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Evolving spatial conservation prioritization with intraspecific genetic data

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Abstract :

Spatial conservation prioritization (SCP) is a planning framework used to identify new conservation areas on the basis of the spatial distribution of species, ecosystems, and their services to human societies. The ongoing accumulation of intraspecific genetic data on a variety of species offers a way to gain knowledge of intraspecific genetic diversity and to estimate several population characteristics useful in conservation, such as dispersal and population size. Here, we review how intraspecific genetic data have been integrated into SCP and highlight their potential for identifying conservation area networks that represent intraspecific genetic diversity comprehensively and that ensure the long-term persistence of biodiversity in the face of global change.

Highlights

► Conservation area networks on land and sea need to be expanded to meet the objectives of the post-2020 global biodiversity framework. ► Spatial conservation prioritization (SCP) is a rigorous framework to identify suitable areas for protection on the basis of scientific data. ► Integrating intraspecific genetic data in SCP can help identify networks of conservation areas that are more representative of biological diversity and likely better at ensuring its long-term persistence.

Keywords : adaptive genetic diversity ; biodiversity features ; evolutionarily significant units ; reserve design ; systematic conservation planning

Main

The benefits and challenges of intraspecific genetic data for spatial conservation prioritization

Facing worldwide declines in biodiversity and nature's contributions to people [1], the post-2020 global biodiversity framework under discussion by the UN will prescribe to create "ecologically representative and well-connected" networks of conservation areas (CAs) that cover 30% of marine, aquatic and terrestrial habitats, and to ensure that 90% of within species genetic diversity is maintained by 2030 (see www.cbd.int/conferences/post2020). To achieve these goals, spatial conservation prioritization (SCP) is an effective framework to identify new CAs on the basis of the spatial distribution of conservation costs and **biodiversity features** (see **Glossary**) such as species and ecosystems [2].

Over time, SCP has evolved to integrate increasingly complex aspects of biodiversity, such as connectivity, ecosystem services and functional diversity [3–5]. Recently, attempts have been made to use intraspecific genetic data to gain knowledge on several aspects of species' biology that are critical for their conservation (see also **Online Supplemental Information Table S1**). In particular, genetic data can provide information on intraspecific genetic diversity, dispersal and population size [6,7]. The published studies listed in **Table S1** show that such information can increase the **comprehensiveness** of CA networks and the long-term persistence of biodiversity. However, the successful integration of intraspecific genetic data with other types of data in SCP presents challenges. Here, we briefly review the available techniques to estimate intraspecific genetic diversity, dispersal and population size from intraspecific genetic data and we discuss how to best integrate them in SCP.

Obtaining unbiased information from intraspecific genetic data

Intraspecific genetic diversity

Species are not static in time and show phenotypic variation throughout their range. This intraspecific diversity, which arises through the interplay of environmental and genetic variation, has consequences for population viability, community and ecosystem functioning, and nature's contributions to people [8,9]. Intraspecific variation is an important asset that can allow species to persist in the face of rapid environmental change, such as those expected from the outcomes of global climate change [10]. There is evidence that intraspecific genetic diversity has declined in many wild species [11,12]; therefore, the post-2020 biodiversity framework will commit to protecting intraspecific genetic diversity and CAs can be a valuable tool to reach this objective [13].

Intraspecific genetic diversity can be partitioned into within-population diversity and between-population diversity, analogous to partitioning species diversity into alpha and beta components [14]. Within-population genetic diversity can be measured using metrics such as allelic richness and observed and expected heterozygosity, while between-population genetic diversity can be represented by metrics of genetic differentiation [15]. Genetic differentiation can be used to identify conservation units below the species level, such as management units (MUs) and evolutionarily significant units (ESUs) [16]. The maintenance of genetic differentiation between MUs implies significant demographic isolation or selection against immigrants, which justifies considering them as distinct conservation units [16]. Conversely, genetically homogenous sets of individuals cannot be considered as MUs given that the level of migration that is sufficient for genetic homogeneity might not be sufficiently high to ensure **demographic connectivity** [17,18].

