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Title: Inter-basin dispersal through irrigation canals explains low genetic structure in *Diplomystes cf. chilensis*, an endangered freshwater catfish from Central Chile

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1 Inter-basin dispersal through irrigation canals explains low genetic structure in *Diplomystes* cf.  
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15

16 Abstract

17 Biotic homogenization in freshwater ecosystems is a growing concern among conservation  
18 biologists. Recent phylogeographic data has shown low genetic structure between some basins  
19 from Central Chile, hypothesizing that either current dispersal through irrigation canals or  
20 incomplete lineage sorting due to recent divergence might explain the observed patterns.

21 However, these hypotheses remain untested despite their potential implications for freshwater  
22 biodiversity and conservation. We used a statistical, model-based framework (approximate  
23 Bayesian computation) to investigate the relative support for each of these hypotheses. Our

24 results show strong support for the model involving current migration between basins, and  
25 rejected the model of recent divergence without migration. These results strongly suggest that  
26 irrigation canals are facilitating the dispersal between basins, posing a serious threat to  
27 biodiversity in Central Chile, an area considered a biodiversity hotspot. Finally, these results  
28 highlight the utility of model-based approaches for determining demographic processes with  
29 potential conservation implications, even with the lack of extensive molecular data.

30 Keywords: Biotic homogenization; biodiversity hotspot; approximate Bayesian computation;  
31 mtDNA; aquatic biota.

32

### 33 Introduction

34 Biotic homogenization is a serious threat to the integrity of endemic species and genetic pools  
35 that can result in the loss of continental, regional, and local biodiversity (Olden et al., 2004).  
36 Human constructions such as the Suez Canal and the opening of the St Lawrence Seaway are  
37 striking examples of human activities that have facilitated the movement of hundreds of  
38 estuarine and freshwater species (Galil, 2000; Ricciardi and MacIsaac, 2000), although better  
39 known examples are provided by the introduction of invasive species at a continental or  
40 worldwide scale (Olden, 2006). These events have shown varied negative effects on the diversity  
41 of the regions impacted, including reduction of  $\beta$ -diversity, species extinctions, and genetic  
42 homogenization (Olden et al., 2004).

43

44 At a smaller scale, a less studied human activity that has the potential to reduce diversity in  
45 freshwater environments is the artificial connection of historically isolated river drainages. A few

46 cases of drainage interconnections facilitating inter-basin fish dispersal have been reported in the  
47 literature. For instance, the Snowy and Murray Rivers in Australia were artificially connected as  
48 the result of a major hydroelectric project during the early 20th century, facilitating the  
49 migration of the fish species *Galaxias brevipinnis*, an aggressive migratory species, into the  
50 Murray basin where the species was previously unrecorded (Waters et al., 2002). Similarly in  
51 New Zealand, Esa et al. (2000) reported that the connection of Otago's two major river systems,  
52 the Taieri and the Cluthathe, by tunnels from mining activities resulted in the introgressive  
53 hybridization of two previously allopatric galaxiid species. Although just a few studies have  
54 reported freshwater fish migration between different river basins through human mediated  
55 connections, they highlight the need for documenting these phenomena and studying its  
56 consequences for regional and local biodiversity.

57  
58 The area of Central Chile concentrates the highest human population density of the country, and  
59 due to optimal climatic conditions, a strong agricultural activity (Fuentes and Hajek, 1979). The  
60 area is drained by small and parallel river basins that originate in the Andes and discharge into  
61 the Pacific Ocean, after running just a few hundreds of kilometers. Due to the constant demand  
62 for water from increasing agricultural activity, a number of projects have altered the natural  
63 hydrological landscape of this area by expanding the irrigation network. Some of these  
64 alterations have resulted in the current connection of previously isolated drainages, such as the  
65 Teno-Chimbarongo Canal in Central Chile that links the Rapel and Mataquito basins, and the  
66 Zañartu Canal connecting the Itata and Biobío basins. Despite the potential threat to the  
67 biodiversity of the region, there is a complete lack of studies addressing this issue, and no reports  
68 of inter-basin dispersal through these canals have been reported up to date. However, there is

69 some evidence suggesting that dispersal through these uncovered, stream-like canals might be  
70 possible. Along with the documented presence of fish in some of these canals, which may be  
71 using them as an extension of their natural habitats (Habit and Parra, 2001; Habit, 1994), a recent  
72 phylogeographic study on a catfish genus has found low genetic structure and shared haplotypes  
73 between these basins (Muñoz-Ramírez et al., 2014). This study, which analyzed patterns of  
74 genetic variation from sequences of mitochondrial DNA, showed that even though a high amount  
75 of genetic diversity was partitioned across river basins with unique lineages in most drainages  
76 across the distribution of this group (Muñoz-Ramírez et al., 2014), some basins in Central Chile  
77 exhibited low inter-basin genetic structure, particularly between the Rapel and Mataquito basins  
78 (Fig. 1).

79  
80 Two hypotheses were suggested in Muñoz-Ramírez et al., (2014) to explain the lack of genetic  
81 structure in these basins. One points out that current migrations between these basins might be  
82 occurring through irrigation canals (e.g. the Teno-Chimbarongo Canal, Fig. 1), reducing genetic  
83 structure by genetic homogenization. The second suggested that the lack of genetic  
84 differentiation could be explained by incomplete lineage sorting resulting from a relatively recent  
85 divergence following the last Pleistocene glaciation. Opportunities for headwater rearrangements  
86 and river captures might have occurred when glaciers melted approximately 10,000 years ago  
87 (Ruzzante et al., 2006).

