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Maintenance of genetic diversity in subdivided populations using genomic coancestry matrices

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Abstract

For both undivided and subdivided populations, the consensus method to maintain genetic diversity is the Optimal Contribution (OC) method. For subdivided populations, this method determines the optimal contribution of each candidate to each subpopulation to maximize global genetic diversity (which implicitly optimizes migration between subpopulations) while balancing the relative levels of coancestry between and within subpopulations. Inbreeding can be controlled by increasing the weight given to within-subpopulation coancestry (λ). Here we extend the original OC method for subdivided populations that used pedigree-based coancestry matrices, to the use of more accurate genomic matrices. Global levels of genetic diversity, measured as expected heterozygosity and allelic diversity, their distributions within and between subpopulations, and the migration pattern between subpopulations, were evaluated via stochastic simulations. The temporal trajectory of allele frequencies was also investigated. The genomic matrices investigated were (i) the matrix based on deviations of the observed number of alleles shared by two individuals from the expected number under Hardy–Weinberg equilibrium; and (ii) a matrix based on a genomic relationship matrix. The matrix based on deviations led to higher global and within-subpopulation expected heterozygosities, lower inbreeding and similar allelic diversity than the second genomic and pedigree-based matrices when a relatively high weight was given to the within-subpopulation coancestries ($\lambda \geq 5$). Under this scenario, allele frequencies moved only slightly away from the initial frequencies. Therefore, the recommended strategy is to use the former matrix in the OC methodology giving a high weight to the within-subpopulation coancestry.

KEYWORDS
allele frequency changes, allelic diversity, expected heterozygosity, genomic coancestry, optimal contributions, subdivided populations

1 | INTRODUCTION

Most populations of endangered species are subdivided into disconnected breeding groups. In nature, the main causes of subdivision are the deterioration of habitats, with the consequent isolation of different subpopulations, and/or the creation of artificial barriers (e.g., roads, railways or fences). In ex situ conservation programmes of wild and domestic species, the fragmentation may be intentional for logistical reasons (e.g., limited space and facilities to keep the population in a single location or ease of managing small subpopulations) or because the subdivision has a clear biological reason, as different subpopulations may be characterized by local adaptations which should be preserved. Regardless, the subdivision has the advantage of reducing the risk of extinction of the global population due to different hazards (e.g., fires, predator attacks and infectious disease outbreaks), as such events could cause the extinction of a particular subpopulation while keeping safe the global population. In fact, one of the criteria of both the Food and Agriculture Organization (FAO) and the International Union for Conservation of Nature (IUCN) for considering a species or breed as critically endangered is that it is concentrated in a restricted area (FAO, 2013; IUCN Standards and Petitions Committee, 2022).

On the other hand, the fragmentation of a population constitutes a danger because it implies a reduced census (and, consequently, a reduced effective population size) in each subpopulation. This could lead to high levels of genetic drift within subpopulations with a consequent increase in inbreeding and loss of genetic diversity at the local level (Falconer & Mackay, 1996). This is despite the fact that, at the global population level, genetic drift could be low. Consequently, when a population has been subdivided, it is convenient to favour gene flow between the different subpopulations to reduce the increase in inbreeding and the risk of extinction.

For an undivided population, the consensus method to maintain genetic diversity is the Optimal Contribution (OC) method that, in the context of conservation programmes, determines the optimal number of offspring (contribution) that each breeding candidate should produce to maximize genetic diversity, measured as expected heterozygosity. This is achieved by minimizing the global coancestry between candidates (Fernández et al., 2003; Villanueva et al., 2004). Fernández et al. (2008) extended the OC method to optimally manage subdivided populations. Their method determines the optimal contribution of each candidate to every subpopulation in the next generation to maximize the global genetic diversity while balancing the relative levels of coancestry between and within subpopulations by including specific weights to each term. This implies that, when the within-subpopulation term is given a high weight, the levels of inbreeding within subpopulations can be better controlled (i.e., the inbreeding levels reached are lower). It must be highlighted that the process implicitly leads to the optimization of the migration pattern between subpopulations in order to achieve the intended distribution of diversity. Fernández et al. (2008) demonstrated, by computer simulations, that their method maintains higher levels of genetic diversity in the global population and equal or lower inbreeding in each subpopulation than the reference methodology of One Migrant Per Generation (OMPG). The OMPG method (Mills & Allendorf, 1996; Wang, 2004) is based on the island model derived by Wright (1931) and was the standard approach to manage subdivided populations in the past. The efficiency of the dynamic method of Fernández et al. (2008) has been demonstrated not only with simulated but also with real data (Ávila et al., 2011; Caballero et al., 2010) and has been implemented in the software METAPOP2 (López-Cortegano et al., 2019).

As originally proposed, the method of Fernández et al. (2008) used pedigree information to compute coancestries and optimize contributions. However, pedigree-based genetic relationships between individuals in wild populations and in many domestic populations are unknown, especially those between individuals belonging to different subpopulations. In such situations, relationships can be estimated using genetic marker information. In fact, for undivided populations it has been shown that, when the number of markers is large enough, the use of molecular-based (genomic) coancestries in the OC method leads to a more efficient maintenance of genetic diversity than the use of pedigree-based coancestries (de Cara et al., 2011, 2013; Gómez-Romano et al., 2013). The increase in the efficiency of management is due to the fact that genomic coefficients measure the actual proportion of loci that two particular individuals have in common (i.e., they give the realized relationships) while pedigree-based coefficients give only expectations of these proportions, which can differ from the exact proportions. The potential benefit of using genomic coancestries in the management of subdivided populations is worth investigating to determine if the comparison with pedigree-based management produces the same results as in the undivided population scenario.

Several authors (Frankham, 2008; Lacy, 2000; Meuwissen et al., 2020; Saura et al., 2008) argue that maximizing global genetic diversity, per se, may have negative consequences given that the population genetic composition is modified. For instance, in the context of an ex situ conservation programme, changing the genetic composition of the population can affect its survival once it is reintroduced to the wild. Management aimed at maximizing diversity may lead to increased frequencies of deleterious recessive alleles and may also disrupt positive interactions between loci which have occurred due to many generations of natural selection (Fernández & Caballero, 2001; Saura et al., 2008; Schoen et al., 1998). It is thus also worthwhile to investigate potential changes in the genetic composition (i.e., in allele frequencies) of the population when applying the OC methodology.

Several genomic coancestry matrices have been proposed (Villanueva et al., 2021) and recent studies with undivided populations have showed that their use in OC can have different consequences in terms of the genetic diversity maintained and the evolution of allele frequencies (Gómez-Romano et al., 2016; Meuwissen et al., 2020; Morales-González et al., 2021). In

particular, results of these previous studies indicate that the use of measures of coancestry based on alleles sharing (e.g., Nejati-Javaremi et al., 1997) in OC resulted in a higher genetic diversity (measured as expected heterozygosity) than the use of coancestry computed from realized relationship matrices commonly used in genetic evaluations in animal breeding (VanRaden, 2008). However, use of the latter maintained allele frequencies closer to those in the base population. Recently, Meuwissen et al. (2020) have shown that use of VanRaden's matrices manages drift and limits changes in allele frequency at the expense of a higher rate of increase in homozygosity. It is expected that use of the different genomic matrices would have also different consequences when managing subdivided populations, not only on the global levels of diversity and the fate of allelic frequencies, but also on the distribution of diversity across subpopulations.

The objective of this study was to evaluate, via stochastic simulations, the efficiency of using genomic coancestry matrices in the OC method for maintaining genetic diversity in subdivided populations. Global genetic diversity, its distribution within and between subpopulations and migration flow between subpopulations were evaluated. Also, the trajectory of allele frequencies under this management method was investigated. Results obtained when using genomic information were compared with those obtained using pedigree information.

2 | MATERIALS AND METHODS

All scenarios simulated involved the management of a subdivided population composed of five subpopulations, mimicking the structure of the captive breeding programme of the Iberian lynx (Kleinman-Ruiz et al., 2019). Management was carried out using the Fernández et al. (2008) development of OC for subdivided populations, directed to the maintenance of genetic diversity in the global population (measured as expected heterozygosity) while restricting the increase in inbreeding within subpopulations by giving different weights to the within-subpopulation coancestry term. Management was carried out for 10 discrete generations to evaluate the different scenarios in the short and long term. Matings were performed within subpopulations (i.e., offspring was always generated from couples belonging to the same subpopulation). Subsequently, offspring migrated to other subpopulations (if required) following the solutions arising from the optimization. Results from implementation of the method using different genomic coancestry matrices were compared with those using the pedigree-based coancestry matrix. The conservation programme started from a base population of 100 individuals, which was created in several steps. First, a population at mutation–drift equilibrium was generated. Second, the population was expanded to have enough individuals for sampling 100 replicates. Third, in some scenarios, extra random mating generations were performed to create subpopulations genetically differentiated before starting the management. The detailed steps taken in the simulations are given below. The simulations were carried out using in-house Fortran 90 codes.

