Research Article

Optimization procedures for establishing reserve networks for biodiversity conservation taking into account population genetic structure

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Abstract

Conservation genetics has been focused on the ecological and evolutionary persistence of targets (species or other intraspecific units), especially when dealing with narrow-ranged species, and no generalized solution regarding the problem of where to concentrate conservation efforts for multiple genetic targets has yet been achieved. Broadly distributed and abundant species allow the identification of evolutionary significant units, management units, phylogeographical units or other spatial patterns in genetic variability, including those generated by effects of habitat fragmentation caused by human activities. However, these genetic units are rarely considered as priority conservation targets in regional conservation planning procedures. In this paper, we discuss a theoretical framework in which target persistence and genetic representation of targets defined using multiple genetic criteria can be explicitly incorporated into the broad-scale reserve network models used to optimize biodiversity conservation based on multiple species data. When genetic variation can be considered discrete in geographical space, the solution is straightforward, and each spatial unit must be considered as a distinct target. But methods for dealing with continuous genetic variation in space are not trivial and optimization procedures must still be developed. We present a simple heuristic and sequential algorithm to deal with this problem by combining multiple networks of local populations of multiple species in which minimum separation distance between conserved populations is a function of spatial autocorrelation patterns of genetic variability within each species.

Key words: biodiversity conservation, population structure, geographic genetics.

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Introduction

One of the fundamental challenges in conservation biology involves the development of theoretical principles and methods for the design of nature reserves (Williams *et al.*, 2004). This is very important because the establishment of reserves is the main strategy adopted by governments to preserve biodiversity, despite many criticisms and potential conflicts with other human activities (Margules and Pressey, 2000; Aaron *et al.*, 2001; Balmford *et al.*, 2001).

The most important criterion to define the reserve system should be to achieve maximum representation of biodiversity but, unfortunately, political and economic interests are usually more important than scientific criteria

(Margules and Pressey, 2000). However, since the early 1980's quantitative methods to establish reserve networks that preserves maximum biodiversity at the smallest possible cost have been available (Church *et al.*, 1996; Pressey *et al.*, 1997; Margules and Pressey, 2000; Cabeza and Moilanen, 2001; Williams *et al.*, 2004). In most practical applications, conservation targets are defined as the occurrence of species or, when distributional data are not available, as vegetation types obtained by remote sensing techniques. As recently discussed by Brooks *et al.* (2004), there is considerable discussion on how hierarchical level biodiversity should be factored into such reserve network models, although there seems to be a consensus that biodiversity patterns are surrogates for population processes and so, when possible, both ecological (abundance, growth rates, demographic stochasticity) and genetic (estimates of inbreeding, gene flow and fitness) data should be incorporate into mod-

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eling to ensure the viability of conservation targets (Pressey, 2004).

Despite these theoretical discussions, it is difficult to add complex patterns of biodiversity at multiple hierarchical levels to quantitative models for conservation planning. Under the risk of introducing a false dichotomy, we believe that conservation genetics has been focused on two slightly different, but not mutually exclusive, approaches (for general definitions see Frankham *et al.,* 2002). On the one hand, rare, endemic or endangered species with narrow current geographic ranges have usually been studied to assess population viability, principally by measuring endogamy and trying to link this estimate with other demographic characteristics such as fecundity and mortality and, consequently, to help minimizing their extinction risks. Due to their narrow ranges and conservation status, such species are usually considered priority conservation targets and will be certainly represented in optimally defined reserve designs. On the other hand, for broadly-distributed and abundant species, genetic data is usually used to analyze population structure to allow the identification of evolutionary significant units (ESUs) and management units (MUs) or other phylogeographic patterns, including those that can be associated with habitat loss or fragmentation by human activities (and, of course, viability analysis of specific populations of these species can also be conducted). Although these species are useful in allowing an explicit understanding of evolutionary and ecological processes driving genetic diversity (including those magnified by human actions), they are usually only marginally considered in reserve design processes. Such populations will, of course, be part of optimum designs 'by default' and will be randomly selected in systems due to the broad overall distribution of the species. However, local populations or genetic variants of non-threatened species are usually not explicitly considered as priority targets, even though genetic analyses can show that they could be treated as independent and unique targets in reserve selection models and subjected, as genetic units, to the same persistence problems of narrow-ranged species. So, if population genetic structure is not explicitly incorporated into regional conservation planning, it is not difficult to imagine that endangered species will have more of their (current) genetic diversity preserved than non-threatened species, which will suffer from loss of genetic variability that may be concentrated into a few populations that were not incorporated (by chance alone) into conservation units.

