

An assessment of European pig diversity using molecular markers: Partitioning of diversity among breeds

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Received 12 October 2004; accepted 17 November 2004

Key words: biodiversity, conservation, genetic marker, pig

Abstract

Genetic diversity within and between breeds (and lines) of pigs was investigated. The sample comprised 68 European domestic breeds (and lines), including 29 local breeds, 18 varieties of major international breeds, namely *Duroc*, *Hampshire*, *Landrace*, *Large White* and *Piétrain*, and 21 commercial lines either purebred or synthetic, to which the Chinese *Meishan* and a sample of European wild pig were added. On average 46 animals per breed were sampled (range 12–68). The genetic markers were microsatellites (50 loci) and AFLP (amplified fragment length polymorphism, 148 loci). The analysis of diversity showed that the local breeds accounted for 56% of the total European between-breed microsatellite diversity, and slightly less for AFLP, followed by commercial lines and international breeds. Conversely, the group of international breeds contributed most to within-breed diversity, followed by commercial lines and local breeds.

Individual breed contributions to the overall European between- and within-breed diversity were estimated. The range in between-breed diversity contributions among the 68 breeds was 0.04–3.94% for microsatellites and 0.24–2.94% for AFLP. The within-breed diversity contributions varied very little for both types of markers, but microsatellite contributions were negatively correlated with the between-breed contributions, so care is needed in balancing the two types of contribution when making conservation decisions. By taking into account the risks of extinction of the 29 local breeds, a cryopreservation potential (priority) was estimated for each of them.

Introduction

Domestication of the pig dates back to the Neolithic age. Remains of domestic pigs dated 7000 years before Christ have indeed been found in China, which is known to be a major and very early centre of pig domestication. The reasons for domestication of the pig are diverse. This animal was considered as sacred in the ancient world and it still is in some countries like Papua New Guinea. Pigs have also been used in England to point for game and in France to root for truffles. Since modern times, however, the pig has mainly been used to produce fat, fresh meat (pork) and various forms of processed meat (ham, bacon, etc...). The increasing demand for food protein is generally considered as the main reason for the recent development of breeds with high lean meat content and for fast genetic changes of production efficiency in modern breeds. Genetic aspects of domestication and breed development have recently been reviewed by Jones (1998), who provides detailed information on the main existing breeds.

A proper evaluation of livestock genetic resources is of fundamental importance. Breeds have to be catalogued and evaluated. The inventory of Mason (1988) provided an early overview of the distribution of pig breeds across the world. Nearly 400 breeds were then exploited, the largest numbers of breeds being found in Asia and Europe. In the second half of the 20th century pig breeding programmes became increasingly efficient. As a consequence, the tendency has been towards the use of a limited number of breeds, which has raised concern as to the maintenance of the species biodiversity. As an example, one single breed, the *Large White* (also called *Yorkshire* in some countries) accounts for about one

third of the pork consumed in the European Union (EU).

The current state of pig genetic resources in Europe is represented by a mix of many local breeds, mostly rare, with some threatened by extinction, and by a small number of intensively selected breeds of international status (e.g. *Large White*, *Landrace*, *Piétrain*, etc...). This situation makes it of particular interest to assess the level of genetic diversity that is present in Europe, in order to maintain genetic variation for characters that are likely to be the targets of current or future selection programmes.

With this aim, a collaborative project, involving 15 European countries, was launched by the EU in 1998. The intention was to sample a large and diverse set of European breeds and use molecular genetic markers for assessing diversity, along the FAO recommendations for measuring domestic animal diversity (Barker et al. 1998). Data necessary to analyse the between-breed as well as the within-breed genetic variation have thus become available (Ollivier et al. 2003). The aspects of breed differentiation, based on classical population genetics methods for subdivided populations, such as *F* statistics and phylogenetic trees, are presented elsewhere (SanCristobal et al., Submitted). The data showed that the pig may be seen as a highly subdivided species over the European continent. In the same paper an attempt was also made to analyse the evolutionary forces involved in the breed differentiation process. In what follows, a detailed analysis of the European pig diversity will be presented. The aim is to quantify individual breed contributions to the present pig biodiversity, to evaluate its potential future evolution, and to discuss recommendations for its management and conservation.

Material and methods

Breeds sampled and genetic markers typed

Altogether, considering the EU project launched in 1998 (termed PigBioDiv) and the pilot diversity study realised within a previous EU Pig Gene Mapping Project (PiGMaP, detailed in Laval et al. 2000), a total of 70 breeds (or lines) was sampled. The 68 strictly European domestic breeds, excluding the European wild pig and the Chinese *Meishan*, were sorted into three categories, namely local breeds (29), national varieties of international breeds (18), and privately owned commercial lines (21), mostly derived from the previous category. The breeds' names, country of origin, category and sample sizes are given in Table 1.