2.1 | Generation of the base population

As stated above, creation of the base population was carried out in several steps. In a first step, a population of size $N = 100$ was simulated during 10,000 generations of random mating to create enough levels of linkage disequilibrium between markers used in the management and other loci in the genome where diversity also needs to be maintained (see below). Using a larger N would have generated unrealistic low levels of linkage disequilibrium. The genome was composed of 20 chromosomes of one Morgan each. Two types of biallelic loci (500,000 single nucleotide polymorphisms [SNPs] and 500,000 "unobserved loci" per chromosome) were simulated. Both types of loci were evenly distributed and interspersed (i.e., SNPs and unobserved loci alternated along a particular chromosome). SNPs and unobserved loci differed simply in their subsequent use. SNP loci were used for computing the genomic coancestry matrices involved in the management and the unobserved loci were used for calculating the different parameters evaluated (i.e., they were used for monitoring purposes). Thus, the effect of using different genomic coancestry matrices in OC can be evaluated on the whole genome and not only on the loci used in the management (i.e., the SNPs). At the beginning of the process, all loci were fixed. The mutation rate per locus and generation (μ) was 2.5×10^{-6} for all loci. When producing the gametes, the number of crossovers per chromosome was drawn from a Poisson distribution with mean equal to one. Crossovers were randomly distributed without interference. At the end of the process, the expected heterozygosity measured at both types of loci had stabilized, thus approaching a mutation–drift equilibrium.

In a second step, the population was expanded during four generations to create enough individuals to sample 100 different replicates with 100 individuals each. During this expansion, each individual was randomly mated to eight different individuals and each mating produced one offspring. Thus, the number of individuals was quadrupled each generation. At the end of this process, the population consisted of 25,600 individuals (half females and half males).

Each replicate was created by initially sampling 100 individuals (half of each sex) at random from the expanded population. Then two different population structures were simulated. These mainly reflected contrasting levels of differentiation between subpopulations in the base population ($t = 0$ thereafter) where management started (Figure 1):

1. Scenarios "Equal" (E). In these scenarios, all subpopulations were equally related, and all individuals had equal or very similar inbreeding coefficients at $t = 0$. This was a consequence of randomly distributing individuals among subpopulations directly from the expanded population. There was a total of five subpopulations comprising 10 males and 10 females each

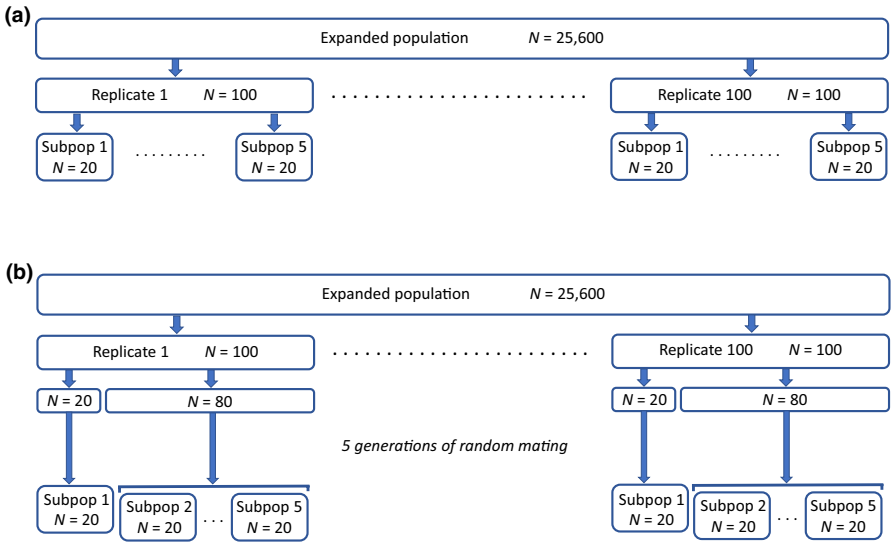

FIGURE 1 Diagram of the steps given to generate the base population in scenarios with different population structures: Equal (a, all subpopulations were equally related) and Unequal (b, subpopulation 1 was genetically differentiated and more inbred than the other four subpopulations).

(Figure 1a). At $t = 0$ pedigree-based inbreeding coefficients were zero. Pedigree-based coancestry coefficients between and within subpopulations were also zero except self-coancestries which had a value equal to 0.5 (consequently, the average coancestry within subpopulations was one divided by twice the number of individuals in the subpopulation, i.e., 1/40 in our simulations). At this generation, the genomic coefficients of coancestry between and within subpopulations and the genomic inbreeding coefficients within subpopulations were very similar across subpopulations. Only loci segregating in a particular replicate at $t = 0$ were used in the management (SNPs) and in calculation of the parameters evaluated (unobserved loci). The average number of SNPs and unobserved loci still segregating at $t = 0$ across replicates in the global population was 48,830 and 48,720, respectively. Expected heterozygosity for the global population computed with all loci (SNPs and unobserved loci) still segregating was 0.193.

2. Scenarios "Unequal" (U). In these scenarios, one of the subpopulations was generated to be genetically differentiated and more inbred than the other four at $t = 0$. To obtain this specific structure, the 100 individuals initially sampled from the expanded population were divided into two groups. One of the groups was composed of 10 males and 10 females and the other group was composed of the remaining individuals (40 males and 40 females). Then, five discrete generations of random mating were carried out within each group, keeping size and sex ratio constant (Figure 1b). Afterwards, the largest group was divided into four subpopulations of equal size (i.e., 10 males and 10 females each). These four subpopulations (subpopulations 2–5) together with the subpopulation isolated before (subpopulation 1) constituted the base population ($t = 0$) from which management started. Pedigree was recorded during the five random mating generations and, therefore, pedigree-based coancestries and inbreeding coefficients at $t = 0$ had nonzero values. Note that, in these scenarios, the pedigree-based and the genomic coancestries between an individual of subpopulation 1 and individuals from any of the other subpopulations were higher than the coancestries between individuals of subpopulations 2–5. This translates into a greater genetic differentiation between subpopulation 1 and the rest of the subpopulations. Similarly, inbreeding coefficients were higher in subpopulation 1 than in the rest. As before, only loci segregating in a particular replicate at $t = 0$ were used and, on average, they were 48,519 SNPs and 48,376 unobserved loci. Expected heterozygosity for the global population computed with all loci (SNPs and unobserved loci) still segregating was 0.188.

2.2 | Management method

In all scenarios, management was performed following the methodology proposed by Fernández et al. (2008). Briefly, the aim of the methodology is to determine the contributions (i.e., the number of offspring from each potential parent) that maximize the global amount of diversity (measured as expected heterozygosity) in the next generation. As we deal with subdivided populations, this diversity can be partitioned into within- and between-subpopulation diversity. Consequently, the objective function to be minimized also includes two terms: one related to the coancestry coefficient between subpopulations (B) and another term related to the coancestry coefficient within-subpopulations (W). Additionally, these terms can be weighted differentially by including a factor (λ). Specifically, the formulation would be $B + \lambda W$, where $B = \sum_{k=1}^{n} \sum_{l \neq k}^{n} \sum_{i=1}^{N} \sum_{j=1}^{N} f_{ij} c_{ik} c_{jl}$, $W = \sum_{k=1}^{n} \sum_{i=1}^{N} \sum_{j=1}^{N} f_{ij} c_{ik} c_{jk}$, λ is a weighting factor, n is the number of subpopulations, N is the number of individuals in the global population, f_{ij} is the coancestry coefficient between individuals i and j, and c_{ik} is the contribution of candidate i to subpopulation k (i.e., the number of offspring generated by that candidate to be raised in subpopulation k and, consequently, restricted to be a positive integer). Thus, this formulation reflects that, when dealing with a structured (subdivided) population, the contribution of a particular individual can be partitioned into its contribution to each subpopulation. Note that B is the term corresponding to the coancestry of candidates

TABLE 1 Scenarios simulated (marked with *) that varied in combinations of the initial population structure, the weight given to the within-subpopulation coancestry (λ), the coancestry matrix used in the optimization, and the frequencies used when computing the genomic coancestry matrices $\Theta_{L\&H}$ and Θ_{VR2}.

Population structure[b]	λ	Frequencies used[c]	Coancestry matrix[a]		
			Θ_{PED}	$\Theta_{L\&H}$	Θ_{VR2}
Equal	1	Global	*	*	*
	5	Global	*	*	*
	10	Global	*	*	*
Unequal	1	Global	*	*	*
	5	Global	*	*	*
	10	Global	*	*	*
	1	Subpopulations		*	*
	5	Subpopulations		*	*
	10	Subpopulations		*	*

[a]Θ_{PED}: pedigree-based matrix; $\Theta_{L\&H}$: Li and Horvitz genomic matrix; Θ_{VR2}: VanRaden genomic matrix.

