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## OPEN Valorization of feral pigs in the tropics, from the genetic characterization to the re-domestication

Nicolas Degras<sup>1</sup>, Yann Labrune<sup>2</sup>, Nathalie Mandonnet<sup>1</sup>, Mélain Bructer<sup>3</sup>, Katia Benony<sup>3</sup>, Claudine Vertueux-Degras<sup>4</sup>, Gisèle Alexandre<sup>1</sup>, Nausicaa Pouillet<sup>1</sup> & Jean-Luc Gourdine<sup>1</sup>✉

Feral pigs may serve as a valuable genetic resource for the future, offering potential interesting gene pool for adaptation to climate change and the preservation of biodiversity. The main objective of this study was to identify the genetic structure of feral pigs from the Caribbean island of Martinique, measure the inbreeding rate of a Creole population re-domesticated in 2016 from captured feral pigs, and evaluate its evolution to the present day. We hypothesized that feral pigs, like Creole breeds of the Americas, have been shaped by a unique cross-breeding process linked to the historical context of the Caribbean. A total of 121 animals were genotyped and 76 were compared with referenced mainstream genotypes and Creole breeds from the Americas. Re-domestication efforts were carried out through a holistic approach, involving researchers, farmers, consultants, and development actors. The results showed that feral and semi-feral pigs in Martinique belong to the creole pig breeds, with more than 20% Iberian genetic admixture. The majority of domesticated pigs groups studied including re-domesticated creole pigs exhibit a significantly lower proportion of runs of homozygosity compared to feral pigs, suggesting a better control of inbreeding, thanks to structured breeding programs. The chosen conservation strategy was the result of a consensus between scientific evidence, practical experience, and field feasibility. A rotational mating system using sire lines among a minimum of five farmers was adopted. This approach is expected to generate, within five years, a pedigree containing information on a total of at least 150 reproducers on 8 generations.

**Keywords** Feral pig, Admixture, Re-domestication, Conservation strategy, Martinique

The regional concentration of livestock farming and the expansion of international trade - such as off-farm feed production (e.g. soybean meal) - have created new geochemical cycles<sup>1</sup> that have global impacts on the environment and biodiversity<sup>2</sup>. Livestock farming systems, which play a major role in biomass transformation and protein production, represent both a critical factor and a driving force in addressing the interconnected challenges of food security, climate change, and biodiversity conservation<sup>3</sup>. The use and management of local breeds can contribute to meeting these challenges<sup>4</sup>, particularly through the conservation of « rustic » animal genetic resources. These breeds are well-adapted – or adaptable – to local conditions<sup>5</sup>, and they also carry potentially valuable alleles that could benefit the future of their species<sup>6</sup>. The Caribbean region provides a unique context for studying local genetic resources and their use in agro-ecological farming systems. Its complex history – including the Taino culture, European colonization and the transatlantic slave trade, as well as Indian migrations – has fostered extensive interactions between continents (Africa, Europe, Asia)<sup>7</sup>. These interactions led to the emergence and development of Creole breeds (CR) in low input systems, such as the Creole pig of Martinique (14°N, 61°W), in the French overseas departments of the Caribbean. The Taino, the first inhabitants of the Caribbean islands, did not domesticate *Sus scrofa domesticus*. This specie was introduced only after Columbus's second voyage in 1493, and likely reached Martinique during the fourth voyage in 1502<sup>8</sup>. Over time, these Iberian pig populations gave rise to a diverse range of genotypes across the Americas-Caribbean region, now referred to as “Creole”. Prior to the rise of intensive livestock farming in the 1970s, the CR pig breed played

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a key role in the subsistence economy of smallholder farmers in Martinique<sup>9</sup>. Nowadays, CR pig farming is in the minority, having largely been replaced by exotic genotypes selected for higher production and reproduction traits.

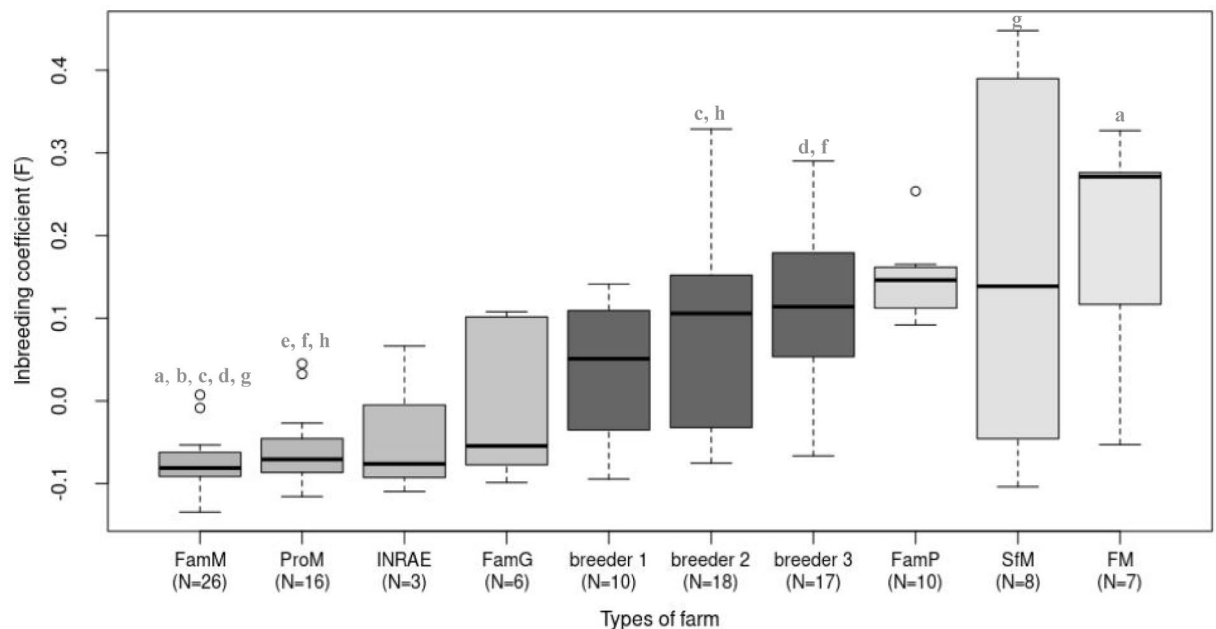
The Regional Natural Park of Martinique (PNRM) has identified some feral pigs in the mountainous regions and aims to develop a niche market for local pig breeds through the re-domestication of these feral pigs. To achieve this, a program involving various stakeholders has been established, using a holistic dashboard approach<sup>10</sup>. Since 2016, feral pigs have been captured, re-domesticated by volunteer farmers, and bred to increase the domestic population. In 2022, the French National Research Institute for Agriculture, Food and Environment (INRAE) collected blood samples from these re-domesticated feral pigs to measure the inbreeding coefficient and monitor the genetic evolution of the population. The aims of the present study were (i) to identify the genetic structure of feral pig population in Martinique; (ii) to measure the inbreeding rate of the re-domesticated creole population sampled in 2022 and assess its evolution compared to the founder population sampled in 2016; (iii) to suggest practical breeding schemes encompassing genetic characterization, the re-domestication process, and inbreeding management.

