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1 **Modelling the effect of in-stream and overland dispersal on gene flow in river networks**

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21

22 **ABSTRACT**

23 Modelling gene flow across natural landscapes is a current challenge of population genetics.
24 Models are essential to make clear predictions about conditions that cause genetic
25 differentiation or maintain connectivity between populations. River networks are a special
26 case of landscape matrix. They represent stretches of habitat connected according to a
27 branching pattern where dispersal is usually limited to upstream or downstream movements.
28 Because of their peculiar topology, and the increasing concern about conservation issues in
29 hydrosystems, there has been a recent revival of interest in modelling dispersal in river
30 networks. Network complexity has been shown to influence global population differentiation.
31 However, geometric characteristics are likely to interact with the way individuals move across
32 space. Studies have focused on in-stream movements. None of the work published so far took
33 into consideration the ability of many species to disperse overland between branches of the
34 same network though. We predicted that the relative contribution of these two dispersal
35 modalities (in-stream and overland) would affect the overall genetic structure. We simulated
36 dispersal in synthetic river networks using an individual-based model. We tested the effect of
37 dispersal modalities, i.e. the ratio of overland / in-stream dispersal, and two geometric
38 parameters, bifurcation angle between branches and network complexity. Data revealed that if
39 geometrical parameters affected population differentiation, dispersal parameters had the
40 strongest effect. Interestingly, we observed a quadratic relationship between p the proportion
41 of overland dispersers and population differentiation. We interpret this U-shape pattern as a
42 balance between isolation by distance caused by in-stream movements at low values of p and
43 intense migrant exchanges within the same branching unit at high values of p . Our study is the
44 first attempt to model out-of-network movements. It clearly shows that both geometric and
45 dispersal parameters interact. Both should be taken into consideration in order to refine
46 predictions about dispersal and gene flow in river network.

47

48

49 **1. Introduction**

50 Dispersal is a key life history trait for population processes as it contributes to gene flow,
51 prevents local extinction, and determines the probability of patch recolonization (Hanski,
52 1999; Clobert et al., 2001; Bullock et al., 2002; Bowler and Benton, 2005; Ronce, 2007). The
53 spatial distribution of dispersal events across an area determines preferential connections and
54 gene flow level between patches. Connectivity level between demes affects migration-drift
55 equilibrium and the overall level of genetic differentiation of populations. Modelling dispersal
56 in landscapes is thus an essential step to investigate the relationships between the distribution
57 of habitat patches, connectivity networks and the resulting spatial genetic structure of
58 populations (Campbell et al. 2007). Model outputs help to build predictions for instance about
59 the effect of connectivity on the inbreeding level and the potential for local adaptation of
60 demes which are both major issues from a theoretical and conservation point of view.

61 Natural environments are anisotropic which means that heterogeneity in landscape
62 composition and spatial organisation causes individuals to move along preferential pathways
63 across the landscape matrix (Gustafson and Gardner, 1996; Béliste, 2005). Many studies
64 attempted to model gene flow in different types of landscapes (Nuismer et al., 2003; Cushman
65 et al., 2006; Shaw et al., 2006; Ceddia et al., 2007; Vuilleumier and Fontanillas, 2007). Still,
66 river networks can be considered as a particular case of landscape matrix (Campbell et al.
67 2007). The peculiarity arises from their topology. River networks are continuous stretches of
68 habitats, suitable for breeding or dispersal, connected in a dendritic (i.e. branching) pattern.
69 The “biological” distance between two sites is not defined by the straight-line distance
70 (Euclidian distance) but by the length of the watercourse between the two points (Fagan,
71 2002). Consequently, the geometrical configuration of the river network determines the
72 distribution of distance between breeding sites. The distance following the watercourse (Little
73 et al., 1997) and the number of branches (Gardner et al., 2003) are parameters that could
74 affect dispersal of individuals, gene flow patterns and ultimately spatial genetic structure.
75 However, in river networks, individuals do not necessarily disperse along a watercourse (i.e.
76 in-stream dispersal). They can also move between branches (i.e. overland dispersal) if all life
77 stages are nor strictly aquatic, or if floods connect different watercourses.

78 In species whose dispersal is restricted to the watercourse, movements are constrained
79 by water flow, network topology, and physical barriers to dispersal such as bordering
80 terrestrial habitat (Slatkin, 1985; Rissler et al., 2004; Lowe et al., 2006). It results from these

81 properties that gene flow occurs preferentially along branches (Ward et al., 1994; Bilton et al.,
82 2001; Beck and Pruett-Jones, 2002; Power and Dietrich, 2002; Peckarsky et al., 2005). Gene
83 flow is generally asymmetric as more individuals move downstream following the water flow
84 than the other way round (Hernandez-Martich et al., 1995). In addition, the hierarchical
85 structure of river networks tends to isolate populations living in different branches from each
86 others (McGlashan et al., 2001). Individuals are then distributed among different watercourses
87 when they move upstream, whereas they are concentrated, joining at confluences, when they
88 move downstream (Power and Dietrich, 2002). These two types of movement are expected to
89 result in decreased genetic diversity upstream (Schmidt et al., 1995) and increased genetic
90 differentiation between branches (Power and Dietrich, 2002). In addition, upstream
91 populations are more sensitive to genetic drift because of their geographic isolation (Fraser et
92 al., 2004). Therefore, the genetic structure of populations is supposed to reflect the
93 hierarchical structure of the river network (Meffe and Vrijenhoek, 1988). This assumption
94 was verified in 56% of fish species (Awise, 2000), the freshwater prawn, *Macrobrachium*
95 *australiense* (Cook et al., 2002), and the white-clawed crayfish *Austropotamobius pallipes*
96 (Grandjean et al., 1997).

97 Nevertheless, genetic patterns do not always match the spatial organization of the river
98 network because of barriers to dispersal caused by dams (Hurwood and Hughes, 1998;
99 McGlashan and Hughes, 2000) or out-of-network dispersal (Hurwood and Hughes, 2001). A
100 number of species like freshwater insects (Kovats et al., 1996; Miller et al., 2002; Petersen et
101 al., 2004; Macneale et al., 2005) or amphibians (Lowe, 2002) shows overland and in-stream
102 dispersal. For these organisms, overall genetic differentiation is supposed to decrease with the
103 level of overland connectivity between nearby but independent watercourses (Gibbs et al.,
104 1998). This prediction has recently received support from an empirical study in the Banded
105 damselfly, *Calopteryx splendens* (Chaput-Bardy et al., 2008). Genetic analyses revealed that
106 gene flow preferentially occurred along watercourses. However, overland dispersal accounted
107 for the mismatch between the spatial genetic structure and the river network structure.