Standard DNA marker technologies were applied, namely *single sequence repeat* (SSR or so-called microsatellites) on all 70 breeds, and *arbitrary amplification of fragment length polymorphism* (AFLP) on a subset of 59 breeds (the 11 PiGMaP breeds being only typed for microsatellites). The number of loci typed was 50 (or 26 in the 11 PiGMaP breeds) for microsatellites and 148 for AFLP. The details on the populations and the microsatellite markers can be obtained at the database established by the Roslin Institute (Russell et al. 2003) <http://www.databases.roslin.ac.uk/pigbiodiv/>.

DNA was extracted from blood samples in each country and dispatched to the relevant genotyping laboratories. The genotyping of microsatellites was shared between Labogena at Jouy-en-Josas (34 loci, using an ABI multi-capillary sequencer) and Wageningen University (16 loci, using an ABI 377 sequencer). The data previously collected in the PiGMaP project were made comparable to the PigBioDiv data by using a set of four control animals typed in both projects. All genotypes were transferred to the project database mentioned above. AFLP fingerprints were generated as described by Vos et al. (1995). In our study, jointly realised in the laboratories of PIC at Cambridge and Keygene Company at Wageningen, four enzyme combinations *EcoRI/TaqI* were chosen based on previous AFLP analyses on pigs. A dominant scoring system was created using proprietary software and the data also transferred to the project database. More

details on the typings can be found in Groenen et al. (2003) for microsatellites and Plastow et al. (2003) for AFLP.

Analysis of diversity

Between-breed diversity

Pairwise genetic distances between the breeds appear to be the most relevant parameters in the context of between-breed diversity. Multi-locus Reynolds distances (Reynolds et al. 1983) were calculated for microsatellites using the Phylip software (Felsenstein 2000), whereas for AFLP we used the average of locus-specific distances, setting a zero value for pairwise identically monomorphic loci. Standard Nei multi-locus distances (Nei 1972) were calculated via Phylip for both markers. The four corresponding distance matrices are given in the online Appendix.

Weitzman (1992, 1993) has provided an analytical framework able to guide conservation policies through the use of a diversity function. The approach can be extended to the situation of livestock breeds diversity, as advocated by Thaon d'Arnoldi et al. (1998). Given a set S of n species (or breeds), among which $n(n-1)/2$ pairwise distances are known, one may define a distance d_i between any species i from S and its closest neighbour in the set $S \setminus i$, defined as the set S excluding i . The diversity function V is defined by Weitzman (1993) as "the maximum, over all members of the set, of the distance of that member from its closest relative in the set plus the diversity of the set without that member", such as:

$$V(S) = \text{maximum over } S \text{ of } [d_i + V(S \setminus i)]. \quad (1)$$

One can see that, after setting the arbitrary initial value $V(i)$ to zero, $V(S)$ is a sum of $n-1$ distances. Equation (1) also allows calculating the diversity of any remaining subset of S . The relative loss of diversity resulting from the extinction of any given breed k may then be defined as:

$$V_k = 1 - V(S \setminus k)/V(S), \quad (2)$$

where $V(S)$ and $V(S \setminus k)$ are diversities as defined in (1). V_k is termed the *contribution of breed 'k' to between-breed diversity* (CB), previously called marginal loss of diversity by Laval et al. (2000).

Table 1. Breeds sampled in PigBioDiv and PiGMaP (ordered by country)

Breed/line code ^a	Country of origin	Breed/line name (company ^b)	Breed/line category ^c	Sample size
BEPI01	Belgium	Belgian Piétrain	I	46
CZPR01	Czech Republic	Presticke	L	50
DEAS01	Germany	Angler Sattelschwein	L	56
DEBB01	"	Bunte Bentheimer	L	47
DEDU03	"	Duroc line (S)	C	49
DEHA02	"	Hampshire line (BHZP)	C	60
DELR02	"	German Landrace	I	50
DELR14	"	Landrace line (BHZP)	C	55
DELW02	"	German Large White	I	52
DELW10	"	Large White line (BHZP)	C	50
DEMA01	"	Mangalica	L	29
DEPI03	"	German Piétrain	I	51
DESH01	"	Schwäbisch-Hällisches Schwein	L	45
DKLR04	Denmark	Danish Landrace (contemporary)	I	52
DKLR05	"	Danish Landrace (1970)	I	30
DKSO01	"	Sortbroget	L	50
ESNC01	Spain	Negro Canario	"	18
ESNI01	"	Negro Iberico	"	48
ESMJ01	"	Manchado de Jabugo	"	36
ESRE01	"	Retinto	"	68
FILR06	Finland	Finnish Landrace	I	56
FRBA01	France	Basque	L	46
FRCR01	"	Créole (Guadeloupe)	"	44
FRDR01	"	DRB synthetic line (SCAPAAG)	C	50
FRGA01	"	Gascon	L	56
FRLA01	"	Laconie synthetic line (PAL)	C	49
FRLI01	"	Limousin	L	56
FRLR01	"	French Landrace	I	51
FRLR13	"	Landrace line (FH)	C	51
FRLW01	"	French Large White (dam line)	I	50
FRLW08	"	Large White line (FH)	C	50
FRLW09	"	Large White line (PAL)	C	46
FRLW12	"	French Large White (sire line)	I	34
FRNO01	"	Normand (or Blanc de l'Ouest)	L	52
FRPI02	"	French Piétrain	I	50
FRPI05	"	Piétrain line (FH)	C	48
FRTM01	"	Tia Meslan synthetic line (PAL)	C	49
GBBK01	United-Kingdom	Berkshire	L	50
GBBL01	"	British Lop	"	35
GBBS01	"	British Saddleback	"	42
GBDU02	"	Duroc line (PIC)	C	50
GBGO01	"	Gloucester Old Spots	L	53
GBHA01	"	Hampshire line (PIC)	C	50
GBLB01	"	Large Black	L	52
GBLE01	"	Leicoma synthetic line (PIC)	C	50
GBLR10	"	Landrace line (PIC)	"	50
GBLR11	"	"	"	50
GBLR12	"	"	"	48
GBLW05	"	Large White line (PIC)	"	50
GBLW06	"	"	"	50
GBLW07	"	"	"	50
GBMW01	"	Middle White	L	38