## Results

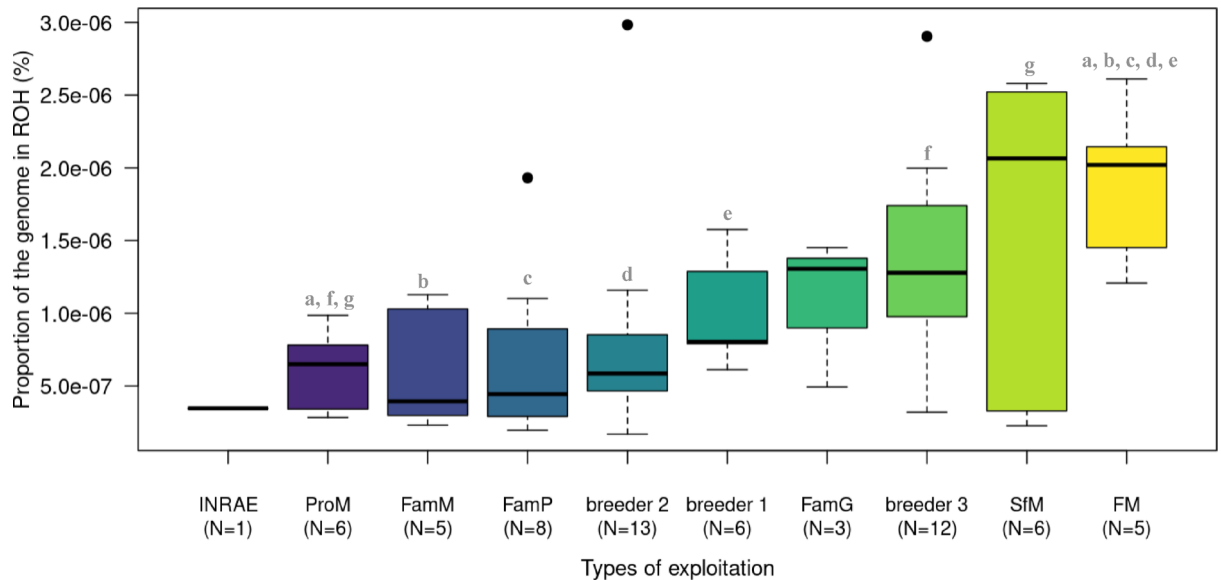
### Inbreeding of pig populations of Martinique

Figure 1 shows the inbreeding coefficients of the different pig groups sampled in 2016 and 2022. The results show that feral and semi-feral pigs exhibit the highest inbreeding levels. In contrast, pigs from professional and family farms in Martinique and Guadeloupe display low inbreeding coefficients, comparable to those of Creole pigs raised at INRAE. Highly significant differences ( $a: P < 0.001$ ) were observed between the inbreeding coefficients of feral pigs (FM) and pigs from family farms in Martinique (FamM). Pigs from the three creole pig farmers (Breeder 1, Breeder 2, Breeder 3) show intermediate inbreeding levels – higher than those of farmed pigs but lower than those of feral and semi-feral. Notably, the FamP group (pigs from specific family farms in Martinique) shows a relatively high inbreeding coefficient compared to other domesticated pigs. Re-domesticated creole pigs from Breeder 1 and Breeder 2, along with FamP pigs – potential ancestors of some re-domesticated feral pigs – display significantly higher inbreeding coefficients than pigs from family farms (FamM) and professional farms (ProM) in Martinique ( $b, c, d: P < 0.001$ ;  $e, f, h: P < 0.01$ ).

Figure 2 illustrates the proportion of the genome in ROH for local pigs across various farms. A total of 194 ROH segments were identified in 65 individuals out of the 121 pigs genotyped in Martinique and Guadeloupe. The ROH results follow the same trend as the inbreeding coefficient, confirming a significant difference between domestic and feral pigs. Domesticated pigs from professional farms (ProM), family farms (FamM and FamP), as well as re-domesticated creole pig from feral population raised by Breeder 1 and Breeder 2, exhibit significantly



**Fig. 1.** Inbreeding coefficient (F) per farm. P-value (P). *a, b, c, d: P < 0,001; e, f, g: P < 0,01; h: P < 0,05.* Breeder 1,2,3 : Re-domesticated feral pigs by three volunteer farmers in the PNRM program; FM: Feral pigs are animals captured by hunters or PNRM staff; SfM: Pigs crossed with feral pigs by farmers and kept on their farms; FamM: Pigs reared in family farms in Martinique; FamP: Pigs raised on family farms that are potential parents of CRM re-domesticated feral pigs; ProM: Pigs that are reared by pig professional farmers; FamG: Pigs reared in family farms in Guadeloupe; INRAE: Creole pigs that are conserved at the INRAE experimental facilities. Each boxplot represents, from top to bottom: the maximum value, the third quartile, the median (in bold), the first quartile, and the minimum value.



**Fig. 2.** Proportion of the local pigs' genome in ROHs in per farm. *P*-value (*P*). *a*:  $P < 0,001$ ; *b*, *c*, *d*, *e*:  $P < 0,01$ ; *f*, *g*:  $P < 0,005$ . 194 ROH detected in 65 individuals among the 121 individuals genotyped in Martinique and Guadeloupe. Breeder 1,2,3 : Re-domesticated feral pigs by three volunteer farmers in the PNRM program; FM: Feral pigs are animals captured by hunters or PNRM staff; SfM: Pigs crossed with feral pigs by farmers and kept on their farms; FamM: Pigs reared in family farms in Martinique; FamP: Pigs raised on family farms that are potential parents of CRM re-domesticated feral pigs; ProM: Pigs that are reared by pig professional farmers; FamG: Pigs reared in family farms in Guadeloupe; INRAE: Creole pigs that are conserved at the INRAE experimental facilities. Each boxplot represents, from top to bottom: the maximum value, the third quartile, the median (in bold), the first quartile, and the minimum value.

fewer ROH regions compared to feral pigs (FM) (*a*:  $P < 0,001$ ; *b*, *c*, *d*, *e*:  $P < 0,01$ ). The short length of the box plots for domesticated creole pigs and feral pigs suggests relatively older inbreeding events. In contrast, the extended length of the box plot for the semi-feral group (SfM) indicates more recent inbreeding.