108 Two network parameters are likely to influence the effect of overland dispersal on
109 genetic structure. (i) The mean angle between two branches joining at a confluence is also of
110 importance as the Euclidean distance between two sites of adjacent branches decreases with
111 the bifurcation angle. (ii) For a given area, the number of branches that receive migrants from
112 other branches increases with the complexity of the network, i.e. the number of branches,
113 owing to the higher density of watercourses. For organisms with strict in-stream dispersal,

114 higher complexity is expected to promote differentiation between regions of the network (sub-
115 catchments). In contrast, it is expected to lower population differentiation when overland
116 dispersal allows gene flow between otherwise distant branches. In genetic terms, overall
117 population differentiation is expected to be positively correlated with the mean bifurcation
118 angle but the relationship with network complexity is less straightforward.

119 In summary, it can be predicted that the population genetic structure in a river network
120 depends on the geometry of the river network, the dispersal modalities used by the species,
121 and the presence of barriers. The first mathematical models investigating the effect of river
122 network topology on genetic patterns were carried out a few decades ago (Sawyer, 1978;
123 Meffe and Vrijenhoek, 1988). However, a revival of interest in the effect of river structure on
124 dispersal or gene flow has been occurring (Charles et al., 2000; McGlashan and Hughes,
125 2000; Fagan, 2002; Lowe, 2002; Neuenschwanger, 2006; Labonne et al., 2008; Cote et al.,
126 2009). Recently, Labonne et al. (2008) demonstrated using simulations the effect of the size
127 and the number of branches on connectivity as well as on metapopulation persistence.
128 However, none of these authors attempted to model out-of-network dispersal. The effects of
129 bifurcation angles and network complexity on genetic structure remain to be investigated for
130 species or life stages able of out-of-network dispersal (Campbell Grant et al., 2007) (Fig. 1).
131 In the present study, we used an individual based model to simulate in-stream and overland
132 dispersal and tested the effects of the branching pattern, bifurcation angles and the probability
133 of overland dispersal on the overall genetic structure of demes in the network.

134

135 2. Materials and methods

136 2. 1. Modelling of synthetic river networks

137 River networks have two main properties. Firstly, they are made of segments (watercourse
138 stretches) and confluence points that form a branching network (Ganio et al., 2005). The
139 geometry of a network is characterized by the hierarchical structure of watercourses
140 (segments) categorized in orders. Many classification systems have been put forward but we
141 decided upon Strahler's system (Strahler, 1957) that is the most widely used. The
142 classification system is as follows: (i) headwaters are considered as first order stream
143 segments, (ii) when two stream segments within the same order $\omega = i$ merge, the stream
144 segment resulting from this confluence is considered as order $\omega = i+1$, (iii) when two stream
145 segments of different orders, $\omega = i$ and $\omega = j$ merge, the stream segment resulting from this
146 confluence is of order $\omega = \max(i,j)$ (Strahler, 1957). The river network order corresponds to
147 the highest index value of a segment. This classification puts forward general geometric laws.
148 Among them, Horton's laws (Horton, 1945) describe the way stream networks are organized.
149 These laws express the so-called bifurcation ratio R_B and length ratio R_L , also known as
150 Horton's ratios. A great number of experimental studies on stream networks (Tarboton et al.,
151 1990; Rosso et al., 1991) revealed that these ratios are rather stable and fluctuate between 3
152 and 5 for R_B and between 1.5 and 3.5 for R_L . Horton's laws also make it possible to work out
153 the R_B and R_L (equation 2), where \bar{l}_k is the average value of the morphometric lengths of k
154 order and N_k is the number of morphometric lengths of k order.

155

$$156 \quad R_L = \frac{\bar{l}_k}{\bar{l}_{k-1}}, \quad R_B = \frac{N_{k-1}}{N_k} \quad (2)$$

157

158 2. 2. Modelling in-stream and overland dispersal in synthetic river networks

159 In our synthetic networks, each node is connected to one or two upper nodes (upstream) and
160 one lower node (downstream). Upstream and downstream dispersal is allowed. Dispersal is
161 defined as the fraction m of adults that move out of their natal node before breeding, so it is
162 different from effective migration. Among dispersers, a fraction $(1-p)$ of adults disperse in-
163 stream, i.e. along the watercourse, and a fraction (p) disperses overland, i.e. between branches

164 of the network. River networks are discretized into evenly spaced nodes. Each node is a
165 potential breeding site. Individuals can disperse up to four nodes when moving in-stream, and
166 to an equivalent distance when moving overland to another branch. The dispersal distribution
167 is uniform so that individuals can reach any node within a 4-node range. We allowed p to vary
168 between 0 and 1. A zero value indicates that only in-stream dispersal occurs. When $p=1$, all
169 adults disperse overland when possible. As a general rule for $p>0$, individuals disperse in-
170 stream if no site can be reached by an out-of network movement. Bifurcation angle α
171 determines the overland distance between two nodes on adjacent branches but not their in-
172 stream distance. Successful overland dispersal is more likely for low values of α as distances
173 between branches are shorter. On the contrary, in-stream dispersal should prevail in network
174 with high values of α .

175 Boundary nodes (boundaries of the river catchment) are linked to upper nil nodes. For these
176 nodes we consider that individuals disperse out of the network. The reason is that boundary
177 nodes receive fewer migrants (only from one direction) and are thus more prone to genetic
178 drift. They could thus bias the estimation of the overall population structure.

179

180 *2. 3. Colonization, demographic and genetic parameters*

181 Individuals were introduced from the lowermost node. We allowed colonization of the entire
182 network from this single node. The carrying capacity K for each node was fixed to 100 adults.
183 If the number of adults after migration in a population exceeded K , then a sample of K
184 individuals was randomly drawn from the pool of resident and migrant adults. Extra
185 individuals were not allowed to breed. Strictly monogamous pairs were formed randomly
186 from the sample of adults. Each pair produced 5 offspring so that no variation in breeding
187 success occurred. There was no overlap between generations.

188 Individuals were characterized by ten bi-allelic loci with a mutation rate of 10^{-8} like
189 SNP (Single Nucleotide Polymorphism) markers (Brumfield et al., 2003). A population,
190 defined as all adults present on a given node. Sex of new individuals were drawn at random.
191 Individuals of the initial sample (first generation on the lower node) were heterozygous for
192 the ten loci. By this way all simulations start with the same initial conditions : allele
193 frequencies set at 0.5 for the ten loci. For all subsequent generations and populations egg
194 genotype resulted from the random sampling of one allele from each parent. Hardy-Weinberg
195 equilibrium was assumed for each population.