88  
89 The consequences of potential connections between historically isolated basins might bring  
90 unforeseen impacts to the diversity of this region, which is considered an important hotspot of  
91 biodiversity (Myers et al., 2000). Thus, it is urgent to know whether these basins are exchanging

92 fauna. However, testing these hypotheses with molecular data requires the use of methods that  
93 rigorously assess the relative support of these alternative scenarios and not simply rely on *ad hoc*  
94 explanations of the molecular patterns (Knowles, 2003). Current model-based approaches have  
95 proven to be powerful tools to test alternative demographic models, allowing the assessment of  
96 competing historical scenarios and the estimation of important demographic parameters  
97 (Bertorelle et al., 2010; Csilléry et al., 2010; Fagundes et al., 2007). In this study, we use a  
98 model-based simulation approach (approximate Bayesian computation) that allows the  
99 probabilistic comparison of alternative demographic models and the simultaneous estimation of  
100 demographic parameters to test whether current dispersal through irrigation canals or incomplete  
101 lineage sorting resulting from recent divergence better explain the observed genetic patterns in  
102 an endangered catfish, *Diplomystes cf. chilensis*.

103

## 104 Material and Methods

### 105 *Study system*

106 Central Chile is considered a hotspot of biodiversity (Myers et al., 2000). This area is also one of  
107 the most threatened in Chile as it concentrates high levels of urbanization, forestry, and  
108 agriculture (Aronson et al., 1998; Azócar et al., 2007). One of the rarest, but also interesting  
109 group of fish inhabiting these rivers are the diplomystids, a group of endangered catfish  
110 recognized as one of the earliest branching lineages in the diverse order Siluriformes (Arratia,  
111 1987; Sullivan et al., 2006). Diplomystids species are rare, have low fecundity (Vila et al., 1996),  
112 and exhibit generally low genetic diversity compared with other co-distributed fish species  
113 (Muñoz-Ramírez et al., 2014; Victoriano et al., 2012). All Chilean species are considered  
114 Endangered (CONAMA 2008). Their geographic distribution has decreased in recent times as

115 they have gone extinct from two basins in the north part of their distribution (Aconcagua and  
116 Maipo basins; Muñoz-Ramírez et al., 2010), presumably as a consequence of habitat  
117 deterioration and the introduction of exotic species (Arratia, 1987). In this regard, irrigation  
118 canals may pose a new type of threat for their survival and a challenge for their conservation  
119 which needs to be investigated.

120

#### 121 *Haplotype network*

122 We reconstruct a haplotype network focusing on the northern distribution of the genus to  
123 highlight the shallow relationships between lineages from different basins in this region (Fig. 2).  
124 This was done by using the same sequences (GenBank's accession numbers JX648663–  
125 JX649064) and following the same methodology as in Muñoz-Ramírez et al. (2014), using the  
126 software Network 4.610 (Bandelt et al., 1999) for build the haplotype network, and DnaSP 5.0  
127 (Librado and Rozas, 2009) to infer the haplotypes and their frequencies.

128

#### 129 *Simulation analyses*

130 The approximate Bayesian computation (ABC) approach can be briefly described as follows (for  
131 more details about this statistical technique see the reviews of Bertorelle et al., 2010, Csilléry et  
132 al., 2010, and Sunnåker et al., 2013). A large number of genealogies are simulated assuming  
133 different combinations of parameter values and demographic models. Simulations that produce  
134 genetic patterns (reduced to summary statistics) close to the observed patterns are retained for  
135 posterior analyses. Posterior probabilities of the models are estimated by the relative proportion  
136 of simulations retained by each model, and parameter values are then estimated based on the  
137 selected model and the posterior distribution of its parameters. We used an ABC approach as

138 implemented in the ABCtoolbox (Wegmann et al., 2010), using SIMCOAL 2.0 (Laval and  
139 Excoffier, 2004) to simulate the data, and a command line version of the program Arlequin 3.5  
140 (arlsuostat) (Excoffier and Lischer, 2010) to calculate the summary statistics of each simulation.  
141 We focussed on two river basins to build our models, The Rapel and the Mataquito Basins,  
142 because they i) represent a monophyletic sample of individuals (see Fig. 2), ii) exhibit the lowest  
143 levels of between-basin genetic structure, and iii) allow reducing the complexity of the models  
144 being compared (see the schematic representation of the models in Fig. 3). The first model (Fig.  
145 3A) represents the historical scenario of divergence after the last glaciation with no admixture  
146 (hereafter the “Model I”). The second model (Fig. 3B) represents the scenario of current inter-  
147 basin dispersal through artificial canals (hereafter Model II). These two models are similar,  
148 except in that in the Model II, basins are allowed to interchange individuals in recent times (since  
149 100 years ago). Model parameters are fully described in Table 1. All model parameters being  
150 sampled were drawn from a uniform distribution to allow an unbiased exploration of the  
151 parameter space. Regardless of the prior distribution chosen, posterior distribution can usually be  
152 approximated from the retained simulations with confidence, assuming the model being tested is  
153 a fair representation of the process under study. The parameter T\_DIV (i.e. time since divergence  
154 between basins) was sampled in the range of 2,000 to 5,000 generations (4,000–10,000 ybp).  
155 This range seems reasonable because it is old enough to capture the end of the last glaciation  
156 (assuming a generation time of 2 years), but young enough to allow capturing potential  
157 connective events of a more recent age (up to 4,000 ybp). The effective population size (i.e.  $N_e$ ,  
158 the number of haploid genes in a deme) for the Rapel basin ( $N_{e2}$ ) was set equal to twice the  
159 population size of the Mataquito basin ( $N_{e1}$ ) to take into account the differences in size of the  
160 basins. The Mataquito basin drains an area of  $\sim 6,000\text{Km}^2$  (Source:



161 [http://www.sinia.cl/1292/articles-31018\\_Mataquito.pdf](http://www.sinia.cl/1292/articles-31018_Mataquito.pdf)), whereas the Rapel basin drains an area  
162 of  $\sim 13,000 \text{ Km}^2$  (source: [http://www.sinia.cl/1292/articles-31018\\_Rapel.pdf](http://www.sinia.cl/1292/articles-31018_Rapel.pdf)). Population sizes  
163 were sampled in the range of 10–500 individuals in every simulation. This range is reasonable  
164 given the small size of both basins and the biological characteristics of the species. Population  
165 sizes in the range of 500–2,500 have been reported for a catfish from the Murray-Darling basin  
166 in Australia (Rourke and Gilligan, 2010) inhabiting a basin with an area of 1,000,000  $\text{Km}^2$ , three  
167 orders of magnitude larger than the basins studied here. Furthermore, diplomystids are known to  
168 be rare and of low fecundity (Habit et al., 2006; Vila et al., 1996) which suggests small  
169 population sizes. The mutation rate parameter was sampled in the range of 0.00002 to 0.00008  
170 substitutions per locus per generation and, a generation time of two years was assumed based on  
171 literature (Vila et al., 1996). Regarding sequence evolution of the simulated sequences, a  
172 transition/transversion ratio was set to 0.33. A total of 200,000 data sets were simulated per  
173 model with the same characteristics of the empirical data set used in Muñoz-Ramírez et al.  
174 (2014), which consisted of 36 mtDNA sequences of 2073 base pairs in length (13 and 23  
175 sequences from the Rapel basin and the Mataquito basin, respectively; GenBank's accession  
176 numbers JX648663–JX648698 and JX648864–JX648899). The Tajima's D neutrality index (a  
177 commonly used statistic to infer demographic expansion),  $\pi$  (the average number of pairwise  
178 differences), and  $S$  (the number of polymorphic sites) were used to summarize intra-basin genetic  
179 patterns, whereas  $F_{st}$  (a measure of the degree of population subdivision) was used to  
180 characterize the genetic structure between the basins. These statistics were chosen because they  
181 are usually highly informative about pattern of genetic diversity at the population level. Only  
182 those simulations that produced summary statistics very close to the observed patterns  
183 (Euclidean distance of 1 or smaller between the observed and the simulated summary statistics)

184 were retained for further analyses. A post-sampling regression adjustment was performed under  
185 the ABC-GLM approach to improve the estimation of parameters (Leuenberger and Wegmann,  
186 2010). Based on the results from the model selection procedure, the best supported model was  
187 then used to estimate some additional parameters, such as  $N_1$  and  $N_2$  as independent free  
188 parameters and the migration rate between basins ( $m$ ). Here, both  $N_1$  and  $N_2$  were sampled from  
189 a uniform distribution and range 10–250. Migration rate was sampled from a uniform  
190 distribution with range 0.01–0.3 (proportion of the population per generation).

191

## 192 Results

193 The summary statistics produced the following results when applied to the empirical dataset:

194  $S_{\text{Mataquito}} = 1$ ,  $S_{\text{Rapel}} = 0.9359$ ,  $D_{\text{Mataquito}} = -0.9180$ ;  $D_{\text{Rapel}} = -0.7748$ ,  $\pi_{\text{Mataquito}} = 1.7628$ ,  $\pi_{\text{Rapel}} = 4.2051$ ,

195  $F_{st} = 0.0614$ . The results from the simulations showed that Model I (no admixture) was unable to

196 reproduce the observed patterns described above (see Fig. 4 for an example with two summary

197 statistics). For example, Fig.4 shows that although Model I was able to reproduce  $\pi$  values close

198 to the observed in a small proportion of simulations,  $F_{st}$  values produced by this model were far

199 from those observed from the empirical data. On the contrary, Model II (recent admixture)

200 produced simulated patterns that were very close to the observed patterns (Fig. 4). This pattern

201 was consistent across all summary statistics studied, but more accentuated for  $F_{st}$ . (Fig. 5).

202 Based on the model selection procedure, the posterior probability of Model II was 1.0 versus a

203 value of 0.0 for the Model I. This means that all the retained simulations (1237 simulations or

204 0.3%) were obtained from Model II and none was retained from Model I since all simulations

205 from model I produced genetic patterns that were over the minimum Euclidean distance to the

206 observed summary statistics. In addition, the marginal density of Model II was 10341.8 resulting

207 in a p-value of 1, while the marginal density of Model I was  $4736E^{-241}$ , resulting in a p-value of  
208 0. Based on these results, we then used Model II to estimate some demographic parameters of  
209 interest. We found that  $N_e$  were 49.1 and 18.6 for the Rapel and the Mataquito basins,  
210 respectively (Fig. 6A–B). The migration rate ( $m$ ) between basins was 0.23, indicating that a 23%  
211 of each population is migrating between basins per generation (Fig. 6C). The mutation rate was  
212 estimated in 0.000027 substitutions per locus per generation (Fig. 6D). The simulated data was  
213 not informative for the time of divergence ( $T_{DIV}$ ; Fig. 6E).

214

## 215 Discussion

216 Our analyses showed that obtaining the observed genetic patterns of low genetic structure  
217 between basins is unlikely from a model without admixture, even for divergences as recent as  
218 2,000 generations ago (or 4,000 ybp). On the other hand, the observed patterns were easily  
219 obtained with a model that takes into account current admixture. These results strongly support  
220 the scenario of dispersal through irrigation canals as the most likely explanation for the observed  
221 genetic patterns, and reject the possibility that they can represent a case of incomplete lineage  
222 sorting due to recent divergence. The generality of this finding needs to be investigated with  
223 other taxa, but similarly low genetic structure in another catfish (*Trichomycterus areolatus*;  
224 Unmack et al., 2009) suggests that dispersal between basins might be a more general  
225 phenomenon involving several species. Furthermore, the presence of these canals connecting  
226 other basins further south (e.g. the Itata and Biobio basins; Habit, 1994) suggests that the impact  
227 on biodiversity might be even more geographically widespread than currently recognized,  
228 involving distinct biogeographic areas, and unique freshwater fish assemblages (Dyer, 2000).