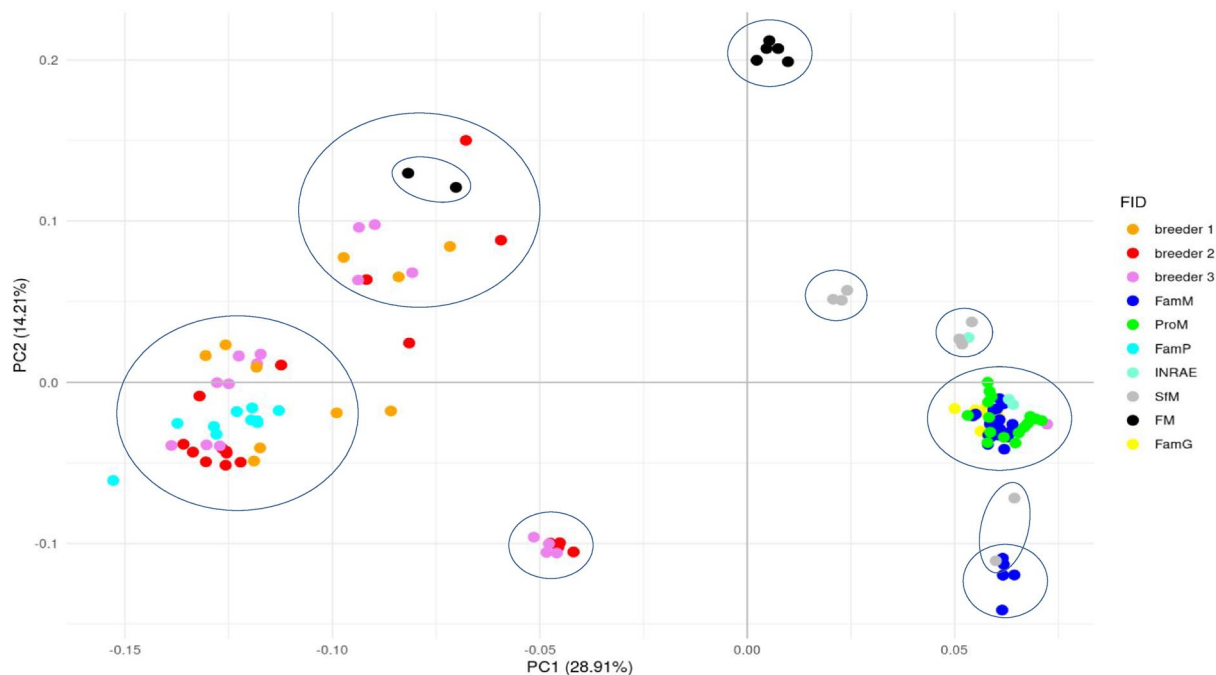
### Genetic diversity between pigs of Martinique

Figure 3 presents the results of the PCA analysis. Genetically similar individuals appear closer together based on the 13,578 SNPs markers used. The analysis revealed that the pigs assumed to belong to CR breed actually represent a wide range of genotypes. Based on Fig. 3, ten distinct groups can be identified. Among the feral pigs, two groups emerge: one that is genetically distant from domesticated pigs, and another that is closer to domesticated creole pigs. The domesticated creole pigs in Martinique are divided into three groups: one group is closely related to two feral individuals, suggesting a potential kinship; another group is genetically similar to nine pigs from family farms in Martinique (FamP), indicating possible familial ties; and a third group is genetically distinct from both of the above, pointing to different family origins. In addition, there is a large cluster consisting of pigs from professional and family farms in both Martinique and Guadeloupe, along with Creole pigs from the PTEA facility. Within the family-farmed pigs in Martinique, one subgroup stands out as genetically differentiated from the main cluster. The semi-feral pigs form three distinct groups. Two of these are positioned genetically between the feral pigs and those from family and professional farms, reinforcing their intermediate status. The third group includes two individuals closely related to pigs from family farms in Martinique.

### Genetic admixture of pigs of Martinique

The analysis of the genetic structure of the different pig populations studied was conducted using a variable number of clusters (*K*), ranging from 7 to 20. The cross-validation error reveals a minimum at  $K = 10$ , suggesting that the genetic structure of the dataset is best explained by ten ancestral origins. Based on these results, we chose  $K = 10$  to estimate ancestry coefficients, capturing the contribution of seven mainstream breeds along with Chinese ancestry. The results of the unsupervised analysis at  $K = 10$  (Fig. 4) show that the genetic structure of Chinese breeds (Jinhua, Jinguha), Iberian, Duroc, Piétrain, Hampshire, Gascon, and to a lesser extent, Large White and Landrace, is relatively homogeneous. These European and Chinese breeds were therefore used as reference genotypes to study the genetic structure of pigs in Martinique - particularly the feral population.

The supervised analysis at  $K = 10$  shows that similar to Creole pig populations across the Americas, the feral and semi-feral pigs of Martinique carry a notable Iberian genetic component ( $> 20\%$ ). Estimates of ancestral composition show that this Iberian contribution is, on average, higher in feral pigs from Martinique than in semi-feral pigs from Martinique or Creole pigs from Guadeloupe, the other French Caribbean island (Table 2). Specifically, the main genetic components of feral pigs in Martinique derive from the Landrace and Iberian breeds, whereas Creole pigs in Guadeloupe show stronger influence from the Large White and Landrace breeds.



**Fig. 3.** PCA of genetic distances between animals genotyped in Martinique and Guadeloupe (The two French Caribbean islands). Breeder 1,2,3 : Re-domesticated feral pigs by three volunteer farmers in the PNRM program; FID: Family identifier, FM: Feral pigs are animals captured by hunters or PNRM staff; SIM: Pigs crossed with feral pigs by farmers and kept on their farms; FamM: Pigs reared in family farms in Martinique; FamP: Pigs raised on family farms that are potential parents of CRM re-domesticated feral pigs; ProM: Pigs that are reared by pig professional farmers; FamG: Pigs reared in family farms in Guadeloupe; INRAE: Creole pigs that are conserved at the INRAE experimental facilities.