Table 1. (Continued)

Breed/line code ^a	Country of origin	Breed/line name (company ^b)	Breed/line category ^c	Sample size
GBPI04	"	Piértrain line (PIC)	C	50
GBT01	"	Tamworth	L	42
ISLR09	Iceland	Icelandic Landrace	I	35
ITCA01	Italy	Calabrese	L	19
ITCS01	"	Cinta Senese	L	30
ITCT01	"	Casertana	L	28
ITDU01	"	Italian Duroc	I	50
ITLR03	"	Italian Landrace	I	50
ITLW03	"	Italian Large White	I	50
ITNS01	"	Nera Siciliana	L	50
NLLW04	The Netherlands	Dutch Large White (sire line)	I	30
NOLR08	Norway	Norwegian Landrace	I	50
PLPU01	Poland	Pulawska Spots	L	48
PTBI01	Portugal	Bisaro	L	60
SELR07	Sweden	Swedish Landrace	I	24
SELS01	"	Linderödssvin	L	36
SEWPO1	"	Wild pig from Poland	Wild	12
CNMS01	France and UK (sampling)	Meishan	Imported	61
Total	16 countries	70 breeds/lines	29 L/18 I/21 C/ 2 other	3223

^aThe breed code is a concatenation of a 2-letter country code, a 2-letter breed (or synthetic) code, and a 2-digit variety (or line) code. For example, ISLR09 is the Icelandic variety of Landrace numbered 09 in the project. PiGMAP breeds are in bold.

^bBundesHybridZuchtProgram (BHZP), France Hybrides (FH), Pen Ar Lan (PAL), Pig Improvement Company (PIC), Schaumann (S) and Société Coopérative Agricole pour l'Assainissement et l'Amélioration Génétique du Cheptel Porcin (SCAPAAG).

^cLocal breed (L), national variety of international breed (I), purebred or synthetic commercial line (C).

This parameter may be considered as an estimate of the genetic originality of each breed. The method, however, becomes computationally demanding when the number of breeds is high, as in our case. A specific software has been developed and applied here (Derban et al. 2002), available at <http://www-sgqa.jouy.inra.fr/diffusions.htm>. The analysis was limited to the 68 strictly European domestic breeds defined previously, using the distances calculated from the microsatellite data, and to a subset of 58 breeds (excluding *Meishan* and the 11 PiGMAP breeds) for the AFLP data. For such large numbers of breeds, individual CBs were calculated using the approximation proposed by Thaon d'Arnoldi et al. (1998).

A loss of diversity can also be calculated by extending Equation (2) to any subset of breeds, thus leading to a diversity breakdown among groups of breeds instead of among individual breeds. This was applied to the three categories of breeds as defined in Table 1, allowing the contribution of each group to the overall between-breed diversity to be evaluated.

Weitzman (1993) proposed to use the diversity function for defining conservation policies in the long-term by taking into account the risks of extinction. Based on extinction probabilities of each breed over a given period of time, an expected diversity, $E(V)$, can be defined, given the various extinction-survival patterns which may occur with given probabilities, and assuming those events to be independent. The *marginal between-breed diversity* (MB) of a given breed is then obtained as minus the partial derivative of $E(V)$ with respect to the extinction probability of each breed, which expresses the increase in $E(V)$ with respect to the decrease in extinction probability. Another useful parameter also proposed by Weitzman is the percentage change in $E(V)$ per percentage decrease in extinction probability, that he calls elasticity of diversity or conservation potential. Since $E(V)$ is linear in each of the extinction probabilities, MBs are constant and therefore conservation potential measures the increase in $E(V)$ that would result from making a breed safe. In livestock species, where cryopreservation is available, it may be assumed that extinction probability can be set to

zero. One can then define for each breed a *cryo-preservation potential* (CP) analogous to the conservation potential of Weitzman and establish cryopreservation priorities (Thaon d'Arnoldi et al. 1998; Ollivier 1998). This analysis was performed on the subset of 29 local breeds, using extinction probabilities derived from the breed information available in the database of the European Association for Animal Production (EAAP-AGDB at <http://www.tiho-hannover.de/einricht/eaap/index.htm>) and FAO (DAD-IS at <http://www.fao.org/dad-is/>). The inbreeding expected after 50 generations was taken as the probability of extinction of each breed $P(\text{ext})$, so that $P(\text{ext}) = 1 - \exp(-50/2N_e) \approx 25/N_e$, where N_e is the effective population size defined by Wright (1931) as $N_e = 4N_mN_f/(N_m + N_f)$, combining the number of breeding males (N_m) and females (N_f) reported in the breed.