229

230 Migration between basins may impact biodiversity at different scales (Olden, 2006). At a  
231 population level, the impact of these inter-basin migrations has the potential to erode genetic  
232 differentiation that has been accumulating for thousands of years with the inevitable consequence  
233 of a lack of overall regional genetic diversity (Olden et al., 2004) and the disruption of local  
234 adaptations (Storfer, 1999). At the species level, homogenization may result in the introgressive  
235 hybridization between closely related species with the potential result of species merging, and  
236 consequently, a lack of species richness (Rhymer and Simberloff, 1996). In addition, it may  
237 cause extinctions by competitive exclusion. With scarce knowledge on the ecology of species, it  
238 is hard to predict whether ecologically similar species from different basins may coexist if they  
239 migrate into adjacent basins or the exclusion of the less competitive species will take place. In  
240 the case of diplomystids, the scarce literature about their ecology suggest that species and  
241 populations from different basins occupy the same trophic niche (Beltrán-Concha et al., 2012)  
242 and similar habitats (Arratia, 1983), which would suggest that either strong negative interactions  
243 or complete genetic homogenization may occur, depending on the degree of reproductive  
244 isolation between lineages. Finally, regional diversity may still decrease without extinctions by  
245 the simple fact of homogenization of the unique biotas of each basin. In other words, the  
246 distinctiveness of different biogeographic provinces can be reduced as endemics of each basin  
247 spread to adjacent areas, in detriment of the  $\beta$  diversity of the region (Olden, 2006).

248

249 Our results exemplify the power of ABC methods to distinguish between different demographic  
250 scenarios in general, and demonstrate they can be successfully applied to test hypotheses in the  
251 context analyzed here in particular. Additional multilocus data may add statistical power to

252 estimate multiple demographic parameters more accurately. However, the approach used here  
253 proved to be powerful enough for model testing.

254

255 Although our results are robust and provide strong evidence of inter-basin dispersal for *D. cf.*  
256 *chilensis*, confirmation and quantification with more direct types of evidence (e.g. mark and  
257 recapture techniques) would help to better estimate the magnitude of organismal movement  
258 between basins and the degree of impact on the aquatic community. Are all species equally likely  
259 to migrate between basins? When and under what conditions they migrate? What will be the  
260 consequences for the biodiversity of the region? What species will be more affected? What can  
261 be done to reduce the potential impact of this new threat? All these questions remain to be  
262 investigated and further research needs to be conducted to fully understand the impact of this  
263 poorly known, but probably common, environmental alteration on the conservation of freshwater  
264 biodiversity. Answers to these questions will be key to not only better assess the impacts of these  
265 alterations, but also to better plan and manage future developments in a region that face  
266 increasing water demands.

267

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370 Figure 1 Study area in Central Chile showing river basins and a representation of the Teno-  
371 Chimbarongo canal. Black dots are localities from where *Diplomystes cf. chilensis* were sampled  
372 (for more details about sampling see Munoz-Ramírez et al. 2014)

373 Figure 2 Haplotype network based on a 2073 bp region of mitochondrial DNA. (A), haplotype  
374 network of the entire family (from Muñoz-Ramírez et al. 2014). (B), detail on the Clade I or  
375 North clade representing the species *D. cf. chilensis*. Note the low genetic structure between the  
376 Rapel and the Mataquito basins, as shared haplotypes between both basins are common

377 Figure 3 Models tested by the ABC approach. In both models, the divergence time (T\_DIV) was  
378 set to 2,000–5,000 generations in the past (4,000–10,000 ybp) and the effective population size  
379 ( $N_e$ ) to 10–500 individuals for both basins. The difference between these two models was that in  
380 the admixture model, basins were allowed to interchange individuals at a rate of 10% of the total  
381 population per generation

382 Figure 4 Values for two summary statistics produced by simulations under the two models  
383 investigated in this study. Only 1% of the simulations (i.e. the retained simulations) are shown.  
384 Model I corresponds to the model without admixture, whereas Model II corresponds to the  
385 model with admixture. The intersection of the red lines corresponds to the observed values from  
386 the empirical data. Note that the x axis was reduced to better show the data

387 Figure 5 Results from the summary statistics obtained from the simulated data under the Model I  
388 (no admixture) and model II (recent admixture).  $F_{st}$  was calculated between basins. The red  
389 dashed line represents the value obtained from the empirical data

390 Figure 6 Posterior densities for parameters in Model II. This model is a modification of model II  
391 (best supported model) used for hypotheses testing, and include the population size of Rapel  
392 basin ( $N_{e2}$ ) as a free parameter (i.e. not constrained to be twice the population size of the Rapel  
393 basin), and the migration rate parameter ( $m$ ). (A), Population size of Mataquito basin ( $N_{e1}$ ). (B),  
394 population size of Rapel basin ( $N_{e2}$ ). (C), migration rate ( $m$ ). (D), divergence time ( $T_{DIV}$ ). (E),  
395 mutation rate (MTDNA\_RATE).

