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

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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

Abstract

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

1. Introduction

Human activities fragment habitats worldwide, with agriculture and/or settlements 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 matrilines 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

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

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

2.2.2. Landscape models

We compared the classical isolation by distance (IBD) model in which the explanatory variable is the Euclidean distance between groups with isolation by remoteness resistance (R) and isolation by land resistance (L). Since absolute values for remoteness and land resistances 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 GenAlEx

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 *Fst* [*Fst*/(1-*Fst*)] 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

13

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

14

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

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

682   for all the other models are in Appendix C.

| Models | df | MLPE | | |
		AICc	ΔAICc	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.

698
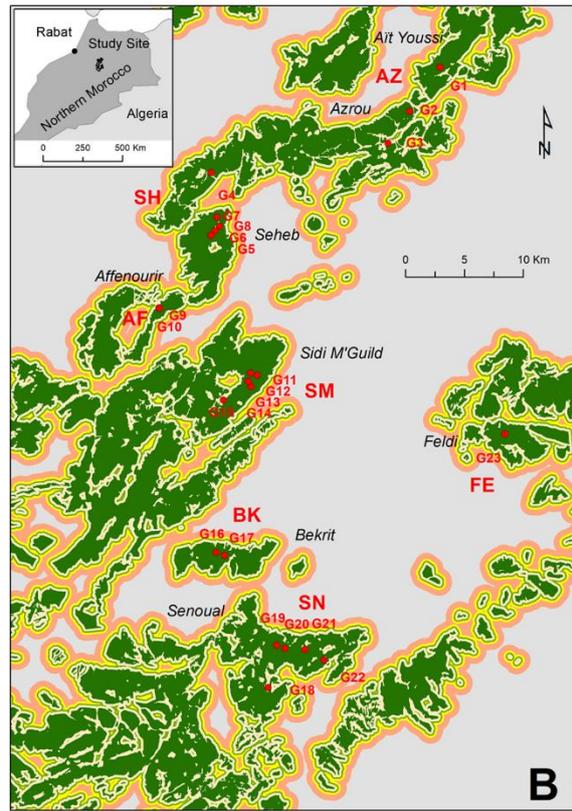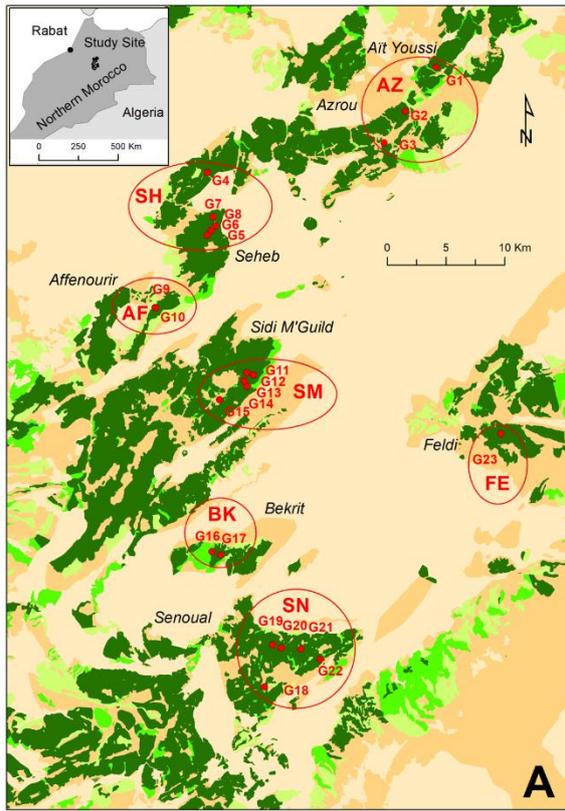
Habitats

- • Sampled groups
- ■ Undamaged forest
- ■ Degraded forest
- ■ Oak coppices
- ■ Open areas
- ■ Human activities

Remoteness distance

- • Sampled groups
- ■ 0
- ■ < 200m
- ■ < 300m
- ■ < 500m
- ■ <1000m
- ■ > 1000m

699