ESUs are populations or groups of populations that have evolved independently and can be identified by reconstructing phylogenetic trees within species [16,19]. ESUs are important conservation units because a

comprehensive view of biodiversity includes the full set of nested clades representing phylogenetic relationships among organisms [20]. In addition, regions with maximum phylogenetic diversity for a given taxon will also have the greatest trait diversity and thus potential to respond evolutionarily to future environmental change [21]. Finally, focusing on ESUs instead of species can help conserve biodiversity when taxonomy is uncertain [22]. Although the identification of ESUs has frequently relied on finding monophyletic clades [19], the general agreement is that ESUs should not be designated solely on the basis of genetic distinctiveness: ecological exchangeability and existence of genetic adaptations are among the proposed criteria to define ESUs [16,23,24]. Furthermore, the steps and choice of methods involved in reconstructing phylogenies can influence the inferred relationships among population units [25,26].

A further distinction can be made between **neutral genetic diversity** and **adaptive genetic diversity** according to the effects of genetic variation on individual and population fitness [27]. However, the effect of different alleles on the fitness of individuals and the viability of populations is seldom known, especially for non-model organisms. Genotype-phenotype association studies aim to identify genes responsible for phenotypic variation through correlative tests between variation in phenotypic traits and genetic variation [28]. Such genes can be considered important for the viability of populations when the phenotypic traits studied are of key importance for the persistence of populations and the identified genes have sufficiently large phenotypic effects for their variation to significantly affect phenotypic variation [29]. A second set of methods (**outlier tests** and **environmental association analyses**) investigate the signatures of selection to detect candidate loci underlying local adaptation [30,31]. However, it is always difficult to distinguish the signatures of positive selection from those of genetic drift [30] and, even when adaptive loci have been identified with high confidence, the effects of their genetic diversity on population persistence usually remain unknown [29]. Faced with these challenges, it is often difficult to partition neutral from adaptive genetic diversity. One possibility is using genome-wide genetic variation as a proxy for the viability of populations [32]. However, for some cases where genetic variation in phenotypic traits has been

quantified, neutral genetic variation has proven to be a poor predictor of adaptive genetic variance [33]. Furthermore, genomic techniques allow typing thousands of loci and if all these loci were included as biodiversity features, they could lead to computationally prohibitive problems and redundant information. As large genomic data sets accumulate [34], there is a need to consider how measures of intraspecific genetic diversity can be used in SCP.

Dispersal

The post-2020 global framework emphasizes that biodiversity should be protected through "well-connected systems" of CAs. The functioning of systems of CAs as well-connected networks depends critically on the dispersal of organisms, which facilitates recolonization after catastrophic disturbances (**demographic rescue**) and allows the spread of adaptive variants that increase the viability of local populations facing environmental change (**genetic rescue**). In some species, dispersal can be studied using telemetry methods, but these techniques are not practical for many animal and plant species that disperse during life stages (such as larvae or seeds) when they are too small to be equipped with emitters. In these cases, genetic techniques can be a useful alternative to estimate dispersal at the temporal scale of a few generations in the past (**Box 1**). Four types of methods have been identified to estimate dispersal from genetic data: assignment tests [35], parentage analysis [35–37], analysis of the pattern of isolation-by-distance [37] and clinal analysis [38]. The results are estimates of dispersal probabilities between sites (summarized in a **dispersal matrix**) and dispersal distances (summarized in a **dispersal kernel**). Each of these methods has strengths and weaknesses (reviewed in [7,35]): for example, the accuracy of assignment tests depends on the degree of genetic differentiation between populations, while parentage and clinal analyses require intensive sampling or sequencing efforts [35] and cannot realistically be applied to a large number of species occupying an area being considered for SCP. However, gaining direct dispersal data for a small number of representative taxa could be useful to complement other, more feasible genetic approaches, such as the analysis of isolation by distance [37].