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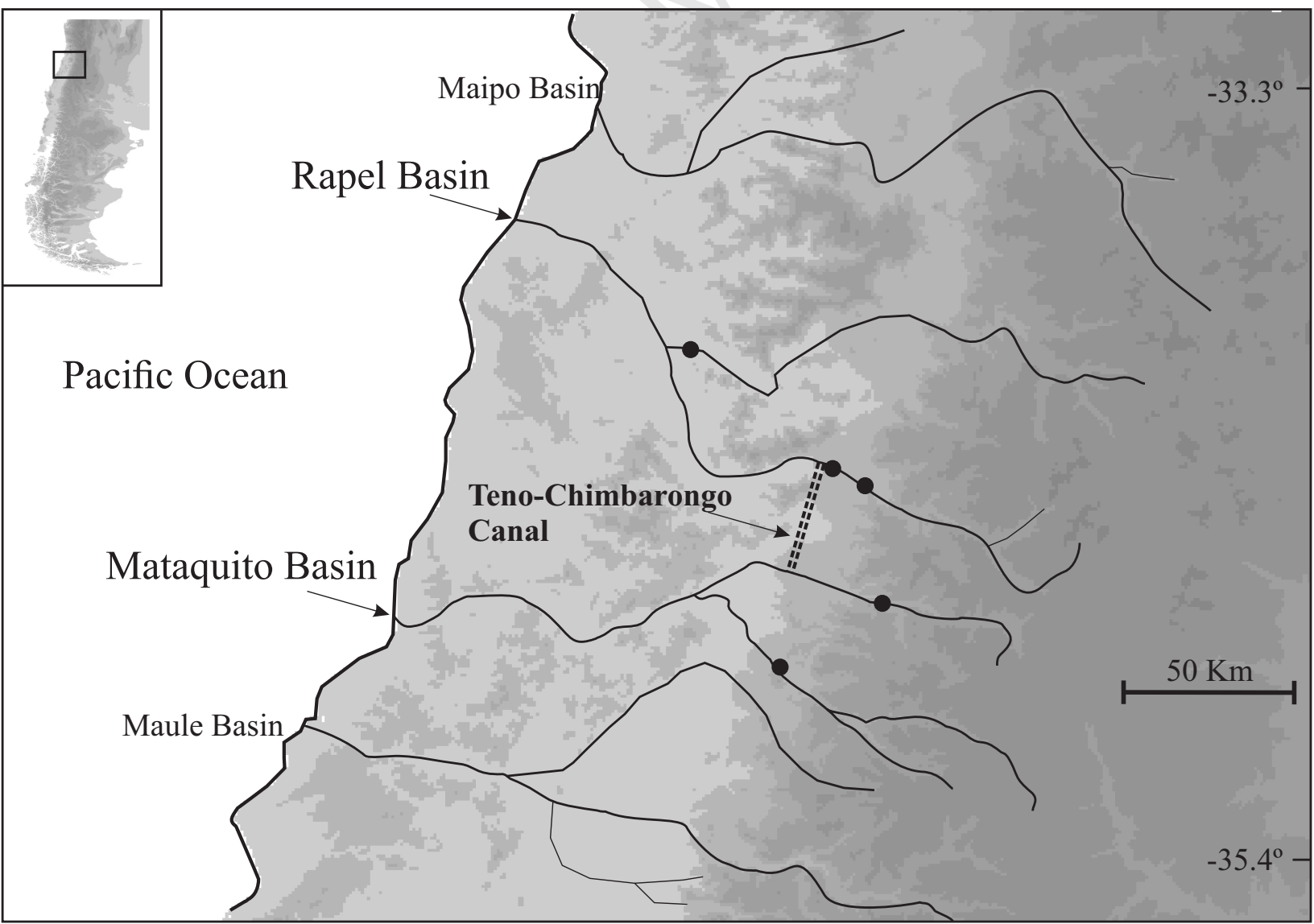
- 398 1. Using a model-based statistical approach, we found strong evidence that the endangered  
399 catfish *Diplomystes cf. chilensis* is dispersing between historically isolated basins through  
400 irrigation canals.
- 401 2. The high levels of migration between basins inferred suggest high dispersal capabilities.
- 402 3. Population sizes inferred were very low, suggesting the species might be especially vulnerable  
403 to future habitat alterations.