In order to reduce the computing time needed to consider the large number of extinction-survival patterns (2^{29} for microsatellites), the MBs were approximated by assuming additivity of the breed contributions, but using exact individual CBs. It was shown empirically that such an approximation is tightly correlated with the exact value when the number of breeds becomes large. In addition, $E(V)$ may be written as a function of any breed probability of extinction P_k , as $E(V) = P_k E(V|\text{breed } k \text{ extinct}) + (1 - P_k) E(V|\text{breed } k \text{ safe})$. Since additivity of CBs implies $E(V|\text{breed } k \text{ safe}) - E(V|\text{breed } k \text{ extinct}) = \text{CB}_k$, it also implies $\text{MB} = -\partial E(V)/\partial P_k = \text{CB}_k$. The MBs are then equal to the CBs and independent from the probabilities of extinction. The CPs easily follow as $\text{CP}_k = \text{CB}_k P_k$.

Within-breed diversity

Within-breed expected heterozygosity under Hardy-Weinberg equilibrium (H) is usually considered as a relevant measure of within-breed diversity (see Nei 1973). Taking H as the within-breed diversity function, the loss of within-breed diversity due to the extinction of any breed k may be derived, in a way similar to the loss of between-breed diversity defined in (2), as:

$$H_k = 1 - H(S \setminus k)/H(S), \quad (3)$$

where $H(S)$ is the average within-breed heterozygosity of the whole set S and $H(S \setminus k)$ the average within-breed heterozygosity of the set S excluding breed k (Ollivier and Foulley, 2005). H_k is termed

the *contribution of breed 'k' to within-breed diversity* (CW). Also, as previously with V , a within-breed diversity breakdown was performed over the three categories of breeds defined in Table 1. Here the *marginal within-breed diversity* of each breed (MW, similar to MB), taking into account its probability of extinction, was identical to its CW, since additivity of CWs over breeds strictly held.

Results

Individual breed contributions to diversity

The diversity considered is the overall between-breed diversity of the 68 strictly European domestic breeds or lines, thus excluding the wild pig sample as well as the Chinese *Meishan* breed. The results show that the individual contributions to between-breed diversity (CB) ranged from 0.04 to 3.94% for microsatellites (Table 2). For AFLP, the range was 0.24 to 2.94% (individual contributions not shown). Similar results were obtained with the standard Nei distances and will not be discussed further.

The individual breed contributions to within-breed diversity (CW) are also shown in Table 2. They varied very little for microsatellites, namely from -0.43 (French *Basque*) to 0.35% (French *Créole*), and slightly more for AFLP, from -0.94 to 1.07% (individual contributions not shown). The two types of markers also differed in the correlation between CB and CW, which was negative for microsatellites and near zero for AFLP. By definition, CWs strictly parallels the breed heterozygosity pattern. Local breeds showed more heterogeneous internal diversities, in keeping with the extreme CWs highlighted above for two local breeds.

Breed group contributions to diversity

Diversity was partitioned among the three categories of breeds defined (Table 3), for both types of markers and for within- as well as between-breed diversity (Table 3). The highest contribution to between-breed diversity was provided by the group of local breeds, followed by the commercial lines and the group of international breeds. Differences in group contributions, however, were larger for microsatellites than for AFLP. A reverse order was observed for the within-breed contri-

Table 2. Microsatellite-derived contributions (%) to between-breed (CB) diversity, based on Reynolds distances among 68 European domestic breeds and lines, and to within-breed (CW) diversity based on within-breed expected heterozygosity (CB and CW defined in text, breed/line codes given in Table 1)

