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1 **A multiscale analysis of landscape resistance reveals genetic isolates in an**
2 **endangered forest-specialist species the Barbary macaque (*Macaca***
3 ***sylvanus*)**

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23

24 **Abstract**

25 In forest-specialist mammals, forest loss may induce resistance to animal movement and
26 reduce gene flow between populations, and thereby increase genetic erosion and
27 extinction risks for populations. Understanding how landscape features affect gene flow
28 is of critical importance for conservation. Using landscape genetic tools at multiple
29 spatial scales, we assessed the effects of landscape heterogeneity (in particular the
30 presence of wide open or rural habitats) on gene flow in an endangered forest-specialist
31 species – the Barbary macaque (*Macaca sylvanus*) –, in its major forest site in Morocco.
32 We genotyped 248 individuals from 23 macaque groups using 11 microsatellite loci. We
33 modelled different scenarios of isolation by landscape resistance. We further tested the
34 relationships between genetic distance and isolation by resistance, after controlling for
35 the effect of isolation by distance. Our results revealed a significant genetic structure and
36 a disruption of gene flow even in geographic proximity. Whatever the spatial scale,
37 remoteness from the forest edge beyond 1km acted as a barrier to macaque movements.
38 In addition, at a fine scale, human-dominated areas were also detected as a barrier. The
39 detection of private alleles in each population suggests an ongoing process of isolation.
40 The preservation of the Barbary macaque implies 1) strictly avoiding all silvicultural
41 practices (in particular clear-cutting of holm oak forests) that could contribute to increase
42 distances between forest patches, 2) restoring corridors between forests, 3) and
43 preserving key small forest patches as potential stepping stones facilitating macaque
44 dispersal.

45 **1. Introduction**

46 Human activities fragment habitats worldwide, with agriculture and/or settlements
47 making up most of the matrix between remaining patches of optimal habitats (Ellis et al.,

48 2010). In particular, forests can be fragmented because of agricultural land expansion and/or
49 inadequate silvicultural practices (Foley et al., 2005). Heterogeneous and fragmented
50 landscapes potentially limit gene flow because functional connectivity between suitable
51 habitat patches is reduced (Manel and Holderegger, 2013; Taylor et al., 1993). A lack of
52 connectivity leads to populations that are isolated from one another (Kupfer et al., 2006), a
53 loss of genetic diversity within populations, and increased extinction risks, especially for
54 small populations (Haddad et al., 2015).

55 Species sensitivity to habitat fragmentation depends on the ecological and behavioural
56 flexibility of the species dispersal characteristics: habitat generalists with high potential
57 dispersal may be less sensitive to habitat fragmentation than other species (Amos et al., 2014;
58 Engler et al., 2014; Goossens et al., 2016) because they are able to cross the inhospitable
59 matrix at suitable periods and adjust their travelling activities across time and space [e.g.
60 elephants (Graham et al., 2009)]. By contrast, in habitat-specialist species, potential dispersal
61 can decrease with the increasing distances to refuges, the increasing probabilities of
62 encountering predators (Gubili et al., 2017), or with physiological constraints that condition
63 their greater fidelity to site [e.g. increasing water requirements in amphibian species (Mims et
64 al., 2015)]. The inhospitable matrix can therefore become a barrier to dispersal (Moraes et al.,
65 2018) and impede the recolonisation of void habitat patches by habitat-specialist species
66 (Haddad et al., 2015). For these species, the functional connectivity between suitable habitats
67 can be particularly sensitive to the distance to refuges and the quality of the matrix.

68 Understanding the relationships between landscape structure and patterns of gene flow
69 is all the more crucial for conservation strategies regarding endangered and habitat-specialist
70 species. However, in heterogeneous habitats, patterns of landscape resistance to dispersal can
71 be difficult to assess because factors limiting animal mobility can be hidden depending on the

72 spatial scale of analyses (Anderson et al., 2010; Aylward et al., 2020; Jackson and Fahrig,
73 2012). For instance, the consequences of landscape heterogeneity on squirrel monkey (*Saimiri*
74 *oerstedii*) populations in Costa Rica from palm oil plantations were detected only at a large
75 scale and went undetected at a fine scale, indicating that this matrix habitat mainly limits long
76 dispersal events (Blair and Melnick, 2012). Therefore, investigations of the links between
77 landscape and the genetic structure of populations should be conducted at different spatial
78 scales (Harrisson et al., 2013) in order to detect the landscape determinants of local and long-
79 distance dispersal.

