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

Pascaline Le Gouar^{1*}, Dominique Vallet¹, Aude Ernoult², Eric J. Petit^{1,3}, Yann Rantier², Stéphane Dréano⁴, Mohamed Qarro⁵, Nelly Ménard¹,

¹ UMR 6553, ECOBIO: Ecosystems, Biodiversity, Evolution, CNRS/University of Rennes 1, Biological Station of Paimpont, Paimpont, France,

² UMR 6553, ECOBIO: Ecosystems, Biodiversity, Evolution, CNRS/University of Rennes 1, Rennes, France,

³ ESE, Ecology and Ecosystem Health, INRAE, Institut Agro, Rennes, France,

⁴ Univ Rennes, CNRS, IGDR (Institut de génétique et développement de Rennes) - UMR 6290, F-35000 Rennes, France

⁵ Ecole Nationale Forestière d'Ingénieurs, Salé, Rabat, Morocco,

Corresponding authors: Pascaline Le Gouar, UMR6553 ECOBIO, CNRS/University of Rennes1, Station Biologique, 35380 Paimpont, France. pascaline.legouar@univ-rennes1.fr. Tel : + 33 299618173.

Nelly Ménard, UMR6553 ECOBIO, CNRS/University of Rennes1, Station Biologique, 35380 Paimpont, France. nelly.menard@univ-rennes1.fr

ORCID :

Pascaline Le Gouar: <https://orcid.org/0000-0001-5309-3667>

Nelly Ménard: <https://orcid.org/0000-0003-4122-9330>

Eric J. Petit: <https://orcid.org/0000-0001-5058-5826>

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.,

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

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

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

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

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

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

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

2. Materials and Methods

2.1. Study area and sample collection

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

2.2. Landscape resistance computation

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

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

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

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

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

2.3. Genetic analyses

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

2.3.1 - Cluster analyses

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

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

2.3.3 - Population genetic statistics

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

2.4. Testing the influence of landscape on genetic structure

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

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

3.-Results

3.1 - Genetic structure and genetic diversity

Out of the 376 samples, 248 samples were genetically identified as unique individuals (their genotypes are available in Dataset S1). Simulations from 10 independent runs in GENELAND constantly identified seven main clusters (K). We then considered the number of populations to be seven ($K=7$) in the subsequent analyses (Fig. 1A, B, see also Voronoi tessellation in Appendix F). They included one to five sampled groups. We noticed that the two AZ and SH populations included groups hosted in two different forest fragments (Aït Youssi-Azrou and Azrou-Seheb, respectively). H_E and Allelic richness varied from 0.44 to 0.58 and from 2.70 to 3.87, respectively (Table 2). Genetic diversity indexes were lowest in population FE where two loci were fixed while one locus was fixed in BK. We noticed the presence of private alleles in all populations, which reached 4 in the two SN and SM populations (Table 2).

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

3.2. Link between genetic distance and remoteness and land resistances

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

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

4. Discussion

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

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

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

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

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

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 palliatus* 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

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

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

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

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

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

4.3. Implications for conservation

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

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

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

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

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

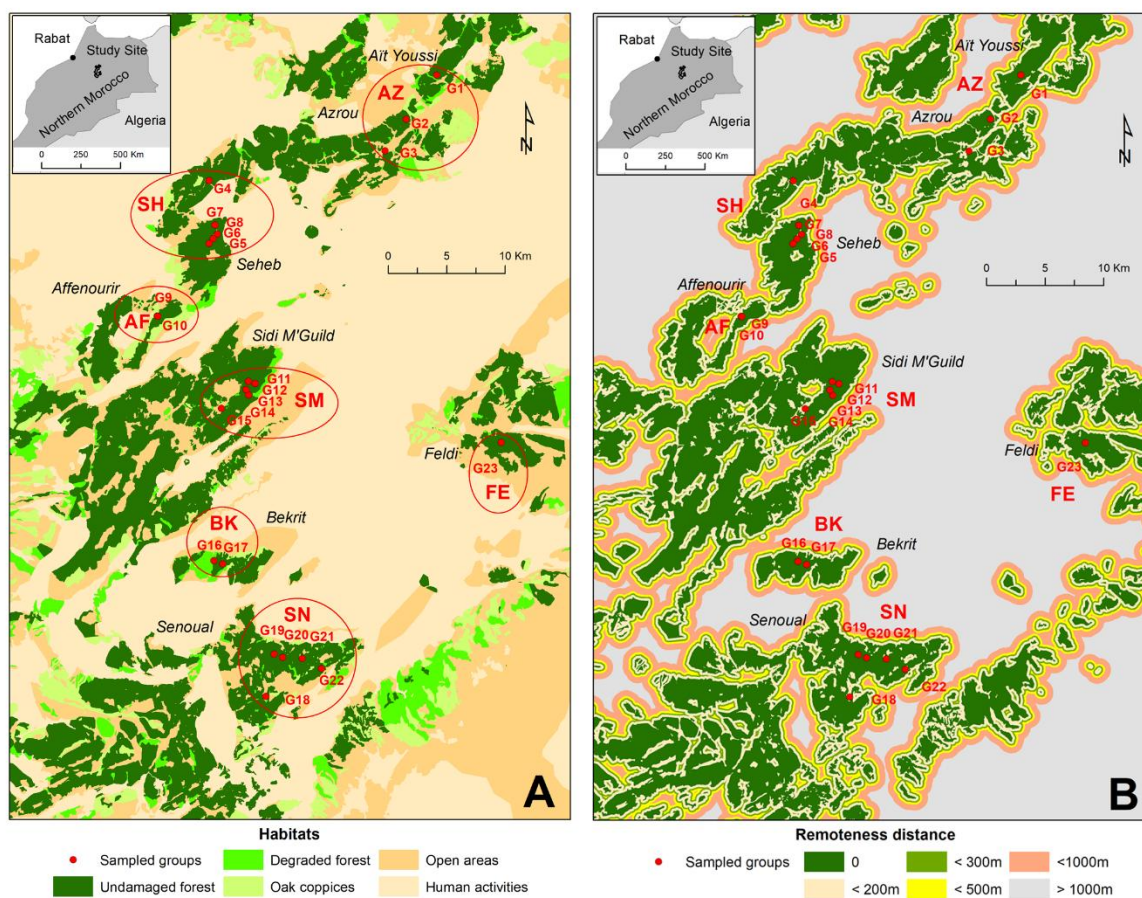
Table 3. Selection of the top 4 models from 39 MLPE models (see Table 1 for 38 scenarios and IBD) computed at four spatial scales corresponding to the whole population, and three sets of forest patches, SP1, SP2, and SP3. The best models ($\Delta\text{AICc} < 2$) are in bold. Results for all the other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

Models	df	MLPE		
		AICc	Δ 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

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

Figure legends

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



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