196

197 *2. 4. Test of network geometry and dispersal characteristics on genetic structure*

198 We modeled three river networks representative of many catchments observed in natural
199 environment. The Horton parameters for the selected networks were as follows: Network A
200 $\omega=3, R_L=2, R_B=2$; Network B $\omega=3, R_L=2, R_B=3$; and Network C $\omega=3, R_L=2, R_B=4$. For each of
201 these three river networks, we created six additional networks with different values of α , the
202 bifurcation angle between two branches joining at a confluence. We set α respectively to 15,
203 30, 45, 60, 75, and 90 degrees. Higher values are not expected to occur frequent. Keeping α
204 constant across the whole network could cause crossings between higher order branches. In
205 order to avoid this problem, we used a simple rule. Each bifurcation angle involving one last
206 order segment was set to α . Angles for all other bifurcations were set to $\alpha/2$.

207 A total of 18 networks were synthesized, the Fig. 2 represents some of them. Size was
208 fixed so that the distance between the lower and upper node was 26 nodes. Network size, i.e.
209 the number of nodes, was 54 for $R_B=2$, 88 for $R_B=3$, and 132 for $R_B=4$.

210 For each network we selected six values of p , the fraction of overland dispersers: 0,
211 0.2, 0.4, 0.6, 0.8, and 1. For all 36 combinations of α and p we ran 20 replicates. In addition,
212 we replicated these simulations for all parameter combinations at two dispersal levels ($m= 0.1$
213 and 0.2). Each simulation was run for 300 generations. Preliminary tests using the more
214 complex network (Network C) showed that this length was sufficient to reach migration-drift
215 equilibrium for the range of network sizes we simulated (Fig. 3). Overall, we ran 4320
216 simulations (3 networks $\times 6\alpha \times 6p \times 2m \times 20$ replicates).

217 We computed the mean and the variance of the overall F_{ST} value for each for α and p
218 combinations and m values. We thus included all populations and all individuals in the
219 computation of the F statistics. For each network, we visualized the effect of α and p on F_{ST}
220 and F_{ST} standard deviation as a response surface fitted using the weighted least square method
221 using STATISTICA 7.1 (StatSoft, Inc, 1984-2005).

222 Generalized linear models (GLMs) were constructed to test for the influence of R_B , α ,
223 p and their interactions on F_{ST} . We carried out a factorial analysis including all factors and
224 their pairwise interactions. We used a squared term of p to test for non-linear effect of this
225 variable (McCullagh and Nelder, 1983). GLMs assumed a normal error structure, as the
226 response variable ($\log F_{ST}$) was adjusted to a Gaussian distribution. A stepwise Akaike's
227 Information Criterion with a backwards selection procedure was used to select the most

228 parsimonious model from the complete model: $\log(F_{ST}) \sim R_B + \alpha + m + p + p^2 + R_B:\alpha + R_B:m + R_B:p +$
229 $R_B:p^2 + \alpha:m + \alpha:p + \alpha:p^2 + m:p + m:p^2 + p:p$ (Burnham and Anderson, 2002). For each model
230 considered we also calculated the percentage deviance explained (%DE) as a measure of
231 goodness-of-fit. Model selection was carried out using used the StepAIC function in MASS
232 package available in R (R project for statistical computing, ver. 2.8.1, [http://www.r-](http://www.r-project.org/)
233 [project.org/](http://www.r-project.org/)).

234

235 3. Results

236 *Connectivity and dispersal modality*

237 Figure 4 shows that, in synthetic river networks, the distribution of pairwise distances differs
238 for the two modalities of dispersal considered. The probability of reaching a node is higher for
239 out-of-the-network dispersal than for in-stream dispersal for all distances (Fig. 4). In addition,
240 the probability difference between in-stream and overland dispersal increased with R_B .
241 Finally, the difference depended on the bifurcation angle as it increased with α for a given R_B
242 (Fig. 4). Thus, this graph shows that the level of network complexity R_B influences the
243 probability of successful dispersal. It is also indicative of an interaction between network
244 geometry, R_B and α , and dispersal modalities on the biological connectivity of the whole river
245 network.

246

247 *Effect of dispersal parameters m and p*

248 The complete model, $\log(F_{ST}) \sim R_B + \alpha + m + p + p^2 + R_B:\alpha + R_B:m + R_B:p +$
249 $R_B:p^2 + \alpha:m + \alpha:p + \alpha:p^2 + m:p + m:p^2 + p:p^2$, gave a good fit to the dataset (residual adjustment test,
250 $p > 0.1$). According to the model selection procedure (Stepwise AIC), the two best models
251 accounted for more than 86.5% of explained deviance (Table 1). The best model, Model 1,
252 contained all variables (R_B , α , m , p and p^2) and all but one interaction $\alpha:m$, and the second
253 best model, Model 2, was the complete model (Table 1). Results of both models were strongly
254 similar; consequently we chose to show the results for Model 1 only. Most interactions were
255 significant although their residual deviance was small (Table 2). The large sample size of
256 simulations might have caused the undue detection of small effects without little biological
257 sense. We thus focused our analysis on the main significant effects and interactions.

258 The main factors influencing F_{ST} were the migration rate m (residual deviance = 83.49,
259 $p < 0.0001$, table 2), and squared overland dispersal p^2 (residual deviance = 31.78, $p < 0.0001$)
260 (Table 2, Fig. 6). Dispersal rate m had the most influential effect on F_{ST} (Table 3). For $m = 0.20$
261 the response surface was strongly flattened, which outlined the fact that F_{ST} weakly responded
262 to variations of the bifurcation angle α , and the proportion of overland dispersers p when m
263 was high enough (Fig. 6). Surprisingly, we found a quadratic relationship between F_{ST} and p .
264 F_{ST} decreased for values of p between 0 and 0.5. It increased for values of p above 0.5 (Fig. 6).
265 A similar relationship was logically observed for the standard deviation of F_{ST} (Fig. 7). Thus,
266 a minimum of genetic differentiation was reached for intermediate values of p .

267 In order to make sure that the quadratic relationship was not an artefact caused by
268 dispersal rules, we ran additional simulations where overland disperser died when they could
269 not reach a node. We carried out ten replicates for two values of the bifurcation angle ($\alpha = 15$
270 and 90°) on the following network: $\omega = 3$, $R_B = 3$, $m = 0.1$. Results showed again a quadratic
271 relationship between p and F_{ST} (data not shown). The only difference was null F_{ST} values for
272 $p = 1$ as individuals could not disperse overland out of the initial node and thus could not
273 colonize the network.

