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Julie Pierson, Ariane Bernard Laurent, Yann Magnani, Stéphane Marin, Sonia Said, Alain Caizergues

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1 **Euclidean distances *versus* effective pathways: a GIS approach for**
2 **testing the effects of dispersal constraints on spatial genetic structure**
3 **of Black grouse (*Tetrao tetrix* Aves, *Tetraoninae*) populations.**

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7 Julie Pierson¹, Ariane Bernard-Laurent¹, Yann Magnani¹, Stéphane Marin¹, Sonia Saïd²
8 and Alain Caizergues³

9

10 1 ONCFS, Direction des études et de la recherche, CNERA Faune de Montagne, soit
11 90, impasse "Les Daudes", BP 41, 74 320 Sévrier, France

12 2 ONCFS, Direction des études et de la recherche, CNERA Cervidés Sanglier, 1 place
13 Exelmans 55000 Bar Le Duc, France

14 3 ONCFS, Direction des études et de la recherche, CNERA Avifaune Migratrice, 53,
15 Rue Russeil, 44000 Nantes, France

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24 Corresponding author: Alain Caizergues (a.caizergues@oncfs.gouv.fr)

25

25 **Abstract.**

26 Radio-tracking of juveniles and genetic studies have previously suggested that mountain
27 ridges may represent barrier to dispersal for the Black grouse. In the present study, we
28 assessed the potential of a more straightforward approach to test the effect of these
29 topological features on Black grouse dispersal. We simply compared correlations
30 between genetic distances and geographic distances assuming that if mountain ridges
31 truly represent barriers to dispersal for the Black grouse, correlation coefficients should
32 improve when using pairwise distances taking into account dispersal barriers (or
33 effective pathways) instead of straight-line (Euclidean) distances. We computed
34 effective pathways using the Geographic Information System (GIS) package
35 ARCVIEW 3.2 and its extension PATHMATRIX especially designed to determine
36 least-cost pathways from a landscape matrix in which all habitat types are given a
37 specific cost. Whatever the type of distance used (Euclidean distances *versus* effective
38 pathways) a highly significant isolation-by-distance effect was observed. The
39 correlation between geographic and genetic distances slightly improved when the
40 effective pathways instead of Euclidean distances were used. However, these
41 improvements were very small suggesting either that mountain ridges are “permeable”
42 barriers to dispersal or that the prerequisite for using the GIS approach efficiently were
43 not fully satisfied.

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48 **Keywords:** Aves, dispersal constraints, genetic differentiation, GIS, least cost analysis,
49 microsatellites.

50

50 **Introduction**

51 Describing population spatial structure and understanding its determinants is a key issue
52 for conservation/management purposes (Frankham et al 2002). In this perspective, the
53 challenge it is not only to assess habitat requirements, but also to identify landscape
54 components that effectively impede movements between populations (Coulon et al
55 2006; Vos et al 2001).

56 The Black grouse (*Tetrao tetrix*) is a galliform bird living in forested areas of
57 northern and central Europe, but also in open moors of British Isles as well as in the
58 Alps. Over the last 50 years, human activity has greatly diminished in numerous areas
59 formerly occupied by the Black grouse, resulting in the extirpation of the species owing
60 to the closure of forest canopy. In the Alps, the distribution of Black grouse has
61 remained stable over the 25 years, but populations have declined because of changes in
62 land use practices (spreading of ski resorts, land abandonment) (Arlettaz et al 2007;
63 Bernard-Laurent 1994). Legally speaking, the Black grouse is now considered as a
64 major conservation concern (Storch 2000), although the species is not threatened but
65 included in Annex I of the EU Birds Directive (79/409/EEC) as a species for which
66 special habitat conservation measures are required.