These two views are usually not considered simultaneously in the context of establishing broad-scale, regional conservation planning, despite the large amount of current literature discussing the conservation implications of population and metapopulation genetic structure (see Hanski and Gilpin 1997). Conservation genetics have been focused on the ecological and evolutionary persistence of targets (species or other intraspecific units), especially when dealing with narrow-ranged species and their representation, but no generalized solution for where to concentrate conservation efforts for multiple targets with different genetic characteristics have yet been achieved.

In this paper, we outline a theoretical framework in which these two approaches to conservation genetics could be explicitly incorporated into the broad-scale reserve network models used to optimize biodiversity conservation based on multiple species data.

Principles of reserve network design

Methods to find reserve networks by optimization usually start by asking 'what is the minimum cost necessary to represent all targets' (Williams *et al*., 2004). One general principle underlying this process is complementarity, which states that different units in the conservation system must try to deal with different targets such that that there is minimum of overlap of targets and minimum redundancy in the system.

In the simplest form, the cost of a reserve network or system may be defined by its total area or simply by the number of reserves (usually of equal size). However, it is not uncommon to include as costs more complex variables that express the difficulty of incorporating a spatial unit into the network, such complex variables including the human population living in the region, price of land, agricultural potential of the area, probability of habitat loss, and even the spatial aggregation of reserves (which minimize transport and other management costs) (Briers, 2002; Chown *et al*., 2003). On the other hand, conservation targets usually include a list of different species or vegetation types, but can also include other ecological processes or can weight species differentially depending on their endangered status, potential impact on humans or their evolutionary history (Seal *et al*., 1998; Secherest *et al*., 2003; Diniz-Filho, 2004).

In a simple example (Figure 1A), if one wants to find the minimum number of sites that represent all four species (targets) in a region to generate an optimum reserve network, two sites must be preserved in order to get at least one 'population' of each species (the minimum representation problem). Although this is a simple example with an intuitive solution, mathematically, this is a problem of integer linear programming (ILP) and can be very complicated when dealing with large matrices and several costs and weights, or when multiple objectives for each target are desired such as the conserve of at least two or three populations of each species.

Mathematically, the information as to whether a species (or any other conservation target) is present or not in a set of sites is contained in a species-by-sites (m x n) matrix **A**, whose elements (A_{ij}) are unity if a species is present and zero if it is absent. Also, a vector **X** of dimension n determines whether or not a site is included (also coded as 1 or 0)
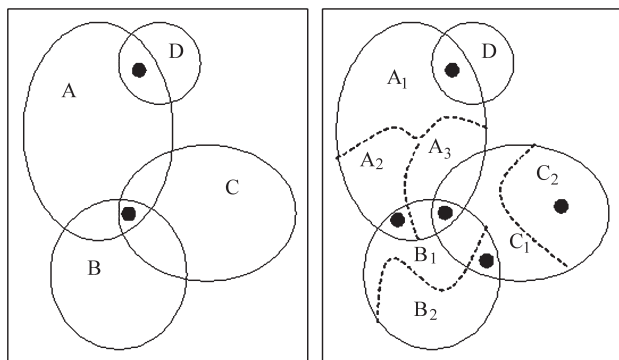
Figure 1 - The discrete concept. (A) Two different local populations need to be conserved for a optimum and minimum representation of four species; B) if a discrete population structure could be assigned for some of the species (three intraspecific units for species A and two intraspecific units for species B and C) a total of 5 sites would be needed to conserve all genetic structure within and between species.

