 8), a result that underlines the role of elevation as a key mediator of functional  
232 connectivity in tropical landscapes (Worboys, Francis & Lockwood, 2010).

233 Despite global concerns with the negative effects of habitat degradation on tropical  
234 biodiversity (Barlow et al., 2018), only 25 studies have so far explicitly assessed the effect of  
235 habitat loss on gene flow. From these, only 12 found reduced gene flow with increasing habitat  
236 loss, and a single study reported a significant isolation by deforestation in an army ant (Fig. 8). In

237 contrast to other flying insects where both females and males disperse, army ants queens are  
238 permanently wingless, so gene flow is restricted and mainly driven by male dispersal (Jaffé,  
239 Moritz & Kraus, 2009; Pérez-Espona, McLeod & Franks, 2012). This result suggests that the  
240 effect of habitat loss on gene flow is difficult to detect, as species with extremely restricted  
241 dispersal are more likely to show large effect sizes and thus be less susceptible to type-II errors  
242 (false negatives). Additionally, time-lags in the responses to landscape changes have been shown  
243 in several species (Hanski & Ovaskainen, 2002; Jackson & Sax, 2009), and barriers to gene flow  
244 are more difficult to detect in species with longer generation times (Landguth et al., 2010).  
245 Alternatively, perhaps many tropical organisms are in fact able to maintain high levels of gene  
246 flow across degraded and heterogeneous landscapes (Jaffé et al., 2016).

247

## 248 **Conclusions**

249 Our study reveals important knowledge gaps regarding landscape effects on gene flow in tropical  
250 organisms, which prevent making cross-species generalizations. However, cross-species patterns  
251 of genetic connectivity provide important insights into common barriers to gene flow or  
252 differential responses to land use changes (Poelchau & Hamrick, 2012; Lanes et al., 2018). Such  
253 knowledge is particularly important to inform conservation actions seeking to safeguard  
254 ecosystem function, and not only target species (Manel & Holderegger, 2013b). Our work  
255 nevertheless provides some useful guidelines to help fill these knowledge gaps: 1) Increased  
256 efforts are needed to study unrepresented taxonomic groups and tropical areas outside the  
257 Americas, as well as generate more spatially explicit environmental data in the tropics; 2) The  
258 adoption of genotyping by sequencing and individual-level approaches could substantially  
259 increase statistical power and shed light into both neutral and adaptive patterns of genetic  
260 variation; 3) Using statistical methods based in maximum-likelihood to relate genetic and spatial  
261 data (such as MLPE models), could minimize type-I errors, result in more accurate parameter  
262 estimates (which account for multiple landscape and environmental predictors), and help  
263 establish a common model-selection framework across landscape genetic studies; 4) Reporting  
264 statistical power and testing for possible time-lags, could help provide more confidence in  
265 landscape effects on gene flow, and thereby make IBR estimates comparable across studies.