80 The Barbary macaque (*Macaca sylvanus*) is a forest-dependent and endangered social
81 species whose distribution range is restricted to a human-modified and heterogeneous
82 landscape across northern Algeria and Morocco. Its decline led to a recent change of its IUCN
83 threat status from ‘Vulnerable’ to ‘Endangered’ species (Butynski et al., 2008) and to place it
84 in Appendix I of CITES (CITES, 2017). There is a global need to determine how landscape
85 heterogeneity affects functional connectivity among forest patches and in turn the genetic
86 structure of Barbary macaque populations, potentially leading to the formation of small
87 genetic isolates at higher risk of extinction (Benson et al., 2016). The Barbary macaque is a
88 social species which forms multimale-multifemale groups of 10-88 individuals (Ménard,
89 2002; Ménard and Vallet, 1993b). Similar to other macaque species (e.g. *M. fuscata*, *M.*
90 *mulatta*, *M. fascicularis*, Gachot-Neveu and Ménard, 2004; Melnick, 1987), females are
91 philopatric in terms of attachment to their natal group and their home range, while males
92 disperse. Nevertheless, permanent group fission between matriline is also considered as a
93 way by which females disperse so that social groups can be considered as relevant units of
94 dispersal (Lefebvre et al., 2003; Ménard, 2017). Natal dispersal of males usually occurs near
95 adulthood, and then adult males disperse several times in their life. Empirical observations of

96 dispersing males indicated that at least 30% of them immigrated into immediate neighbouring
97 groups. Therefore, the Barbary macaque shows rather low potential dispersal owing to female
98 philopatry and the putative usual short dispersal distance of males (Ménard and Vallet, 1996;
99 Taub, 1977). In addition, although the Barbary macaque spend more than 50% of its diurnal
100 activities on the ground (Ménard and Vallet, 1997), as a forest-specialist species, Barbary
101 macaque social groups are reluctant to cross large open areas (in the order of 200m) between
102 forest edges (Ménard and Vallet, 1996). Similarly, we suspect that the ability of dispersing
103 males to venture far from forest edges remains limited. Barbary macaques are not dependent
104 on cultivated food. Crop-foraging remains anecdotal in the Middle Atlas, occurring only in
105 rare cases where crops are in contact with the forest edge.

106 Because the Barbary macaque is forest-dependent with low potential dispersal, we
107 assumed that gene flow, and consequently genetic structure and diversity, were highly
108 affected by distance between forest fragments and the presence of open areas. We
109 hypothesized that (1) non-forest matrices were more resistant to gene flow as the distance
110 increased between the edges of forest fragments, (2) open areas or anthropogenic rural
111 landscape greatly limited macaque dispersal between forest patches as compared to dispersal
112 within continuous forest. We employed stratified non-invasive genetic sampling in several
113 forest patches and landscape genetic tools to evaluate these hypotheses and we tested the level
114 of connectivity between forest patches at different spatial scales (Anderson et al., 2010). We
115 finally discuss how the identification of the degree of isolation of the populations, their
116 genetic status, and the landscape variables that limit gene flow can be used to adapt
117 management actions in favour of the Barbary macaque.

118 **2. Materials and Methods**

119 *2.1. Study area and sample collection*

120 The study area covered 3,472 km² in the Middle Atlas region in Morocco where the
121 forested area is highly fragmented (Fig. 1). The areas managed by foresters covered 1,402
122 km² including unforested areas and forest patches mainly composed of mixed evergreen
123 cedar-oak forests (*Cedrus atlantica* and *Quercus rotundifolia*, Ménard et al., 2014). The
124 remaining areas were mainly devoted to agricultural or pastoral activities, and human
125 settlements (see Appendix A for details on the vegetation mapping). Five land-cover
126 categories were defined according to the ecological requirements of Barbary macaques, in
127 particular their movement (see below): “undamaged forests” containing tall mature trees;
128 “degraded forests” with cedars heavily pruned by shepherds; “oak coppice” (tree height: 2-5
129 meters) resulting from silvicultural practices; “open areas” including open grasslands or very
130 low oak coppice (< 2 m high), and “human-dominated areas” devoted to agricultural or
131 pastoral activities, or human settlements (Fig. 1A). Between 2006 and 2009, we collected 376
132 fecal samples from 23 wild Barbary macaque groups distributed in eight forest patches (Fig.
133 1, see details on procedure and sample distribution in Appendix B).

134 2.2. Landscape resistance computation

135 2.2.1. Resistance maps based on “remoteness” and “land”

136 Resistance maps were built based on two approaches. In the first approach, we
137 considered the remoteness from forest edges (hereafter called “remoteness resistance”). The
138 remoteness resistance map was built with six categories of distances from the forest edge.
139 First, “1” was attributed to every location within forest patches. Then, five classes of
140 distances were mapped, with five buffers built outside forest patches using ArcGis 10.5.1
141 (Environmental Systems Research Institute, 2017): < 200m (based on our studies on focal
142 groups indicating that they did not move away from forest edges by more than 200m, Ménard
143 and Vallet, 1996), < 300m, < 500m, < 1000m, > 1000m. These remoteness distances

144 corresponded to edge-to-edge distances between forest patches of < 400m, < 600m, < 1000m,
145 < 2000m, > 2000m, respectively. Then, resistance values were assigned to each distance
146 category (Fig.1B and Table 1).