[b]Equal: all subpopulations were equally related; Unequal: one of the subpopulations was genetically differentiated and more inbred than the other four.

[c]Global: using initial frequencies in the global population; Subpopulations: using the average initial frequencies of the subpopulations involved in the calculation of a particular coancestry coefficient.

generating offspring to be allocated to different subpopulations (and, thus, it is proportional to the diversity between subpopulations in the next generation), *W* is the term corresponding to the coancestry of candidates generating offspring to be reared in the same subpopulation (and, thus, it is proportional to the diversity within subpopulations) and λ is a factor balancing the relative importance of within-subpopulation coancestry and, consequently, the level of inbreeding for each subpopulation. In this study, the relative weight given to within-subpopulation coancestry (λ) took values of 1, 5 or 10. The higher the value of λ, the lower the expected levels of within-subpopulation coancestry and inbreeding.

The methodology also allows us to restrict the number of migrants by imposing the constraint $\sum_{k=1}^{N}\sum_{l\neq k}^{n} c_{ik} \leq 2\,nM$, where *M* is the maximum number of individuals allowed to move (on average) from one subpopulation to another subpopulation per generation. In all scenarios this value was restricted to 1, implying that the maximum total number of migrants allowed per generation was five. This is a rate acceptable for most conservation programmes when considering the logistic problems that the movement of individuals may have (Mills & Allendorf, 1996; Wang, 2004). Constraints to guarantee that the subpopulation sizes and the sex ratio were kept constant across generations were also applied. In addition, given that breeding was imposed to be performed within subpopulations, the sum of contributions (number of offspring) of females breeding in subpopulation *k* to subpopulation *l* was forced to be equal to the sum of contributions of males breeding in subpopulation *k* to subpopulation *l*. Optimization was performed using a simulated annealing algorithm that is described in detail in Fernández and Toro (1999). All restrictions were satisfied by penalizing solutions not fitting them during the search performed by the algorithm.

Management was implemented using three estimates of coancestry (*f*), including one estimate derived from the pedigree (f_P) and two estimates derived from genomic information (i.e., from the SNPs segregating at $t = 0$). The two genomic coancestry coefficients used were:

1 $f_{L\&H}$: the coancestry coefficient describing the excess of observed number of alleles shared by two individuals relative to the expected number under Hardy–Weinberg equilibrium (Li & Horvitz, 1953; Toro et al., 2002). Specifically, the coancestry coefficient between individuals *i* and *j* was computed as

$$f_{L\&H(i,j)} = \frac{\sum_{k=1}^{S} f_{OBS(i,j)k} - S + 2\sum_{k=1}^{S} p_k(1-p_k)}{2\sum_{k=1}^{S} p_k(1-p_k)},$$

where $f_{OBS(i,j)}$ is the proportion of alleles shared by both individuals, *S* is the number of SNPs and p_k is the frequency of the reference allele of SNP *k* at $t = 0$.

2 f_{VR2}: the coancestry coefficient computed from the genomic relationship matrix obtained using method two described in VanRaden (2008) and proposed by Amin et al. (2007). Specifically, the coancestry coefficient between individuals *i* and *j* was computed as

$$f_{VR2(i,j)} = \frac{1}{2S}\sum_{k=1}^{S} \frac{(x_{ki} - 2p_k)(x_{kj} - 2p_k)}{2p_k(1-p_k)},$$

where x_{ki} is the genotype of individual *i* for SNP *k*, coded as zero, one or two for genotypes *AA*, *AB* and *BB*, respectively, and p_k is the allele frequency as defined for $f_{L\&H}$.

These coefficients have been widely used in the literature, but under different names (see Table 1 of Villanueva et al., 2021). Here, we used the terminology given in Villanueva et al. (2021). Matrices constructed with coefficients f_{PED}, $f_{L\&H}$ and f_{VR2} will be referred to as Θ_{PED}, $\Theta_{L\&H}$ and Θ_{VR2}, respectively. Θ_{VR2} differs from $\Theta_{L\&H}$ in that with Θ_{VR2} rare alleles contribute more to the coancestry coefficient than common alleles (Gómez-Romano et al., 2016; Morales-González

et al., 2021). In fact, the correlation between VanRaden's and Li and Horvitz's coefficients increases when only SNPs with high minimum allele frequency (MAF) are used (Morales-González et al., 2020, 2021; Villanueva et al., 2021).

Coefficients $f_{L\&H}$ and f_{VR2} depend on allele frequencies at $t = 0$. In the case of a subdivided population, it is unclear which frequencies should be used as they could be those in the global population or the averages of frequencies of the two subpopulations to which two particular individuals belong. In scenarios E, allele frequencies were similar for all subpopulations and therefore only global frequencies were used to compute $f_{L\&H}$ and f_{VR2}. In scenarios U, both approaches (global or average subpopulation frequencies) were considered.

Summarizing, the scenarios simulated are combinations of four factors: (i) the population structure (E or U); (ii) the weight given to the within-subpopulation coancestry (λ); (iii) the coancestry matrix used in the optimization ($\boldsymbol{\Theta}_{PED}$, $\boldsymbol{\Theta}_{L\&H}$ or $\boldsymbol{\Theta}_{VR2}$); and (iv) the frequencies used when computing $\boldsymbol{\Theta}_{L\&H}$ and $\boldsymbol{\Theta}_{VR2}$. The different scenarios are summarized in Table 1.

2.3 | Parameters estimated

Management scenarios were compared in terms of the genetic diversity retained in the global population and its distribution between and within subpopulations. All parameters were computed using the unobserved loci. Genetic diversity in the global population (H_T) was measured as the expected heterozygosity. Genetic diversity within subpopulations (H_S) was measured as the average expected heterozygosity across subpopulations. Expected heterozygosity was computed for each generation as $1 - \sum_{k=1}^{L} \sum_{l=1}^{2} p_{kl}^2$, where L is the number of loci and p_{kl} is the frequency of allele l of locus k (calculated for the global population or for subpopulations). The genetic diversity between subpopulations was calculated as $D = H_T - H_S$. This parameter reflects the degree of differentiation (distance) between subpopulations and is equal to Nei's minimum genetic distance (e.g., Toro & Caballero, 2005; Toro et al., 2002).

Another measure of genetic diversity used was the number of segregating loci at a given generation t, both at the global level and within subpopulations. It is given as the percentage of loci that continued segregating at t relative to those segregating at $t = 0$. Note that the number of segregating loci is a measure of allelic diversity when biallelic loci are used.

The average molecular inbreeding was computed as the observed homozygosity (i.e., the proportion of homozygous loci), in the global population (F_T) and within a particular subpopulation i (F_{Si}).

The different scenarios were also compared in terms of the evolution across generations of the average frequency of the minor allele (measured at the global population level but also within subpopulations) and in terms of the migration pattern. Specifically, the migration pattern was focused on the number of migrants sent to and received by subpopulation 1 because, as stated above, this subpopulation was genetically differentiated (and more inbred) at $t = 0$ in scenarios U. Results presented for all parameters are averages across the 100 replicates.

3 | RESULTS

Increasing λ from one to five led to different results for expected heterozygosity, allelic diversity, levels of inbreeding and changes in the average allele frequency. However, increasing λ from five to 10 led to almost the same outcomes. For this reason, only the results for $\lambda = 1$ and $\lambda = 5$ are shown.

3.1 | Genetic diversity

When management was based on $\boldsymbol{\Theta}_{PED}$ or $\boldsymbol{\Theta}_{VR2}$, the expected heterozygosity both in the global population (H_T) and within subpopulations (H_S) decreased across generations in all scenarios (Table 2). The opposite trend was observed for the genetic distance between subpopulations (D), indicating that the subpopulations diverged over time. While H_T was insensitive to the value of λ, H_S was slightly lower (and D was slightly higher) for the lowest λ.

On the other hand, when the management was based on $\boldsymbol{\Theta}_{L\&H}$, H_T increased across generations, and consequently reached values higher than those achieved when the management was based on $\boldsymbol{\Theta}_{PED}$ or $\boldsymbol{\Theta}_{VR2}$ after a single generation of management. By contrast, H_S decreased across generations when using $\boldsymbol{\Theta}_{L\&H}$ in the optimization. For $\lambda = 1$, this decrease was greater than when using $\boldsymbol{\Theta}_{PED}$ or $\boldsymbol{\Theta}_{VR2}$. Thus, using $\boldsymbol{\Theta}_{L\&H}$ with $\lambda = 1$ led to higher differentiation among subpopulations (i.e., higher D) than using other coancestry matrices. However, for $\lambda = 5$, H_S decreased less when using $\boldsymbol{\Theta}_{L\&H}$ than when using $\boldsymbol{\Theta}_{PED}$ or $\boldsymbol{\Theta}_{VR2}$ and still kept higher levels of H_T. Therefore, it seems that the use of $\boldsymbol{\Theta}_{L\&H}$ with $\lambda = 5$ in OC could be the strategy to follow as it leads to higher levels of genetic diversity both in the global population and within subpopulations than the use of $\boldsymbol{\Theta}_{PED}$ or $\boldsymbol{\Theta}_{VR2}$. For $\lambda = 5$, D values were similar when using different coancestry matrices.