266

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270

271 **Supplemental Information**

272 Supplemental Datasets.

273

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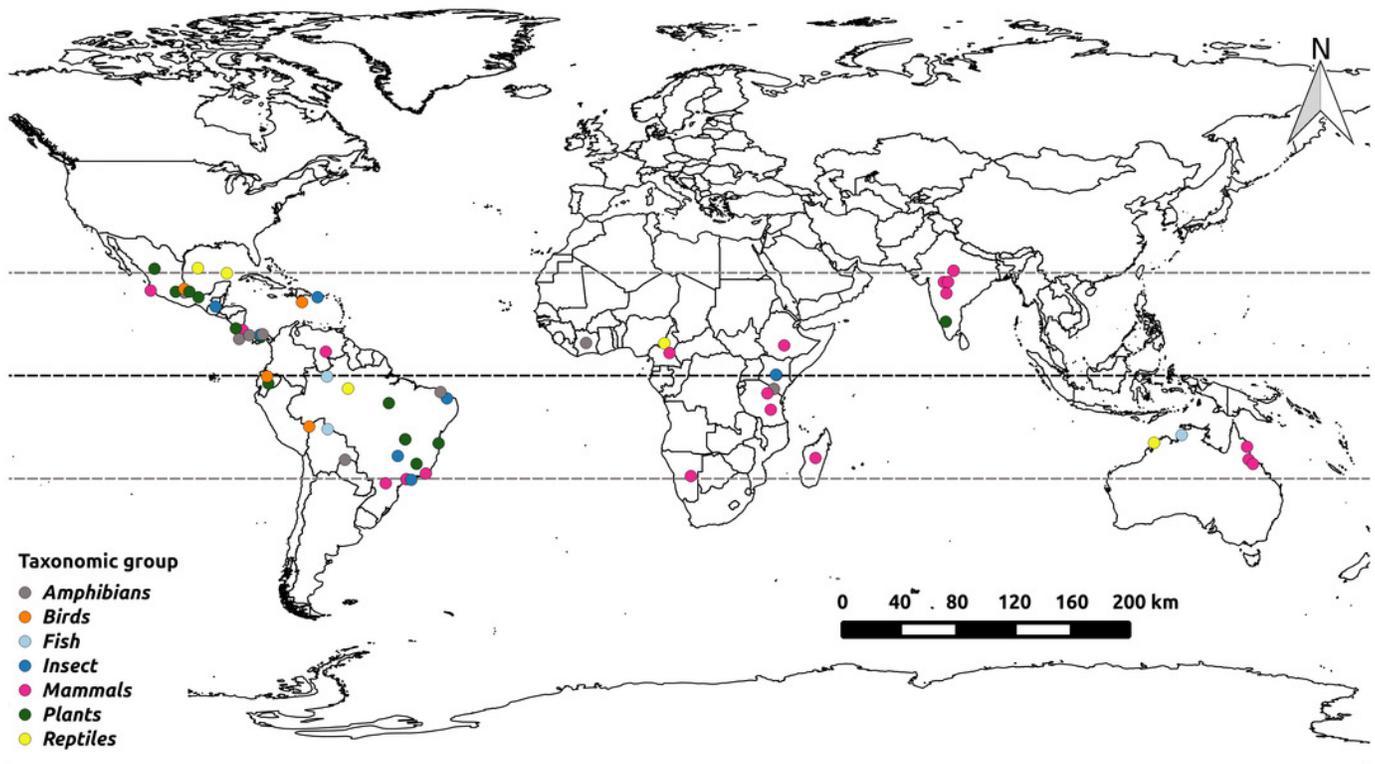
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456

# Figure 1

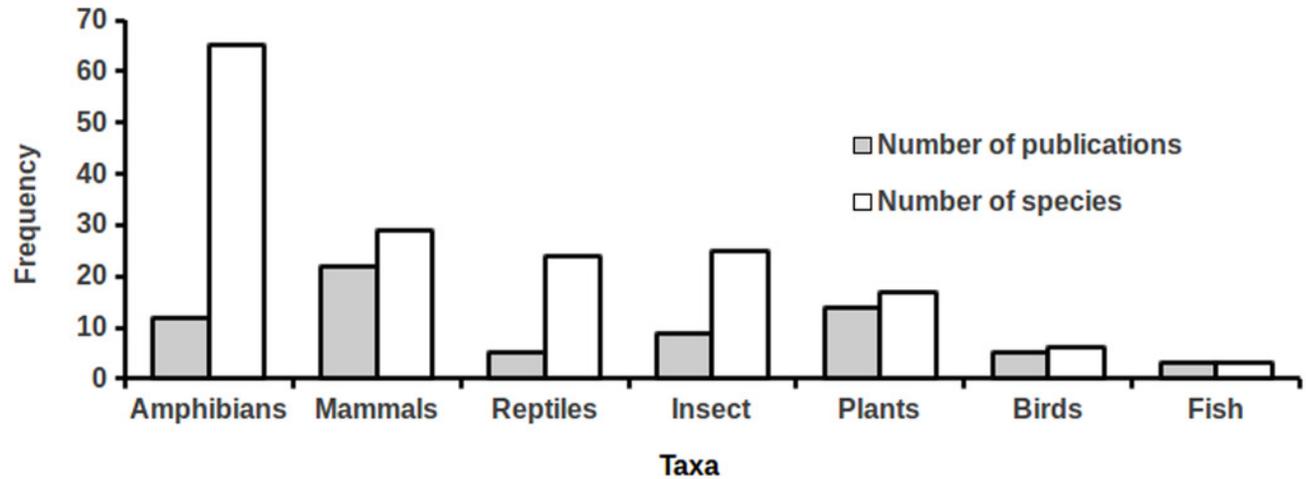
Sampling locations of the surveyed studies.