BREED/LINE	CB	CW
Local breeds		
DEAS01	0.98	0.20
FRBA01	3.94	-0.44
DEBB01	2.00	0.06
PTBI01	1.43	0.24
GBBK01	2.86	-0.33
GBBL01	1.62	0.17
GBBS01	1.05	0.04
ITCA01	2.75	-0.23
FRCR01	0.58	0.35
ITCS01	2.84	-0.21
ITCT01	2.32	0.08
FRGA01	2.35	-0.10
GBGO01	2.59	-0.29
GBLB01	2.40	-0.13
FRLI01	2.48	-0.23
SELS01	1.89	0.01
DEMA01	3.01	-0.25
ESMJ01	2.60	-0.37
GBMW01	2.45	-0.10
ESNC01	3.19	-0.28
ESNI01	0.56	0.08
FRNO01	2.37	-0.08
ITNS01	1.13	0.31
CZPR01	0.48	0.26
PLPU01	1.97	0.03
ESRE01	0.04	0.09
DESH01	1.19	0.28
DKSO01	1.80	0.00
GBTA01	3.27	-0.24
National varieties of international breeds		
ITDU01	0.25	-0.02
FRLR01	0.32	0.15
DELR02	1.96	0.17
ITLR03	0.49	0.17
DKLR04	0.85	-0.06
DKLR05	1.04	0.02
FILR06	0.95	-0.03
SELR07	0.83	0.05
NOLR08	1.37	-0.02
ISLR09	1.30	0.29
FRLW01	0.73	0.14
DELR02	0.47	0.16
ITLW03	0.35	0.14
NLLW04	2.03	-0.12
FRLW12	0.28	0.17
BEPI01	1.00	0.09
FRPI02	0.23	0.07
DEPI03	0.78	0.06

Table 2. (Continued)

BREED/LINE	CB	CW
Commercial lines		
FRDR01	1.68	0.14
GBDU02	0.97	-0.17
DEDU03	1.54	-0.13
GBHA01	1.67	-0.17
DEHA02	1.07	-0.04
FRLA01	1.27	-0.02
GBLE01	0.78	0.08
GBLR10	0.85	-0.01
GBLR11	1.25	-0.01
GBLR12	0.79	-0.02
FRLR13	0.91	0.07
DELR14	1.32	0.04
GBLW05	0.90	0.06
GBLW06	0.80	0.02
GBLW07	1.60	-0.16
FRLW08	1.22	-0.07
FRLW09	0.89	0.02
DELR10	1.82	-0.08
GBPI04	1.38	0.00
FRPI05	1.58	-0.11
FRTM01	2.34	0.25
TOTAL:	100.00	0.00

Overall between-breed diversity on the Reynolds distance scale: 11.549. Sum of individual CBs: 11.281 (individual CBs are expressed relative to this sum). Average expected heterozygosity: 0.555.

contributions, the international breeds contributing most to this diversity followed by the groups of commercial lines and local breeds. The differences between the three groups were larger, in relative value, with AFLP as compared to microsatellites.

Marginal diversities

The 29 European local breeds of this study are all registered in the European and FAO databases, which keep an updated account of the number of breeding boars and sows in each breed. Based on this information, the effective sizes and probabilities of extinction are given in Table 4. Because of the additivity of CBs, assumed on the grounds of the quasi-identity of breed contributions (CB) and marginal diversities (MB), as explained above, the MBs given in Table 4 were identical to CBs. While Table 2 provides a short-term evaluation of genetic diversity, Table 4 addresses long-term evolution of diversity by integrating extinction

Table 3. Breed groups contributions to diversity based on Reynolds distances

Group	Number of breeds per group		Group contribution (%)			
	Microsatellites	AFLP	Between-breed		Within-breed	
			Microsatellites	AFLP	Microsatellites	AFLP
Local breeds	29	23	55.9	44.0	-1.9	-4.0
National varieties of international breeds	18	14	15.4	21.9	2.1	6.2
Commercial lines	21	21	28.7	34.1	-0.5	-1.4
Total or average	68	58	100.0 ^a	100.0 ^a	0.555 ^b	0.114 ^b

^aOverall between-breed diversity on the Reynolds distance scale: 11.549 for microsatellites and 4.490 for AFLP.

Sum of group contributions: 10.976 for microsatellites and 4.485 for AFLP (group contributions are expressed relative to these sums).

^bAverage within-breed expected heterozygosity.

probabilities. This, in a way, combines genetic originality (or uniqueness) and risk status. Table 4 shows how the long-term approach modified the conservation priorities. When the marginal gain of diversity from cryopreserving each breed (its cryopreservation potential CP) was considered, considerably larger differences than in MB appeared among the different breeds, since they ranged from 0 to 21% in their potentials based on microsatellites, and similarly for AFLP (results not shown). This was particularly exemplified by the Spanish *Manchado de Jabugo* and *Negro Canario*, which both received an enhanced priority since they combined genetic originality and high degree of endangerment.

Marginal within-breed diversities (MW), not shown in Table 4, can easily be derived from Table 2, since MWs were equal to their corresponding CWs, as previously mentioned. The low variation of the breed contributions mentioned above therefore also applied to marginal within-breed diversities.

Discussion

Numerous surveys of genetic diversity based on genetic markers have been performed on farm animal species, including the pig. However, most of these studies, have been rather limited, both in the number of breeds sampled and in the number of markers used: see, for the pig, van Zeveren et al. (1995), Li et al. (2000), Martinez et al. (2000), Laval et al. (2000), Ollivier et al. (2001), and Sun et al. (2002). The studies carried out since 1995 (Ollivier et al. 2003) allowed the collection of a

unique set of data, given the number of markers (nearly 200 loci) and of breeds (70).