in the reserve network. Based on these elements, the minimum representation is:

$$\text{Minimize } \Sigma\, x_j \tag{1}$$

$$\text{Subject to } \Sigma\, a_{ij}x_j \geq 1, \text{ for } i = 1,\dots, m \tag{2}$$

$$x_j \in \{0, 1\} \tag{3}$$

The objective function (1) minimizes the number of sites, whereas inequalities (2) ensure that each species will be represented at least once in the final set of sites. The integral in (3) ensures that each state variable x_j is either zero or one, making the problem an integer one (Rodrigues *et al.*, 2000). This problem is NP-complete, so that the difficulty of guaranteeing an optimum solution increases exponentially with the number of targets *m*. However, different computational algorithms based on heuristic or meta-heuristic procedures can be used to solve this problem. A very simple approach is to use a sequential and heuristic search, the so-called 'greedy' approach (Church *et al.*, 1996; Pressey *et al.*, 1997) which consists of first finding the site with the largest overlap of species (*i.e.* the site with maximum richness) and choosing it as the first selected site in the network and then assuming that all species present in this site are already preserved. The next step is to choose the site that has maximum richness for species *not present in the first site* (maximum complementarity), and select it as the next one to be added to the network. The search continues until all species are added to the system. Although this approach is quite simple and can easily be applied to large matrices, it does not produce optimal solutions (Pressey *et al.*, 1997) and standard ILP techniques such as 'branch-and-bound', or computational techniques such as simulated annealing (Possingham *et al.*, 2000; Cabeza and Moilanen, 2001; Rodrigues *et al.*, 2002a), need to be used to find these optimum solutions. The modeling process can also be improved by adding more elements, such as differential weighting of both conservation targets and sites (for

more complex models see Rodrigues *et al.*, 2000). For example, when all targets (species) need to be represented at least *b* times the inequality (2) becomes

$$\text{Subject to } \Sigma\, a_{ij}x_j \geq b, \text{ for } i = 1,\dots, m \tag{2a}$$

In terms of types of targets, the general idea is to include species as targets (but see Pressey, 2004) based on their distribution maps. However, population level processes can make this decision much more difficult because of issues related both to persistence and representation. For example, Gaston *et al.* (2001) and Araújo and Williams (2001) both showed that if only distributional data (occurrence of multiple species in a region) is considered optimization procedures based on the complementarity described above tend to find networks whose units are located at the periphery of the range of most species if bounded ecological communities occur in the region concerned (for a more recent approach see also McCarthy *et al.*, 2005). Under classic central-periphery demographic models, the persistence of such species and populations may be problematic, although other models do exist. Alternative models of population structure under other historical scenarios were discussed by Hampe and Petit (2005).

In terms of representation, does defining species as coherent and unique evolutionary units ensure biodiversity representation? In other words, is it enough to conserve one or a few randomly chosen populations of many species, even if they are above the minimum viable population sizes needed for their persistence. We believe that it is not only possible, but better, to define targets within each species taking into account their internal ecological and evolutionary genetic structure and to consider this structure in the reserve design process.

There have been long discussions in conservation genetics about this issue, but centered on the concept of evolutionary significant units (ESUs) and management units (MUs) for intraspecific conservation (for reviews see Crandall *et al.*, 2000; Fraser and Bernatchez, 2001). Also, the population genetic structure of a species is strongly dependent on its breeding system and demographic parameters (Loveless and Hamrick 1984) as well as regional events of historical partition (vicariance) which simultaneously affect multiple species with similar life-history parameters (Avise 2000; Lapointe and Rissler 2005). Thus, our basic aim in this paper is to define how the outcome of these debates can be incorporated into the previously discussed models for reserve network that have been designed to simultaneously conserve multiple species. We suggest two possible solutions, one assuming discrete patterns (the discrete concept) and the other assuming continuous patterns of population structure processes in geographical space (the continuous variation in geographic space concept).

The discrete concept of population genetic structure

The discrete concept refers to the situation when it is possible to clearly allocate the genetic variability of a species distributed in geographic space in such a way that different groups of local populations can be distinguished from each other based on various different criteria. In this case, the solution is straightforward: each of these spatial units must be used as a target in optimization routines so that a species whose range is divided into k_i units will have a target equal to at least k_i samples spatially structured for species i (Fig. 1B). However, note that this is different from simply increasing the conservation goals for each species as expressed in inequality (2a) because such choices within the ranges of the species are not a simple function of minimum overlap between ranges but instead depend on genetic structure.