Taxonomic groups are indicated by colors.



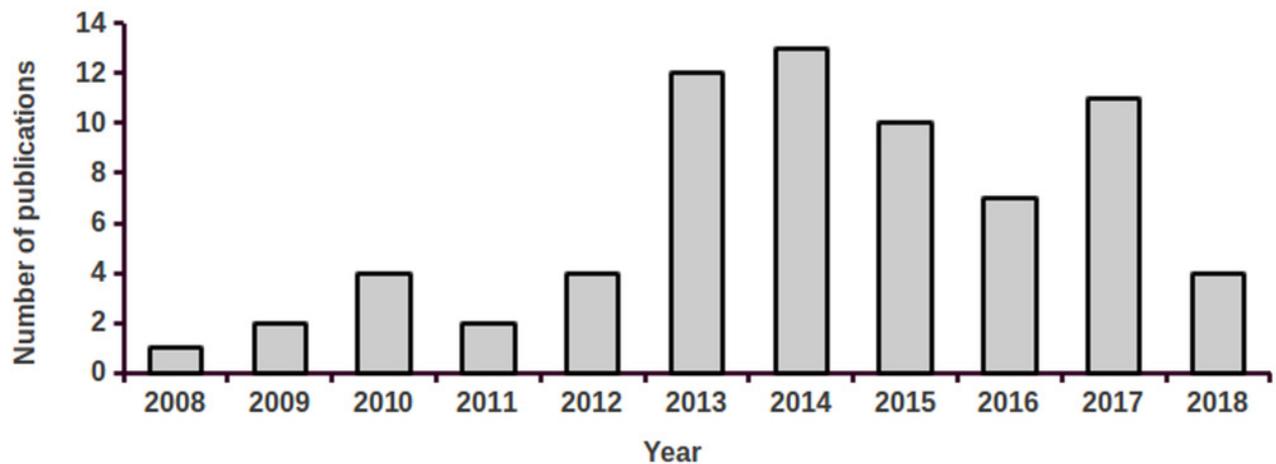
## Figure 2

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



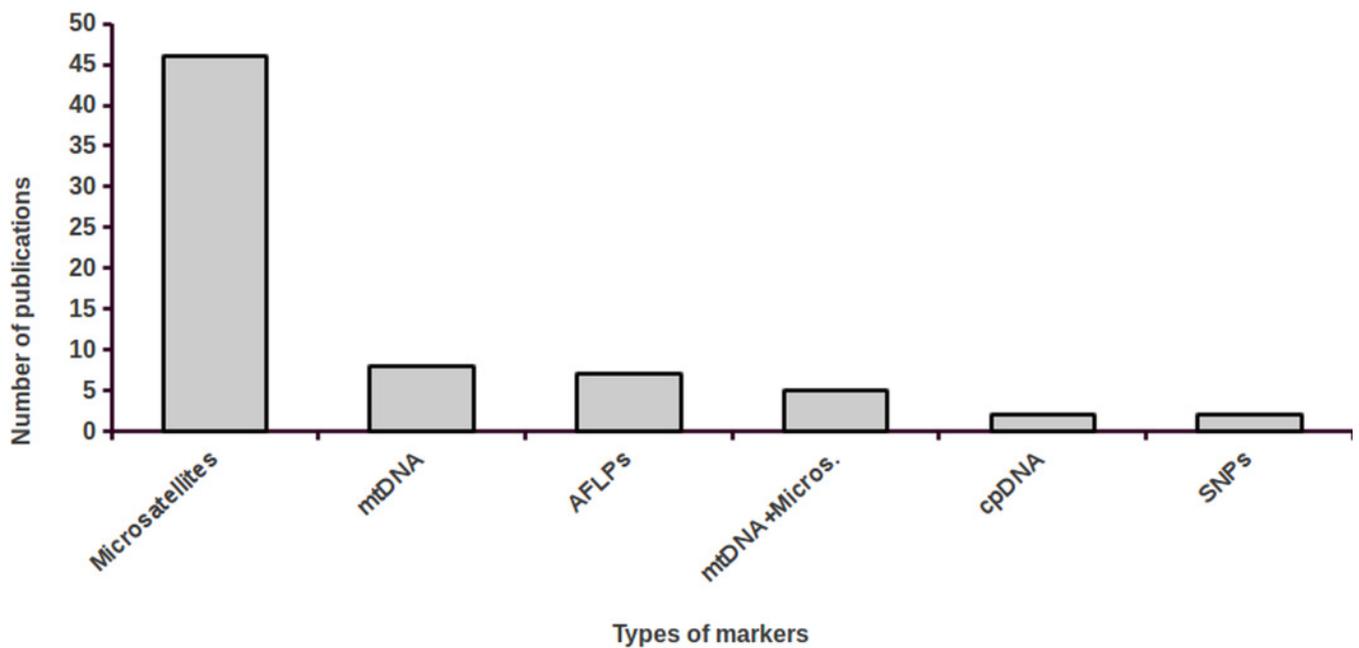