Notably, similar to the Creole pigs of Brazil, the feral pigs of Martinique also display a Chinese genetic component (> 10%). In contrast, pigs from family and professional farms in Martinique exhibit a strong genetic influence from the Large White and Duroc breeds, with minimal Iberian ancestry.

### Breeding scheme selected for ex situ conservation programme

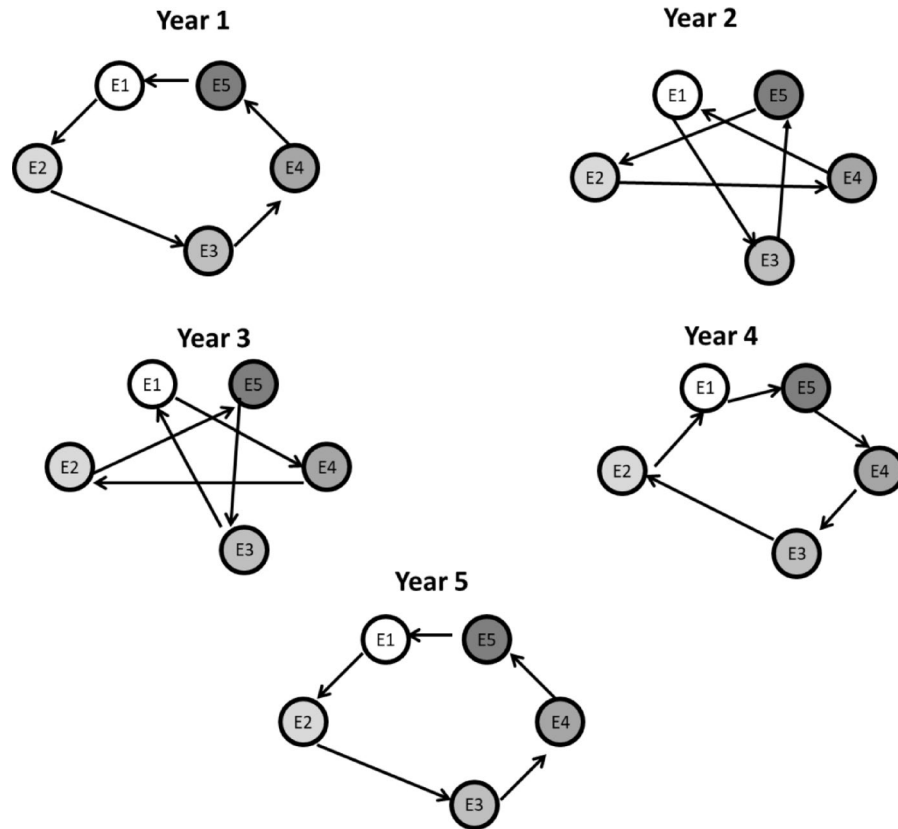
Figure 5 shows the main principles of the breeding scheme for the conservation of feral pigs. A low inbreeding rate should be maintained through rotational mating of sire lines, involving a minimum of five farmers. This minimum number was agreed upon through stakeholders' discussions, balancing the need for at least four distinct herd groups for conservation purposes and the practical limitations of small-scale farming systems (i.e., a maximum of two boars and six sows per farm). Each circle in the Fig. 5 represents either an individual farm or a group of herds. The following rules have been validated by the stakeholders: (i) minimum genetic diversity: the number of sire and dam lines must be at least 10; each herd or group of herds must maintain these lines by replacing boars with their sons and sows with their daughters; (ii) avoiding inbreeding: sows must be mated with boars born in different herds or herd groups; mating animals born within the same herd is strictly prohibited; (iii) high turnover of sires: the number of boars annually should be maximized, and their replacement rate should be as rapid as possible; boars should be used for only one year and then replaced by their male offspring; in contrast, sows should be retained for as long as feasible, ideally for up to eight litters. By the end of the fourth rotation in this circular mating scheme, the pedigree of the creole pig breed in Martinique is expected to include data on at least 150 reproducers across eight generations.

### Discussion

It is now well established that the use and management of local farm animal genetic resources can help address many of the global challenges we face, by preserving genotypes that may be essential in the future<sup>4</sup>. The creole pig breed, in particular, has been shaped by a unique crossbreeding history closely tied to the region's colonial and agricultural past<sup>4</sup>. The main strengths of the Creole breeds lie in their adaptation to the humid tropical environment. These include heat tolerance<sup>11,12</sup>, an enhanced ability to utilize tropical forages and crops, better mobilization of body reserves, and greater resistance to ecto- and endo-parasites than exotic genotypes<sup>13</sup>.

In our study, we detected a genetic structure comprising 10 ancestral origins. These findings are consistent with previously published data<sup>14</sup> identifying 8 ancestral origins, which highlight the extreme complexity of pig genetic structure across the Americas. Although they share the same name, Creole (CR) pigs differ between American territories, as they result from complex admixture processes involving breeds of diverse origins – shaped by each territory's unique colonial history between the 15th and 19th centuries<sup>15</sup>. Despite their genetic diversity, CR pigs share a common feature: a predominant Iberian genetic contribution<sup>14</sup> ranging from 13 to





**Fig. 5.** Rotational mating plan with maximum avoidance of inbreeding. Each small circle E represent a herd or a regional group of herds, arrows represent the rotation mating (from the first to the fifth generations for maximum avoidance of inbreeding scheme).

72%. In the present study, estimates of ancestral composition show that feral pigs in Martinique, like many pig populations across the Americas, carry a substantial proportion of Iberian ancestry – averaging 24%. Interestingly, the presence of feral pigs in Martinique was already noted in the 17th century. Labat<sup>16</sup> described them as follows: “The maroon pigs found on the islands are of two kinds, and it is easy to distinguish between them. Those of the Spanish breed, that is to say, of those first introduced by the Spaniards at the beginning of their discoveries, are short and stocky, with large heads and short snouts. The second breed comes from the domestic pigs that escaped from the pens where they were kept. They are no different from those in France, from where their ancestors were brought, and it does not appear that these two breeds have intermingled...”. Our results show that the proportion of Iberian ancestry is higher in feral pigs from Martinique than in the Creole pigs from Guadeloupe (24 vs. 20%), the other Francophone territory in the Caribbean. This difference may be attributed to the more isolated breeding of feral pigs, which live in the wild and are less exposed to crossbreeding compared to farm-raised pigs<sup>17</sup>. Contrary to the expectations or beliefs of some farmers, our analysis reveals that most pigs from family and professional farms have little to no Iberian genetic contribution. In cases where no pedigree information was available, we selected animals for genotyping based on their phenotypic resemblance to Creole pigs. This study highlights the value of genomic tools in identifying the genetic origins of animals in the absence of pedigree data. Indeed, genetic markers such as SNPs provide a powerful means to trace and evaluate the ancestry of sampled animals.