147 In the second approach we ranked land cover types, i.e. landscapes of increasing resistance to
148 movements, from forest areas to human-dominated open areas (hereafter called “land
149 resistance”, see below). We ordered the resistance values of the five land cover categories
150 according to scientific literature on habitat suitability based on Barbary macaque density
151 estimated in each type of land cover (Fa, 1984; Taub, 1977) and on habitat use within home
152 ranges (Ménard, 2002; Waterman et al., 2019). “Undamaged forest” was the optimal habitat,
153 with tall mature trees as refuges against danger, where resistance to macaque movement was
154 assumed to be the lowest. “Degraded forest” was less favourable to macaque movement
155 because pruned cedars offered poor visual protection and the reduced width of the canopy
156 prevented macaques from escaping via trees. In “oak coppice”, macaques had to travel on the
157 ground with a relative visual protection against predators. “Open areas”, and “human-
158 dominated areas” were the least permeable areas because they did not provide protection
159 against predators; “human-dominated areas” were related to the highest predation risk (Table
160 1 and see Appendix A for details and illustrations). Roads were not considered because there
161 is no highway in the study area and macaque groups easily cross roads when they are included
162 in their home ranges.

163 2.2.2. *Landscape models*

164 We compared the classical isolation by distance (IBD) model in which the explanatory
165 variable is the Euclidean distance between groups with isolation by remoteness resistance (R)
166 and isolation by land resistance (L). Since absolute values for remoteness and land resistances
167 were not available, we tested relative values based on previous knowledge of habitat

168 suitability and use (Fa, 1984; Ménard, 2002; Waterman et al., 2019). Those relative values
169 have the advantage to be easily understood and used by stakeholders. Because of uncertainty
170 on the values of those resistances, we tested a large range of resistance values (from 1 to
171 1000), including scenarios with low differences among remoteness and land resistances and
172 scenarios with high maximized differences among remoteness and land resistances (Beier et
173 al., 2009). For all the scenarios (n = 38), we kept the hierarchical order of resistance costs
174 based on biological data (Bowman et al., 2020, Table C1, appendix C). For isolation by
175 remoteness resistance, we tested 13 scenarios of remoteness resistance to determine to what
176 extent an increasing resistance cost linked to the distance from the forest edge restricts gene
177 flow. Concerning isolation by land resistance, we tested 25 scenarios of resistance costs that
178 differed in the relative costs attributed to the various land cover categories (Table C2). Only
179 best models that explored gradual resistance costs or a potential threshold effect linked to a
180 specific landscape feature are presented in the main text (Table 1). The land and remoteness
181 resistance maps (Fig. 1A, B) were each converted into raster-grids at a 100m cell size
182 resolution. Each 100m x 100m pixel of each raster was attributed to a resistance level
183 category, i.e. the cost.

184 For each scenario, we assessed between-group connectivity across the study area using the
185 circuit theory, which assumes that dispersing animals have limited knowledge of the
186 landscape (McRae, 2006; McRae et al., 2008). This method is becoming the standard method
187 linking landscape and population genetics [see a review in Dickson et al. (2019)]. It integrates
188 all possible existing paths for each pair of sampled groups and computes the cumulated cost
189 between two locations. Distance costs were extracted with Circuitscape v4.0.5 (McRae, 2006;
190 McRae et al., 2008). We measured Euclidean distances, such as the shortest distance between

191 two sampled groups. In all, we computed 38 distance cost explanatory variables and the IBD
192 model.

193 *2.3. Genetic analyses*

194 DNA extraction, PCR amplification and genotyping were performed as described in (Vallet et
195 al., 2008). Barbary macaques were genotyped at 11 tetranucleotide autosomal microsatellite
196 loci using fluorescently labelled primers and multiplex amplifications whenever possible (for
197 details on the procedures, on the loci, PCR set-up and thermocycling profiles, quality control
198 of consensus genotypes, see Appendix D). Only individual faeces successfully genotyped at a
199 minimum of seven loci were retained for further analyses. This threshold ensured reliable
200 individual identification ($P(ID)_{sib} < 0.01$, see Appendix D for details). We used Genecap
201 software (Wilberg and Dreher, 2004) to detect and exclude all duplicate samples (Appendix
202 D).

203 *2.3.1 - Cluster analyses*

204 After the final set of unique individual genotypes was established, we explored the pattern of
205 population structure within the study area by clustering samples based on their allele
206 frequencies using GENELAND (version 3.3.0; Guillot et al., 2005), which incorporates
207 geographic coordinates as priors in a Bayesian model. The program estimates the number of
208 clusters within a sample of individuals and assigns individuals to clusters by minimising
209 Hardy-Weinberg and linkage disequilibria within populations. GENELAND also uses the
210 geographic coordinates of each individual as part of the clustering process (Guillot et al.,
211 2005). We used the spatial model with null alleles and uncorrelated allele frequencies. We
212 performed 10^5 iterations, out of which every 100th observation was retained, and we assumed
213 a maximum of 10 clusters. In GENELAND analyses, we specified the uncertainty attached to
214 the coordinates of the sampled social groups as 1,000m, which took into account that they

215 could have been observed at locations of their home range other than the geo-referenced
216 sampling sites. We considered each cluster as a population.