67 Numerous studies aiming to better understand the causes of the decline of Black
68 grouse populations in the Alps have been carried out since 20 years (Bernard 1981;
69 Caizergues and Ellison 1997; Caizergues and Ellison 2000; Caizergues and Ellison
70 2002; Ellison et al 1988; Magnani 1988). A major aim of these studies was to collect
71 data on dispersal movements in order to better understand the spatial organisation of
72 Black grouse populations. In this context, radio-tracking studies showed that dispersing
73 juveniles were reluctant to cross high mountain ridges culminating above their natural
74 habitat (i.e., above 2300 m a.s.l.) and more generally that movements between

75 favourable habitat patches were always performed along forest drainages i.e. following
76 the axes of valleys (Caizergues and Ellison 2002). Later, indirect evidence supporting
77 that high ridges impede Black grouse dispersal could be gathered using a genetic
78 approach. More particularly, the genetic differentiation between local populations was
79 found to be almost seven times higher in the Alps where Black grouse have to cope with
80 mountains ridges constraining dispersal than in Finland where no such constraints exist
81 (Caizergues et al 2003b). Unfortunately, because the stronger genetic differentiation in
82 the Alps compared to Finland could also be due to a naturally more fragmented habitat
83 in the former, firm conclusions concerning the influence of mountain ridges on the
84 spatial organisation of Black grouse populations could not be derived.

85 In the present paper, we adopted a straightforward approach to assess the effects
86 of mountains ridges on the spatial genetic structure of Black grouse populations in the
87 Alps. Using a least-cost-pathway analysis with a Geographic Information System
88 software, we computed distances incorporating the effects of mountain ridges on Black
89 grouse dispersal (distances hereafter called effective pathways). Then we compared the
90 strength of the correlation between genetic distances and these effective pathways to the
91 correlation obtained between the same genetic distances and (straight-line) Euclidean
92 distances. This kind of approach has previously been successfully applied to several
93 biological models although never in birds (Hamilton et al 2006; Michels et al 2001;
94 Spear et al 2005; Stevens et al 2006; Verbeylen et al 2003). We predicted an
95 improvement of the correlation when using effective pathways instead of Euclidean
96 distances if, as expected, mountains ridges effectively impede dispersal movements of
97 Black grouse.

98 **Materials and methods**

99 *Study area*

100 The study site almost covers the whole French Alps as well as portions of Swiss and
101 western Italian Alps, representing an area of about 45,000 km². The topography consists
102 in a succession of valleys, ridges and high mountains with altitudes mainly comprised
103 between 200 and 4800 m a.s.l (Figure 1).

104 *Sampling and genetic methods*

105 Tissues (skin, muscles, toes, liver) were collected from Black grouse legally shot by
106 hunters during the autumns 1997 – 2000. This period does not exceed the average
107 generation time of the Black grouse which has been estimated to 4-5 years (Caizergues
108 and Ellison 1997).

109 Analyses were performed both at the individual and population levels. Four
110 hundred and thirty six samples grouped in 18 entities (populations) were used in the
111 analyses at the population level. Analyses performed at the individual level included a
112 sample of 152 individuals selected to cover as homogeneously as possible the larger
113 area possible (Figure 1). We did not use the whole sample in the individual based
114 approach because it would have implied the calculation of 94830 least-cost paths which
115 represented a computing time exceeding 80 hours.

116 Each individual retained was characterised with at least 10 of the 14
117 microsatellites loci whose properties are described in details in Caizergues *et al.*
118 (2003b). DNA extraction were performed using DNeasy Tissue Kits (Qiagen Inc.)
119 following manufacturer protocols. Amplifications were carried out on PTC 100
120 thermocycler using Touch Down procedures (Don et al 1991) in volumes of 10 µl
121 containing 1 µl of extraction product (see Caizergues et al 2003b for details).

122 *Statistical analyses of genetic data*

123 Previous analyses of a subsample of the material presented here did not detect
124 significant linkage disequilibrium between pairs of loci (Caizergues et al 2003b).
125 Therefore, only tests of Hardy-Weinberg proportions and the basic statistics averaged
126 over loci are presented here.