Our analyses suggest a notable contribution of Chinese ancestry in the genetic makeup of feral and semi-feral pigs in Martinique, ranging from 9 to 11%. This could be explained by: i) indirect introgression through the incorporation of Chinese genes into European breeds to improve prolificity<sup>18</sup>; ii) direct introgression via the historical or more recent importation of Chinese pig genotypes into Martinique. Historical records support this hypothesis. Pigs from Asia were introduced to regions of the Americas during maritime trade between 1685 and 1841. Labat<sup>16</sup> reported, “The French ships that stopped at the islands on their return from Siam and China brought another pig breed - short legged, with very little hair and a very large belly”. Additionally, in rural regions of Guadeloupe and Martinique, elderly people use the term “Siam pigs” to refer to the Creole pig (Gourdine, personal communication).

Our results on inbreeding management show that re-domesticated creole pigs from Breeders 2 and 3 have lower inbreeding coefficients than feral pigs (FM), but a significantly higher coefficients than pigs from family farms (FamM) and professional farms (ProM) in Martinique. These differences can be explained in two ways. First, the re-domesticated creole pigs likely exhibit intermediate levels of inbreeding because they originated from a mix of FM and FamM pigs. Second, the higher inbreeding levels observed in these re-domesticated pigs, compared to FamM and ProM pigs, may be due to the lack of formal breeding plans. In contrast, pigs from

FamM and ProM farms benefit from more structured breeding practices, which aim to minimize inbreeding. As shown by Zhao et al.<sup>19</sup>, although various breeding strategies exist, they generally aim to support reproduction while limiting the accumulation of inbreeding within the population. In contrast, the absence of structured breeding plans for re-domesticated creole pig – partly due to change in PNRM governance in 2016<sup>20</sup> – negatively impact the breeding practices of Breeders 2 and 3. During this period, these pigs were not managed under controlled breeding protocols, likely increasing the probability of mating between closely related individuals. The lack of genealogical information for rare breeds increases the risk of unintentional inbreeding by farmers<sup>21</sup>.

Overall, the majority of domesticated pig groups - including re-domesticated creole pigs – exhibit a significantly lower proportion of runs of homozygosity (ROH) compared to feral pigs. ROH is a recognized method for analyzing inbreeding in animal genetic resources<sup>22,23</sup>. These results suggest that the management of animal genetic resources through structured breeding plans contributes to better control of inbreeding. Windig and Kaal-Lansbergen<sup>24</sup> proposed a herd management strategy based on a rotational breeding system, in which each herd serves as a donor for another in a cyclic manner. This approach has been shown to effectively limit the accumulation of inbreeding while remaining practical for implementation in conservation breeding programs. We drew inspiration from these studies<sup>24</sup> to engage with stakeholders in discussing conservation strategies.

The holistic approach used in this study was both iterative and adaptive. All partners recognized the genetic uniqueness of the feral pigs in Martinique, which have adapted to the natural conditions of the tropical humid island. This breed could provide many products (marketable or not) and fulfil different ecological or social roles<sup>25</sup>. Moreover, the feral pig could play a role in climate-smart livestock systems and contribute to human health benefit<sup>26</sup>. Within this framework, researchers provided a foundation of scientific rigor in support of the public interest – specifically, in the management of the feral pig in Martinique as a common good. This collaborative and constructive environment, established gradually over time, led to the development of a conservation management plan aimed at reducing the risk of losing valuable genetic traits. While methods for conserving genetic diversity remain an active area of genetic research<sup>27,28</sup> many are based on simulation studies. These methods can be effective and widely applied – but only if they are adapted to the specific structure and functioning of the farms involved<sup>29</sup>. The breeding scheme in the present study resulted from a consensus between scientific recommendations and the partners' knowledge of the regional context – including the dynamics of breeder networks, the capacity for genetic material exchange, and the advantages and limitations of the proposed genetic management strategies. In our breeding scheme of Fig. 5, during the first year and in line with Fig. 3, it may be beneficial for each of the five illustrated farms to include a sample of individuals representing the five identified Creole pig groups in Martinique (two FM and three SfM). This initial distribution would ensure genetic diversity from the outset. This method of conservation breeding has been showed to be one of the most effective alternatives for avoiding high levels of inbreeding, particularly in the absence of detailed pedigree information from pedigree or high-density genotyping data<sup>30–32</sup>. However, rotational mating methods alone may not be sufficient to maintain genetic diversity when the population carries deleterious inbreeding load<sup>33</sup>. In the long term, it will be essential to structure the mating plan using for instance the optimal contribution selection theory<sup>30,34</sup>. This approach has been shown to allow for the selection of animals to improve traits on interest - such as meat quality - while maintaining low levels of inbreeding<sup>35</sup>.

In the present study, we carried out a genetic characterization of the feral pig population in Martinique. It is an essential step for the conservation and potential valorisation of local breed resources. Our findings show that the feral and semi-feral pigs share a genetic structure comparable to that of Creole breeds across the Americas, notably marked by a high proportion of Iberian genetic inheritance. These results also highlight the relevance of the saying “*do not judge a book by its cover*”. They show how genetic markers serves as powerful tools for objectively distinguishing “true Creole” pigs from those that merely resemble them phenotypically – underscoring the importance of molecular tools in guiding conservation and breeding efforts.