217 *2.3.3 - Population genetic statistics*

218 Population allele frequencies, the mean number of alleles per locus, the number of private
219 alleles, and expected (H_E) heterozygosity in each population were estimated using GenAEx
220 (Peakall and Smouse, 2012). We also used this program to quantify within- and between-
221 population components of genetic variation, carrying out an analysis of molecular variance
222 (AMOVA) with 9,999 permutations. Allelic richness was estimated using Fstat 2.9.3 (Goudet,
223 2001). We thus computed global F_{ST} , population pairwise F_{ST} ($N = 21$) and group pairwise
224 F_{ST} values ($N = 253$) with 1,000 resamplings by correcting for the presence of null alleles
225 (Appendix E for details) using FreeNA (Chapuis and Estoup, 2007). In order to test if a recent
226 migration event occurred amongst the 23 sampled groups, we used the partial Bayesian
227 method of Rannala and Mountain (1997) implemented in GeneClass2 (Piry et al., 2004) to
228 identify first-generation migrants and their potential source amongst the sampled groups.

229 *2.4. Testing the influence of landscape on genetic structure*

230 We tested if remoteness resistance (R), land resistance (L), and the isolation by distance
231 (IBD) explained pairwise genetic distances between groups [$D_{gen} = F_{ST}/(1-F_{ST})$]. The null
232 model was IBD measured by calculating all logarithmic pairwise Euclidian distances. We
233 used maximum-likelihood population effects (MLPE) mixed models that are recognized as
234 the most optimal approach to account for non-independence of pairwise datasets (Clarke et
235 al., 2002) - but see also a review in Row et al. (2017). We used the general least square
236 models (*gls* function) explaining the logit of pairwise F_{st} [$F_{st}/(1-F_{st})$] by the different
237 scenarios of path costs.

238 We based our model selection on Akaike's information criterion corrected for small sample
239 size (AICc, Burnham and Anderson, 2002) and we estimated model weights on all models
240 (library 'MuMIn', Barton, 2019). All variables and distance matrices were log-transformed to
241 improve linearity for statistical association tests. Statistics were performed with R (R
242 Development Core Team, 2019). We investigated the different models at four spatial scales: a
243 global scale that included the whole population (all sampled groups), and three smaller scales
244 that included different sets of forest patches. The smaller scales were defined by removing the
245 most isolated forest patches successively (based on their remoteness and separation from
246 others by human-dominated landscapes) to test if the significant landscape resistance factor
247 varied with the spatial scale, suggesting that different factors might act on local and long-
248 distance dispersal.

249 **3.-Results**

250 *3.1 - Genetic structure and genetic diversity*

251 Out of the 376 samples, 248 samples were genetically identified as unique individuals (their
252 genotypes are available in Dataset S1). Simulations from 10 independent runs in
253 GENELAND constantly identified seven main clusters (K). We then considered the number
254 of populations to be seven ($K=7$) in the subsequent analyses (Fig. 1A, B, see also Voronoi
255 tessellation in Appendix F). They included one to five sampled groups. We noticed that the
256 two AZ and SH populations included groups hosted in two different forest fragments (Aït
257 Youssi-Azrou and Azrou-Seheb, respectively).

258 H_E and Allelic richness varied from 0.44 to 0.58 and from 2.70 to 3.87, respectively (Table 2).
259 Genetic diversity indexes were lowest in population FE where two loci were fixed while one
260 locus was fixed in BK. We noticed the presence of private alleles in all populations, which
261 reached 4 in the two SN and SM populations (Table 2).

262 The AMOVA showed that 9% of total genetic variation was among social groups, while the
263 difference among populations (as clustered in GENELAND) explained 10% of variation. The
264 remaining variation (81%) was explained by differences within groups. Global F_{ST} among
265 populations was 0.11 (CI: 0.09-0.13) and population pairwise F_{ST} values ranged from 0.074 to
266 0.203 (Appendix G). The average Euclidian distance between populations was 23 km (range:
267 7-44 km). The mean F_{ST} value across groups within populations was 0.05 (CI: 0.04-0.06).
268 Most social groups were found to be significantly differentiated from one another based on
269 F_{ST} group pairwise values, with significant values ranging from 0.02 to 0.34 (see details in
270 Appendix G). However, non-significant values were found in 15 group pairs, of which 12
271 pairs implied groups belonging to the same population. Three non-significant pairwise F_{ST}
272 values implied groups belonging to different populations and different forest patches (see
273 details in Appendix G). We detected at least seven first-generation migrants (Appendix H).
274 Six migrants sampled in four populations originated from another group belonging to their
275 own population. One of them likely originated from a group located in an adjacent forest
276 fragment less than 5 km away (from G1 to G2, Fig. 1, see details in Appendix H). The
277 seventh migrant originated from an adjacent population and an adjacent forest fragment 7-9
278 km away (from G7 to G9, Fig. 1, appendix H).