Table 3 shows the evolution of allelic diversity (measured as the percentage of unobserved loci segregating at a given generation) in the global population (L_T), within subpopulation 1 (L_{S1}), and averaged across subpopulations 2–5 ($L_{S2\text{-}5}$). L_T barely decreased in the global population throughout the management period regardless of the coancestry matrix and the value of λ used. For $\lambda = 1$, $L_{S2\text{-}5}$ decreased faster when using $\boldsymbol{\Theta}_{L\&H}$ than when using $\boldsymbol{\Theta}_{PED}$ or $\boldsymbol{\Theta}_{VR2}$ in OC. Differences in $L_{S2\text{-}5}$ across scenarios using different matrices almost disappeared for $\lambda = 5$. Given that all subpopulations were equally related initially in scenarios E, the percentage of loci that remained segregating at $t = 0$ and at subsequent generations in subpopulation 1 (L_{S1}) was the same as in the rest of the subpopulations ($L_{S2\text{-}5}$). However, in scenarios U, L_{S1} at $t = 0$ was lower than $L_{S2\text{-}5}$, as expected. Management over generations reduced the differences between L_{S1} and $L_{S2\text{-}5}$. This reduction was faster with $\lambda = 5$, and at $t = 10$ L_{S1} and $L_{S2\text{-}5}$ were very similar regardless of the matrix used.

TABLE 2 Average expected heterozygosity in the global population (H_T) and within (H_S) and between (D) subpopulations across generations (t) when contributions are optimized using pedigree-based (Θ_{PED}), Li and Horvitz ($\Theta_{L\&H}$) and VanRaden (Θ_{VR2}) coancestry matrices for two different weights given to the within-subpopulation coancestry (λ) and two different population structures. Matrices $\Theta_{L\&H}$ and Θ_{VR2} were computed using the initial allele frequencies in the global population.[a]

			Θ_{PED}			$\Theta_{L\&H}$			Θ_{VR2}		
Population structure	λ	t	H_T	H_S	D	H_T	H_S	D	H_T	H_S	D
Equal	1	0	0.192	0.189	0.004	0.192	0.189	0.004	0.192	0.189	0.004
		1	0.192	0.187	0.005	0.193	0.184	0.010	0.192	0.187	0.005
		5	0.190	0.180	0.010	0.195	0.174	0.021	0.190	0.179	0.011
		10	0.188	0.174	0.014	0.196	0.169	0.027	0.188	0.173	0.015
	5	0	0.192	0.189	0.004	0.192	0.189	0.004	0.192	0.189	0.004
		1	0.192	0.187	0.005	0.193	0.187	0.006	0.192	0.187	0.005
		5	0.190	0.180	0.010	0.194	0.183	0.010	0.190	0.181	0.009
		10	0.188	0.177	0.011	0.194	0.183	0.011	0.188	0.177	0.010
Unequal	1	0	0.188	0.180	0.008	0.188	0.180	0.008	0.188	0.180	0.008
		1	0.188	0.178	0.010	0.189	0.176	0.013	0.187	0.178	0.009
		5	0.186	0.173	0.013	0.190	0.167	0.024	0.186	0.172	0.013
		10	0.184	0.169	0.015	0.191	0.162	0.030	0.183	0.167	0.016
	5	0	0.188	0.180	0.008	0.188	0.180	0.008	0.188	0.180	0.008
		1	0.188	0.179	0.009	0.189	0.179	0.009	0.187	0.179	0.008
		5	0.186	0.176	0.010	0.189	0.178	0.011	0.185	0.176	0.010
		10	0.183	0.172	0.011	0.189	0.177	0.012	0.183	0.172	0.010

[a]Standard errors ranged from 6.58×10^{-5} to 4.87×10^{-4} for H_T and H_S.

Summarizing, allelic diversity in the global population remained almost at its initial levels in all scenarios. However, H_T was always higher when using $\Theta_{L\&H}$ than when using Θ_{PED} or Θ_{VR2}. The advantage of $\Theta_{L\&H}$ held for $\lambda = 5$ when considering genetic diversity within subpopulations, as a similar level of allelic diversity and more expected heterozygosity (H_S) was retained when using this matrix.

3.2 | Inbreeding

Table 4 shows inbreeding for the global population (F_T), subpopulation 1 (F_{S1}) and the average for subpopulations 2–5 ($F_{S2\text{-}5}$) across generations for the different scenarios. Note that F_T is simply the average inbreeding across subpopulations. As expected, strategies that led to higher/lower H_S (Table 2) led to lower/higher inbreeding (Table 4). Recall that, as matings were at random in each subpopulation, the expected ($1-H_S$) and observed (F_S) homozygosity must be similar.

Management using $\Theta_{L\&H}$ reduced the levels of inbreeding (F_T, F_{S1} and $F_{S2\text{-}5}$) in the first and second (not shown) generations for any value of λ and for both population structures, but for $\lambda = 1$, after the initial decrease there was a faster increase than when using Θ_{PED} and Θ_{VR2}. Consequently, at $t > 2$ global and subpopulation inbreeding levels were higher with $\Theta_{L\&H}$ than with Θ_{PED} or Θ_{VR2}. However, for $\lambda = 5$ the rate of increase in global and subpopulation inbreeding was faster with Θ_{PED} and Θ_{VR2} than with $\Theta_{L\&H}$ and, thus, management using the latter led to less inbreeding. As expected, inbreeding was very similar in all subpopulations under scenarios E and it was lower for $\lambda = 5$ than for $\lambda = 1$ (Table 4). In scenarios U, the difference in inbreeding between subpopulation 1 (initially more inbred) and the remaining subpopulations was effectively reduced by the management, and this reduction was faster for $\lambda = 5$.

3.3 | Change in allele frequencies

Under scenarios U, subpopulation 1 started management ($t = 0$) with an MAF lower than other subpopulations (Figure 2) due to the greater genetic drift that it suffered as it was isolated from the rest during the five previous generations. When using $\Theta_{L\&H}$, the average MAF in subpopulation 1 and in the global population always increased across generations. This is due to the greater efficiency of $\Theta_{L\&H}$ to maintain expected heterozygosity, which takes the highest value at intermediate frequencies. By contrast, when using Θ_{PED} and Θ_{VR2}, the average MAF decreased in the global population, but this decrease was less pronounced than the increase observed with $\Theta_{L\&H}$; that is, Θ_{PED} and Θ_{VR2} maintained frequencies closer to the initial values than $\Theta_{L\&H}$. The difference between MAF in the global population and in subpopulation 1 became smaller over time, especially with $\lambda = 5$ and when using Θ_{PED} or Θ_{VR2}.

3.4 | Migrants

In scenarios E, on average, each subpopulation sent one individual to (and received one individual from) another subpopulation across

TABLE 3 Average allelic diversity (measured as the percentage of loci segregating) in the global population (L_T), in subpopulation 1 (L_{S1}) and average percentage in subpopulations 2–5 ($L_{S2\text{-}5}$) across generations (t) when contributions are optimized using pedigree-based (Θ_{PED}), Li and Horvitz ($\Theta_{L\&H}$) and VanRaden (Θ_{VR2}) coancestry matrices for two different weights given to the within-subpopulation coancestry (λ) and two different population structures. L_{S1} and $L_{S2\text{-}5}$ values obtained with Θ_{PED} and L_T, L_{S1} and $L_{S2\text{-}5}$ values obtained with $\Theta_{L\&H}$ and Θ_{VR2} are those deviated from L_T obtained with Θ_{PED}. Matrices $\Theta_{L\&H}$ and Θ_{VR2} were computed using the initial allele frequencies in the global population.[a]