127 Departures from Hardy-Weinberg expectations were assessed for each locality
128 using exact tests implemented in GENEPOP (3.3 version, 2001, Raymond & Rousset
129 1995; Rousset 2000).

130 *Modelling geographical distances.*

131 All geographical distances were computed using the GIS software ARVIEW version
132 3.2. Effective pathways (or least cost distances) measure the shortest distance between
133 two entities obtained by minimising the costs of moving through the various
134 components of the landscape defined by the user. We modelled effective pathways
135 (between individuals and between populations) with the PATHMATRIX extension of
136 ARCVIEW 3.2 (Ray 2004) using a three components landscape matrix derived from the
137 topological model of the study area. These three landscape components were defined as
138 follow:

- 139 1) Natural habitats of Black grouse ranging between 1600 and 2300 m
140 a.s.l. The species is assumed to move with minimal constraints in his
141 natural habitats.
- 142 2) Mountain ridges culminating above the altitude of 2300 m a.s.l. which
143 are assumed to act as total barriers to Black grouse movements.
- 144 3) Habitats below 1600 m (valleys), which may be costly to cross but that
145 do not represent absolute barriers to dispersal.

146 The delineation of landscape components was achieved on ARCVIEW 3.2 using
147 a raster topological model of the study area with a 200 m resolution grid. Tests
148 performed with 20, 50, 100, 200, 500 m grids showed that a 200 m resolution was the
149 best compromise between computation time and a reliable representation of the putative
150 constraints to dispersal.

151 Effective pathways were computed using the value 1 as an arbitrary cost of
152 moving across natural habitats. To make mountain ridges act as absolute barriers to
153 movements their cost was set at 10000. Valleys up to 10 km wide do not seem to
154 represent a problem for Black grouse (Caizergues et al 2003b). However, undertaking
155 flights in open spaces might entail higher risks in terms of predation than moving under
156 the sheltering canopy of favorable habitats. For this reason, a cost of 2 was set to
157 habitats below an altitude of 1600 m (valleys).

158 The Euclidean distances are simply the straight-line distances between two
159 entities. They don't take landscape structure into account. These distances were also
160 computed on PATHMATRIX but the same cost for the three habitats types was set. In
161 the analyses performed at the population level, pairwise geographical distances were
162 calculated between the barycenter of individuals constituting each of the populations.

163 *Correlations between genetic and geographical distances.*

164 Tests of correlation between genetic and geographical distances were performed in
165 SPAGeDi version 1.2 software (Hardy and Vekemans 2002) with a permutation
166 procedure equivalent to the test of Mantel (Manly 1986; Mantel 1967). SPAGeDi was
167 also employed to compute the various estimates of genetic distances/kinship
168 coefficients. SPAGeDi is of particular interest compared to other genetic packages
169 because it allows importing matrixes and propose a larger collection of genetic distance
170 estimators than most other packages.

171 The statistic $F_{st}/(1-F_{st})$ was used as an estimate of the genetic distances between
172 populations because it is expected to vary linearly with the logarithm of distances and
173 therefore provide unbiased estimates of regression slopes (Rousset 1997). Loiselle's
174 kinship coefficient (Loiselle et al 1995) and the \hat{a} distance (Rousset 2000) were used to
175 characterize the genetic relationships between individuals. Loiselle's kinship coefficient
176 offers both a low bias and a low sampling variance (Hardy and Vekemans 2002). The \hat{a}
177 distance suffers from a higher sampling variance but can be compared to analyses
178 performed at the level of populations because it is a generalization of the $F_{st}/(1-F_{st})$
179 estimator.