279 *3.2. Link between genetic distance and remoteness and land resistances*

280 At the large spatial scale of the whole sampled groups, the best model (R2) with the lowest
281 AICc among the 38 models tested indicated that a maximum resistance to dispersal beyond 1
282 km from a forest edge significantly explained the gene flow between groups (Table 3), while
283 there was no significant effect of land resistance or IBD (see results in appendix C for details
284 on all models and comparison with the least-cost path approach). Therefore, a distance
285 beyond 1 km from the forest edge seemed too costly and limited gene flow. We then explored

286 a smaller spatial scale, after excluding the Feldi forest (with FE population, SP1, see Fig. C1,
287 Appendix C) that was the most isolated from other forests by Euclidean distance (20-27 km)
288 and by wide human-dominated landscapes (Fig. 1A). This spatial scale remained quite large
289 with about 48 km between the most distant forests (Aït Youssi and Senoual) and an average
290 distance of 20 km between the forests. A maximum travel cost beyond 1 km from the forest
291 edge remained the main explanatory factor of resistance to gene flow (Table 3, see also
292 Appendix C for details). By contrast, by restricting the spatial scale while excluding Feldi,
293 Senoual and Bekrit forests (around 30 km between the most distant forests and 10 km
294 between forests on average, SP2 set, Table 3, Fig. C1, Appendix C) we revealed a significant
295 effect of human-dominated landscapes on the macaques' dispersal potential (model L2, Table
296 3). In addition, the second plausible model (R2) included remoteness resistance that was
297 found to limit gene flow when the distance from the forest edge beyond 1km was set to the
298 maximum cost. At a third finer scale (SP3 set, Table 3, see Fig. C1, Appendix C), a maximum
299 cost beyond 1 km from the forest edge appeared the most relevant explanatory factor of
300 dispersal limitation. This SP3 set included four forests (Aït Youssi, Azrou, Seheb,
301 Affenourir). At this scale, the shortest distance between two neighbor forests was lower than
302 at other scales and was free of human-dominated landscape. IBD was not significant when
303 controlling either for remoteness or habitat resistance. Apart from human-dominated habitats,
304 we did not detect that the other habitats restricted the gene flow. We did not find a limitation
305 to dispersal below 1 km from the forest edges.

306 **4. Discussion**

307 We identified seven genetic populations in the Barbary macaques sampled across a
308 large area and several forest patches of the Middle Atlas region. Most populations were
309 hosted in separate forest patches. The moderate gene diversity and the presence of private

310 alleles in all Barbary macaque populations strongly suggest an ongoing global process of
311 isolation. Indeed, although absolute values of resistances were not available, using robust
312 hierarchical relative values we found that landscape resistance impacts Barbary macaque
313 dispersal movement more than Euclidean distance does as it has been shown in other forest
314 specialist species (Moraes et al., 2018; Ruiz-Gonzalez et al., 2015). To our knowledge, the
315 only previous study on Barbary macaque genetic structure, in a region of a similar area in
316 Algeria, showed significant IBD between groups but it did not explore to what extent
317 landscape heterogeneity had an impact on genetic structure and diversity of populations (von
318 Segesser et al., 1999).

319 We highlighted that whatever the spatial scale, a distance beyond 1km from a forest
320 edge limited macaque dispersal movement and gene flow. By contrast, anthropogenic rural
321 land cover limited gene flow between forest patches at a specific spatial scale only. Therefore,
322 our study highlights the usefulness of landscape genetic tools to improve our understanding of
323 gene flow among Barbary macaque populations and the importance of a multiscale approach
324 to estimate dispersal responses depending on different landscape variables (Blair and
325 Melnick, 2012; Galan-Acedo et al., 2019; Gestich et al., 2019; Quéméré et al., 2010; Ruiz-
326 Gonzalez et al., 2015).

327 *4.1. Influence of distance on the non-forest matrix resistance to Barbary macaque gene flow*

328 The nearest differentiated populations, which were located in separate forest patches,
329 were 7-9 km apart, a distance within a 2-3 day range length of groups (up to 3 km per day,
330 Ménard et al., 2013; Ménard and Vallet, 1997). This distance corresponds approximately to
331 the smallest spatial scale of male dispersal and can be considered as the landscape grain size
332 of interest (Baguette and Van Dyck, 2007). The observed genetic differentiation between
333 populations occurred over relatively small geographic distances suggesting that functional

334 connectivity was globally limited. Similar to other habitat specialist mammals [*Martes martes*
335 (Ruiz-Gonzalez et al., 2015); *Canis simensis* (Gottelli et al., 2013)], forest loss or human
336 expansion into the Barbary macaque habitats could disrupt gene flow at a small scale.