274

275 *Effect of network parameters*

276 The geometry of the network (i.e. the number of branches and the bifurcation angle between
277 branches) significantly affected the overall genetic structure. According to the positive values
278 of their coefficients, an increase in R_B or α was reflected by an increase in F_{ST} (Table 3).
279 These two factors respectively took 3.99 ($p < 0.0001$) and 7.38 ($p < 0.0001$) of the residual
280 deviance (Table 2). Fig. 7 illustrates the overall effect of α on F_{ST} . When overland dispersal
281 occurs, overall population differentiation increases with distance between branches. However,
282 Fig. 6 and Table 2 show that the level of network complexity R_B influenced the relationship
283 between the two variables ($R_B: \alpha$, residual deviance = 1.05, $p < 0.0001$). Similarly, F_{ST}
284 increased with bifurcation ratio. Thus, population genetic differentiation increased with
285 network complexity R_B . Here again, the relationship between this variable and F_{ST} was not
286 strictly linear but strongly affected by the interaction with p the proportion of overland
287 dispersers (residual deviance = 5.61, $p < 0.0001$).

288 **4. Discussion**

289 We investigated the effects of network geometry and dispersal modalities on the genetic
290 differentiation of populations. To our knowledge, this study is the first attempt to explicitly
291 consider out-of network dispersal, i.e. movements of individuals between branches. Results
292 clearly showed that dispersal and network characteristics not only influence the overall level
293 of population differentiation but the way they interact is important too. As a consequence,
294 both factor types should be considered jointly when investigating population processes in
295 river networks.

296

297 *Effect of network parameters*

298 Variation of the bifurcation ratio R_B strongly influences the density of watercourses when
299 keeping constant the catchment area. An individual dispersing out-of-the network has thus a
300 better chance to reach another branch in highly than in poorly ramified networks. Fig. 3 and 4
301 show that the number of nodes that can be reached is higher when dispersing overland than
302 when dispersing in-stream, and that the difference tends to increase with R_B . They clearly
303 illustrate the importance of considering the different dispersal pathways available to
304 individuals.

305 Simulations revealed that overall F_{ST} was positively related to R_B . For a given
306 dispersal range, the fraction of movements within branches of the same branching unit
307 increased with the number of branches. In biological terms, this means that differentiation
308 between sub-catchments is favored when network complexity increases. As predicted the
309 bifurcation angle α affected the genetic structure too. Individuals have better opportunities to
310 successfully disperse overland in network with low values of α because of the reduced mean
311 pairwise distance between sites. Consistently, we observed a positive relationship between α
312 and the overall level of population differentiation. Thus, the simulation results support our
313 initial predictions about the relationships between river network parameters and the level of
314 population differentiation. F_{ST} tended to increase with network complexity and bifurcation
315 angle between branches, i.e. with decreasing opportunity for successful overland dispersal.
316 However, the effect of network parameters did not only consist in linear changes of the
317 overall F_{ST} value. Interactions between R_B and p contributed to the bending of the surface
318 response.

319

320 *Effect of dispersal parameters m and p*

321 Dispersal m and the proportion of overland dispersers p appeared as the major factors
322 contributing to population differentiation. The reduction in deviance when these factors were
323 considered was much greater than for any other factor. Dispersal alone seemed to be the most
324 influential on F_{ST} , as shown on Fig. 4. Doubling its value from 0.1 to 0.2 caused a strong
325 flattening of the surface response whatever the combinations of the other parameters. Such a
326 result suggests that moderate to strong migration would cancel the effect of network
327 geometry. Thus, the effects of other factors would only be detected under a range of low
328 dispersal rates.

329 Unexpectedly, we observed a quadratic relationship between p , the proportion of
330 overland dispersers, and population differentiation F_{ST} . The effect was reinforced with
331 increasing values of R_B . We interpret the curvilinear shape of this relationship as the effect of
332 a balance between two mechanisms. Without overland dispersal, gradual differentiation
333 according to an isolation by distance pattern occurred (results not shown). It results that nodes
334 located close to the outlet and in distant branch tended to differentiate because they were
335 located far apart. In contrast, genetic differentiation was strongly reduced when overland
336 dispersal was allowed, i.e. when regular exchanges of migrants between branches could
337 occur. However, F_{ST} increased again for high values of p when most migrants dispersed out-
338 of-the network. Under such conditions, migration is expected to occur mostly within sub-units
339 (sub-catchment) of the network. Accordingly, in-stream dispersal was very low, reducing the
340 effect of effective migration along the network. Stronger population differentiation for low
341 and high values of p is thus likely to be accounted for by the relative effects of the two
342 dispersal modalities.

343

344 *Perspectives and current limits of investigations of dispersal in river networks*

345 We developed an individual-based model to predict spatial genetic structure of organisms able
346 to disperse in-stream and out-of-the network. We believe that this study can be useful to
347 improve our understanding of population processes in river networks and we hope it will help
348 stimulating other investigations on the topic. Nevertheless, we have to keep in mind that
349 synthetic networks still represent simpler versions of natural river networks. For this reason,
350 the effects on ecological processes of some of investigated factors, like network geometry,
351 might be over- or under-estimated. Owing to computation constraints, our synthetic networks

352 represented only a part of the range of all existing networks. Much larger values of R_B can be
353 observed for larger catchments. Moreover, we found that most variables interacted to affect
354 the overall population differentiation. Thus, we cannot extrapolate our findings to higher
355 levels of complexity yet. We focused on a restricted range of R_B values. Even if this range
356 encompasses a large proportion of catchments observed, we are still unable to predict the
357 shape of the surface response for very complex networks.

358 We used dichotomic networks and the bifurcation angle α was fixed, i.e. all branches
359 split with the same angle. Dichotomy is not an absolute rule in river network geometry and it
360 would be highly interesting to consider the influence of this geometric factor in future studies.
361 Moreover, α is far from being constant. The variance of α may be of some importance and
362 ought to be considered too, even if we do not expect that drastically different conclusions
363 would be drawn as the bifurcation angle was not the strongest effect we detected. Finally,
364 natural river networks are subjected to stochastic factors (e.g. flood, drought, pollution)
365 affecting intrinsic population growth rates, carrying capacities and deme extinction
366 probability. These factors were not considered in our simulations. We kept the demographic
367 part of the simulation quite simple. However, there are few reasons for demographic
368 stochasticity such as local extinctions and re-colonisations to reduce overall population
369 differentiation. Demographic stochasticity is usually shown to work the other way round as it
370 reduces metapopulation effective size (Whitlock and Barton, 1997).

371 Considering overland dispersal opens new questions. For instance, river networks are
372 modelled as objects completely isolated from external influences. In particular, no exchanges
373 of migrants between neighboring catchments or other water bodies are allowed. In real
374 situations, the closest branch to a river network can belong to a completely different
375 catchment. If it makes no difference for strictly aquatic species, this situation has to be
376 considered for species able of out-of-network movements. Such a situation is more likely to
377 be observed in higher order segments (upstream parts) and is more likely in flat areas where
378 terrestrial barriers to dispersal maybe less stringent than in areas with strong elevation
379 variations. Overland movements from one valley to another could be simply impossible for
380 many species when large altitude changes are required.