Census and effective population size

Various statistical frameworks are available to estimate **census population size** N_c from samples of individuals from natural populations typed with molecular markers [39]. These methods offer a valuable alternative to direct observation for obtaining estimates of population density in species that are difficult to observe and count, such as aquatic animals. For example, close-kin mark-recapture is an extension of traditional mark-recapture approaches where each juvenile carries the "marks" of its parents within its DNA [40]; using this method with a panel of 8,961 SNPs, Hillary *et al.* [41] estimated that N_c in the white shark *Carcharodon carcharias* population in eastern Australia and New Zealand ranges between 2,500–6,750 individuals. Intraspecific genetic data are also useful to estimate **effective population size N_e**, which is related to the risk of **inbreeding depression** and loss of genetic diversity [42], through several statistical frameworks applicable to a variety of life-histories [43]. Although uncertainty increases when the real N_e is large, with appropriate sampling designs and sufficient numbers of genetic markers, genetic data can provide precise and unbiased estimates of N_c and N_e, in some cases using the same dataset [44]. Temporally repeated sampling can provide estimates of population trends in time and thus help identify declining populations [45].

Integrating information obtained from intraspecific genetic data in spatial conservation prioritization

SCP can be treated as a mathematical problem using equations linking the spatial distribution of biodiversity features and conservation costs [46] (**Box 2**). While there are different formulations of SCP problems [46], almost all of them involve four parameters: the representation level r_{ij} of biodiversity feature j in site i, the cost c_i of protecting site i, the spatial target T_j for biodiversity feature j, and the adjacency cost cv_{ih} between site i and h. The general principle to integrating the estimates from intraspecific genetic data is to link them explicitly to the parameters of SCP (**Figure 1**).

158 *Intraspecific genetic diversity*

159 There are various ways to integrate information on intraspecific genetic diversity into SCP. The simplest
160 approach is to use alleles as biodiversity features instead of (or in combination with) species ("AL" method
161 in **Table 1**), but it can be difficult to decide which and how many genetic markers and alleles to consider as
162 biodiversity features. Estimates of within-site diversity, such as allelic richness and heterozygosity, can be
163 used as biodiversity features ("GM"); however, defining a target of representation T_j for them is not
164 meaningful since T_j considers the total sum of a biodiversity feature across the planning area and such
165 genetic metrics are not additive across space. These metrics could be better integrated as cost layers, for
166 example by setting costs proportional to the inverse of allelic richness to select sites with high local genetic
167 diversity ("CS" method). Another option is to use site-specific metrics to rank sites according to the metric
168 of interest (e.g. sites with low and high allelic richness) and split the taxon (species or conservation unit)
169 occurrence layer into several distinct layers with specific representation targets ("ST" method).

170 Conservation units (MUs and ESUs), when present, can also be used directly as biodiversity features ("CU"
171 method). As an alternative to using ESUs, the branches of the phylogenetic tree can be used directly as
172 biodiversity features to assign higher priorities to older genetic lineages [22,47]. This approach may be
173 useful because conserving lineages separated by longer branches results in protecting larger amounts of
174 genetic diversity, compared to conserving more closely related lineages. In addition, using branches
175 ensures cost-effective protection as deeper branches representing shared evolutionary histories are only
176 accounted for once in the prioritization [48].

177 Some species do not have a discrete spatial genetic structure that permits researchers to unambiguously
178 identify conservation units. A solution to this problem is to use continuous measures of genetic distance
179 [49] in the 'environmental diversity' formulation of the SCP problem ("ED" method), used to identify a set
180 of conservation priority sites on the basis of continuous intraspecific variation (genetic or environmental
181 [50]).

Importantly, as genetic sampling is usually sparse, there will not be enough observations to measure the spatial occurrence r_{ij} of alleles, conservation units or genetic metrics nor to measure costs c_i in all sites. This requires a spatialization step to go from sampled points to values for all sites in the regular grid (planning units) used in SCP. This can be done using several methods relying on sampled genetic data only (e.g. inverse distance weighting) or making use of environmental variables (e.g. **ecological niche models**). **Supplementary Table 1** indicates the methods used for each published paper that incorporates genetic data in SCP. There is currently no comparison of the various methods to infer genetic data to cover unsampled sites (see **Outstanding questions**).