			Θ_{PED}			$\Theta_{L\&H}$			Θ_{VR2}		
Population structure	λ	t	L_T	L_{S1}	$L_{S2\text{-}5}$	L_T	L_{S1}	$L_{S2\text{-}5}$	L_T	L_{S1}	$L_{S2\text{-}5}$
Equal	1	0	100.0	−14.6	−14.7	+0.0	−14.6	−14.7	+0.0	−14.6	−14.7
		1	99.9	−19.2	−19.3	−0.2	−25.6	−25.8	+0.0	−19.3	−19.3
		5	99.6	−27.9	−27.9	−0.3	−37.3	−36.8	+0.0	−28.6	−28.5
		10	99.3	−32.0	−32.3	−0.4	−40.2	−40.4	+0.0	−34.0	−33.7
	5	0	100.0	−14.6	−14.7	+0.0	−14.6	−14.7	+0.0	−14.6	−14.7
		1	99.9	−19.2	−19.3	+0.0	−20.4	−20.6	+0.0	−19.2	−19.2
		5	99.6	−27.4	−27.4	−0.1	−28.8	−28.8	+0.0	−27.1	−27.2
		10	99.3	−31.2	−31.0	−0.1	−31.7	−31.5	+0.0	−30.8	−30.8
Unequal	1	0	100.0	−39.4	−23.2	+0.0	−39.4	−23.2	+0.0	−39.4	−23.2
		1	99.9	−38.8	−26.7	−0.1	−40.9	−30.8	+0.0	−37.9	−26.1
		5	99.7	−37.0	−32.3	−0.3	−42.4	−39.5	+0.0	−37.3	−32.7
		10	99.5	−37.4	−35.5	−0.3	−43.6	−42.6	−0.1	−38.6	−36.6
	5	0	100.0	−39.4	−23.2	+0.0	−39.4	−23.2	+0.0	−39.4	−23.2
		1	99.9	−36.1	−25.6	+0.0	−36.6	−26.6	+0.0	−36.2	−25.6
		5	99.7	−31.3	−31.6	−0.1	−33.6	−32.8	+0.0	−32.7	−31.6
		10	99.4	−34.1	−34.3	−0.1	−35.7	−35.2	+0.0	−34.5	−34.7

[a]Standard errors for the number of unobserved loci segregating were less than 1.47×10^{-2}.

generations (results not shown). For $\lambda = 1$, this was also the case in scenarios U when using $\Theta_{L\&H}$ or Θ_{VR2} computed from the global initial frequencies or Θ_{PED} (Figure 3a,c, dotted lines). However, for $\lambda = 5$ (Figure 3a,c, dashed lines), whatever the matrix used in OC, subpopulation 1 always sent three or four migrants to other subpopulations in the first generation and, as the generations went by, the number of migrants sent decreased (one migrant after four or five generations). Also, for $\lambda = 5$ the migrants received by subpopulation 1 from the rest was initially on average slightly above one and after a few generations (about five) stabilized around one. These outcomes are a reflection of the balance between maximizing genetic diversity and controlling within-subpopulation inbreeding implicit in the method. Note that subpopulation 1 was the most inbred but also was the most genetically differentiated (i.e., it harboured particular genetic information) and, thus, moving individuals from subpopulation 1 helped to reduce inbreeding in subpopulations 2–5. The differential migration rate toward subpopulation 1 led to similar expected heterozygosities (Table 2), the same percentage of loci segregating (Table 3) and similar levels of inbreeding (Table 4) in all subpopulations at $t = 10$.

3.5 | Effect of using different initial allele frequencies when computing $\Theta_{L\&H}$ and Θ_{VR2}

Using the initial allele frequencies of subpopulations to compute $\Theta_{L\&H}$ and Θ_{VR2} led to similar allelic diversity (data not shown) but, in general, to lower expected heterozygosity (H_T and H_S) and higher inbreeding (F_{S1} and $F_{S2\text{-}5}$) than using initial frequencies in the global population (Table 5). Genetic differences between subpopulations (D) increased when using local frequencies. The largest difference between using global and subpopulation frequencies was for Θ_{VR2}, particularly with $\lambda = 5$. It was interesting to note that management based on Θ_{VR2} computed using allele frequencies of subpopulations led to the same results for different values of λ (Table 5 and Figures 2 and 3b,d).

Figure 2 shows that management with Θ_{VR2} computed with subpopulation frequencies led to greater changes in MAF than when the matrix was computed using global frequencies (except in subpopulation 1 with $\lambda = 1$). At a global level, the use of $\Theta_{L\&H}$ was more insensitive to the frequencies used, although this was not the case for subpopulation 1. Specifically, the use of subpopulation frequencies made the MAF of subpopulation 1 rise less, which implies that the allele frequencies were kept closer to those in the base population than when using global frequencies (Figure 2a,c). Also, for the global population, frequencies were closer to the initial values with $\Theta_{L\&H}$ than with Θ_{VR2} when using subpopulation frequencies.

Migration flow changed greatly when the frequencies of subpopulations were used to estimate the genomic coancestry matrices (Figure 3). In scenarios using Θ_{VR2}, subpopulation 1 sent and received one migrant on average in all generations for any λ. However, in scenarios using $\Theta_{L\&H}$ and $\lambda = 1$, subpopulation 1 sent four or five

TABLE 4 Average molecular inbreeding in the global population (F_T), subpopulation 1 (F_{S1}) and subpopulations 2–5 ($F_{S2\text{-}5}$) across generations (t) when contributions are optimized using pedigree-based (Θ_{PED}), Li and Horvitz ($\Theta_{L\&H}$) and VanRaden (Θ_{VR2}) coancestry matrices for two different weights given to the within-subpopulation coancestry (λ) and two different population structures. Matrices $\Theta_{L\&H}$ and Θ_{VR2} were computed using the initial allele frequencies in the global population.[a]

			Θ_{PED}			$\Theta_{L\&H}$			Θ_{VR2}		
Population structure	λ	t	F_T	F_{S1}	$F_{S2\text{-}5}$	F_T	F_{S1}	$F_{S2\text{-}5}$	F_T	F_{S1}	$F_{S2\text{-}5}$
Equal	1	0	0.807	0.807	0.807	0.807	0.807	0.807	0.807	0.807	0.807
		1	0.807	0.807	0.807	0.804	0.805	0.804	0.807	0.807	0.807
		5	0.814	0.813	0.814	0.815	0.815	0.815	0.813	0.813	0.813
		10	0.819	0.819	0.819	0.822	0.822	0.822	0.819	0.820	0.819
	5	0	0.807	0.807	0.807	0.807	0.807	0.807	0.807	0.807	0.807
		1	0.807	0.807	0.807	0.805	0.805	0.805	0.807	0.807	0.807
		5	0.813	0.812	0.813	0.808	0.809	0.808	0.812	0.812	0.812
		10	0.816	0.816	0.817	0.809	0.809	0.809	0.815	0.815	0.815
Unequal	1	0	0.814	0.825	0.811	0.814	0.825	0.811	0.814	0.825	0.811
		1	0.815	0.826	0.812	0.812	0.824	0.810	0.815	0.827	0.812
		5	0.820	0.828	0.819	0.822	0.830	0.822	0.820	0.828	0.819
		10	0.825	0.829	0.824	0.829	0.833	0.829	0.825	0.830	0.824
	5	0	0.814	0.825	0.811	0.814	0.825	0.811	0.814	0.825	0.811
		1	0.814	0.825	0.811	0.813	0.823	0.810	0.815	0.825	0.812
		5	0.817	0.818	0.817	0.814	0.815	0.814	0.817	0.818	0.817
		10	0.821	0.821	0.821	0.815	0.815	0.815	0.821	0.820	0.821

[a]Standard errors ranged from 1.45×10^{-4} to 5.16×10^{-4}.

migrants per generation without receiving any contribution from other subpopulations for the whole period of management. For $\lambda = 5$, the initial large contribution of subpopulation 1 (i.e., five migrants sent to other subpopulations) gradually decreased with time, stabilizing at around two migrants. In parallel, a small number of individuals (average < 1) was received by subpopulation 1 in all generations in scenarios using $\Theta_{L\&H}$ and $\lambda = 5$.

4 | DISCUSSION

This study has compared the use of different coancestry matrices (pedigree-based and genomic matrices) in the management of a subdivided population through OC methodology in the framework of a conservation programme. Comparisons were made in terms of the genetic diversity maintained in the total population, in terms of its distribution between and within subpopulations, and in terms of the average global and within-subpopulation molecular inbreeding. Results showed that management based on matrices Θ_{PED} and Θ_{VR2} led to similar outcomes, and that the use of $\Theta_{L\&H}$ led to higher global genetic diversity than the use of Θ_{PED} and Θ_{VR2} for any weight given to subpopulation diversity (i.e., for any value of λ). Moreover, in scenarios where more weight was given to the within-subpopulation coancestry ($\lambda \geq 5$), the use of $\Theta_{L\&H}$ also led to higher local genetic diversity, lower inbreeding levels and similar allelic diversity. Using local allele frequencies to construct the genomic coancestry matrices instead of the global frequencies implied, in general, lower genetic diversity and higher inbreeding.

Results for the different parameters have been given for the unobserved loci which are not used in calculating coancestry and, thus, they are not directly under selection. However, unobserved loci are in linkage disequilibrium with the markers used in the management and this disequilibrium drives changes in the same direction in both types of loci (De Cara et al., 2011; Gómez-Romano et al., 2013; Morales-González et al., 2021; Toro et al., 2020; Woolliams & Meuwissen, 2022).