381 It is obvious from these considerations that the field of investigation is still vast. The
382 present study is a first attempt to study gene flow patterns in river networks when different
383 dispersal modalities are available. It completes other simulation studies or methods that have
384 been developed recently to analyze population genetic structure (Neuenschwander 2006,

385 Labonne et al. 2008). The development of predictive methods specifically designed to address
386 this issue is still highly required. Such methods are obviously important for basic science but
387 they are also badly needed for conservation purpose given the general degradation of
388 freshwater habitats and the reduction and fragmentation of populations they harbor. We hope
389 this work, by considering the possibility of different dispersal modalities, will contribute to
390 improve our understanding of population processes in river networks.

391

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397

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532

533 **Figure captions**

534

535 Figure 1: Bifurcation angle α and dispersal pathways in river networks. In-stream dispersal is
536 unaffected by α (up). In contrast, overland dispersal is very sensitive to variation of α as the
537 fraction of the network receiving migrants from a node increases when α decreases (down).
538 Circles indicate the dispersal range and diamonds the nodes that can actually be reached from
539 the focal node.

540

541 Figure 2: Examples of synthetic river network used for simulations in the present study. River
542 order ω and branch length ratio R_L were respectively 3 and 2. The bifurcation ratio R_B varied
543 between 2 and 4. The figure shows only two values of the bifurcation angle α , 15 and 60
544 degrees.

545

546 Figure 3: Variation of F_{ST} in river networks with different bifurcation angles α , and levels of
547 branching complexity R_B : (a) $R_B=2$, $\alpha=15^\circ$, (b) $R_B=2$, $\alpha=90^\circ$, (c) $R_B=4$, $\alpha=15^\circ$, (d) $R_B=4$,
548 $\alpha=90^\circ$. Graphs show 20 replicates for each sets of simulation where $\omega=3$ (river network
549 order), $R_L=2$ (the length ratio), $m=0.1$ (dispersal rate), $p=0.6$ (overland dispersal rate) are
550 constant. Results indicate that migration-drift equilibrium is reached by the 300th generation.
551 We used this value as the maximum number of iterations in the study.

552

553 Figure 4: : Cumulative probability of the number of nodes that can be reached from any site
554 against the distance to the focal node. Functions are given for 3 levels of network complexity
555 R_B , 2 bifurcation angles and two dispersal modalities (in-stream and overland). The vertical
556 lines indicate the maximal dispersal distance in our simulations.

557

558 Figure 5: Response surface of overall F_{ST} -value to bifurcation angle α and branching
559 complexity R_B . Estimations were made using a weighted least square method on F_{ST} values
560 for 20 replicates of each combination of α and R_B

561

562 Figure 6: Response surface of overall F_{ST} to bifurcation α , and branching complexity R_B .
563 Estimations were made using a weighted least square method on standard deviation of F_{ST}
564 values for 20 replicates of each combination of α and R_B .

565

566 Figure 7: Interaction between p , the proportion of terrestrial dispersers, the bifurcation angle
567 α , and network complexity R_B . on overall population differentiation F_{ST} . Triangles: $\alpha=90^\circ$,
568 diamonds $\alpha=15^\circ$.

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571 **Table 1.** Generalized linear models after a stepwise AIC for the relationship between genetic
572 differentiation ($\log F_{ST}$), branching ratio of the river network (R_B), bifurcation angle between
573 branches (α), migration rate (m), proportion of overland dispersal (p), and the quadratic term
574 (p^2). For each model are shown the number of parameters (k), log-likelihood (LL), change in
575 Akaike's Information Criterion (ΔAIC), AIC weight (wAICc), and the percentage deviance
576 explained (%DE) in the $\log F_{ST}$ response variable.

577

Model	Variables	k	Log-likelihood	ΔAIC	AIC weights	%DE
1	complete model without the interaction $\alpha:m$	22	5305.831	0.0	0.514	86.51
2	complete model	23	5305.943	0.1	0.486	86.51

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582 **Table 2.** ANOVA results of the most parsimonious GLM (see Model 1 in the Table 1). Df is
 583 the degree of freedom and Df Resid the degree of freedom of the residual deviance.

584

	Df	Residual deviance	Df Resid	Deviance	F	p
NULL			4319	160.801		
R _B	2	3.999	4317	156.802	396.438	< 0.0001
α	1	7.376	4316	149.427	1462.368	< 0.0001
m	1	83.490	4315	65.936	16553.809	< 0.0001
p	1	0.024	4314	65.912	4.795	0.02859
p ²	1	31.782	4313	34.13	6301.440	< 0.0001
R _B :α	2	1.046	4311	33.084	103.697	< 0.0001
R _B :m	2	0.094	4309	32.991	9.300	< 0.0001
R _B :p	2	5.609	4307	27.382	556.011	< 0.0001
R _B :p ²	2	2.895	4305	24.487	286.962	< 0.0001
α:p	1	0.511	4304	23.976	101.387	< 0.0001
α:p ²	1	0.795	4303	23.181	157.659	< 0.0001
m:p	1	0.030	4302	23.151	5.983	0.01448
m:p ²	1	0.614	4301	22.537	121.695	< 0.0001
p:p ²	1	0.850	4300	21.687	168.457	< 0.0001

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591 **Table 3.** Effect of branching ratio of the river network (R_B), bifurcation angle between
592 branches (α), migration rate (m), proportion of overland dispersal (p), and the quadratic term
593 (p^2), on between genetic differentiation ($\log F_{ST}$). Here is presented the most parsimonious
594 Model 1 from the complete model. We used a Generalized Linear Model and applied a
595 stepwise AIC with a backward selection procedure (see methods). R_{B2} and m_{10} were taken as
596 reference.