A simple variation of conservation goals among species (by creating a parameter b for each species, b_i), generated under a linear (or any other function) relationship between the number of population conserved and the intraspecific genetic diversity (say, by increasing the number of conserved populations for species with more genetic variability) would, of course, increase the chance of selecting populations representing different evolutionary units within species. In this case, inequality (2) would be

$$\text{Subject to } \Sigma\, a_{ij}x_j \ge b_i, \text{ for } i = 1,\dots, m \qquad (2b)$$

However, since this model is not spatially explicit about the intraspecific genetic units, it would fail in many situations, depending on the spatial covariation of population genetic structure among units of different species.

The division of the geographic range of a species into multiple units can appear under distinct criteria and by many evolutionary processes but, in general, depends on isolation caused by long-term historical processes such a barrier to gene flow. This will result in relatively high F_{ST} values and a clear geographic structure of populations, which could be clearly visualized by clustering and ordination techniques. Distinct phylogeographic units, as defined by Avise (2000), based on mtDNA could be used as conservation targets in the same way as the 'classical' concept of evolutionary significant units based on reciprocal monophyly of mitochondrial haplotypes. Crandall *et al.* (2000) and Fraser and Bernatchez (2001) discussed the validity of defining ESU's based on only mtDNA.

Under a purely stochastic process of population differentiation by historical isolation, the number of units within a species will increase monotonically with the size of the geographic range to form a broken-stick distribution of fragmented ranges (MacArthur, 1972) in which species with wide geographic ranges are divided more into subunits whereas narrowly distributed species are more genetically homogeneous. As a consequence, there will appear a rela-

tionship between the geographic-range size-frequency distribution (RSFD) of targets and the number of reserves in the network designed to conserve the population genetic structure of multiple species.

However, the situation is often more complex because barriers can simultaneously affect, or not affect, various species in the system. If the barrier affects gene flow simultaneously in multiple species the subunits for different species will be spatially congruent in such a way that the overall number of reserves in the system will slowly increase in relation to the number of species in the system, this relationship being even more accentuated if the range of the species are more or less of the same size (Figure 2). This increase will be slower than if barriers randomly affect different species because intraspecific spatial units will not be spatially congruent so that the final number of reserves necessary to conserve all species will increase faster in relation to the number of species. This variation in historical effects tends to occur when one is dealing with species with very different life histories and ecological characteristics in such a way that variable population structures within species will be found in the same area.

In some sense, this process is already happening for some taxonomic groups for which the biological species concept is being 'replaced' by phylogenetic concepts to define species, in a process that has recently been called 'taxonomic inflation' (Isaac *et al.*, 2004). For this reason, many
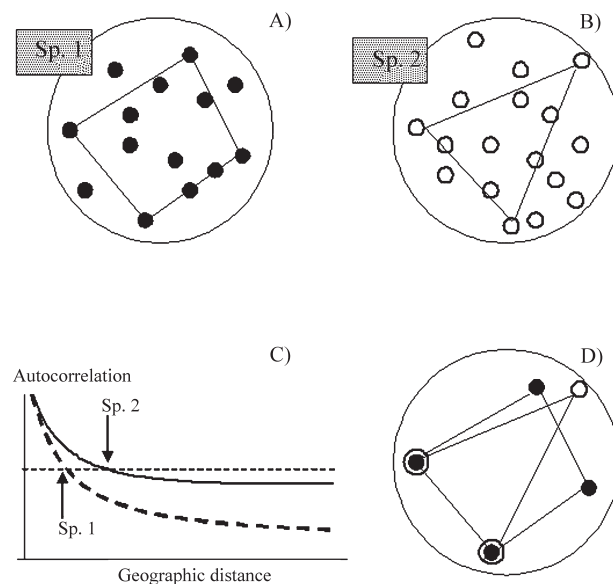

Figure 2 - The continuous concept. This shows a simple example for two different species (populations with open (A) and closed (B) circles). Networks of local populations for each species are designed using genetic variability spatial correlograms (C), which indicated different genetic patch sizes. The superimposition of these two networks indicates that five sites are necessary to better conserve continuous genetic variation, two of them with both species, and three of them containing one species each. This is one possible solution, since other networks could be obtained for each species.

recent papers have suggested that conservation targets must be better defined by measurements of phylogenetic diversity and not necessarily by discrete, and often arbitrary, units such as species (Faith, 1992; Crozier, 1997; Rodrigues *et al*., 2002b; Sechrest *et al*., 2003; Onal, 2003, Tôrres and Diniz-Filho, 2004; Bickford *et al*., 2004).