## Figure 3

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



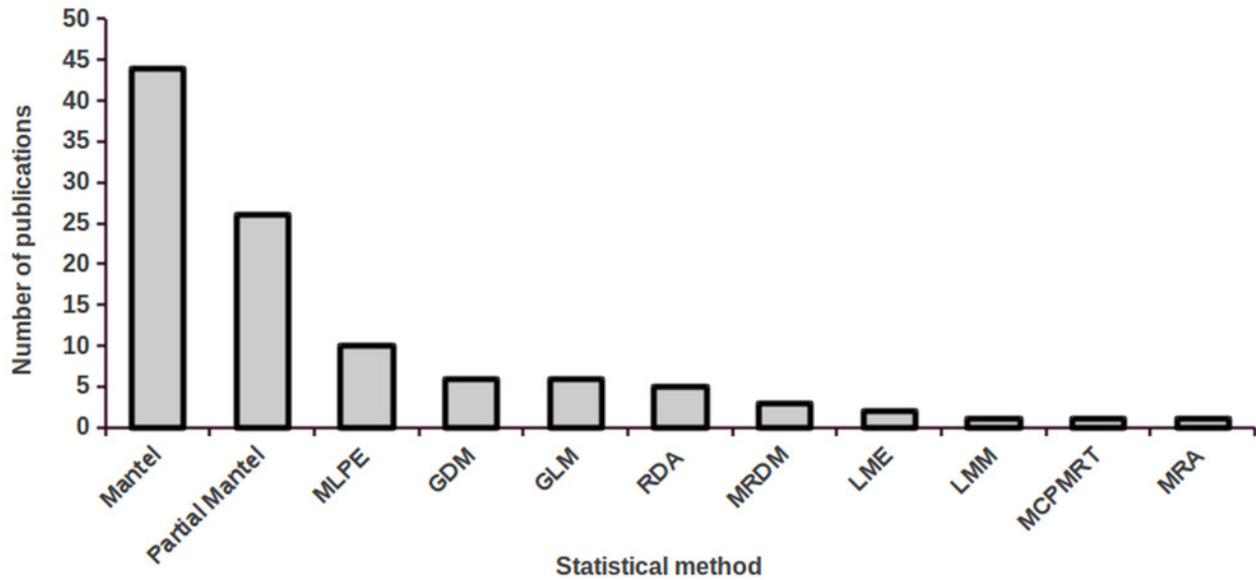
## Figure 4

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



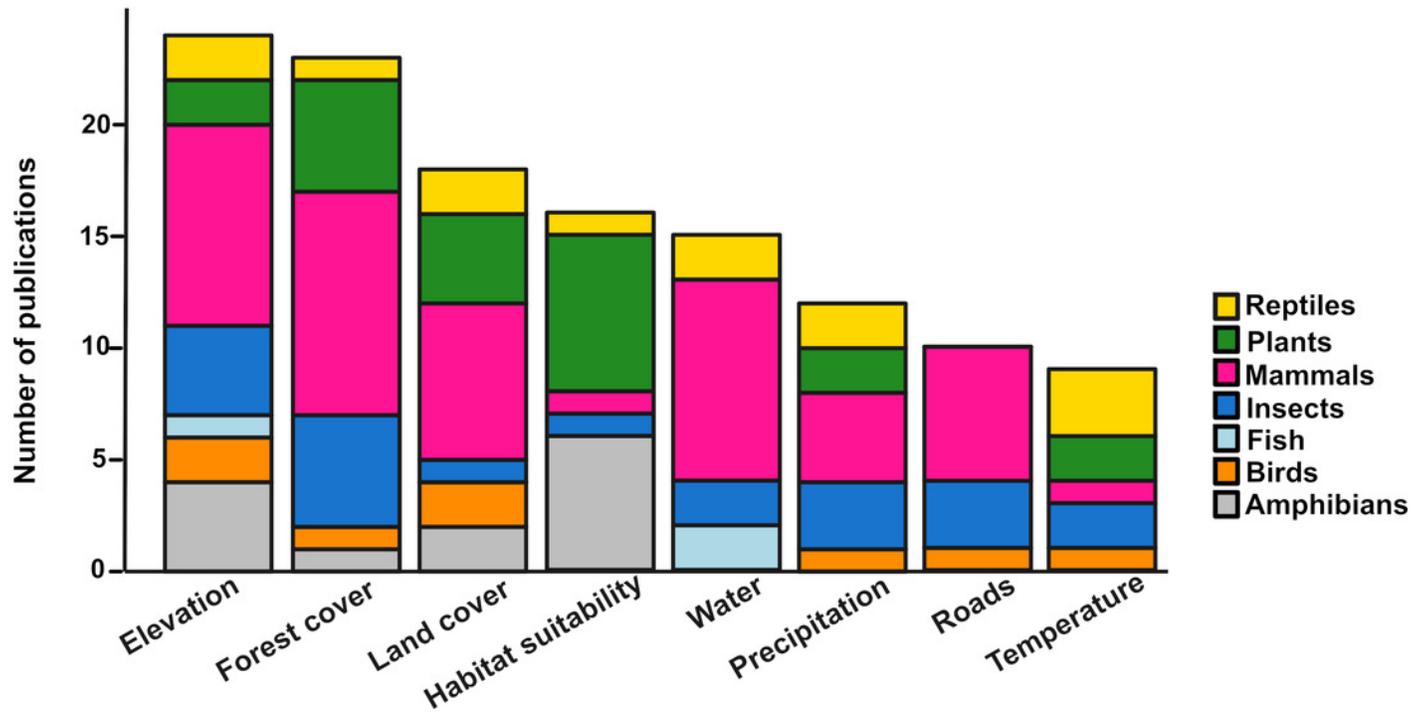