In population genetics and conservation biology studies using neutral molecular markers, genetic diversity is usually measured as expected heterozygosity (Nei, 1973) or as allelic diversity, that is the mean number of alleles per marker (Allendorf et al., 2013; Toro et al., 2009), which is equivalent to the percentage of segregating loci for biallelic markers. Most conservation studies dealing with managing and monitoring genetic diversity have focused on heterozygosity because high levels of heterozygosity also imply high levels of additive genetic variance and, thus, strong potential responses to selection (Falconer & Mackay, 1996). In addition, heterozygosity is inversely related to inbreeding and inbreeding depression. Consequently, the OC methodology has been directed to maximization of the expected heterozygosity by using coancestries between candidates. However, allelic diversity is also a very relevant parameter in conservation genetics (Luikart et al., 1998; Nei et al., 1975; Vilas et al., 2015). Thus, both expected heterozygosity and allelic diversity should be

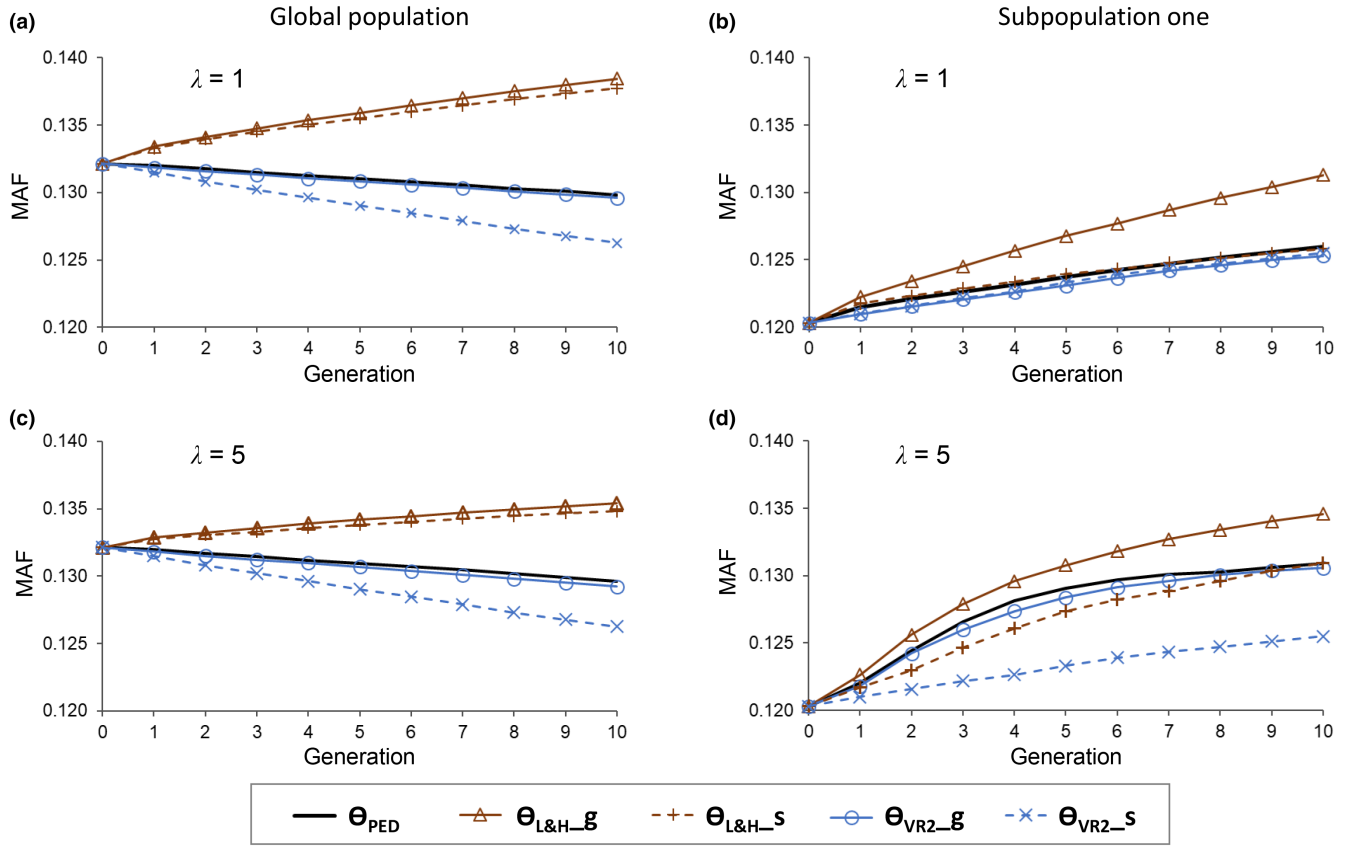

FIGURE 2 Average frequency of the minor allele (MAF) in the global population (left panels) and in subpopulation 1 (right panels) across generations when contributions are optimized using pedigree-based (Θ_{PED}), Li and Horvitz ($\Theta_{L\&H}$) and VanRaden (Θ_{VR2}) coancestry matrices and two different weights are given to the within-subpopulation coancestry ($\lambda = 1$ and $\lambda = 5$), for scenarios with Unequal population structure. Matrices $\Theta_{L\&H}$ and Θ_{VR2} were computed using global (subscript "_g") or subpopulation initial allele frequencies (subscript "_s").

evaluated and accounted for in the management of populations. In addition, it can be argued that in a conservation programme genetic variability should be preserved as closely as possible to that of the original population. Thus, management leading to changes in allele frequencies could be undesirable, especially in ex situ conservation programmes (e.g., Saura et al., 2008; Toro et al., 2020).

Different genomic coancestry matrices have been described in the literature (e.g., Villanueva et al., 2021) including those used here ($\Theta_{L\&H}$ and Θ_{VR2}). One of the simplest genomic matrices is that of Nejati-Javaremi et al. (1997) where the coancestry between two individuals is computed as the proportion of alleles shared by both individuals. This matrix (also called IBS matrix or similarity matrix) has been used in previous studies applying the OC method for managing genetic conservation programmes (de Cara et al., 2011, 2013; Eynard et al., 2016; Gómez-Romano et al., 2013). Also, the software METAPOP2 (López-Cortegano et al., 2019) implements such a matrix calculated from multi-allelic markers for the management of subdivided populations. Although this matrix has not been considered here, it has a correlation of one with $\Theta_{L\&H}$ (Villanueva et al., 2021) and therefore the same results are expected from the use of both coancestry matrices.

In the context of subdivided populations, our study has shown that the use of $\Theta_{L\&H}$ in OC was able to maintain higher expected heterozygosity than and similar allelic diversity to Θ_{VR2}. For undivided populations and using a reduced number of multi-allelic markers in the management, Fernández et al. (2004) also found that OC was able to give higher expected heterozygosity than and the same allelic diversity as a method specifically aimed at maximizing the latter. However, the use of matrices constructed from a large number of biallelic markers (SNPs) in OC can lead to different outcomes, as shown by Meuwissen et al. (2020) and Morales-González et al. (2021). These studies compared the use of genomic $\Theta_{L\&H}$ (a matrix with a correlation of one with the matrix used by Fernández et al., 2004) and Θ_{VR2} in OC and showed that $\Theta_{L\&H}$ led to higher levels of expected heterozygosity but to lower levels of allelic diversity than Θ_{VR2}. Morales-González et al. (2021) argued that, when the average H_E is maximized, the low allelic diversity found may be a consequence of the fact that rare alleles have little effect on H_E: that is, many loci can be fixed without a reduction in H_E, provided the remaining loci increase their MAF to get closer to intermediate values.