The continuous variation in geographic space of genetic variation

In many situations, genetic variability cannot be partitioned into discrete groups of populations but is a continuous function of geographic space in such a way that statistical and mathematical procedures, including those designed to establish ESUs, used to establish evolutionary units based on discrete structures will not work, generating a recent debate on theory and methods for intraspecific conservation (see Paetkaeu, 1999).

We have previously suggested that statistical analysis of genetic variation by spatial autocorrelation could be useful to define 'operational' units for conservation (Diniz-Filho and Telles, 2002). Spatial autocorrelation measures the similarity between samples for a given variable as a function of spatial distance (Sokal and Oden, 1978a,b; Griffith, 1987; Legendre and Legendre, 1998; Diniz-Filho *et al*., 2003; Epperson, 2003). For quantitative or continuous variables such as allele frequencies, abundance and species richness Moran's coefficient (*I*) is the most commonly used coefficient in univariate autocorrelation analyses and is given as

$$I = \left(\frac{n}{S}\right)\left[\frac{\sum_i\sum_j (y_i - \bar{y})(y_j - \bar{y})w_{ij}}{\sum_i (y_i - \bar{y})^2}\right] \qquad (4)$$

where *n* is the number of samples (local populations), y_i and y_j are the values of the allele frequencies in populations *i* and *j*, $\bar{y}$ is the average of *y* and w_{ij} is an element of the matrix **W**. In this matrix, $w_{ij} = 1$ if the pair *i, j* of local populations is within a given distance class interval (indicating populations that are 'connected in this class') and $w_{ij} = 0$ when the converse is true. The value of S is the number of entries (connections) in the **W** matrix. The value expected under the null hypothesis of the absence of spatial autocorrelation is $-1/(n - 1)$. Detailed computations of the standard error of this coefficient are given in Griffith (1987) and Legendre and Legendre (1998).

Moran's *I* usually varies between -1 for maximum negative autocorrelation and +1 for maximum positive autocorrelation. Non-zero *I* values indicate that allele frequencies in local populations connected at a given geographic distance are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected for randomly associated pairs of populations. The geographic distances can be partitioned into discrete classes to create successive **W** matrices which result in different *I* values for

the same variable and allows autocorrelation to be evaluated as a function of spatial distance using a graph called a spatial correlogram which furnishes a descriptor of the spatial pattern in the data. When multiple allele frequencies are analyzed, average correlograms can be calculated. Alternatively, analogous multivariate correlograms can be computed based on pair-wise genetic distance matrices such as Nei's genetic distances, or any other appropriated form, using Mantel tests (Diniz-Filho and Telles, 2002; Telles *et al*., 2003). A similar reasoning can be based on the procedure proposed by Wagner *et al*. (2005), who recently generalized variograms based on Analyses of Molecular Variance (AMOVA) to describe continuous genetic structure in microsatellite data.

The basic idea of the procedure devised by us (Diniz-Filho and Telles, 2002) is that the intercept of the spatial correlogram (or the average intercept calculated for many variables), which is the spatial distance at which the autocorrelation statistics become non-significant (hereafter called D_C), furnishes a distance at which local populations become statistically independent from each other (see also Diniz-Filho, 2001). Sampling populations separated by this distance will minimize redundancy while at the same time ensuring that a high level of genetic variability is included with less effort. As recently pointed out by Manel *et al*. (2003) in the context of the new field of 'landscape genetics', although this procedure still need to be tested and evaluated it can furnish an initial basis for working with the continuous distribution of genetic variability and evolutionary processes in geographic space.

To apply the concept of operational units developed by us in the context of multiple species it would be necessary to use an algorithm that finds the minimum number of overlapping sites that are, for each species, situated at a given distance D_C defined by the intercept of the correlogram. In a first approximation, if all species have the same D_C value as consequence of similar life-histories and ecology affecting the dynamic of genes among local populations in similar ways and if the spatial process is stationary and forms no strong clinal structures (for a discussion of the impact of non-stationary in the method see Telles *et al*., 2003) the problem is reduced to finding the minimum number of sites (reserves) that conserve all species for a given time and in which all reserves are situated at least at a distance D_C from each other. In this case the number of local populations to be conserved within each species will be a function of the size range, since larger ranges can be covered with more populations situated at a distance D_C apart. Again, if the RSFD is constant (*i.e.* all species have approximately the same range), the number of populations to be conserved within each species is given by the ratio between D_C and the range extent (defining the parameter *b* in inequality 2b). The overall problem is also reduced to finding the minimum number of reserves that conserve all species a given time when all reserves are situated at least at a dis-

tance D_C from each other. This could be easily implemented in standard conservation planning programs such as SITES by defining the minimum separation distance based on the D_C value established by autocorrelation analysis.

