FURTHER DEVELOPMENTS ON WEITZMAN'S APPROACH TO ASSESS CONSERVATION OF GENETIC DIVERSITY

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INTRODUCTION

The preservation of biodiversity, and, in particular, the conservation of genetic diversity in livestock has been lately an important focus of attention (Thaon d'Arnoldi *et al*., 1999 ; Eding and Meuwissen, 2001). Weitzman's diversity measure (Weitzman, 1992) provided a new way of studying the diversity of a set of breeds or species with a well defined diversity function based on pairwise distances –*e.g.*, genetic distances–. It gathers a number of nice, both intuitively and algebraically, properties (Weitzman, 1992 ; Thaon d'Arnoldi *et al*., 1999 ; Eding and Meuwissen, 2001), not verified by other common diversity measures (Weitzman, 1992). It has been applied, for example, in Thaon d'Arnoldi *et al*. (1999), Laval *et al*.(2000) or Cañon *et al*. (2001).

Weitzman (1993) suggested a methodology to study the evolution of diversity with time, allowing a criterium for decision making on the distribution of resources. It is based on probabilities of extinction for each breed and is suitable for any diversity measure. However, the non-availability of an objective definition for those probabilities of extinction has kept these ideas away from practical application. Another drawback of Weitzman's approach, as noted by some authors (Caballero and Toro, 2001 ; Eding and Meuwissen, 2001) is that only between-breeds information is taken into account, while the potential knowledge of within-breed data is ignored. We intend to eliminate these two disadvantages by calculating probabilitites of *genetic extinction*. We will study the behaviour of this approach and its appropriateness for assessing decision making in the conservation of genetic diversity with an example set of local French and Spanish cattle.

MATERIAL AND METHODS

Biologic material. A set of 8 local French and Spanish cattle breeds from European project Contract Fair1 CT 95-0702 –see Cañón *et al*. (2001) for details–, was selected to perform the analysis. A total of 50 animals per breed were genotyped for 10 microsatellite type marker loci, and their allelic frequencies were recorded.

Genetic diversity. Weitzman's diversity measure and partial contributions of each breed and node were computed. For breed *i*, partial contribution is $PC_i = \left(D(Q) - D(Q \setminus i)\right)/D(Q)$,where Q is the set of all breeds, $Q \backslash i$ the set of all breeds minus breed *i* and $D(\bullet)$ the diversity function. In an analogous way the contributions of each node can be calculated. The hierarchical tree resulting from the algorithm, together with the values of partial contributions, is depicted in

Figure 1. In contrast with Weitzman (1992) this is not a *maximum likelihood* tree, since there is no such likelihood to be maximised and there are some errors in Weitzman's formulae. However, it provides a natural representation of the grouping of the different breeds, as well as a graphical view of the importance of each one in terms of diversity. Reynolds genetic distance (Reynolds *et al*., 1983) was used for the analysis.
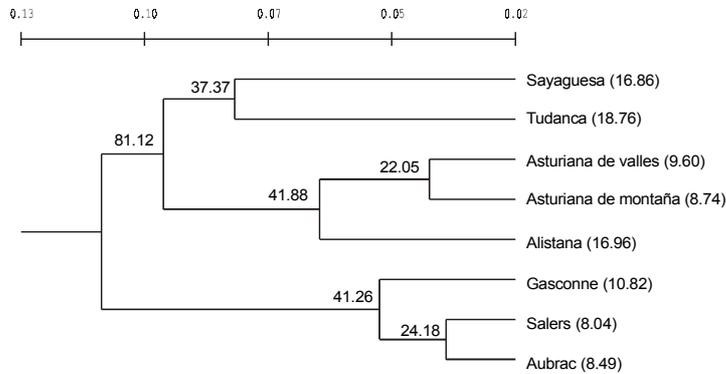

Figure 1. Hierarchical tree showing the grouping of the 8 breeds and the partial contribution of each breed and each node (in %)

Expected diversity, marginal diversity and conservation potential. If we can measure the diversity of a set of breeds Q and of any of its subsets, and we find a way of ascertaining the probability of any breed becoming extinct after a number t of generations, we can view the diversity at generation t, D_t, as a random variable taking values in the space of the subsets of Q, $\wp(Q)$, in such a way that for each $S \in Q$, $D_t(S)$ takes the value of the diversity of set S, with a probability $P_t(S)$ equal to the probability of all the breeds in S having survived after generation t and all the breeds in $Q \backslash S$ having become extinct by generation t. We can define then the *expected diversity at time t*, ED_t, as the expected value of D_t, this is, $ED_t := E[D_t] = \sum_{S \in \wp(Q)} P_t(S)D(S)$. This

definition is not the one used by Weitzman (Weitzman, 1993), since we discard the discount factor he includes and we do not accumulate the sum over the generations.