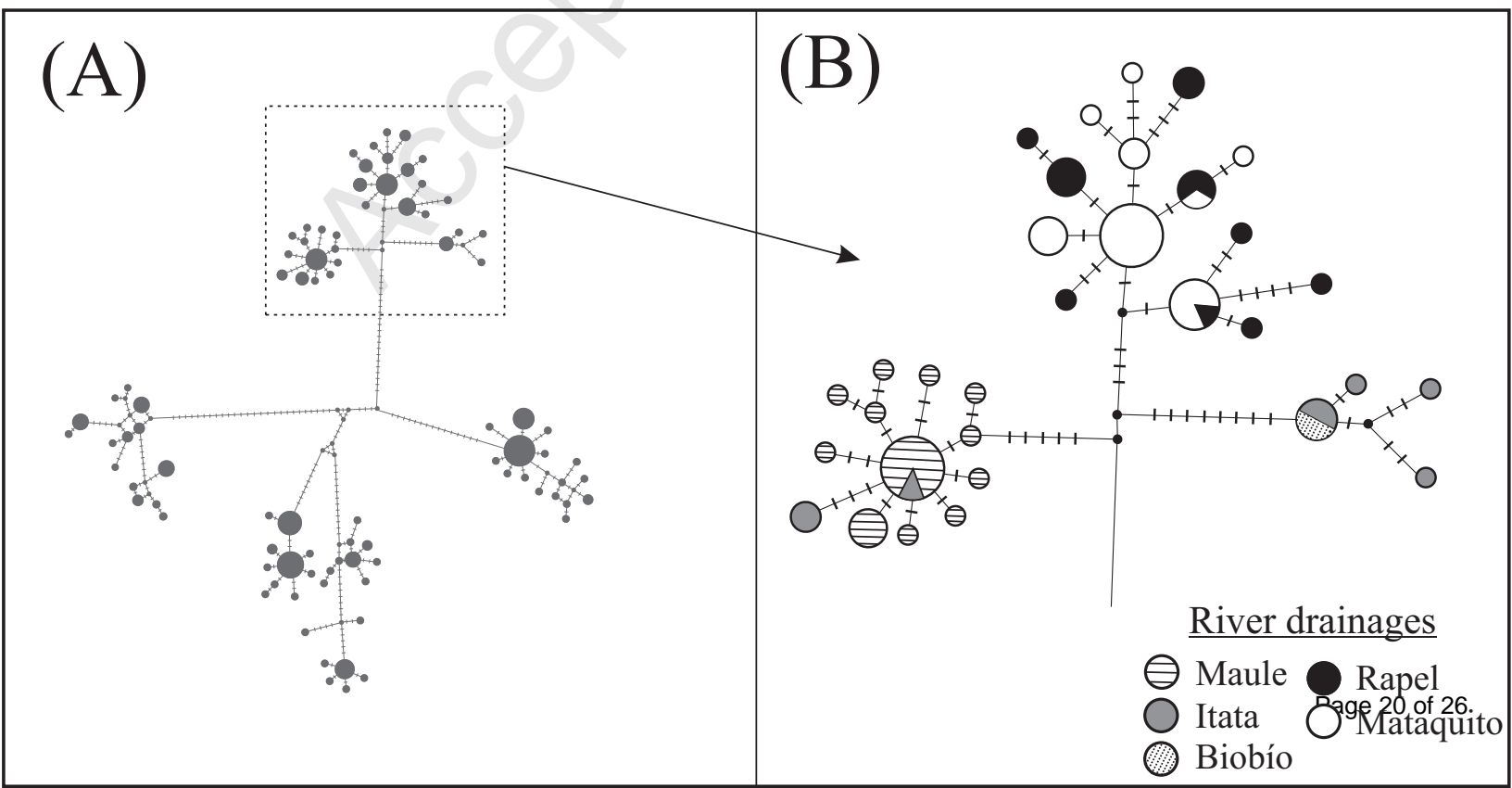
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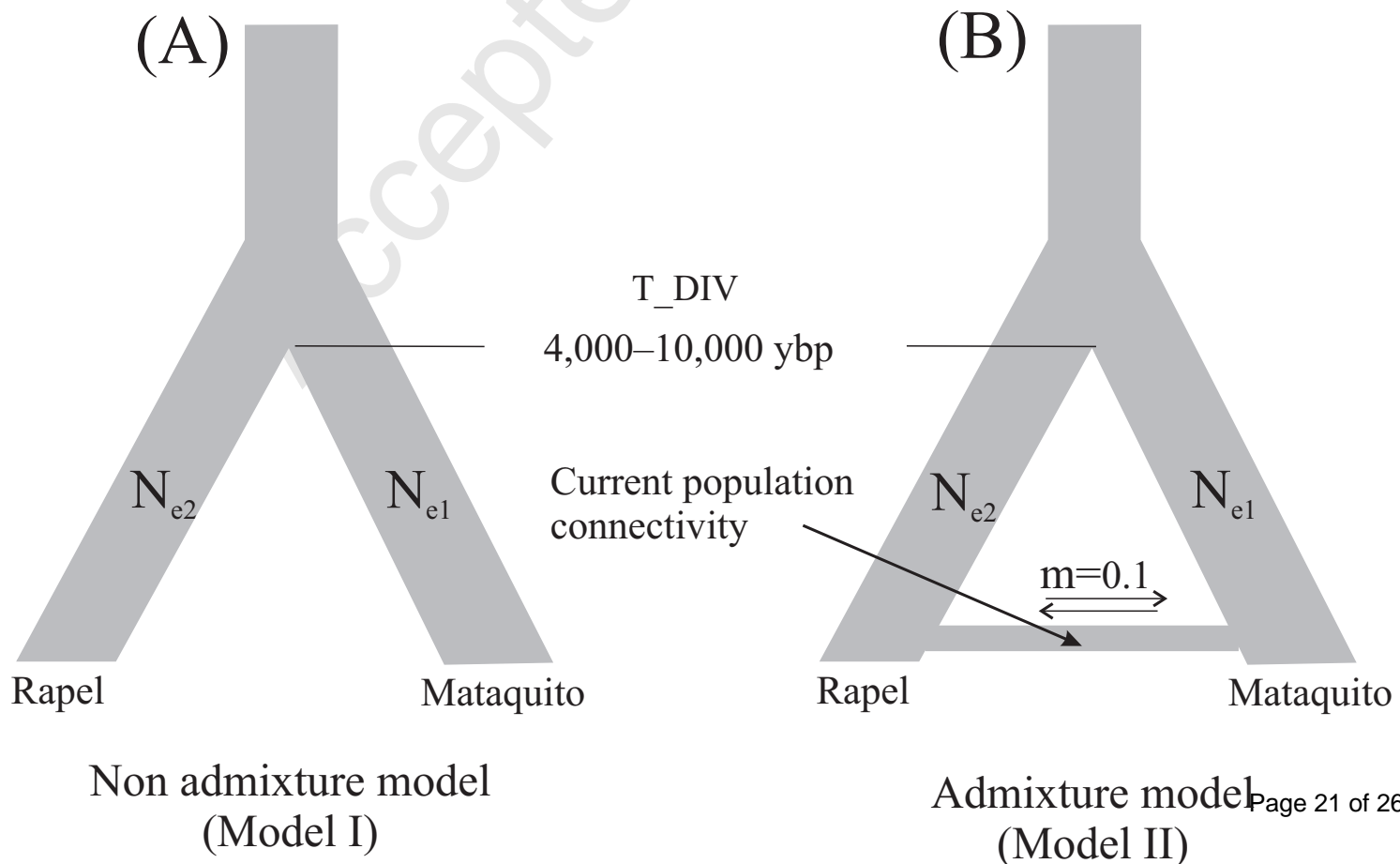
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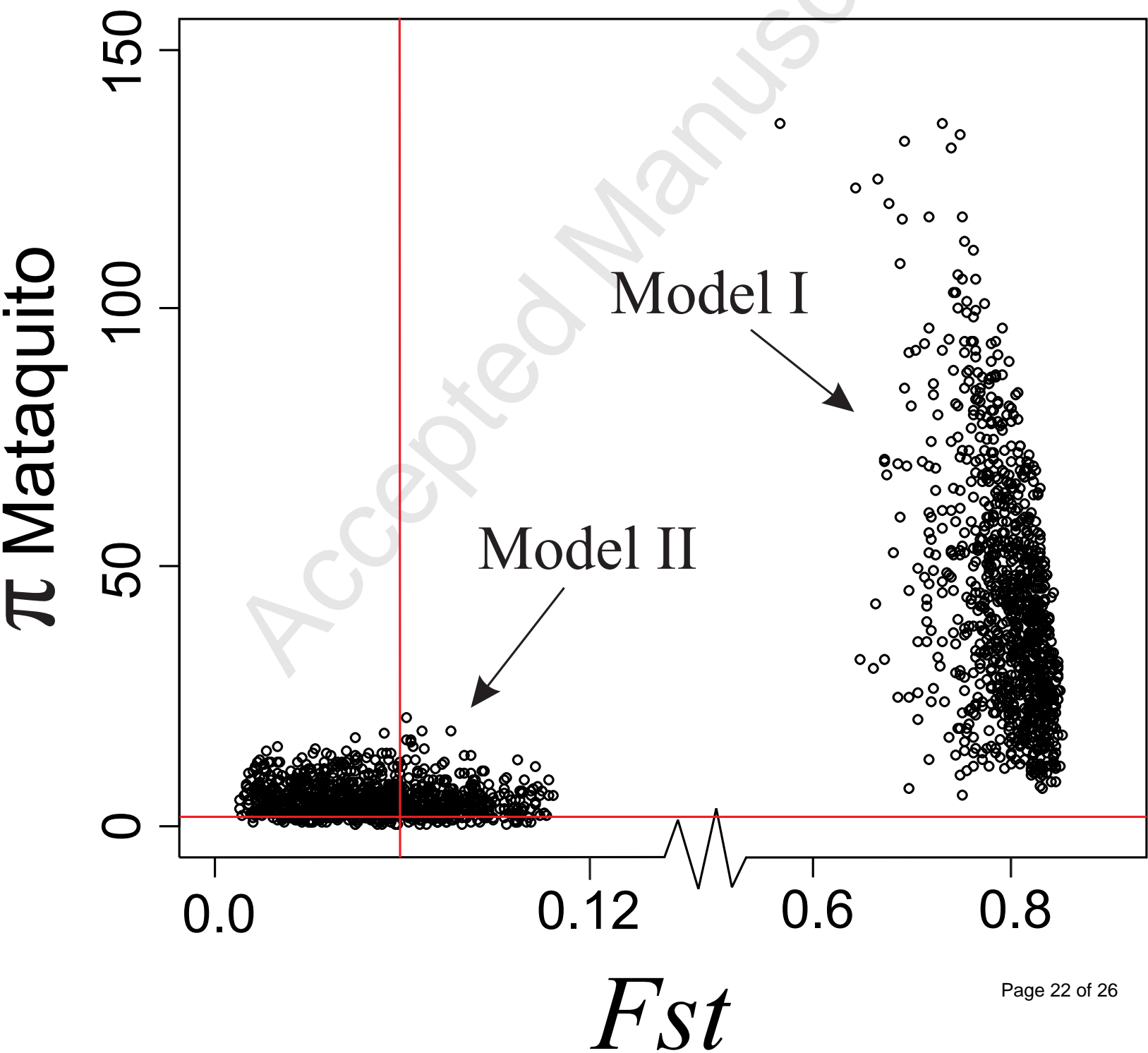