597

	Estimate	SE	t	p
(Intercept)	-9.63E-01	7.77E-03	-123.99	< 0.0001
R_{B3}	1.30E-01	8.42E-03	15.397	< 0.0001
R_{B4}	1.89E-01	8.42E-03	22.471	< 0.0001
α	-3.71E-04	1.11E-04	-3.343	0.00084
m_{20}	-2.52E-01	5.69E-03	-44.234	< 0.0001
p	-8.73E-03	3.94E-04	-22.166	< 0.0001
p^2	1.45E-04	6.90E-06	21.048	< 0.0001
$R_{B3}:\alpha$	5.00E-04	1.03E-04	4.843	< 0.0001
$R_{B4}:\alpha$	1.46E-03	1.03E-04	14.167	< 0.0001
$R_{B3}:m_{20}$	2.03E-02	5.29E-03	3.829	0.00013
$R_{B4}:m_{20}$	1.92E-02	5.29E-03	3.634	0.00028
$R_{B3}:p$	-6.86E-03	2.76E-04	-24.829	< 0.0001
$R_{B4}:p$	-8.22E-03	2.76E-04	-29.743	< 0.0001
$R_{B3}:p^2$	5.35E-05	2.65E-06	20.149	< 0.0001
$R_{B4}:p^2$	5.65E-05	2.65E-06	21.297	< 0.0001
$\alpha:p$	6.55E-05	4.40E-06	14.876	< 0.0001
$\alpha:p^2$	-5.31E-07	4.23E-08	-12.556	< 0.0001
$m_{20}:p$	-2.54E-03	2.26E-04	-11.275	< 0.0001
$m_{20}:p^2$	2.39E-05	2.17E-06	11.032	< 0.0001
$p:p^2$	-5.33E-07	4.11E-08	-12.979	< 0.0001

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602 **Figure 1**

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$\alpha=60^\circ$

$\alpha=15^\circ$

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In-stream dispersal

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Overland dispersal

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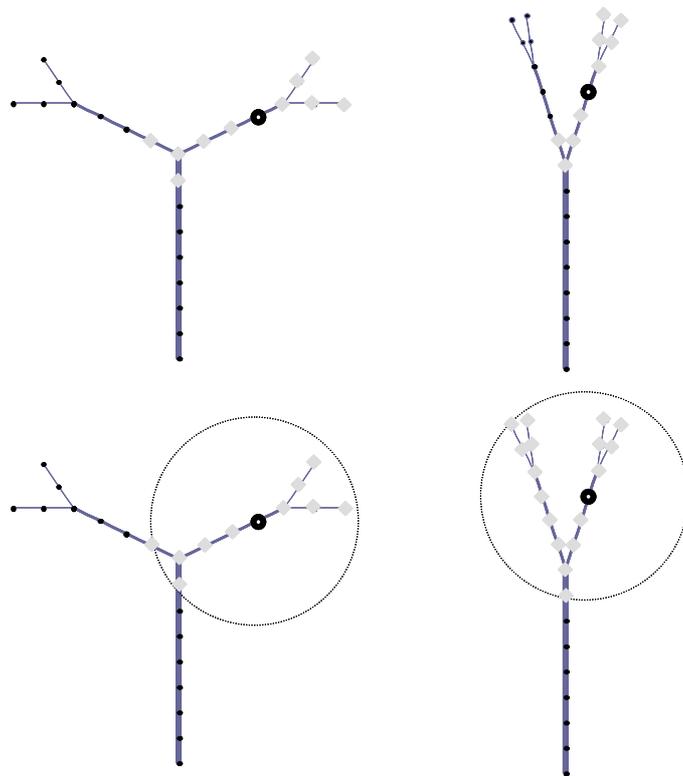
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628 **Figure 2**

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$R_n=2$

$R_n=3$

$R_n=4$

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$\alpha=60^\circ$

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$\alpha=15^\circ$

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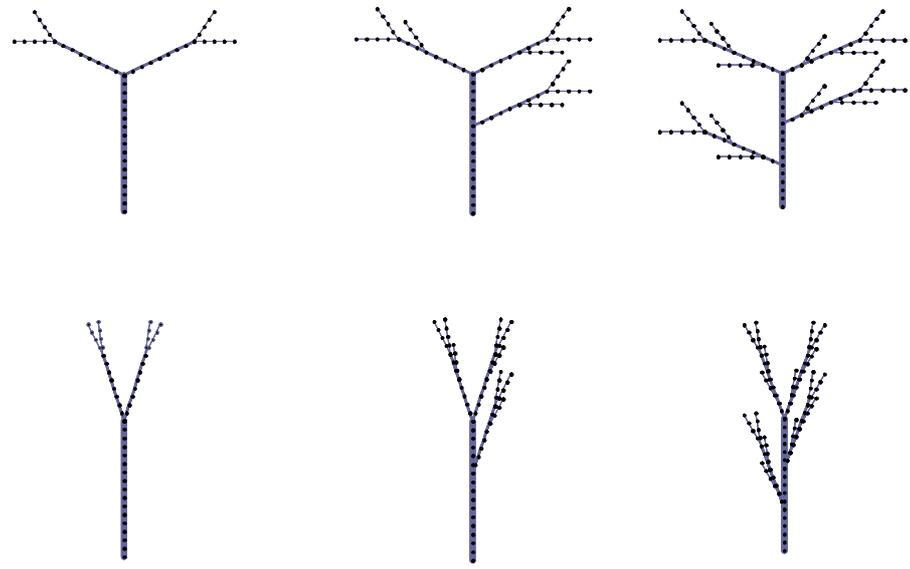
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654 **Figure 3**