180 **Results**

181 *Euclidean distances vs. effective pathways*

182 The characteristics of both Euclidean distances and effective pathways between both
183 individuals and populations are summarized in table 1. The differences between the two
184 types of distances were highly significant (Paired t, test all P values <0.001). The
185 figures showing the effective pathways are very interesting because they allow
186 identifying corridors necessary to maintain dispersal between populations under the
187 hypothesis that mountains ridges 2300 m a.s.l. are dispersal barriers. At least five
188 corridors between the West and East side of the Alpine massif are easily visible on both
189 maps (Figure 2).

190 *Correlations between genetic and geographical distances*

191 Microsatellite polymorphism ranged from 2 to 17 alleles per locus, with a mean
192 of 6.5 (Table 2). Among the 18 populations used in the analyses, only population
193 10 displayed any significant departure from Hardy-Weinberg expectations (Table 2).
194 However, in this population only two 2 loci out of 14 displayed any significant
195 departure from Hardy-Weinberg expectations.

196 The average F_{st} value between populations was 0.049 (SE=0.0039, range: 0 -
197 0.11).

198 Correlations between the genetic distances / kinship coefficient and the
199 logarithms of geographical distances were highly significant either using the individual
200 or the population approach ($P < 0.001$, Tables 3, Figure 3). Regression slopes obtained
201 using $F_{st}/(1-F_{st})$ and the \hat{a} were of the same order of magnitude with confidence
202 intervals largely overlapping (Tables 3). This suggests that the approach based on
203 individuals is as reliable as the approach based on populations despite the high sampling
204 variance of the \hat{a} estimator.

205 At the population level, the correlation between genetic and geographic
206 distances slightly improved when using effective pathways instead of Euclidean
207 distances (Table 3). At the level of the individual, this correlation improved only for
208 Loiselle's kinship coefficient (Table 3). The poorer performance of the analyses using
209 the \hat{a} was probably due to the higher sampling variance of estimator (Vekemans and
210 Hardy 2004).

211 **Discussion**

212 An increasing number of studies explore landscape connectivity using either
213 Geographic Information Systems (e.g., Graham 2001; Larkin et al 2004; Ricketts 2001;
214 Verbeylen et al 2003) or populations genetics approaches (Bouzat 2001; Caizergues et
215 al 2003b; Knutsen et al 2000; Roland et al 2000). In comparison, studies adopting a
216 combination of these two approaches in an integrated manner are scarce (but see
217 (Arnaud 2003; Hamilton et al 2006; Michels et al 2001; Spear et al 2005; Stevens et al
218 2006; Vigneri 2005; Vos et al 2001). Moreover, in most of these studies analyses were
219 carried out at the population rather than the individual level and the integration of

220 landscape structure almost always involved complex assumptions rarely derived from
221 direct observations of the biological model studied.

222 Here we report the results of an explicit landscape genetics analysis in a bird
223 species, specifically the interaction between landscape features and demography and
224 microevolutionary processes (Manel et al 2003). We also show, that maintaining gene
225 flow between Italian and Franco-Swiss Black grouse populations will depend upon our
226 capacity to preserve favourable habitats along five mains corridors.

227 Although most birds usually display good dispersal propensities and therefore
228 little, or no genetic spatial structure at all, we detected not only a highly significant
229 isolation-by-distance effect but also provided support for the negative influence of
230 landscape features such as high ridges on dispersal.

231 However, we concur that as such, our results do not allow to derive firm
232 conclusion about the exact influence of high ridges on Black grouse dispersal, chiefly
233 because only two tests out of three detected an improvement of the correlation
234 coefficient between genetic and geographic distances when the presence of dispersal
235 barriers was taken into account. Moreover, these improvements were small.