337 Our results indicate that, whatever the spatial scale, inter-edge distances greater than 2
338 km (*i.e.* 1 km from a forest edge) highly limits gene flow suggesting that macaque dispersal
339 movement became too costly beyond 1 km from a forest edge. We rather expected to find
340 resistance to dispersal at lower distances, around 400 m between forest edges, due to the
341 reluctance of groups to move away from a distance > 200 meters from the forest edge
342 (Ménard and Vallet, 1996). On the contrary, we revealed the persistence of gene flow between
343 forest patches that were separated by more than 400 meters. Moreover, we detected first
344 migrants between groups living in distant (> 400 m) forest patches. We wonder if migrant
345 males, which are less vulnerable than groups that contain females and offspring, may be able
346 to cross those distances. We currently lack direct observation data on how dispersing males,
347 that move alone, are affected by landscape heterogeneity. Ménard and Vallet (1996) found
348 that male dispersion occurs on short distances; this was corroborated by our genetic analyses,
349 since all the first migrants we detected came from immediate neighbouring groups, within 5-9
350 km of one another, and from a same or very near (< 600m edge-to-edge distance) forest. We
351 hypothesized that some migrant males were able to cross the matrix between more distant
352 forest patches, below the 2km threshold, *i.e.* 1 km from a forest edge. Such long-distance
353 terrestrial movement away from refuges (*i.e.* through the inhospitable matrix) has already
354 been observed in other species such as *Colobus angolensis palliatus* that were found between
355 2 to 4 km from forest (Anderson et al., 2007). However, in the case of local extinctions of
356 isolated Barbary macaque populations, male migration alone cannot effectively recolonise
357 empty forest patches. A recolonisation process would imply the expansion of a neighbouring

358 population as a source, and the formation of a dispersing group of both sexes following group
359 fission, which is the only way for females to disperse (Ménard and Vallet, 1993a). To our
360 knowledge, in social species with female philopatry, the process of dispersal through the
361 landscape by cohesive social groups remains to be investigated, most studies focusing on the
362 movements of males as the dispersing sex. We suspect that the mobility of groups would be
363 lower than that of solitary males dispersing due to socio-ecological constraints, e.g. large
364 groups are more easily detectable by predators, disturbances can disrupt group cohesion, the
365 presence of infants restricts the travel speed, and macaques must reach secure sleeping sites
366 with several tall trees every night.

367 The impact of distance on non-forest matrix resistance to gene flow could be partially
368 mitigated thanks to the possibility for macaque groups or solitary males to cross the matrix
369 during periods of heavy snowfall in winter (during mating period, Ménard and Vallet, 1996),
370 when they are temporarily less subject to human occupation. However, climate change
371 associated with reduced snowy periods can increase landscape resistance to Barbary macaque
372 movements because high-altitude forests are going to be occupied longer by human pastoral
373 activities and settlements near the forests, and transhumance practices partly abandoned (El
374 Aich, 2018).

375 *4.2. Influence of anthropogenic rural areas on Barbary macaque gene flow*

376 *Fst* values indicated genetic differentiation two-fold higher among groups from
377 different populations than among groups from the same population, indicating that gene flow
378 was higher within continuous forest than between forest fragments. Human-dominated
379 habitats, associated with costly remoteness from the forest edge > 1 km, were found to limit
380 gene flow at an intermediate spatial scale (SP2). These two features of the landscape
381 constitute resistance to the dispersal movement of Barbary macaques, likely due to the

382 increased risk of encountering predators, in particular domestic dogs, while being too far from
383 refuges (trees at least 20m tall). Interestingly, whatever the spatial scale, oak coppice and
384 open areas *per se* did not seem to constitute a limitation to macaque dispersal movement and
385 gene flow. The human-dominated habitat effect vanished at the smallest investigated spatial
386 scale when removing the Sidi M'Guild forest. This could suggest that the population of the
387 Sidi M'Guild forest, which is the main population in the largest forest patch, is ongoing an
388 isolation process due both to distance to other forests and human activities in its surroundings.
389 A strong negative effect of human-dominated habitats on gene flow was also found in other
390 forest-specialist species (*Rhinopithecus bieti*, Liu et al., 2009), whereas it was not found in
391 another species (*Saimiri oerstedii*, Blair and Melnick, 2012) where human areas (cattle
392 pastures and residential zones) were small, spread out, isolated from one another. Therefore,
393 this relationship does not seem generalizable as it may depend on landscape composition and
394 configuration.

395 *4.3. Implications for conservation*

396 Reduced gene flow was detectable at all the spatial scales we investigated, except inside
397 forest patches where genetic structure was reduced. Human occupancy around forest patches
398 also contributes to the population isolation process. In particular, population FE can be
399 specifically considered as a genetic isolate due to its loss of connectivity with populations
400 living in other forest patches (> 20km from each other). In support of this, a recent study in
401 the Timahdit region, which includes the Feldi forest fragment that hosts population FE, has
402 shown irreversible land degradation due to desertification and found that 6% of the dense
403 forest disappeared between 1984 and 2007 (Kouba et al., 2018). Some forest-living species
404 showing behavioural adaptability may be relatively resilient to forest reduction because they
405 can temporarily exploit secondary habitats or even colonise urban areas (Maibeche et al.,