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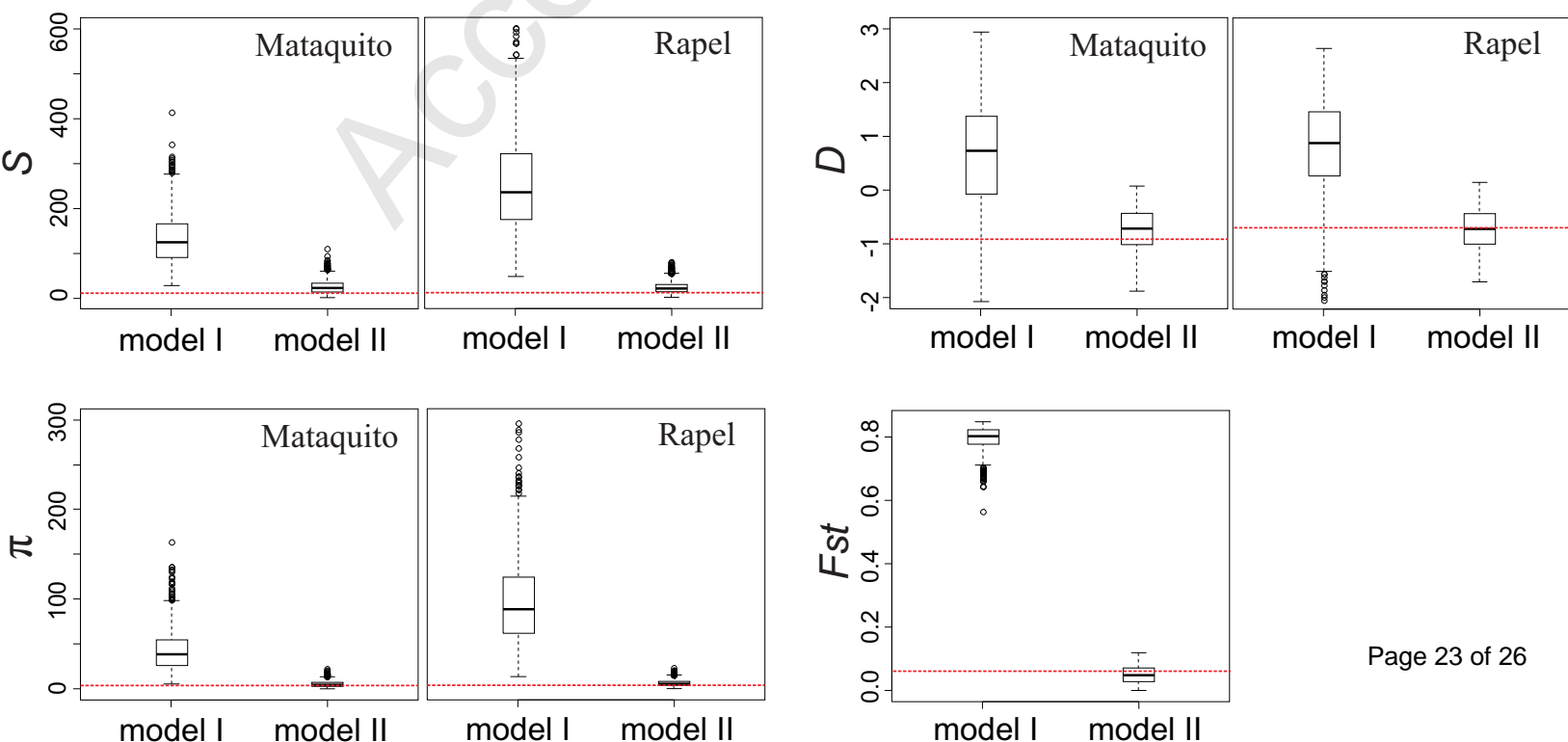
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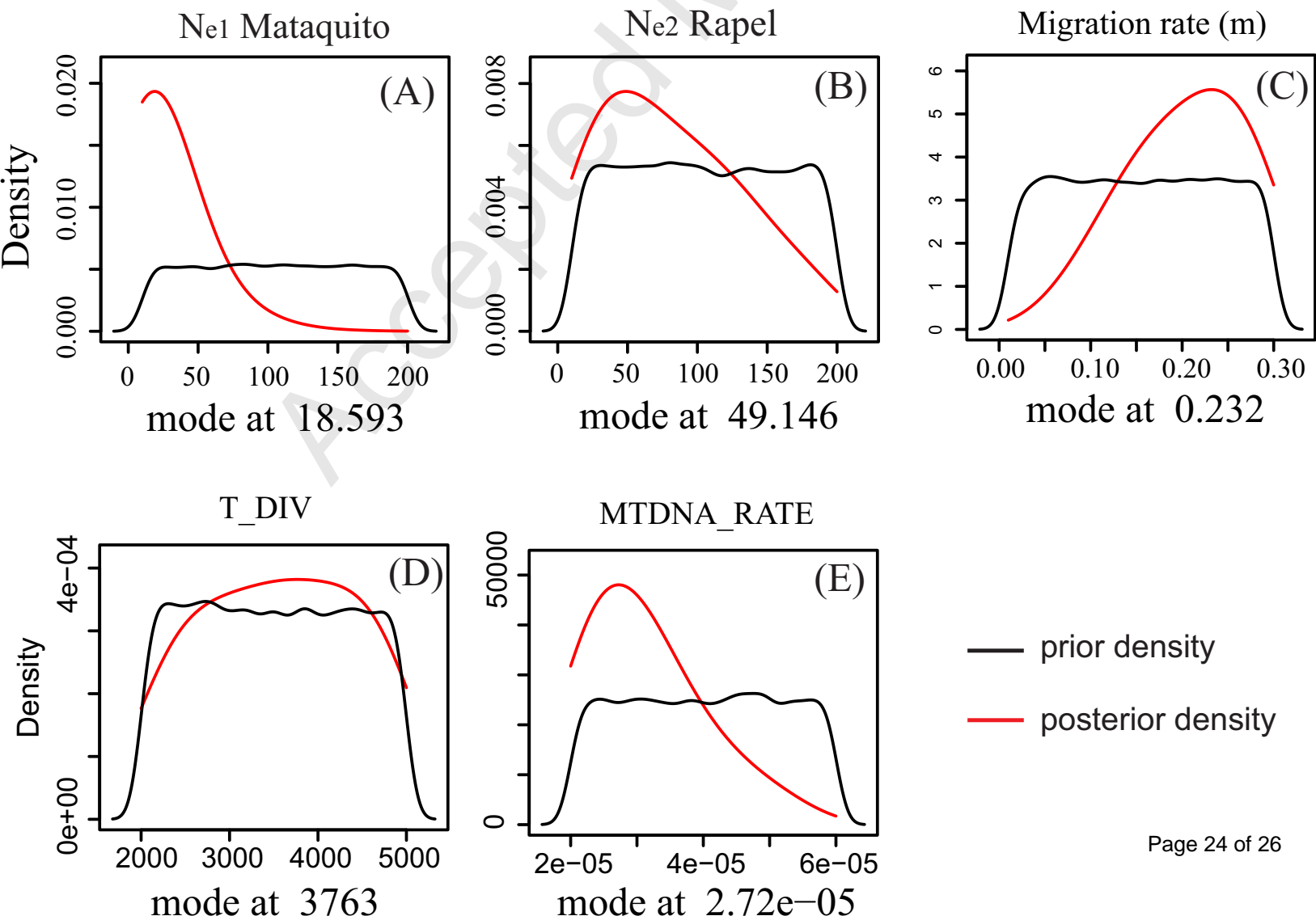