236 Several non exclusive hypotheses might explain why models including effective
237 pathways did not perform much better than model that didn't include them. Firstly, the
238 high variance inherent to all genetic distances estimators (Vekemans and Hardy 2004)
239 would render difficult the detection of small differences between concurrent models.
240 Secondly, barriers occur mainly between the West and East sides of the Alps (Figures 2)
241 while most of our samples come from the West side where numerous passes allow
242 dispersal between neighbouring forest drainages. In other words, our sampling design
243 was probably not optimal to fully exploit the landscape genetics approach simply
244 because the two distances are strongly correlated (Figure 4). Thirdly, owing to the high

245 levels of fragmentation of Black grouse habitats in the Alps, genetic drift could have a
246 more decisive influence on genetic structure of Black grouse populations than
247 previously suspected (Caizergues et al 2003b). This could explain both the higher
248 between-populations genetic differentiation in the Alps than in Finland (Caizergues et al
249 2003b) as well as the relatively poor performance of models taking explicitly dispersal
250 barriers into account. However, in the Alps, Rock ptarmigan populations that
251 experience a level of fragmentation comparable to the Black grouse, did not display a
252 high degree of genetic divergence, with average F_{st} values of 0.01 against 0.049 to 0.07
253 for the Black grouse (present study, Caizergues et al 2003a; Caizergues et al 2003b).
254 Mountain ridges are part of the habitat of Rock ptarmigan meaning that the species, in
255 contrast to Black grouse, doesn't have to cope with barriers to dispersal.

256 Another explanation to the relative poor performance of models taking dispersal
257 into account could be that the mountains ridges do not represent absolute barriers to
258 dispersal contrary to our initial assumption. Although we cannot total discard this
259 hypothesis, direct observations strongly support these topological features do act as
260 natural barriers to dispersal for the Black grouse. These include radio-tracking data of
261 *ca* 100 individuals (Caizergues 1997; Caizergues and Ellison 2002).

262

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265 supporting this project.

266

266 **Table 1.** Summary of characteristics of Euclidean and effective pathways between
 267 populations and individuals (expressed in kilometers).

268

	Populations		Individuals	
	Euclidean distances	Effective pathways	Euclidean distance	Effective pathways
Maximum	284.42	362.59	300.20	371.96
Minimum	17.62	24.12	0.569	0.70
Average	132.05	176.32	119.26	160.41
Median	120.64	171.99	114.40	159.82
Standard deviation	71.35	88.14	70.73	90.37
Paired samples t-test	P<0.001		P<0.001	

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270

271 **Table 2.** Summary statistics of the variability of the 14 microsatellites loci in each of the 18 sampled populations.

272

Population	N	Mean number of alleles	Minimum number of alleles	Maximum number of alleles	Average Ho	Average He
01 (Veglia/Devero)	11	6.07	3	11	0.71	0.77
02 (Vigezzo)	58	8.57	5	13	0.72	0.77
03 (Valais upstream)	15	6.93	4	13	0.79	0.78
04 (Valais downstream)	24	8.14	4	13	0.79	0.78
05 (Giffre)	15	7.71	4	13	0.82	0.79
06 (Aravis/beaufortain)	54	8.64	5	14	0.75	0.78
07 (Tarentaise)	13	6.21	3	10	0.68	0.75
08 (Maurienne upstream)	19	6.36	3	10	0.75	0.74
09 (Maurienne downstream)	49	7.29	4	12	0.73	0.75
10 (Queyras)	57	7.14	4	12	0.71	0.75
11 (Champsaur)	10	5.50	3	9	0.80	0.75
12 (Haut-Var)	18	6.07	4	9	0.76	0.76
13 (Haute-Tinée)	24	6.43	4	13	0.75	0.71
14 (Haute Roya)	45	6.79	4	11	0.75	0.73
15 (Anzasca)	6	5.14	3	7	0.78	0.75
16 (Aosta)	5	4.93	2	7	0.83	0.83
17 (Briançonnais)	6	5.00	3	8	0.73	0.77
18 (Ubaye)	7	5.21	3	8	0.66	0.75

273

273 **Table 3.** Correlation tests between the logarithm of geographical distances (Euclidean
 274 distances vs effective pathways) and genetic distances / kinship coefficient between
 275 individuals (Loiselle's coefficient of kinship and Rousset's \hat{a}) or between populations
 276 ($F_{st}/(1-F_{st})$). r^2 = determination coefficient, a = intercept, b = regression slope value, CI
 277 = confidence interval of b and P-value of the correlation test.