However, in empirical situations, none of these three assumptions of the initial approximation will hold (*i.e.*, D_C-values are not the same for all species, genetic variability is not stationary for all species and RSFD is not a constant) so much more complex optimization models with explicit spatial structure should be developed to deal with these three cases.

Explicit spatial models for reserve design are still in their infancy and have usually focused on the problem of the spatial aggregation of reserves because of the need to minimize management costs (Briers, 2002; Williams *et al.*, 2004). For the working problem we proposed, it would be necessary to find explicit combinations of populations of all species in such a way that distances between reserves are situated at a given distance that respect D_C values for each species within the reserve. The number of populations to be conserved for each species vary and are given by a complex function of the species D_C value and the extent of occurrence when all species are considered simultaneously. Mathematically, the objective function (1) could be rewritten as

$$\text{Minimize} \; \Sigma \, p_i x_j \qquad (1a)$$

were p_i can assume values of 0 or 1 indicating if, for species i, the site j is important or not, in the sense of obeying the minimum distance $D_{C(i)}$ from other sites previously established for the species i. Of course, this function must work under an explicit spatial configurations and, in certain conditions, it may fail to achieve a minimum representation because the result will tend to zero if there is little spatial congruence between the genetic structures of different species. Probably it would be necessary to relax the minimum distance $D_{C\,i}$ iteratively to obtain a solution.

Despite the complexity of this explicit spatial model, we can suggest a simple sequential heuristic algorithm to deal with this situation, as follows:

1. Calculate the spatial correlogram for each species of interest and establish its D_C-values by averaging correlograms of different allele frequencies, intercepts or by combining multiple variables into genetic distances and then calculating a multivariate correlogram;

2. Based on D_C-values and species distribution, calculate all (or many) possible networks for each species, defining multiple possible population of each species as conservation targets;

3. Superimpose the multiple solutions for all species, trying to find best overlap of networks of target populations of all species and then defining the sites for reserves;

A statistical approach could also be adopted to choose between combination of networks, by incorporating a confidence interval of distances among populations, that could be established based on multiple errors of D_C. However, the entire procedure can be very complex if multiple networks exist for each species (once again, a function of D_C in relation to range extent) and if many species and many local populations are analyzed. A small hypothetical example is shown in Figure 2 showing one network for each of the two species in a system. This sequential and heuristic algorithm will almost certainly produce a sub-optimal solution, but computational procedures such as simulated annealing and genetic algorithms could be adapted to search multiple combinations of networks among species and tentatively find the best combinations of sites by avoiding local minimums.

Concluding Remarks

In this paper we discussed some procedures that can be used to take into account genetic population structure in the modern methods used for the spatial design of conservation reserves. The methods discussed focus mainly on the improved representation of biodiversity, since a single population cannot fully represent a broadly-distributed species. If we consider also that overall genetic variability and a more balanced overall heterozygosity can diminish the risk of the extinction of a species, then the approaches proposed here are also important for species persistence.

Methods based on discrete genetic units are relatively simple and can easily be implemented in the standard software for conservation planning based on meta-heuristic procedures, such as SITES, SPOTand C-PLAN, or on linear optimization solutions such as CPLEX. However, methods for dealing with continuous genetic variation within populations are not trivial and optimization procedures must still be developed.

More importantly, the data necessary to incorporate population genetic structure into models is not generally available at present because for any given region the population genetic structure of all species defined as conservation targets should be known based on multiple samples well distributed in geographic space. We hope that a better understanding of the methods and the urgent need for these data to improve conservation planning can furnish guidelines for future research programs in molecular and population genetics. Of course, even if a few species among the targets have been studied, their genetic structure could be taken into account. Genetic data could then play a more explicit and integrating role in conservation, focused not only on the survival of a few flagship populations or species but as a part of general programs to improve the representation and persistence of the entire regional biodiversity.

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