Analysing such a large amount of information raises several difficulties which have been discussed by SanCristobal et al. (2003), and Ollivier and Foulley (2004). Conclusions can be drawn from such data on breed differentiation, phylogenies and on the evolutionary forces generating the diversity observed, as presented in detail elsewhere (SanCristobal et al., Submitted). The wild boar and the Chinese *Meishan* data (see last two lines of Table 1) were deliberately excluded from our diversity analysis, in spite of their potential interest in a broader context of biodiversity. It is indeed well established that the present-day European pig has evolved from both the European wild boar and Chinese domestic breeds introgressed into England during the 18th–19th centuries (e.g. see Jones 1998). However our data showed little evidence of *Meishan* introgressions into specific European breeds, probably because a larger sample of Chinese breeds would have been needed (SanCristobal et al., In preparation). The same remark applies to our wild boar data, given in particular the very small sample investigated (see Table 1). Interestingly, however, the shortest distances to the wild boar were exhibited by breeds raised in the open-air (such as *Créole*, *Nera Siciliana* and Iberian breeds) and might thus reveal accidental inter-crossing with wild boars.

The Weitzman approach to diversity analysis has already been used in several farm animal species such as cattle (Thaon d'Arnoldi et al. 1998; Canon et al. 2001; Simianer et al. 2003), goats (Barker et al. 2001), and pig (Laval et al. 2000; Ollivier et al. 2001). Other approaches to diversity

Table 4. Marginal between-breed diversity and cryopreservation potential of European local breeds (based on Reynolds distances for microsatellites)

BREED/LINE	M	F	N_e^a	P(ext)	MB	CP
CZPR01	110	1870	416	0.0584	1.28	0.28
DEAS01	13	87	45	0.4246	1.26	2.03
DEBB01	10	41	32	0.5404	3.35	6.87
DEMA01	44	80	114	0.1976	4.93	3.67
DESH01	25	139	85	0.2554	3.39	3.27
DKSO01	31	68	85	0.2544	3.87	3.73
ESMJ01 ^b	1	14	4	0.9988	5.51	20.81
ESNC01	6	37	21	0.7020	5.57	14.67
ESNI01	6436	71994	23631	0.0011	1.18	0.00
ESRE01	105	3155	406	0.0597	0.88	0.20
FRBA01	59	306	198	0.1187	6.67	2.99
FRCR01	40	1200	155	0.1491	1.23	0.69
FRGA01	103	543	346	0.0696	3.47	0.92
FRLI01	45	148	138	0.1657	3.84	2.41
FRNO01	33	123	104	0.2135	3.10	2.51
GBBK01	65	212	199	0.1181	4.55	2.03
GBBL01	47	205	153	0.1508	3.12	1.78
GBBS01	54	547	197	0.1194	1.71	0.77
GBGO01	19	503	73	0.2892	4.72	5.18
GBMW01	44	213	146	0.1575	4.06	2.42
GBLB01	42	292	147	0.1565	3.96	2.34
GBT A01	73	281	232	0.1022	5.33	2.06
ITCA01	21	123	72	0.2942	4.92	5.46
ITCS01	87	348	278	0.0859	4.56	1.48
ITCT01	58	40	95	0.2320	4.06	3.56
ITNS01	66	583	237	0.1001	1.40	0.53
PLPU01 ^c	14	239	53	0.3766	2.89	4.11
PTBI01	27	81	81	0.2656	1.90	1.91
SELS01	105	125	228	0.1037	3.29	1.29
Mean (total)	268	2883	964	0.2331	(100.00)	(100.00)

M and F are number of breeding males and females recorded in EAAP-AGDB or DAD-IS (January 2003).

N_e : Effective size, defined as $N_e = 4MF/(M + F)$.

P(ext): Probability of extinction, defined as $P(\text{ext}) = 1 - \exp(-25/N_e)$.

MB: Marginal between-breed diversity (defined in text).

CP: Cryopreservation potential (defined in text).

^aRounded to the next integer.

^bMales and females from DAD-IS (FAO).

^cMales from DAD-IS (FAO).

analysis have been proposed, either based on the classical gene diversity parameters of Nei (1973), as proposed by Petit et al. (1998), who also analysed allelic richness in the same paper, or on the concept of co-ancestry (Eding and Meuwissen 2001; Caballero and Toro 2002). These alternative methods are identical in terms of CW and should be similar to the Weitzman approach in terms of CB. For instance, a correlation of 0.90 was observed between the Weitzman-based breed contributions of Laval et al. (2000) and the

co-ancestry-based between-breed diversity components evaluated by Caballero and Toro (2002) on the same data (Ollivier and Foulley, 2005). It should however be remembered that the Weitzman diversity function cannot increase when a breed is removed, as Equation (1) shows. In other words, CBs cannot be negative, an intuitively appealing property, not shared by other methods, based on variance, which may yield negative breed contributions to breed diversity (Thaon d'Arnoldi et al. 1998).