278

	Genetic distance	Geographic distance	r^2	a	b	95%CI-inf	95%CI-sup	P-value
Individuals	Loiselle's coefficient	Euclidean distances	0.051	0.211	-0.018	-0.020	-0.0172	<0.001
		Effective pathway	0.052	0.215	-0.018	-0.019	-0.0171	<0.001
	\hat{a}	Euclidean distances	0.036	-0.186	0.020	0.016	0.0238	<0.001
		Effective pathways	0.036	-0.187	0.019	0.016	0.0231	<0.001
Populations	$F_{st} / (1-F_{st})$	Euclidean distances	0.439	-0.275	0.027	0.021	0.0346	<0.001
		Effective pathways	0.452	-0.314	0.030	0.023	0.0377	<0.001

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280

280 **Legend of figures**

281 **Figure 1.** Location of the study area and spatial distribution of individuals (open
282 circles) and populations barycentres (black squares). (1 = Veglia/Devero, 2 = Vigezzo, 3
283 = Valais upstream, 4 = Valais downstream, 5 = Giffre, 6 = Aravis/Beaufortain, 7 =
284 Tarentaise, 8 = Maurienne upstream, 9 = Maurienne downstream, 10 = Queyras, 11 =
285 Champsaur, 12 = Haut-Var, 13 = Haute-Tinée, 14 = Haute-Roya, 15 = Anzasca, 16 =
286 Aosta, 17 = Briançonnais, 18 = Ubaye)

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288 **Figure 2.** Least-cost paths as estimated by PATHMATRIX based on (a) Euclidean
289 distances between populations barycentres, (b) effective pathways between populations
290 barycentres and (c) effective pathways between individuals.

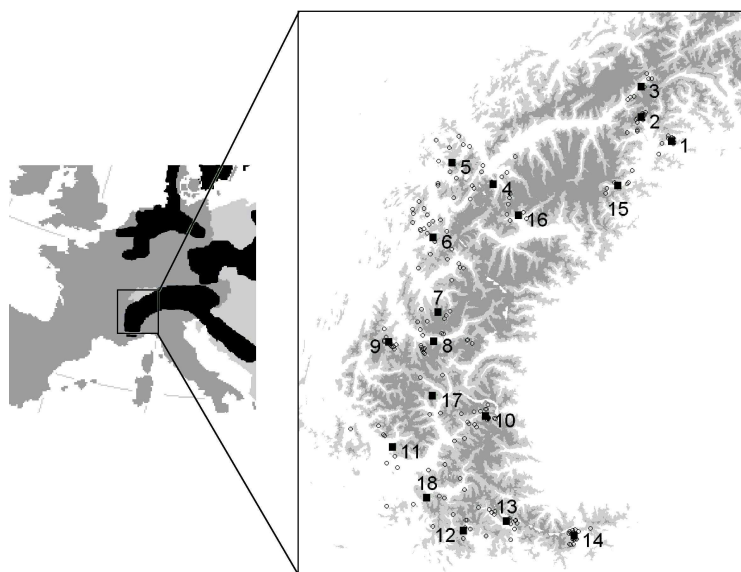
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292 **Figure 3.** Relationship between Euclidean distances (log transformed) and genetic
293 distances/kinship coefficients, and between effective pathways (log transformed) and
294 genetic distances/kinship coefficients.

295

296 **Figure 4.** Relationship between pairwise Euclidean and effective pathways between
297 populations barycentres. r^2 = determination coefficient.