Table 1: Model parameter settings and their prior distributions.

Parameter	description	distribution	Range sampled	comments
<i>Model I</i>				
N1	Effective population size of Mataquito Basin	Uniform	10-250	Units in number of individuals
N2	Effective population size of Rapel Basin	Uniform	20-500	This parameter was set as a complex parameter in the .est file, $N2 = N1*2$
T_DIV	Time since basins became isolated	Uniform	2000-5000	Units in number of generations assuming generation time = 2 years
MTDNA_RATE	Substitution rate for the mtDNA	Uniform	0.00002-0.00006	Values are expressed in substitutions per locus per generation
	Population growth rate	Fixed	0	Population sizes were set to be constant over time
	Ancestral population size	fixed	1.5	The population size before divergence was set to be 1.5 times N2
<i>Model II</i>				
N1	Effective population size of Mataquito Basin	Uniform	10-250	Values expressed in number of individuals
N2	Effective population size of Rapel Basin	Uniform	20-500	This parameter was set as a complex parameter in the .est file, $N2 = N1*2$
T_DIV	Time since basins became isolated	Uniform	2000-5000	Values are expressed in number of generations assuming generation time = 2 years
MTDNA_RATE	Substitution rate for the mtDNA	Uniform	0.00002-0.00006	Values are expressed in substitutions per locus per generation
M	Rate at which individuals migrate between basins	Fixed	0.1	10% of the population per generation (every 2 years)
	Population growth rate	Fixed	0	Population sizes were set to be constant over time
	Ancestral population size	fixed	1.5	The population size before divergence was set to be 1.5 times N2

1. Using a model-based statistical approach, we found strong evidence that the endangered catfish *Diplomystes* cf. *chilensis* is dispersing between historically isolated basins through irrigation canals.
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