## Methods

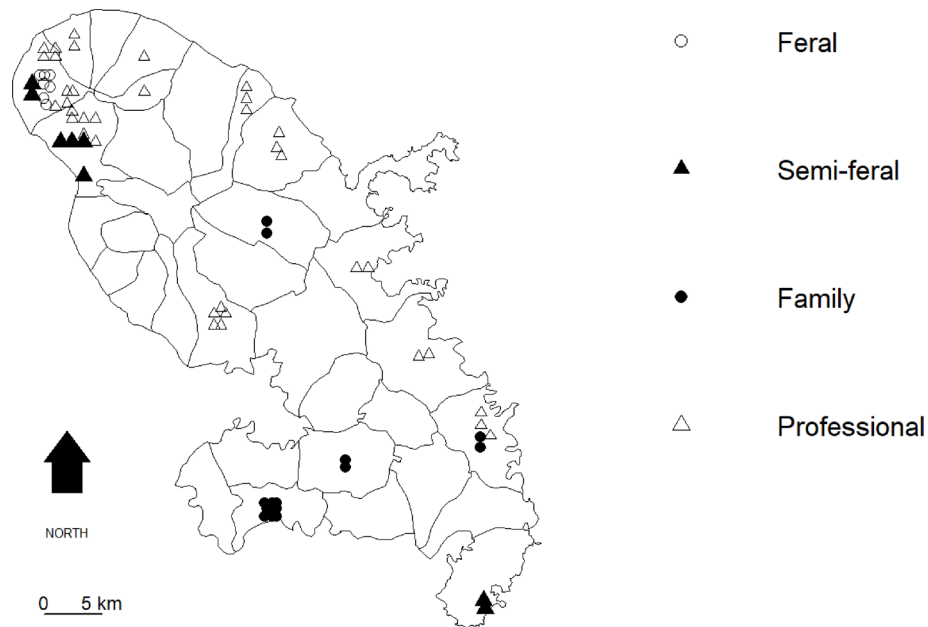
### Location and genotypes sampling

This research was carried out in Martinique, in collaboration with the staff of the animal experimental station, the Tropical Livestock Platform for Agroecology (PTEA) of the French National Research Institute for Agriculture, Food and Environment (INRAE). This experimental unit is accredited for animal experimentation under number A971802, and the involved staff members are trained in animal experimentation and welfare. Animals were treated in accordance with the guidelines and regulations for animal experimentation set by the French Ministry of Agriculture. The protocol (#69-2012-2) was approved by the Ministry of Higher Education and Research, following the advice of the Animal Care and Use Committee of French West Indies and Guyana (N°069). The authors confirm compliance with the ARRIVE guidelines<sup>36</sup>. Informed consent was obtained from all farm owners prior to animal blood sampling.

The animals studied were distributed across 16 of the 34 districts of the island, primarily in areas where agriculture activities predominate. Figure 6 shows the geographical distribution of the genotyped pigs in Martinique according to their origin (feral, semi-feral, pigs reared on family farms, or pigs from professional pig farms). Tourist areas, urban zones, and regions with declining agricultural activity were not included in the study.

### Holistic approach

The overall objective of the present project required scientific and technical expertise across several fields, including genetic characterization, small population management, and farmers' practices. To develop a comprehensive set of specifications - such as conservation schemes for pigs - we adopted a holistic approach. Each partner contributed complementary skills: project coordination was led by the consultancy firm Ruralité Multiservices; technical expertise and territory knowledge were provided by the Agricultural Chamber of



**Fig. 6.** Geographical distribution of pigs genotyped in Martinique.

Martinique, the PNRM, local farmers, and the pig cooperative COOPMAR; and scientific and technical expertise came from INRAE<sup>10</sup>. Experimental protocols – including animal capture, sanitary management, breeding conditions, and mating management – were discussed and regularly updated based on the following principle: proposal originated from scientific expertise; while implementation was guided by the on-the-ground knowledge of the other partners.

#### Animals studied and data used

A non-negligible portion of pig farming in Martinique operates within the popular economy<sup>37</sup> beyond the reach of official oversight and public support. According to the previous investigations by the PNRM, feral pigs roam freely in the mountainous regions of the north of the island. Some of these pigs were captured and raised either in family backyards or in small-scale pig farming operations (referred to as semi-feral pigs). As a result, it was necessary to conduct a survey across the territory of Martinique to identify farmers who may be rearing these animals<sup>38</sup>.

The pigs genotyped in this study came from two distinct groups. The first group includes animals genotyped during surveys conducted across Martinique in 2016. These surveys aimed to identify breeders potentially raising creole pigs. Following these investigations, 76 pigs were genotyped: 7 feral pigs from Martinique, 8 semi-feral pigs, 52 farmed pigs from Martinique, 6 farmed pigs from Guadeloupe and 3 from the PTEA experimental flock of INRAE. All pigs were considered by their owners to belong to the Creole breed, based on morphological aspects such as predominantly black or ash-grey coats, broad and forward-drooping ears, and in some cases, the presence of neck wattles. The second group consists of 45 pigs genotyped in 2022, potentially descended from pigs identified as feral in Martinique in 2016. The animals had not been managed under a specific breeding plan. The purpose of this genotyping was to measure the inbreeding rate of 2022 re-domesticated feral pig population and to assess its genetic evolution since 2016. Blood samples for DNA extraction were collected via jugular venipuncture into two 6-ml tubes containing anticoagulant per pig and stored at 4 °C. After visiting all the farms, the samples were transferred to the laboratory, where they were stored at -20 °C and later transported using dry ice to LABOGENA-DNA – the French reference laboratory for livestock genotyping (ISO 170025 accredited, Jouy-en-Josas, France).

To investigate the potential genetic origins of these pigs, a total of 538 reference mainstream genotypes were used. These data were source from various studies and institutions: (i) 374 pig genotypes from the Americas-Caribbean region and Europe<sup>14</sup>; (ii) 4 genotypes of CR pigs from Guadeloupe studied by Rosé et al.<sup>39</sup> and maintained at the INRAE experimental facilities in Guadeloupe (16°N, 61°W); (iii) 6 pigs considered to be of the CR breed, identified on family farms in Guadeloupe through surveys<sup>17</sup> and (iv) 62 Piétrain and 26 Gascon genotypes provided by INRAE UMR GenPhySE. Table 1 summarizes the pig genotypes used in this study.

First, we applied quality control filtering to the genotype data using Plink, excluding SNPs and individuals based on missingness, minor allele frequency, and Hardy-Weinberg equilibrium thresholds. We then performed linkage disequilibrium (LD) pruning to remove correlated SNPs and retain only independent markers. Then we performed an Admixture analysis in unsupervised mode, meaning that no ancestral reference genotypes were defined beforehand. The software grouped individuals based on their genetic similarities, with the results displayed as color bands on a graph. This first analysis provides a preliminary view of the genetic composition of the studied samples by comparing them to the various genotypes included in the dataset. Next, based on the optimal number of clusters determined using cross-validation, we performed a supervised Admixture