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299 **Figure 1.**

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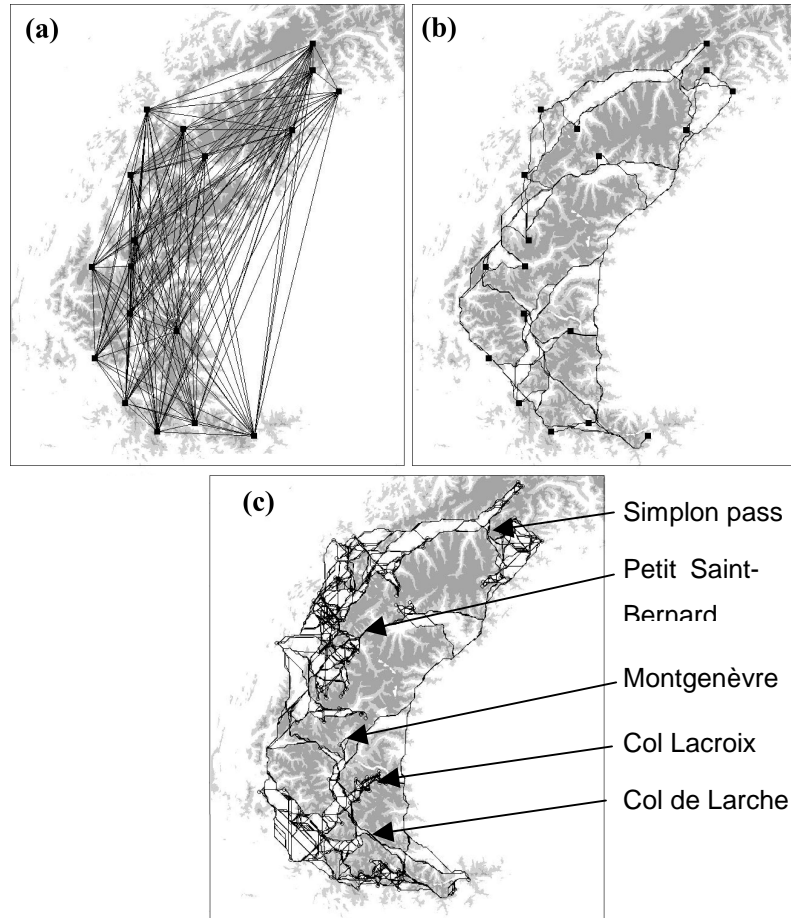
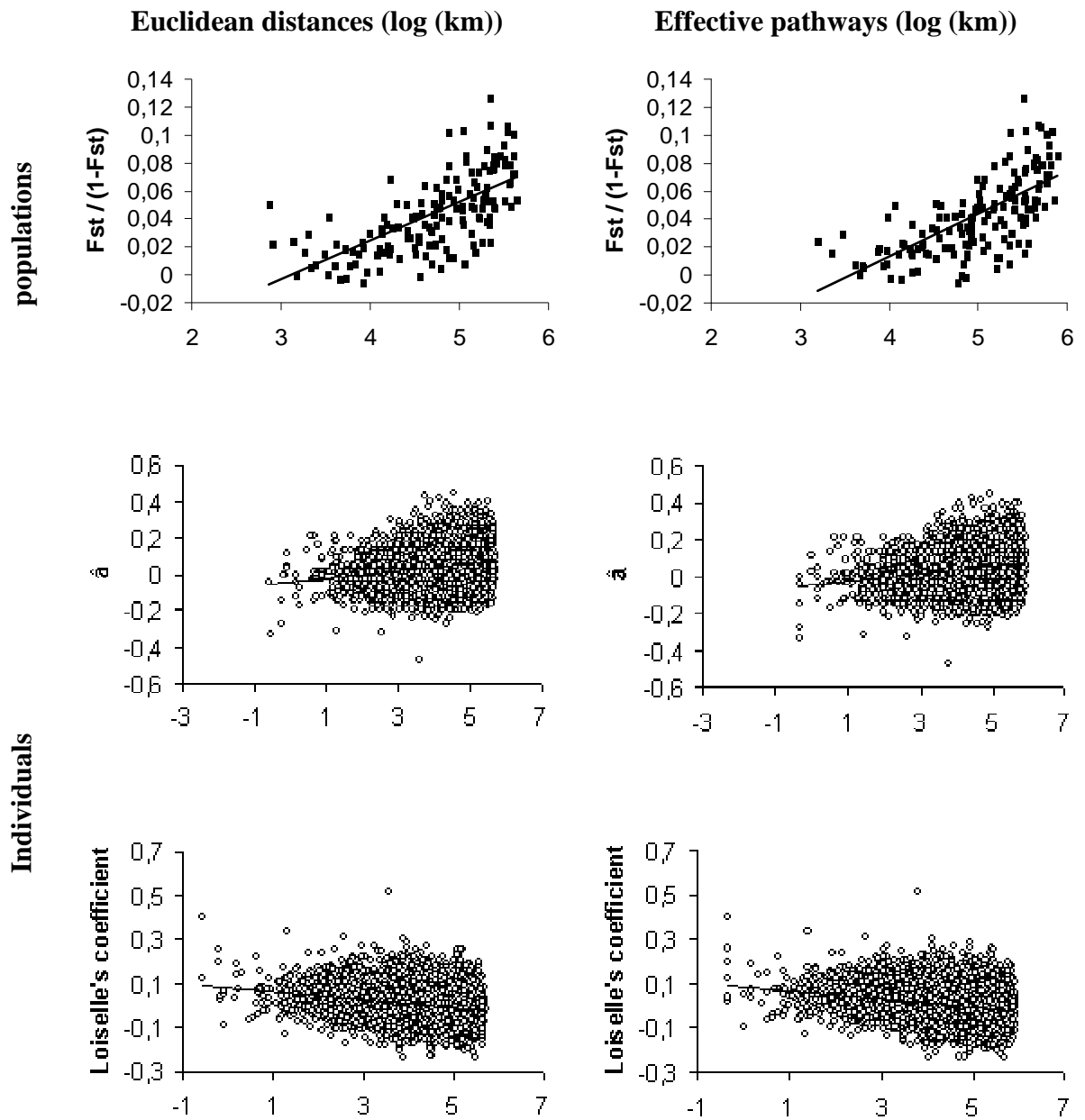