Dispersal

Several methods are available to constrain the sites chosen for protection to be spatially contiguous [46,51,52], such as introducing a boundary cost cv_{ih} for not protecting pairs of bordering sites (**Box 2**). This formulation can easily accommodate the information of dispersal contained in a dispersal matrix, whose elements d_{ij} give the probabilities of dispersal from site *j* to site *i*. Whether it is estimated from genetic data or obtained through other methods, the dispersal matrix can be used to define the cv_{ih} parameter in the SCP problem, which becomes a connectivity penalty cost paid when site *i* is chosen for protection and site *h* is not [53]. Depending on the goals of SCP, researchers can choose the extent to which connectivity should be prioritized by changing parameter *b*, which becomes the connectivity strength modifier (**Equation 2** in **Box 2**)[53]. In other formulations of the SCP problem, the dispersal matrix can be used to maximize metrics of metapopulation performance, such as the expected time to extinction [54,55]. Alternatively, dispersal distances can be used to set the maximal size of CAs and distances between different CAs in a network to ensure that propagules and juveniles generated in one CA can disperse to and recruit in nearby CAs [56,57].

The dispersal matrix can also be used to define site-specific metrics measuring the importance of each site for population persistence using graph theory [58] or matrix analysis [55]. When used as biodiversity

features [58] or costs [59], such site-specific metrics lead to the selection of sites that are well-connected, and this connectivity may enhance persistence within the CA network [58].

Population size

Estimates of N_c and N_e are useful to refine the targets T_j's of species representation that constrain the solution of the SCP problem (**equation 2** in **Box 2**)[60]. These targets define the minimum proportions of the geographical ranges of species that need to be included in the sets of CAs to consider those species adequately covered. Species with smaller geographical ranges are usually given higher proportional targets of representation because they might face a higher risk of extinction than species with larger ranges [61]. Despite being easy to implement, this approach is an approximation for the complexity of demographic, genetic and ecological factors affecting the long-term persistence of species. Estimates of N_c and N_e could help set more appropriate targets, for example by increasing T_j for species that have low numbers of individuals even if their geographical range is large or for species showing a negative temporal trend in abundance. The information provided by population abundance complements that of occurrence in setting conservation priorities [62] and many species are showing signs of declining abundance despite keeping stable geographical ranges [63]. The approach used by the IUCN to classify species into threat categories is also based on criteria of geographical ranges and population abundance [64].

When estimates of N_c and N_e are available per site, they can be used to define SCP problems in terms of abundance: the representation levels (r_{ij}) are the site-specific population numbers and the target T_j is the total species abundance required for long-term persistence, which can be found using population viability analysis or set following the general 50/500 rule [65–67]. This approach requires a comprehensive sampling across the range of the species, or a method to spatialize the estimates of N_c and N_e. While there are several abundance-based species distribution models that predict N_c [68], similar approaches for N_e have yet to be developed.

Building adaptive conservation area networks

A primary goal of well-connected and genetically representative CA networks is to support the persistence of species in the face of anthropogenic disturbance, such as land use and climate change [69]. When loci of large effect on fitness can be identified, there are two alternative conservation strategies that can be adopted to account for future adaptation. First, when the direction of environmental change can be predicted and the relationship between alleles and environmental variables is known, a decision can be made to conserve the alleles that confer stronger adaptation to future environmental conditions, or the sites that show the smallest genetic offset with future predicted conditions [70]. However, focusing on the winners of environmental change relies on many strong assumptions, among which that the populations are optimally adapted to current environmental conditions and that the relationships between alleles and environmental variables are correctly characterized. In addition, when the direction of environmental change is unclear, it is even more difficult to predict biological responses accurately.

A safer strategy is to conserve a portfolio of alleles at adaptive loci (I.e. adaptive genetic diversity) as opposed to conserving only some alleles, as this confers higher adaptation capacity when future environmental conditions are uncertain [71] and buffers the risk of incorrectly characterized gene-environment associations. Depending on the genetic structure of the species, intraspecific genetic diversity can be conserved either by prioritizing sites with the highest within-site diversity (alpha diversity) or by protecting sets of sites with complementary genetic variants to maximize adaptation capacity at the landscape scale (beta diversity; **Box 3**).