406 2015; Singh, 2019). However, limitation of dispersal between forest fragments is a negative
407 consequence for many of them. The adaptability of animals facing landscape heterogeneity
408 can be highly variable in a same landscape depending on the species, even among closely
409 related species [bats, (Albrecht et al., 2007; Ripperger et al., 2013); macaques, (Singh, 2019)].
410 This implies different conservation approaches. For instance, in India, the preservation of a
411 forest specialist macaque (*Macaca silenus*) implied restoring corridors with native vegetation;
412 while the generalist urban macaque (*M. radiata*), threatened by increased macaque/human
413 conflicts, required the protection of hillocks with Hindu temples whose surrounding
414 vegetation constitutes favourable ecosystems (Singh, 2019). The behavioural adaptive
415 abilities of the Barbary macaque appear close to those of *M. silenus*, mainly due to its low
416 potential dispersal through the matrix. However, similarly to *M. silenus* for which forest
417 fragmentation has led to some individuals accepting food from humans (Singh, 2019), some
418 Barbary macaque groups are provisioned along roads crossing forest fragments while others
419 have started to colonise suburban areas whose expansion brought them into contact with
420 forest areas (Maibeche et al., 2015). These behavioural changes naturally go along with
421 decreased fear of humans. We cannot exclude that this declining fear lead them to cross the
422 inhospitable matrix over longer distances in the future. However, this should be unlikely as
423 long as the predation risk is high in the matrix.

424 Our results indicate that if dispersal distances between forest patches increase up to a
425 threshold of 2 km, dispersal will be broken and the populations will become isolated. This
426 could occur if human pressure on the forest increases. In addition, increasing human
427 population and livestock has caused overgrazing of rangelands and reduced grazing areas, and
428 forced herdsmen to use forested areas (pruning cedars for example) to feed their flocks
429 (Kouba et al., 2018). Cedar forests will probably remain only in restricted areas in the future

430 because of global climate change (Cheddadi et al., 2009), with a potential reduction of the
431 Middle Atlas population size and a potentially increasing isolation of small populations.

432 The Middle Atlas region contains the largest forest of the distribution area of the species
433 and is its main reservoir. Given the high vulnerability of the Barbary macaque and the
434 existence of already small forest patches where the risk of extinction of populations can rise
435 following demographic or environmental events, protection strategies should favour
436 connectivity among those forest patches. Habitat restoration is impracticable in the human-
437 dominated landscape where pastoral and agricultural activities are currently well established
438 over the long term. By contrast, habitat restoration should be a crucial priority in areas that
439 depend on forest managers and include oak coppice and open areas. Management of these
440 areas should include avoiding increasing distances between forest patches, favouring the
441 regrowth of oak coppice while abandoning clear-cutting of holm oaks, restoring corridors
442 between forest patches with native vegetation, and preserving key small forest patches as
443 potential stepping stones which promote functional connectivity (Fischer and Lindenmayer,
444 2002).

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670

671 Table 1. Costs used for landscape variables in raster-cost distance analyses of the best
 672 landscape models with Resistance distance (Circuit Theory, calculated using Circuitscape
 673 software). The list of the 38 scenarios is in table C1, appendix C.

Land models	L ₁	L ₂	L ₃	L ₄	L ₅	
Undamaged forests	1	1	1	1	1	
Degraded forests	20	1	1	1	100	
Oak coppices	50	1	1	100	100	
Open areas	80	1	100	100	100	
Human areas	100	100	100	100	100	
Remoteness from forest edge models	R ₁	R ₂	R ₃	R ₄	R ₅	R ₆
Inside forests	1	1	1	1	1	1
< 200m	20	1	1	1	1	100
< 300m	30	1	1	1	100	100
< 500m	50	1	1	100	100	100
< 1000m	80	1	100	100	100	100
> 1000m	100	100	100	100	100	100

674

675 Table 2. Summary genetic statistics for each population.

Population	N	A	He±SD	Ar	Ap
AZ	27	3.73	0.472±0.057	3.13	1
SH	57	4.54	0.572±0.050	3.64	1
AF	12	4.09	0.559±0.056	3.87	1
SM	63	4.73	0.575±0.061	3.71	4
BK	23	3.73	0.500±0.082	3.31	1
SN	55	4.82	0.567±0.056	3.75	4
FE	11	2.73	0.444±0.079	2.70	1

676 N: sample size ; A: mean number of alleles per locus ; H_E : expected heterozygosity; Ar:
677 allelic richness (based on a minimum sample size of 8 individuals) ; Ap: number of private
678 alleles.

679 Table 3. Selection of the top 4 models from 39 MLPE models (see Table 1 for 38 scenarios
680 and IBD) computed at four spatial scales corresponding to the whole population, and three
681 sets of forest patches, SP1, SP2, and SP3. The best models ($\Delta AICc < 2$) are in bold. Results
682 for all the other models are in Appendix C.