Highly unequal contributions of individual breeds to the overall breed diversity were observed here, in spite of the large number of breeds considered, since the highest contribution to microsatellites diversity (3.94%) was 2.7 times the value expected if the breeds had contributed equally (1.47%). Similarly, inequality of contributions appeared when the three categories of populations were considered, since the local breeds contributions were markedly above their expectations assuming equal breed contributions (56 against 43% for microsatellites).

Another way of testing the heterogeneity of breed contributions is to consider their expected statistical distribution under the null hypothesis of homogeneity. Breed contributions are expected to approximately follow the distribution of the distance used, since CBs are differences between a sum of $n-1$ and a sum of $n-2$ distances, as shown by the numerator of V_k in Equation (2). The range of individual breed contributions observed on the Reynolds distance scale for microsatellites was 0.44, i.e. 21 times the standard error (0.021) of this distance evaluated in our situation by SanCristobal et al. (Submitted). This indicates that the variation observed was much greater than expected by chance. It is also worth noting that the highest contribution of the *Basque* breed over the 11 breeds of the pilot study of Laval et al. (2000) was confirmed over the 68 European breeds and lines considered here, as well as the ranking of the ten breeds in common between the two studies ($r=0.97$ between CB of table 2 and pilot study).

The cryopreservation potentials of the European local breeds reported in Table 4 obviously depend on a correct evaluation of their extinction probabilities. Various attempts have been made to classify livestock breeds as to their degree of endangerment (EAAP Working Group 1998), as recently reviewed by Alderson (2003) and Gandini et al. (2004). A common practice is to derive the risk of extinction from the inbreeding increase predicted over a given period of time, knowing the effective population size N_e (Simon and Buchenauer 1993), and keeping in mind that additional inbreeding increase will depend on the intensity of the selection practised. This effective size based on the number of female and/or male breeding individuals is then an essential criterion, as it is also in natural populations (Nunney 2000). It should however be noted that, with overlapping genera-

tions and particularly in early reproducing species like the pig, the census numbers of breeding individuals tend to underestimate the actual rate of increase in inbreeding (Ollivier and James 2004). It should also be stressed that the population sizes given in Table 4 reflect the data provided by each country. In spite of the efforts made to co-ordinate the inventories across countries, the data do not in all cases reflect a comprehensive and updated view of the real situation. In addition, many factors of risk other than population size are known in farm animals, such as demography, breed organisation, and economic competitiveness, all quite difficult to quantify: see for example the evaluations of Reist-Marti et al. (2003) on cattle breeds of Africa.

In any case, ranking breeds for conservation purposes is a difficult task. First of all, there is a need to take into account both between- and within-breed variation (Petit et al. 1998; Barker 2001; Caballero and Toro 2002). Though weighting the respective between-breed and within-breed contributions by F_{ST} and $1-F_{ST}$, as done by Petit et al. (1998) and Caballero and Toro (2002), appears to be a natural way of combining the two components of diversity, different weights may be desirable in some contexts, as pointed out by several authors (Chaiwong and Kinghorn 1999; Piyasatian and Kinghorn 2003; Ollivier and Foulley 2004, Ollivier and Foulley, 2005). In the general context of animal breeding, the relative importance of within-breed and between-breed genetic variability depends on whether priority is given to genetic improvement by selection, efficient cross-breeding systems, or flexibility of production systems, each objective implying different weightings of the two components of diversity.

An example bearing on the French breeds is given in Table 5. Two ways of combining CB and CW were applied, yielding $D_1 = 0.23CB + 0.77CW$, based on the F_{ST} value of 0.23 for microsatellites estimated over the 70 breeds, and $D_2 = 0.83CB + 0.17CW$, which gave five times more weight to the between compared to the within diversity. Table 5 shows that, whilst the *Basque* breed deserves priority for conserving the between-breed diversity of the set considered, on the basis of CB or D_2 , a synthetic line such as *Tia Meslan* should be prioritized in order to maximise the genetic variability of a meta-population combining the existing breeds and lines, on the basis of D_1 . This is not surprising since this line

Table 5. Relative contributions of 16 French breeds/lines to between-breed and within-breed diversity based on microsatellites

BREED/LINE ^a	CB	CW	D_1	D_2
Local breeds				
FRCR01	4.23	1.45	2.09	3.75
FRBA01	14.86	-2.03	1.86	11.99
FRGA01	8.30	-0.50	1.52	6.80
FRLI01	11.73	-1.10	1.85	9.55
FRNO01	8.53	-0.43	1.63	7.00
International breeds				
FRLW01	1.79	0.53	0.82	1.58
FRLW12	<i>1.24</i>	0.67	0.80	<i>1.14</i>
FRLR01	3.76	0.57	1.31	3.22
FRPI02	3.57	0.22	0.99	3.00
Commercial lines				
FRDR01	4.98	0.52	1.54	4.22
FRLA01	6.96	-0.17	1.47	5.75
FRLR13	5.36	0.21	1.39	4.48
FRLW08	5.62	-0.39	0.99	4.60
FRLW09	2.80	-0.01	<i>0.64</i>	2.33
FRPI05	6.16	-0.55	1.00	5.02
FRTM01	10.13	1.01	3.11	8.58
TOTAL	100.00	0.00	23.00	83.00

^aBreed/line code: see Table 1.