| Geographical regions or breeds | Number of genotypes | Abbreviation used |
|--------------------------------|---------------------|-------------------|
| Martinique <sup>1</sup>        |                     |                   |
| Creole                         | 45                  | CRM               |
| Feral                          | 7                   | FM                |
| Semi-feral                     | 8                   | SfM               |
| Family                         | 26                  | FamM              |
| Family parents                 | 10                  | FamP              |
| Professional                   | 16                  | ProM              |
| Guadeloupe <sup>2</sup>        |                     |                   |
| INRAE                          | 7                   | INRAE             |
| Family                         | 6                   | FamG              |
| South America <sup>3,4</sup>   |                     |                   |
| Feral                          | 6                   | FSA               |
| Semi-feral                     | 10                  | SfSA              |
| Creole                         | 110                 | CR                |
| Brasil                         | 30                  | BR                |
| North America <sup>3,5</sup>   | 32                  | USA               |
| Mainstream breeds              |                     |                   |
| Duroc <sup>3</sup>             | 20                  | DU                |
| Hampshire <sup>3</sup>         | 14                  | HA                |
| Large White <sup>3</sup>       | 20                  | LW                |
| Landrace <sup>3</sup>          | 20                  | LR                |
| Iberian <sup>3</sup>           | 15                  | IB                |
| Piétrain <sup>6</sup>          | 62                  | PI                |
| Gascon <sup>6</sup>            | 26                  | GA                |
| Other breeds or other regions  |                     |                   |
| Mediterranean <sup>3,7</sup>   | 22                  | Med               |
| Wild boar <sup>3</sup>         | 13                  | WB                |
| Chinese <sup>3,8</sup>         | 58                  | CH                |

**Table 1.** Origins of the pig genotypes used in this study. <sup>1</sup>Martinique: genotypes are from our study; Creole are feral pigs re-domesticated by three volunteer farmers in the PNRM program; feral pigs are animals captured by hunters or PNRM staff; semi-feral pigs are Pigs crossed with feral pigs by farmers and kept on their farms; family corresponds to pigs reared in family farms; family parents correspond to pigs raised on family farms that are potential parents of CRM re-domesticated feral pigs; professional corresponds to pigs that are reared by pig professional farmers. <sup>2</sup>Guadeloupe: INRAE corresponds to 3 Creole pigs that are conserved at the INRAE experimental facilities and 4 genotypes from the study of Rose et al.<sup>37</sup>; Family corresponds to pigs reared in family farms. <sup>3</sup>Genotypes were obtained from the study of Burgos-Paz et al.<sup>14</sup>. <sup>4</sup>South America: feral corresponds to genotypes of feral and semi-feral pigs from Argentina; Creole corresponds to genotypes of pigs from Argentina, Bolivia, Colombia, Costa Rica, Cuba, Ecuador, Guatemala, Mexico, Peru, and Uruguay; Brasil corresponds to genotypes of 9 Moura pigs from Concordia, 10 Monteiro pigs from Poconé, 9 Piau pigs from Bahia and 2 Nilo pigs from Goias. <sup>5</sup>North America: genotypes are 7 Ossabaw pigs from the Ossabaw island, 10 Yucatan pigs from Indiana and 15 Guinea hog pigs from several USA locations. <sup>6</sup>Piétrain genotypes were obtained from INRAE. <sup>7</sup>Mediterranean corresponds to 14 Bisaro pigs from Portugal, 4 Canarian pigs from Spain, 4 Black Sicilian pigs from Italy. <sup>8</sup>Chinese corresponds to 13 Xiang Pig, 11 Jiangquhai pigs, 17 Jinhua pigs and 17 Meishan pigs from China.

analysis, in which ancestral reference genotypes were specified. This approach enabled us to estimate the relative genetic composition of our study samples by comparing them reference populations. The reference populations were selected based on the study by Burgos-Paz et al.<sup>14</sup> who investigated the genetic structure of Creole pig populations across the Americas. Key ancestral breeds, identified in that study included Iberian, Landrace, Large White, Duroc, Hampshire, and Chinese pigs. To these, we added Piétrain and Gascon genotypes, provided by the INRAE GenPhySE laboratory. These additional genotypes were included based on surveys conducted in 2016, in which breeders in Martinique reported their potential use in crossbreeding<sup>38</sup>. The Table 2 shows the genetic composition using ancestry coefficients from supervised analysis of 10 clusters. Due to the strong genetic similarities observed in the admixture analysis with K = 10 (Fig. 4), the “Chinese” group in Table 2 includes both Meishan and Xiang Pig breeds.

| Geographical regions or breeds <sup>1</sup> | Iberian | Landrace | Large White | Duroc | Chinese | Jinhua | Jiangquhai | Gascon | Hampshire | Piértrain |
|---|---------|----------|-------------|-------|---------|--------|------------|--------|-----------|-----------|
| Martinique <sup>1</sup>                     |         |          |             |       |         |        |            |        |           |           |
| Feral                                       | 0.24    | 0.56     | 0.00        | 0.06  | 0.11    | 0.01   | 0.01       | 0.00   | 0.01      | 0.00      |
| Semi-feral                                  | 0.21    | 0.18     | 0.33        | 0.06  | 0.09    | 0.01   | 0.01       | 0.05   | 0.02      | 0.04      |
| Family                                      | 0.01    | 0.09     | 0.46        | 0.23  | 0.01    | 0.01   | 0.01       | 0.01   | 0.01      | 0.16      |
| Family parents                              | 0.00    | 1.00     | 0.00        | 0.00  | 0.00    | 0.00   | 0.00       | 0.00   | 0.00      | 0.00      |
| Professional                                | 0.02    | 0.10     | 0.39        | 0.30  | 0.01    | 0.01   | 0.00       | 0.01   | 0.00      | 0.16      |
| Guadeloupe <sup>2</sup>                     |         |          |             |       |         |        |            |        |           |           |
| INRAE                                       | 0.20    | 0.13     | 0.37        | 0.07  | 0.03    | 0.01   | 0.01       | 0.04   | 0.04      | 0.10      |
| Family                                      | 0.06    | 0.18     | 0.41        | 0.08  | 0.03    | 0.01   | 0.00       | 0.03   | 0.01      | 0.19      |
| North America <sup>3,4</sup>                | 0.36    | 0.04     | 0.01        | 0.03  | 0.02    | 0.00   | 0.01       | 0.34   | 0.18      | 0.01      |
| South America <sup>3,5</sup>                |         |          |             |       |         |        |            |        |           |           |
| Feral                                       | 0.52    | 0.08     | 0.06        | 0.18  | 0.01    | 0.01   | 0.02       | 0.06   | 0.03      | 0.03      |
| Creole                                      | 0.54    | 0.07     | 0.04        | 0.15  | 0.08    | 0.01   | 0.01       | 0.07   | 0.02      | 0.01      |
| Brasil                                      | 0.52    | 0.05     | 0.02        | 0.16  | 0.17    | 0.00   | 0.01       | 0.03   | 0.01      | 0.03      |
| Mediterranean <sup>3,7</sup>                | 0.30    | 0.30     | 0.28        | 0.04  | 0.01    | 0.00   | 0.00       | 0.02   | 0.02      | 0.03      |

**Table 2.** Predicted genetic composition using ancestry coefficients from supervised analysis of 10 clusters.

<sup>1</sup>See Table 1 for more information about the origin of the breeds. In this table, the category “Chinese” includes similar breeds such as Meishan and Xiang Pig.