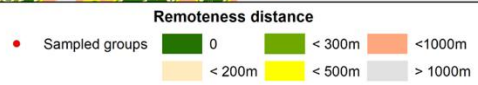
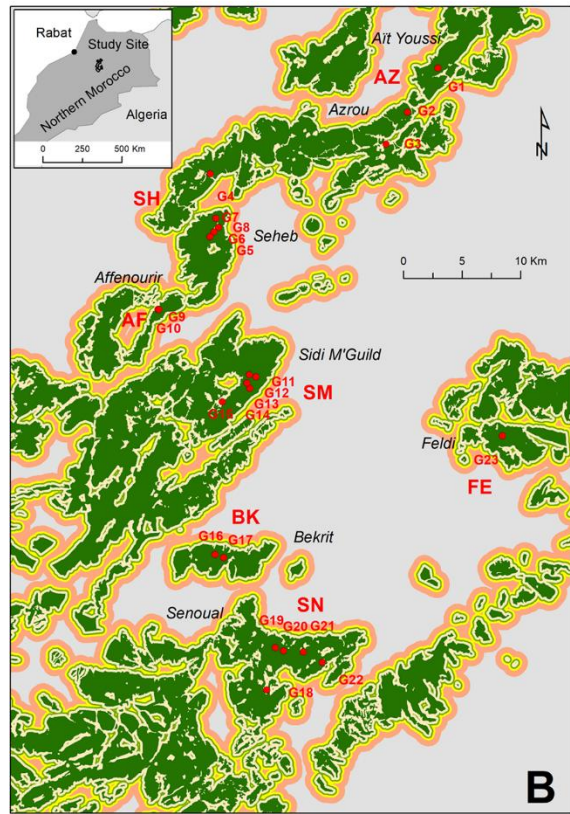
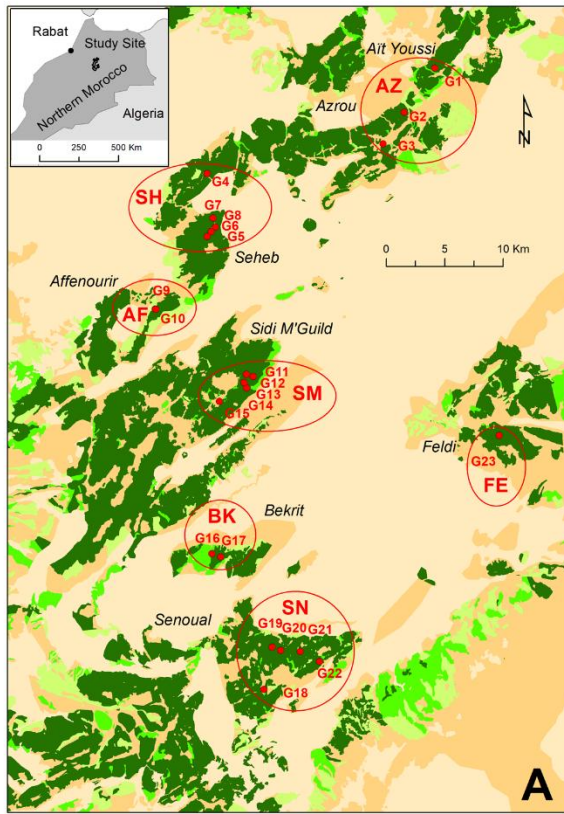
Models	df	MLPE		
		AICc	$\Delta AICc$	weight
Global spatial scale: whole population				
D_{gen} ~ R2 (> 2km edges)	4	-767.13	0	1
D _{gen} ~ L2	4	-750.81	16.32	0
D _{gen} ~ IBD	4	-746.30	20.83	0
D _{gen} ~ R1	4	-745.84	21.29	0
Spatial scale SP1				
D_{gen} ~ R2 (> 2km edges)	4	-690.82	0	1
D _{gen} ~ L2	4	-675.80	15.02	0
D _{gen} ~ IBD	4	-670.53	20.29	0
D _{gen} ~ R1	4	-669.33	21.48	0
Spatial scale SP2				
D_{gen} ~ L2 (anthropogenic areas)	4	-281.33	0	0.65
D_{gen} ~ R2 (> 2km edges)	4	-279.99	1.34	0.33
D _{gen} ~ R3	4	-274.62	6.71	0.02
D _{gen} ~ R5	4	-267.41	13.92	0
Spatial scale SP3				
D_{gen} ~ R2 (> 2km edges)	4	-132.89	0	0.70
D _{gen} ~ R3	4	-130.05	2.85	0.17
D _{gen} ~ L2	4	-128.82	4.08	0.09
D _{gen} ~ R4	4	-127.13	5.77	0.04

683 SP1: includes seven forest patches: Aït Youssi, Azrou, Seheb, Affenourir, Sidi M'Guild,
684 Senoual, Bekrit (the easternmost forest patch, Feldi, being excluded); SP2: includes Aït
685 Youssi, Azrou, Seheb, Affenourir, Sidi M'Guild; SP3: includes Aït Youssi, Azrou, Seheb,
686 Affenourir (see Fig. 1A, B; Fig. C1, Appendix C). AICc: Akaike information criterion for
687 small samples allows selecting the models that fit better to the data with the lowest number of
688 parameters. IBD: Isolation by distance. "> 2km edges" means edge-to-edge distance between
689 two forest patches.

690 **Figure legends**

691 Figure 1. Map of the landscape features of the study area in the Middle Atlas (Morocco),
692 localisation of the sampled Barbary macaque groups (G1-G23), and names (in bold) of the
693 seven genetic populations inferred using GENELAND. (A) Landscape mosaic of habitats; (B)
694 gradient of remoteness distances from the forest edge. The minimum distance between
695 populations was 23 km on average, and ranged from 7 to 43 km. The names of the eight forest
696 fragments where Barbary macaques were sampled are in italics. Red circles delineate
697 population genetics.

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