Concluding remarks: getting the best (out of) genetic data

Despite the potential for improving CA planning, there are still numerous challenges that should be tackled by future research (see **Outstanding questions**). First, information from intraspecific genetic data is affected by various types of uncertainty [72]. Some estimated variables, such as dispersal distance and

population size, can have wide confidence intervals [37,41] and the identity of conservation units and adaptive genetic markers often depends on the methods used [24,30]. There is also limited knowledge about the real effects of intraspecific genetic diversity on the adaptive potential of populations [73]. An important area for future research is to evaluate the impact of these types of uncertainties on the selection of CAs [74] and develop standardized, efficient workflows to integrate the uncertainty of inputs into multi-species SCP [72].

Secondly, characterizing intraspecific genetic diversity requires multiple samples distributed throughout the entire geographic range of species, and possibly replicated in time to estimate population abundance trends. To estimate dispersal and population size, sampling must be carefully planned [35,43]. Multi-species genetic studies are becoming more common [75,76] and efforts are made to bring together genetic data sets for multiple species in free databases [34]. However, intraspecific genetic data are still lacking for many species and attempts to replace them with surrogate variables (e.g. environmental variables) have yielded mixed results [77–79]. Obtaining spatially and temporally replicated genetic samples for multiple species, in line with local conservation priorities and involving all stakeholders [80], remains a main goal for future research.

The scientific community has set ambitious goals to obtain genomic information for wild species: for example, the Earth Biogenome Project aims to sequence all known eukaryotic species in a ten-year timeframe [81]. The availability of genome sequences will undoubtedly help develop genetic markers for wild species, but it will be necessary to understand how to best use the knowledge obtained from reference genomes [82], for example the identification of deleterious mutations and the quantification of mutation load [83], to plan networks of CAs. When genomic data are used to identify putatively adaptive genetic markers, SCP solutions might be similar [85] or substantially different [74,84] to those found using putatively neutral loci or traditional markers such as microsatellites.

Similarly, conserving intraspecific genetic diversity, dispersal and population size might require specific sets of sites that increase conservation costs relative to the surface area needed to conserve species, possibly making it more difficult to reach other conservation objectives. This is likely to happen each time new objectives and constraints are added to the conservation problem. For example, the sites needed to maintain ecosystem services and functional diversity are often different from those needed to conserve species [86,87]. These conflicts in CA siting are eased when the connections between seemingly different objectives are recognized: for example, ensuring that marine reserves ensure population persistence within their borders (biodiversity conservation objective) and fishery supply beyond their borders (ecosystem service objective) can be reconciled by siting them according to the dispersal capacity of the targeted species [88]. This also shows that information obtained from intraspecific genetic data has an added benefit [89] and may justify the extra money and time required to obtain them.

Systematic approaches to biodiversity conservation will be increasingly needed in the near future to reach the targets of the post-2020 global biodiversity framework. Intraspecific genetic data are a wealthy source of information not only for characterizing intraspecific genetic diversity, but also for estimating important demographic parameters such as dispersal and population size. In addition to the framework briefly illustrated here, there might be other ways, which will be important to assess, to expand SCP towards these data. Early examples show that information from intraspecific genetic data is likely to improve the planning of CAs to reach multiple ecological objectives.