Now, if $P_t(i)$ is the probability of extinction of breed i at generation t, then $P_t(S)$ equals $P_t(S) = \prod_{i|P_i \in S} (1 - P_t(i)) \prod_{i|P_i \in Q \backslash S} P_t(i)$. Again, note that this differs slightly from Weitzman's formula, since he considers a one-time period probability and assumes that a species lifetime follows an exponential distribution with that probability as its defining parameter. The

marginal diversity of breed i is defined as $MD_t(i) := -\left.\dfrac{\partial ED_t}{\partial P_t(i)}\right|_{P_t(i)}$. The partial derivative must

be negative, so a minus sign is added to handle positive numbers. In addition, ED_t is a linear function of each $P_t(i)$, so the partial derivative is a constant for any value of $P_t(i)$. The

conservation potential, or *elasticity of diversity* is just the marginal diversity weighted by $P_t(i)$ divided by and the total value of the expected diversity, this is: $CP_t(i) := MD_t(i) \cdot \dfrac{P_t(i)}{ED_t}$.

To incorporate within-breed information and eliminate much of the subjectivness of real extinction probability we will calculate probabilities of *genetic extinction*. We will say that a species is *genetically extinct* when every locus along the genome is fixed in the same allele for all the individuals, this is, when all of them have exactly the same genotype, and it is homozygous in every locus. As it is not possible to have the complete information of the degree of fixation in every gene in the genome, we have computed the probability of fixation at generation *t* of each of the markers used before, performed the analysis with each one and averaged the results over the markers. To avoid too low probabilities, which would mask the results, we have extended the concept of "fixation" to the event of the allele frequency being higher than a certain threshold α. As an example, we have taken $\alpha=0.90$. For a particular locus, the probability of fixation –in strict or extended sense, for $\alpha>0.50$– equals the sum of the probabilities of each of its alleles being fixed. Applying theory of diffusion processes (Krow and Kimura, 1970), and assuming genetic drift is the only effect affecting the population, for a given allele A_i, the probability of its frequency being α or higer equals (García *et al*., 2002)

$$P\big(p_i(t) \geq \alpha\big) =$$

$$= p_0 + \sum_{i=1}^{\infty} (2i+1)p_0(1-p_0)F(i+2,1-i,2,p_0)\Big[(-1)^i + F(-i,i+1,1,\alpha) - F(-i,i+1,1)\Big]e^{\frac{-i(i+1)t}{4N}}$$

where $F(\cdot,\cdot,\cdot,\cdot)$ is the hypergeometric function.

RESULTS AND DISCUSSION
The results obtained with this method applied to the 8 breeds are shown in Table 1. As expected, probability of extinction increases with time. Marginal diversity differs very little from the partial contributions, and the orders of priorities deduced from both quantities are almost the same, with some exceptions, such as Salers or Aubrac. Conservation potential provides very different criteria, since information from its probability of extinction adds or substracts weight from the marginal diversity according to breed. Breeds like Alistana or Asturiana de valles are better positioned, while others, such as Sayaguesa are less prioritized. Conclusive assertions, however, must be made taking both marginal diversity and conservation potential into account. Optimum investment strategies could be found by deriving cost functions for reducing probabilities of extinction and solving the subsequent optimization problem.

Table 2. Mean probabilities of extinction, marginal diversities and conservation potentials through the 16 marker loci

Breed	25 Generations			35 Generations			50 Generations		
	$P_{25}(i)$	$MD_{25}(i)$	$CP_{25}(i)$	$P_{35}(i)$	$MD_{35}(i)$	$CP_{35}(i)$	$P_{50}(i)$	$MD_{50}(i)$	$CP_{50}(i)$
Salers	0.097	8.804	8.455	0.171	9.249	10.290	0.290	9.936	12.181
Aubr	0.109	9.508	10.192	0.185	10.078	12.041	0.306	10.861	13.937
Gasc	0.072	10.688	7.993	0.094	10.571	7.071	0.130	10.480	6.544
Alist	0.221	16.967	32.900	0.353	16.771	34.752	0.528	16.454	33.939
AstM	0.033	9.358	3.146	0.059	9.461	3.772	0.101	9.623	4.308
AstV	0.196	9.735	19.315	0.261	9.715	16.909	0.365	9.632	15.299
Sayag	0.055	18.454	11.769	0.064	18.065	9.374	0.086	17.457	8.104
Tuda	0.032	16.486	6.230	0.045	16.091	5.791	0.069	15.552	5.688

CONCLUSIONS

We have introduced an alternative concept for extinction probability into Weitzman's approach based on an objective way of measuring it and accounting for whithin-breed information. These preliminary results have showed that the behaviour of the method seems to be good, and that it could prove to be a helpful tool in programs for management of biological diversity.

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