Figure 2.

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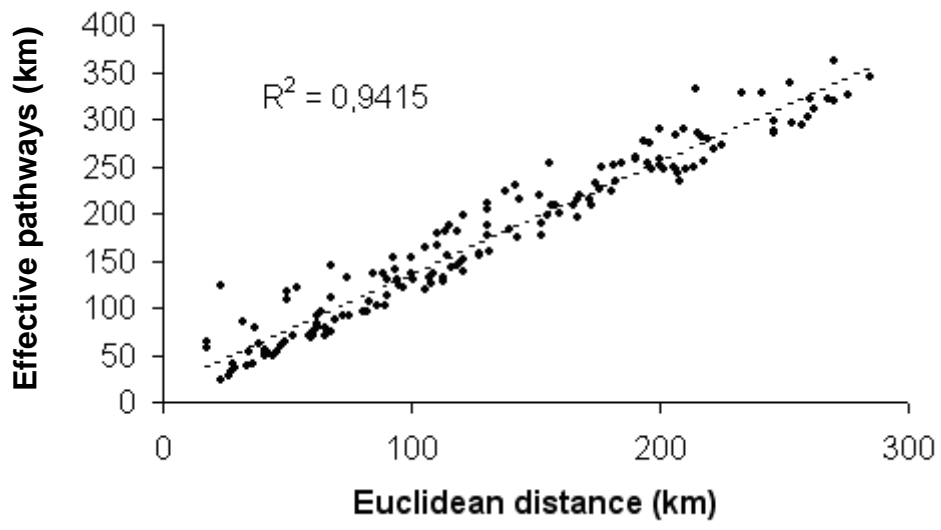
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334 **Figure 3.**

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Figure 4.

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