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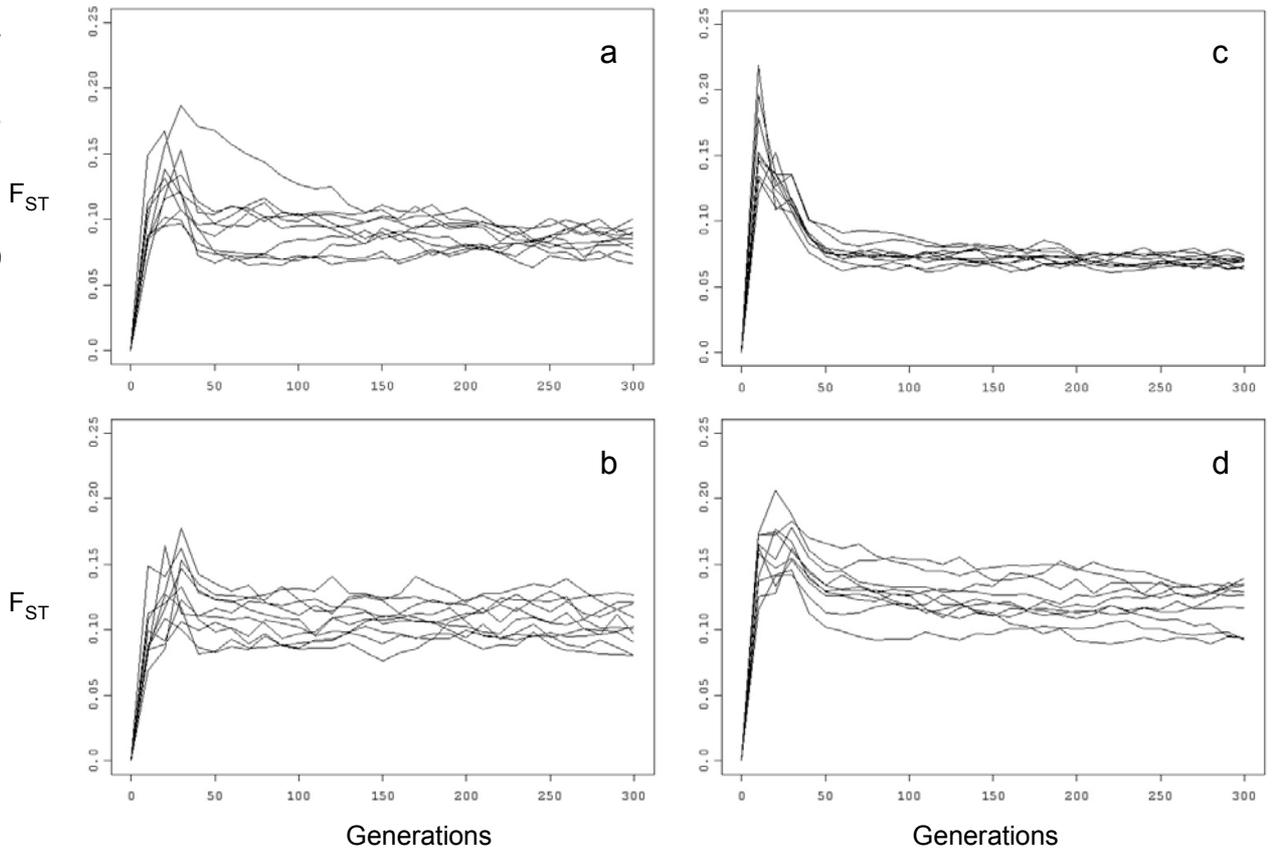
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659 F_{ST}

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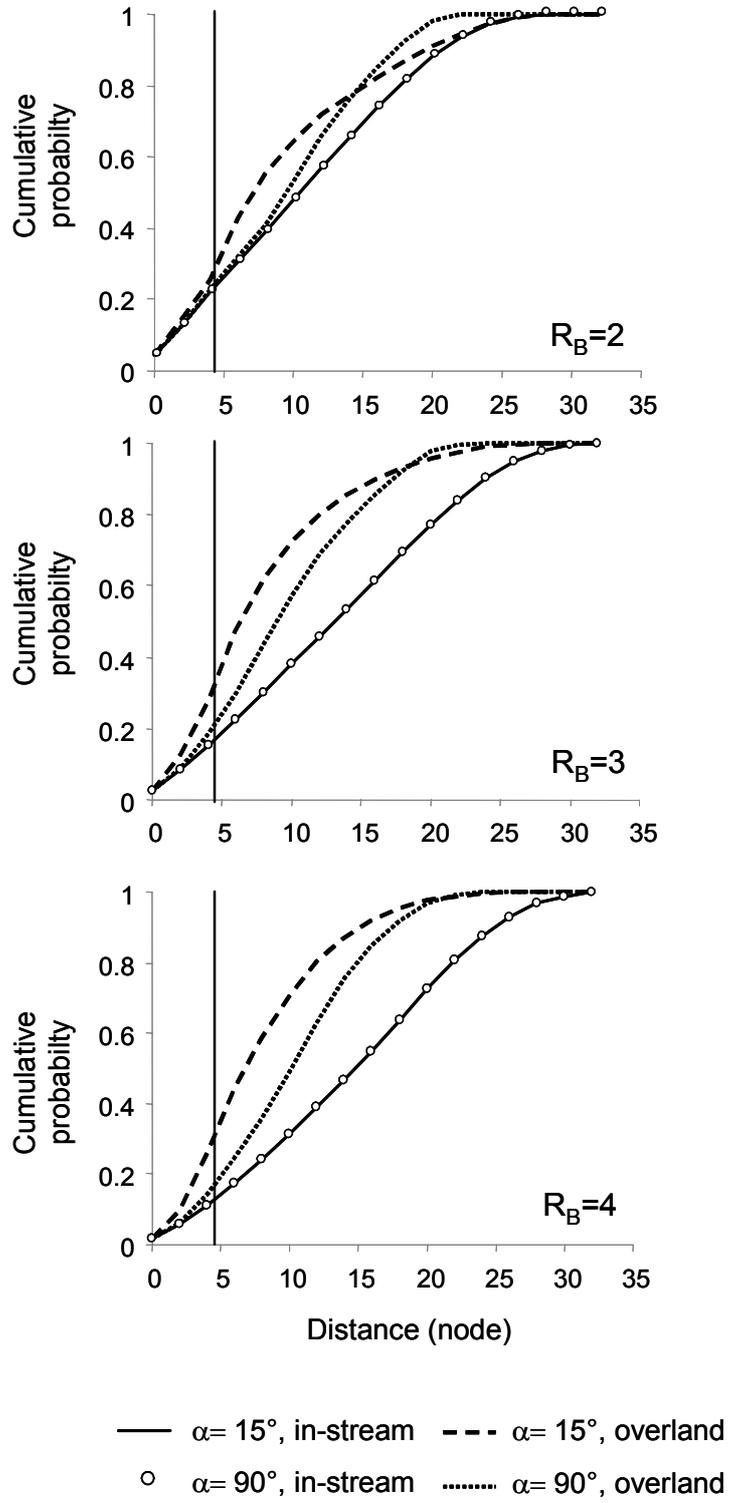