To understand the performance of OC in subdivided populations when using different matrices, we need to consider the fact that in this case global diversity is partitioned into within- (H_S) and between-subpopulation (D) diversity. From an exclusively theoretical point of view, the subdivision of populations can be beneficial for preserving global genetic diversity (Falconer & Mackay, 1996) as, in the long

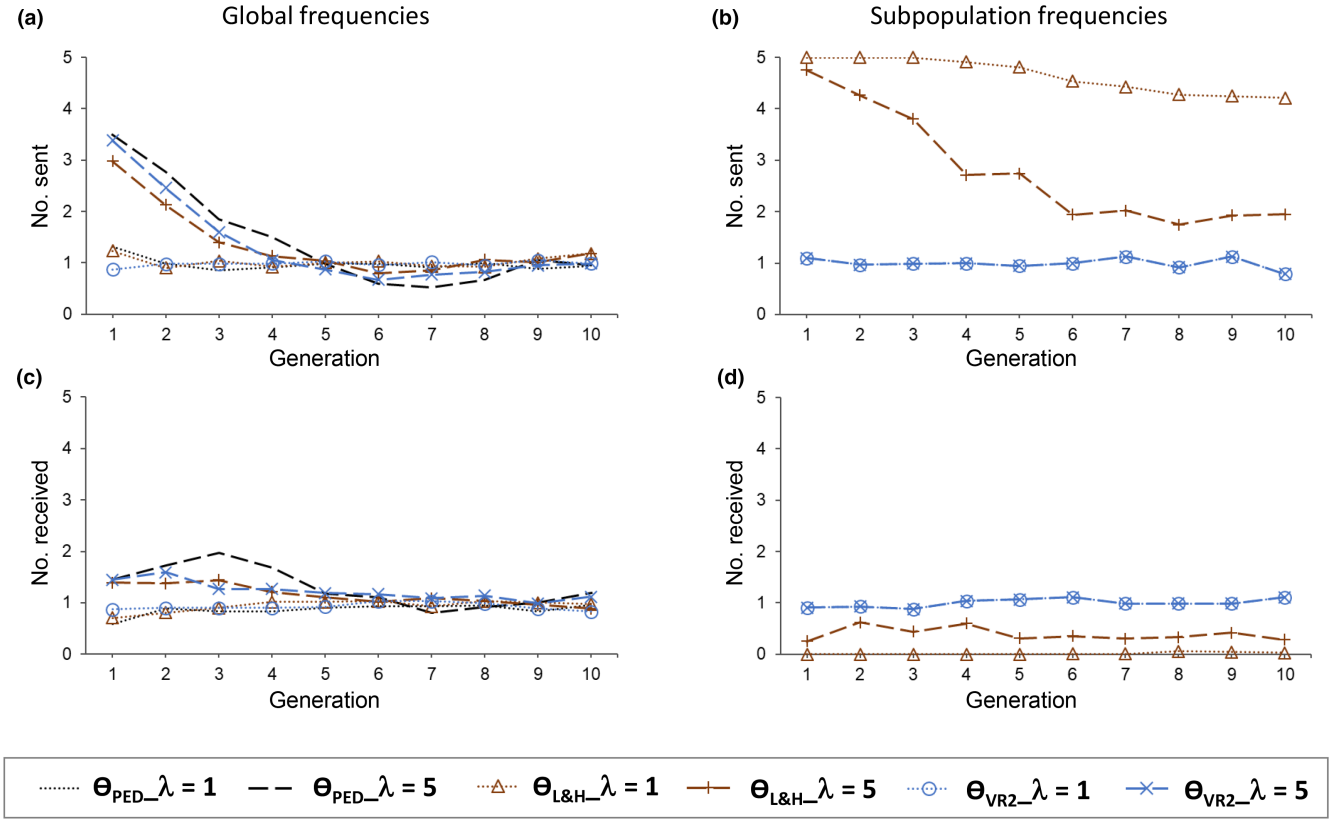

FIGURE 3 Number of individuals sent to and received by subpopulation 1 across generations when contributions are optimized using pedigree-based (Θ_{PED}), Li and Horvitz ($\Theta_{L\&H}$) and VanRaden (Θ_{VR2}) coancestry matrices and two different weights are given to the within-subpopulation coancestry ($\lambda = 1$ and $\lambda = 5$), for scenarios with Unequal population structure. Matrices $\Theta_{L\&H}$ and Θ_{VR2} were computed using global (left panels) or subpopulation initial allele frequencies (right panels).

term, the highest diversity is achieved by maintaining many isolated lines hoping that, by drift, different alleles will be fixed in each of them. This is what happened when using $\Theta_{L\&H}$ and $\lambda = 1$ (i.e., no special weight was given to within-subpopulation diversity) that led to a higher differentiation between subpopulations (higher D) and also the highest global expected heterozygosity. However, allelic diversity was lower than when using Θ_{VR2}. The same results (higher expected heterozygosity and lower allelic diversity with $\Theta_{L\&H}$) were observed for undivided populations in studies comparing these two matrices (Meuwissen et al., 2020; Morales-González et al., 2021). However, when λ was increased to 5, $\Theta_{L\&H}$ was able not only to give the highest heterozygosity but also to give levels of allelic diversity similar to those obtained with Θ_{VR2}. At the global population level, maintenance of the proportion of segregating loci is a reflection of the increased differentiation between subpopulations through the management that makes the fixation of the same allele in all subpopulations unlikely (i.e., for a particular locus, both alleles are likely to be kept in the global population).

Although theoretically subdivision may lead to the maintenance of higher levels of genetic diversity, a high degree of isolation implies higher levels of inbreeding in each subpopulation. The effect of inbreeding depression on fitness will result in an increased risk of extinction of a particular subpopulation, with a net loss of genetic diversity (Charlesworth & Willis, 2009). This problem can be tackled by using an increased weight on the maintenance of within-subpopulation diversity that, consequently, would reduce inbreeding. In doing so, here we have shown that it is possible to keep higher levels of both global and within-subpopulation diversity and lower levels of inbreeding by imposing $\lambda = 5$ when using $\Theta_{L\&H}$. Therefore, it seems that this strategy should be chosen when managing subdivided populations.

In some situations, keeping some degree of differentiation between subpopulations could be advantageous if the interest is to maintain their particular genetic singularity arising from, for example, local adaptations of each subpopulation. In this case, an explicit restriction on the minimum levels of D, F_{ST} (Wright's fixation index) or any other measure of genetic differentiation could be imposed in the optimization either at the global level or at the subpopulations level, as suggested by Fernández et al. (2008). In fact, F_{ST} is related to coancestry through the expression $F_{ST} = (\%f - f)/(1 - f)$, where $\widetilde{f}$ is the mean coancestry within subpopulations and f is the global coancestry (e.g., Caballero & Toro, 2002). Consequently, the restriction on a specific value for the differentiation between subpopulations could be perfectly integrated in the general framework of the OC methodology for subdivided populations.

Besides the main objective of preserving genetic diversity and avoiding inbreeding in conservation programmes, it may also be desirable that certain characteristics previously selected naturally or

TABLE 5 Average expected heterozygosity in the global population (H_T) and within (H_S) and between (D) subpopulations, and average inbreeding in subpopulation 1 (F_{S1}) and in subpopulations 2–5 ($F_{S2\text{-}5}$) across generations (t) when contributions are optimized using pedigree-based (Θ_{PED}), Li and Horvitz ($\Theta_{L\&H}$) and VanRaden (Θ_{VR2}) coancestry matrices for two different weights given to the within-subpopulation coancestry (λ) for scenarios with Unequal population structure. Matrices $\Theta_{L\&H}$ and Θ_{VR2} were computed using initial average subpopulation allele frequencies. Values in parentheses are those that deviated from results obtained when matrices $\Theta_{L\&H}$ and Θ_{VR2} were computed using the initial allele frequencies in the global population (Tables 2 and 4), as a percentage.[a]

		$\Theta_{L\&H}$					Θ_{VR2}				
λ	t	H_T	H_S	D	F_{S1}	$F_{S2\text{-}5}$	H_T	H_S	D	F_{S1}	$F_{S2\text{-}5}$
1	0	0.188 (+0.0)	0.180 (+0.0)	0.008 (+0.0)	0.825 (+0.0)	0.811 (+0.0)	0.188 (+0.0)	0.180 (+0.0)	0.008 (+0.0)	0.825 (+0.0)	0.811 (+0.0)
	1	0.189 (+0.0)	0.176 (+0.0)	0.013 (+0.0)	0.825 (+0.1)	0.809 (−0.1)	0.187 (+0.0)	0.175 (−1.7)	0.012 (+33.3)	0.828 (+0.1)	0.813 (+0.1)
	5	0.190 (+0.0)	0.162 (−3.0)	0.027 (+12.5)	0.840 (+1.2)	0.825 (+0.4)	0.182 (−2.2)	0.160 (−7.0)	0.022 (+69.2)	0.836 (+1.0)	0.829 (+1.2)
	10	0.191 (+0.0)	0.148 (−8.6)	0.042 (+40.0)	0.854 (+2.5)	0.841 (+1.4)	0.177 (−3.3)	0.150 (−10.2)	0.027 (+68.8)	0.844 (+1.7)	0.840 (+1.9)
5	0	0.188 (+0.0)	0.180 (+0.0)	0.008 (+0.0)	0.825 (+0.0)	0.811 (+0.0)	0.188 (+0.0)	0.180 (+0.0)	0.008 (+0.0)	0.825 (+0.0)	0.811 (+0.0)
	1	0.188 (−0.5)	0.179 (+0.0)	0.009 (+0.0)	0.826 (+0.4)	0.810 (+0.0)	0.187 (+0.0)	0.175 (−2.2)	0.012 (+50.0)	0.828 (+0.4)	0.813 (+0.1)
	5	0.188 (−0.5)	0.177 (−0.6)	0.011 (+0.0)	0.821 (+0.7)	0.814 (+0.0)	0.182 (−1.6)	0.160 (−9.1)	0.022 (+120.0)	0.836 (+2.2)	0.829 (+1.5)
	10	0.188 (−0.5)	0.176 (−0.6)	0.012 (+0.0)	0.825 (+1.2)	0.815 (+0.0)	0.177 (−3.3)	0.150 (−12.8)	0.027 (+170.0)	0.844 (+2.9)	0.840 (+2.3)

[a]Standard errors ranged from 1.00×10^{-4} to 6.69×10^{-4} for H_T and H_S and from 1.00×10^{-4} to 1.41×10^{-4} for F_{S1} and $F_{S2\text{-}5}$.

artificially are maintained under relaxed selection during the management period. Some authors have therefore proposed to focus on maintaining allele frequencies as close as possible to those of the original population (e.g., Saura et al., 2008). The matrices used here for management (Θ_{PED}, $\Theta_{L\&H}$ and Θ_{VR2}) influence the trajectory of the allele frequencies in undivided populations, as shown by Meuwissen et al. (2020) and Morales-González et al. (2021). In particular, they observed that matrices Θ_{PED} or Θ_{VR2} led to smaller frequency changes than $\Theta_{L\&H}$, so it can be argued that $\Theta_{L\&H}$ is not suitable for conservation that aims to maintain the original allele frequencies. In this study, we observed the same pattern for subdivided populations when genomic matrices were computed using global allele frequencies and no extra weight was applied to the within-subpopulation coancestry.