## Genotyping and quality control

DNA extraction and blood plasma genotyping were performed by LABOGENA-DNA. The initial genotyping was carried out using the Illumina PorcineSNP60 BeadChip, which contains 61,565 markers. The second round of genotyping, performed in 2022, used the custom PORC-XT\_60K\_V2 porcine chip, developed by Labogena<sup>\*</sup> in partnership with Choice Genetics. This chip is also based on Illumina’s Infinium technology and includes 57,811 SNP markers. The reference genome used was *Sus scrofa* Build 11.1. Quality control of the genotyping data was performed using PLINK 1.09. Markers were excluded if they had more than 5% missing genotypes, a minor allele frequency (MAF) below 1%, or significant deviation from Hardy-Weinberg equilibrium. Additionally, individuals with more than 5% missing genotype data were also excluded. After quality control, a total of 35,657 SNPs across 583 genotypes were retained. Prior to conducting Principal Component Analysis (PCA) and Admixture analysis, we performed linkage disequilibrium (LD) pruning using the --indep flag of PLINK with the following parameters: window size of 60 SNPs, step size of 5 SNPs, and a variance inflation factor threshold of 2. The resulting dataset included 13,578 SNP and 583 genotypes. This LD pruning step helps to reduce redundancy by eliminating SNPs in strong LD, ensuring that the remaining markers represent more independent genetic variation and thereby improving the accuracy of subsequent analyses<sup>40</sup>.

## Calculations and statistical analysis

Principal Component Analysis (PCA), used to estimate genetic distances between individuals in our sample, was performed using PLINK version 1.09<sup>40</sup> with the --pca parameter. This analysis allows for the visualization of genetic similarities and differences among pigs sampled in Martinique. Genetic distances between two individuals were calculated based on kinship coefficients, estimated from allele frequencies at various loci distributed across the 18 autosomes. These distances reflect both shared ancestry and broader population-level genetic divergence.

The inbreeding coefficient was calculated using the --het flag with PLINK 1.09. This analysis computes the observed and expected counts of homozygous autosomal genotype for each sample. The method-of-moments  $F$  coefficient was estimated using the formula:

$$F = \frac{\text{Observed Homozygous Count} - \text{Expected Count}}{\text{Total Observations} - \text{Expected Count}}$$

Initially, an ANOVA test was conducted<sup>41</sup>. While the Shapiro-Wilk test confirmed the normality of residuals, Levene’s test indicated significant variance differences among groups, violating the assumption of homogeneity. As a result, a non-parametric approach was adopted. The  $p$ -value was estimated using the Kruskal-Wallis test, followed by Dunn’s post-hoc test with Bonferroni correction<sup>42</sup> using R software version 4.2.1<sup>43</sup>, and the FSA package version 0.9.6<sup>44</sup>.

Runs of homozygosity (ROH) are one of the primary methods used to assess inbreeding in animal genetic resources<sup>22</sup>. ROHs are defined as continuous chromosomal segments in which all loci exhibit homozygous genotypes<sup>45,46</sup>. These homozygous sequences, presumed to originate from a common ancestor, vary in length depending on the level of inbreeding. Short ROHs typically indicate ancient inbreeding, while long ROHs are suggestive of more recent inbreeding events<sup>22,47</sup>. The ROH parameters used in this study were based on the recommendations of Ceballos et al.<sup>48</sup> and Manunza et al.<sup>49</sup>. ROHs were detected using PLINK 1.09 with the following settings: a minimum ROH length of 1,000 kb (--homozyg-kb 1000), a minimum of 50 SNPs per ROH (--homozyg-snp 50), a maximum of one heterozygous site allowed per ROH (--homozyg-het 1), and a minimum

SNP density of 1 SNP per 100 kb (--homozyg-density 100). The *p*-value for ROH-based inbreeding differences among groups were estimated using ANOVA. The Shapiro-Wilk test confirmed normality of the residuals, and the Levene's test indicated homogeneity of variance among groups. Tukey's HSD test<sup>50,51</sup> and Student's *t*-test were used for pairwise comparisons, with a significance level of 5%, all performed in R software version 4.2.1<sup>43</sup>.

Ancestry proportions for each individual were estimated using ADMIXTURE software version 1.3.0<sup>52</sup>. The optimal number of clusters was determined by minimizing the cross-validation error, using the --cv flag in ADMIXTURE and testing cluster numbers from 7 to 20. This analysis was performed on 121 pig genotypes from Martinique and Guadeloupe to identify the ancestral origins of the sampled populations. To improve estimation accuracy in ADMIXTURE analysis, it is recommended to exclude closely related individuals. Therefore, re-domesticated pigs from Martinique (CRM) were removed, as some individuals from familial farms in Martinique (FamM), as well as from feral (FM), and semi-feral (SfM) populations, were likely close relatives. The final ADMIXTURE analysis was performed on 538 genotypes and 13,578 SNPs.

## Data availability

Sequence data that support the findings of this study have been deposited and are openly available on Research. Data.gouv with the following DOI: <https://doi.org/10.57745/HWCCD5>. We also used the published data from Burgos-Paz et al. 2013 available at Dryad: <https://doi.org/10.5061/dryad.t1r3d>.

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## Author contributions

N.D., G.A. and J-L.G. conceived and designed the project. M.B., K.B. and C.V-D. managed the collection of data. M.B. and K.B. mainly collected the samples and participated to meeting with farmers. N.D. and Y.L. analysed the data. N.D., Y.L. and J-L.G. analysed the data, discussed and interpreted the results. N.D. and J-L.G. wrote the original draft. N.P. and N.M. reviewed the paper. All authors read and approved the final manuscript.

## Declarations

## Ethical approval

The authors confirm compliance with the ARRIVE guidelines. All measurements and observations on animals were performed in accordance with the current law on animal experimentation and ethics (#69-2016-1 from the Animal Care and Use Committee of French West Indies and Guyana) and the experimental protocol was approved by the French Ministry of Agriculture and Fisheries (#A971-18-02) under the direction of J. Fleury

(INRA-PTEA).

### Competing interests

The authors declare no competing interests.

### Additional information

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