662 **Figure 4**

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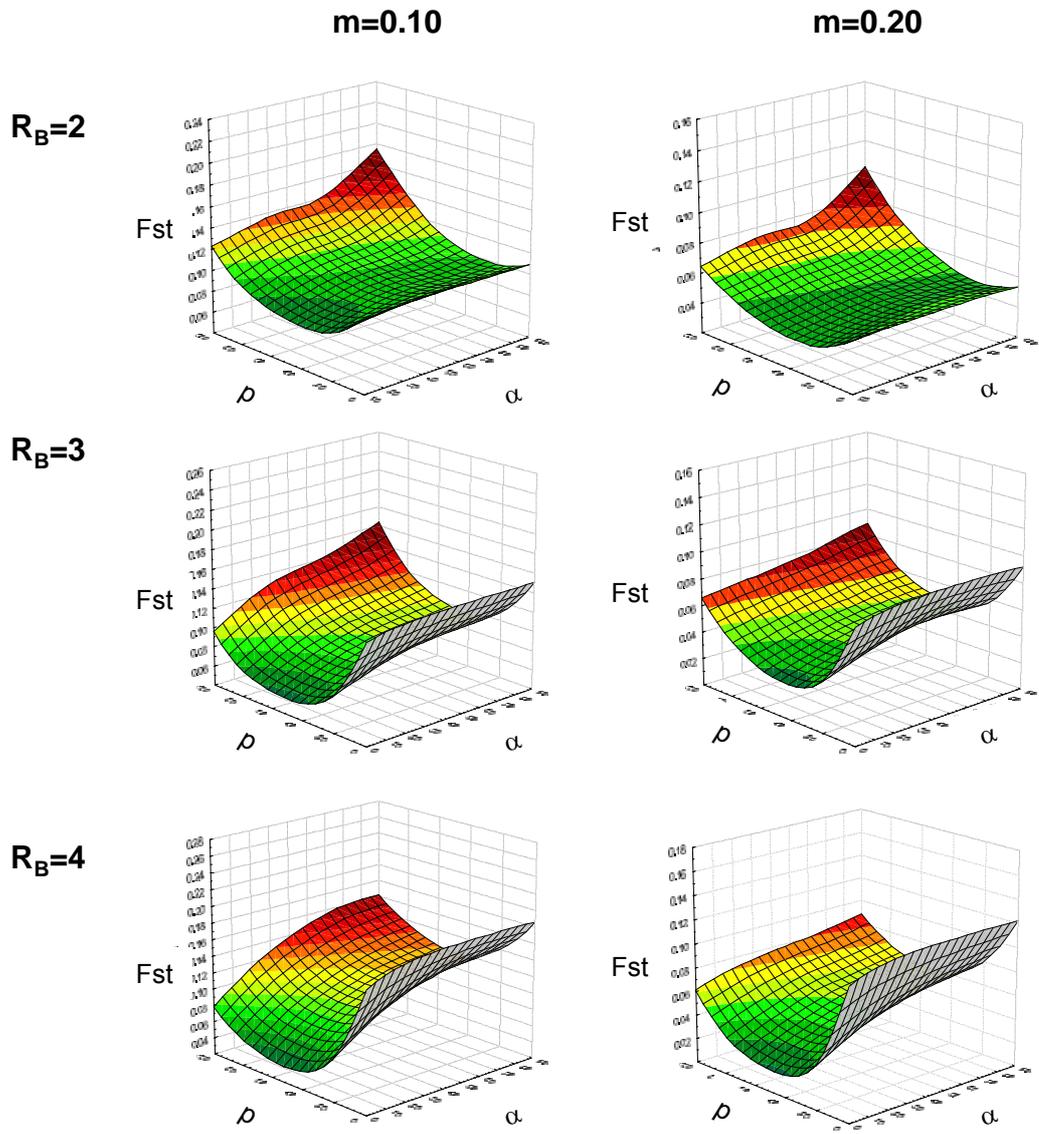


666 **Figure 5**

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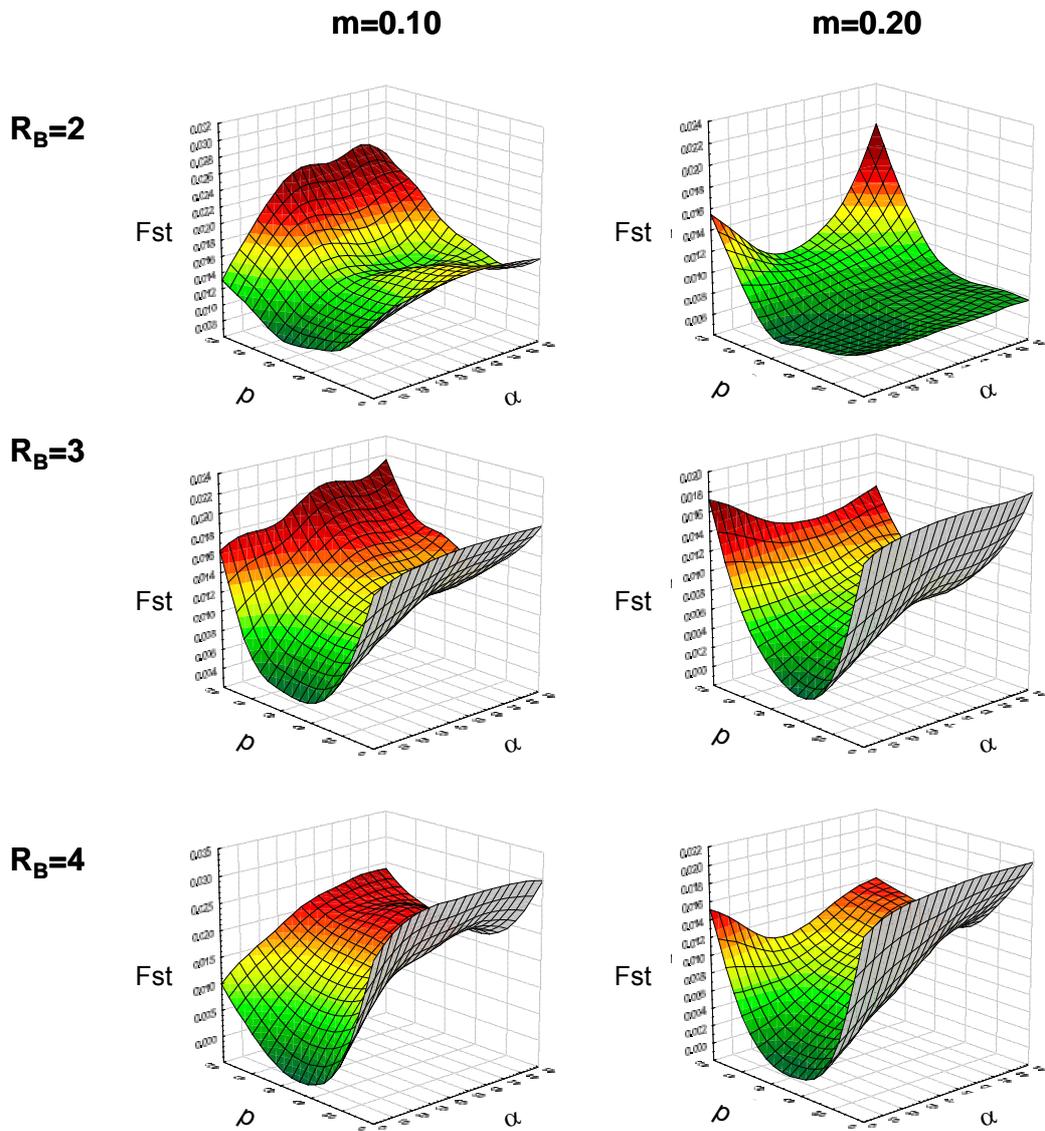
670 **Figure 6**

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Figure 7

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