The genomic matrices used here (i.e., $\Theta_{L\&H}$ and Θ_{VR2}) depend on the allele frequencies in the base population. When the main objective of the conservation programme is to maintain the global diversity of the population, it may be sensible to use the allele frequencies of the entire population to compute these matrices. However, when the main objective is to maintain the singularity of each subpopulation (i.e., when subdivision makes biological sense due to different adaptations or genetic characteristics), using the initial local frequencies could be a better approach. Management based on $\Theta_{L\&H}$ always results in allele frequency changes toward 0.5, and then using subpopulation or global frequencies led to very similar global heterozygosity for any value of λ. Also, very similar within- and between-subpopulation heterozygosities and inbreeding were obtained for $\lambda = 5$ (Table 5). However, with $\lambda = 1$, a higher genetic distance between subpopulations and a higher inbreeding were observed when using subpopulation frequencies, especially in the last generations where migration was reduced (Figure 3). This also happened in all scenarios with management based on Θ_{VR2} (higher differentiation and inbreeding when using subpopulation frequencies). Management based on Θ_{VR2} tends to reduce genetic drift and thus to maintain allele frequencies close to those at $t = 0$ (Meuwissen et al., 2020; Morales-González et al., 2021). Because each subpopulation had different initial allele frequencies, management using subpopulation frequencies would tend to reduce the flow between subpopulations. Consequently, differentiation among subpopulations and within-subpopulation inbreeding are higher than when using global frequencies, for any value of λ. Thus, the initial expectation of a better control of allelic frequency deviation by using local (subpopulation) frequencies in the computation of Θ_{VR2} was not observed in our results. Moreover, the other parameters tested (inbreeding, H_E and segregating loci) were also worse than when using the global initial frequencies. This is due to the fact that rare alleles within each subpopulation are more likely to be lost when using subpopulation frequencies due to a decreased effective population size and increased genetic drift. In fact, with Θ_{VR2}, the average MAF decreased substantially more when using subpopulation frequencies and current frequencies moved away from the original frequencies even more than with $\Theta_{L\&H}$ (Figure 2).

As indicated above, when a population has been subdivided, it is convenient to favour gene flow between the different subpopulations to reduce the increase in inbreeding in each of them, as has been claimed previously (Falconer & Mackay, 1996; Frankham et al., 2002). In scenarios with no extra weight on subpopulation diversity (i.e., $\lambda = 1$), the mixture between subpopulations was carried out in a uniform way; that is, the same number of migrants on average were sent to and received (in this case one) by any subpopulation. This was true irrespective of the coancestry matrix used and even for U scenarios, where subpopulation 1 was more inbred and more differentiated than the rest. In the latter scenarios and for $\lambda = 1$, it seems that there was an equilibrium between the need to reduce the high inbreeding of subpopulation 1 and the need to promote the maintenance of the specific genetic diversity that it harboured. However, with $\lambda \geq 5$, reducing the high inbreeding of subpopulation 1 became the priority and, thus, the number of migrants directed to this subpopulation was initially higher. The pattern of migrant flow was equal for any of the three coancestry matrices used in the OC management when global initial frequencies were used to compute $\boldsymbol{\Theta}_{\mathbf{L\&H}}$ and $\boldsymbol{\Theta}_{\mathbf{VR2}}$. If subpopulation 1 were genetically different from the rest of the subpopulations but not so inbred, the pattern of migration would probably change with an initial tendency of moving individuals preferably from subpopulation 1 to the other subpopulations.

In this study we imposed a restriction on the maximum number of migrants allowed per generation (one migrant per subpopulation). Allowing a higher number of migrants would probably lead to lower inbreeding and to homogenization of the genetic composition of all subpopulations in fewer generations. However, this may not be a realistic scenario due to the cost and risk of moving animals between subpopulations in some scenarios. First, for many species it is an expensive procedure that also implies administrative burden. Moreover, the transportation of animals can cause them stress that can induce maladaptation to the new site and even an increased probability of dying along the way. Regardless, Wang (2004) has shown that relatively small migratory flows (of the order of one migrant per generation and subpopulation; i.e., the OMPG method) are sufficient to maintain levels of inbreeding at acceptable levels. Thus, in this study we limited to five (the number of subpopulations) the number of migrants per generation to make the present results comparable with OMPG as the classical management method applied before the development of OC. Fernández et al. (2008) showed that OC performs better than the OMPG method when relying on pedigree data, as higher levels of diversity were retained and lower levels of inbreeding were generated. Although the OMPG method has not been considered in the present study, we consider that molecular implementation of OC in subdivided populations performs better than OMPG given that the use of marker-based management has led to better results than pedigree-based management in our simulations, and the latter outperform OMPG (Fernández et al., 2008) as stated before. Nevertheless, the OC methodology is flexible and the number of migrants can be increased to the level that could be reasonable for each particular species and conservation programme. Moreover, in the original derivation of the OMPG method, some degree of differentiation between subpopulations was intended to be maintained. If this is the case, the OC methodology could be easily modified to impose a restriction on the minimum value of differentiation (measured as genetic distance or F_{ST}), as the objective function to be optimized implicitly includes calculation of the genetic diversity between populations.

The most likely implementation of the OC method used here is in the management of ex situ conservation programmes that comprise different centres with captive animals. The chosen scenario in this study roughly mimics the real structure of "The Iberian Lynx Ex situ Conservation Program" (https://www.lynxexsitu.es/programa-en.php). This programme involves five centres of similar capacity where the managers aim at having the same numbers of males and females at the different centres. Movements of animals between centres is limited for logistical reasons to levels comparable to those imposed in our simulations (i.e., one migrant per generation). Currently, the management (i.e., contributing parents, mating pattern and translocation of animals between centres) is designed following the principles stablished in this study but relying on pedigree information (Kleinman-Ruiz et al., 2019). Genomic resources have been recently developed for this species (Abascal et al., 2016; Kleinman-Ruiz et al., 2017) and the plan is to implement these resources not only in the ex situ programme but also in the in situ programme. Beyond improving the management of captive animals from the use of genomic information as shown in this study (e.g., increased H_E and allelic diversity and decreased inbreeding), routine genotyping of captive and wild animals will improve the coordination between ex situ and in situ programmes and will allow more accurate management. With routine genotyping, information from an increased number of animals will be able to be included in the management, since it will be possible to estimate the relationships between wild and captive animals. This would allow more precise control of movements of individuals between wild populations (i.e., translocations) to reorganize the diversity and avoid the increase in inbreeding in particular areas. Genomic information would also help to drive decisions on breeding in captive populations (i.e., which animals to breed), accounting for the genetic information which is already present (or lacking) in wild populations in order to release the more adequate individuals. This scenario also applies to many other species. Therefore, the methodology used in this study could have a positive impact in these programmes.

As a general conclusion, our results show that using matrix $\boldsymbol{\Theta}_{\mathbf{L\&H}}$ could be the best option for managing subdivided populations as it leads to higher global diversity and lower inbreeding. Moreover, global allele frequencies should be used to compute the genomic coancestry matrices since higher levels of diversity and lower inbreeding are obtained than when using subpopulation frequencies.

AUTHOR CONTRIBUTION

EM-G: software development, formal analysis, investigation, writing—original draft; BV: supervision, project administration,

funding acquisition, writing—review & editing; MAT: investigation, writing—review & editing; JF: study design, software development, supervision, project administration, funding acquisition, writing—review & editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interests.

DATA AVAILABILITY STATEMENT

The program and the input of parameters necessary to use it are available on GitHub (https://github.com/EliMorGon/Metapopulation).

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