CB: Contribution to between-breed diversity (%).

CW: Contribution to within-breed diversity (%).

Objective $D_1 = 0.23CB + 0.77CW$.

Objective $D_2 = 0.83CB + 0.17CW$.

(in bold highest contribution; in italic lowest contribution).

contains genes coming from two imported Chinese breeds. The example, however, interestingly shows that this line has probably maintained a good deal of its initial diversity since its creation 20 years ago. This is indeed reflected in the diversity observed for both markers.

Marker diversity, even though properly evaluated, needs to be completed by more detailed breed characterisation, as pointed out by several authors (Ruane 2000; Barker 2001; Alderson 2003). This implies setting a balance between genetic diversity and genetic merit, as the latter may be "perceived" (Chaiwong and Kinghorn 1999; Piyasatian and Kinghorn 2003), or, more generally, between distinctiveness and utility (Weitzman 1998). This also raises the important question of assessing the utility of neutral markers in the management of genetic diversity in farm animal species. The concordance between molecular diversity and quantitative trait diversity has been widely debated in the literature on natural popu-

lations (e.g. Lynch et al. 1999), an issue of equal importance in the management of livestock species diversity. Because of the hitch-hiking effects of selected genes on marker loci, marker and quantitative trait loci (QTL) diversities are expected to be correlated, as shown, for instance, by the simulations of Bataillon et al. (1996). A marker-based description of genetic diversity for a set of populations may then be considered as a useful guide for conservation policies in domestic animals (Barker et al. 1998; Barker 2002). Results obtained on natural populations also suggest that the levels of population subdivision for molecular markers are essentially equivalent to, or might even underestimate, the levels of population subdivision for quantitative traits (Lynch et al. 1999). The situation may be different within populations, since Pfrender et al. (2000) found that molecular and quantitative-genetic variations were essentially uncorrelated in 31 natural populations of *Daphnia*, due to the uncertain relationship between heterozygosity and heritability, particularly for quantitative traits with a non-additive genetic basis.

Microsatellite markers (SSR) are currently recommended as the marker of choice for measuring diversity, although AFLP have also been widely used in several species. In our study, the correlation between the individual breed CB of SSR and AFLP was lower than expected for markers supposed to be predominantly governed by genetic drift (correlation of 0.52, not shown). In a pure drift model, Reynolds distances have indeed the same expectation in bi-allelic (AFLP) and multi-allelic (SSR) systems. Overall between-breed diversity was considerably lower in AFLP (Table 3). This may be due to differential departure from the pure drift model (e.g. Barker et al. 2001), but a different genomic coverage cannot be excluded either (Plastow et al., In preparation).

Conclusions

This investigation complements and confirms earlier studies and demonstrates the feasibility of a large-scale evaluation of genetic diversity at the international level. More than half of the total European breed diversity of the pig – based on microsatellites – could be assigned to the local breeds, several of which are presently in danger of extinction. The data collected should provide guidance for

establishing conservation policies within European countries. Commercial opportunities can also be envisaged. For example, the approaches and tools developed in these studies may be used by breeders' associations and breeding companies to evaluate the internal diversity of their populations and for devising strategies of maintenance, development and improvement of their genetic resources. Other indirect benefits of our investigations are the European data repository, created and made publicly available for further research on pig diversity, and a duplicated DNA bank which will serve as a centre of biological resources for future evaluations of genetic diversity using new marker and gene technologies. In the future, genetic polymorphisms reflecting as much as possible functional diversity should continue to be investigated. More generally, the need for an operational framework in defining conservation policies should be emphasised. Based on the results of this study, we recommend to define marginal breed contributions to both within- and between-breed diversity, and to combine those contributions according to the objective of diversity pursued.

Acknowledgements

This work has received support from several programmes of the European Union (contracts BI02-CT94-3044, RESGEN-CT95-012 and BIO4-CT98-0188), which are gratefully acknowledged. Thanks are also due to the providers of the PiGMaP data not involved in PigBioDiv, namely Luc Peelman (Ghent, Belgium), Hermann Geldermann (Stuttgart, Germany), Merete Fredholm (Copenhagen, Denmark), and Leif Andersson (Uppsala, Sweden), and to Henner Simianer (Göttingen) for useful comments and suggestions. We also gratefully acknowledge the constructive comments provided by an anonymous referee.

Appendix

Genetic distances among 70 breeds (microsatellites) and 59 breeds (AFLP)

Microsatellites (50 loci): Multilocus Reynolds and Nei standard distances were obtained via the

GENDIST programme of the Phylip software (Felsenstein 2000).

AFLP (148 loci): Monolocus Reynolds distances from GENDIST were averaged over loci, assuming a zero distance for pairs of identically monomorphic populations; multilocus Nei standard distances were obtained directly from GENDIST.

<http://www.databases.roslin.ac.uk/pigbiodiv/>

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