## Figure 5

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



## Figure 6

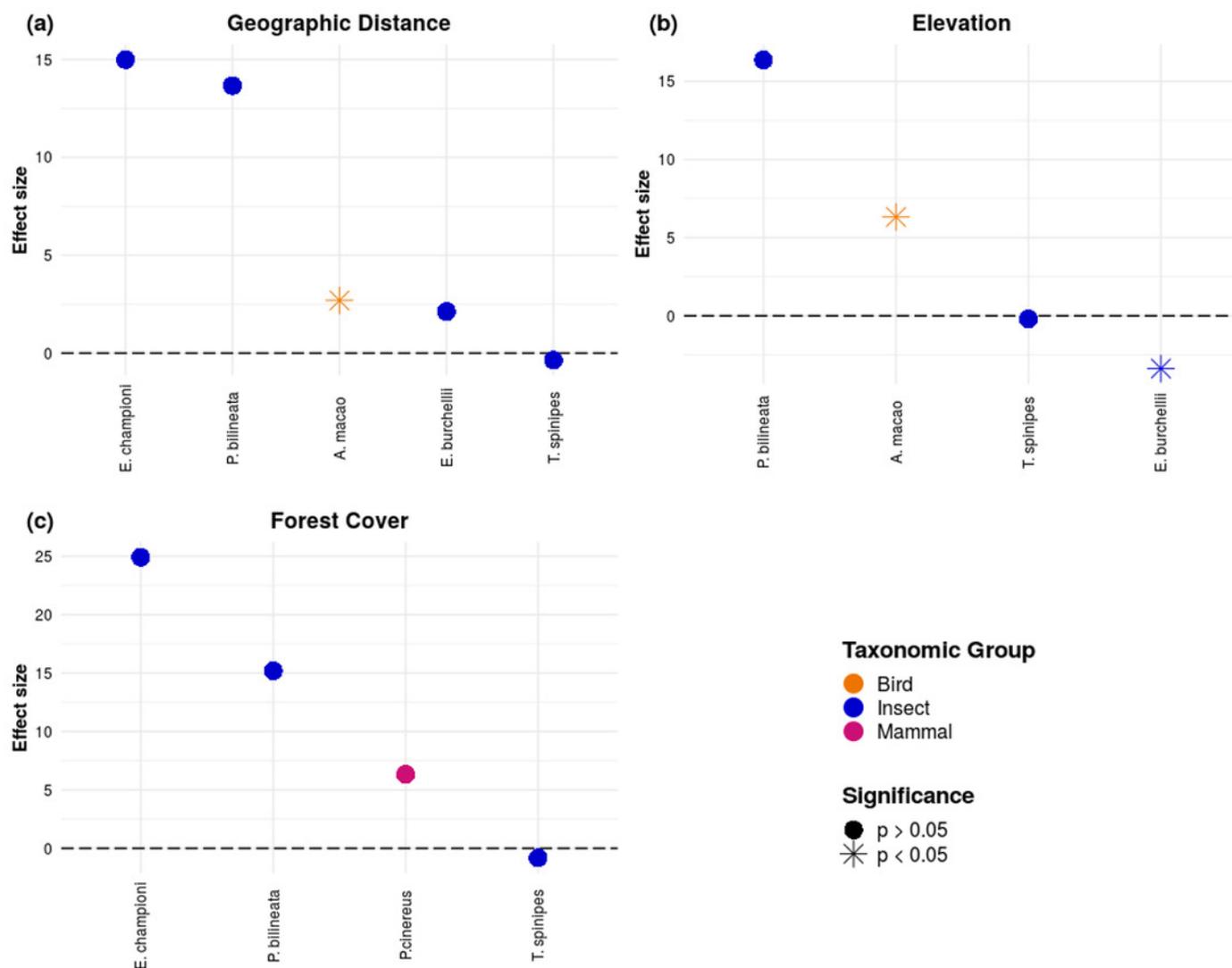
Number of studies focusing on different landscape effects on gene flow for each taxonomic group.



## Figure 7

Individual-level isolation by resistance (IBR) effect sizes.

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



## Figure 8

Population-level isolation by resistance (IBR) effect sizes.

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