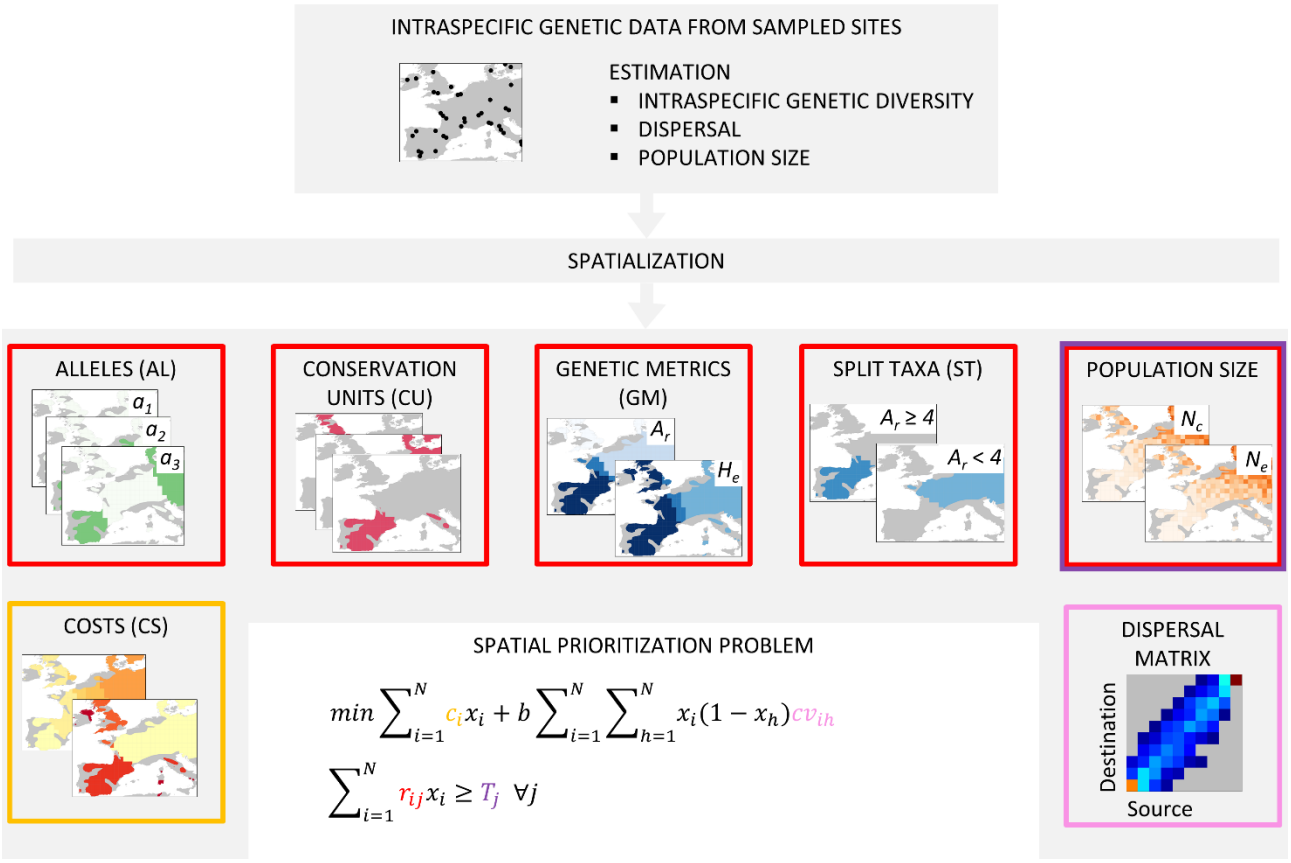

Figure 1. Integration of intraspecific genetic data into the 'minimum set coverage' spatial conservation prioritization (SCP) problem. Intraspecific genetic data can enter the minimum set SCP problem in various ways. Estimates of intraspecific genetic diversity obtained from sampled sites can be converted into spatial layers through a spatialization step. Layers of alleles (AL), conservation units (CU), genetic metrics (GM; such as allelic richness A_r and expected heterozygosity H_e) and split taxa occurrences (ST) can be used as biodiversity features and enter the SCP problem via variable r_{ij}, the representation level of biodiversity feature j in site i. The ST example shows the distribution range of a taxon split into two layers on the basis of the A_r value, with a threshold of 4 alleles. Information on dispersal, arranged in a dispersal matrix, can be used to define the connectivity penalty costs cv_{ih}. Estimates of population size at the species level can be used to refine the specific spatial representation targets T_j and estimates at the site level can be used as a layer to define SCP problems in terms of abundance. All three types of intraspecific genetic data can also be used to define layers of conservation costs c_i (CS). See **Table 1** and main text for detailed explanation of each method and **Box 2** for notation of the SCP problem.

Table 1. Methods to integrate information from intraspecific genetic data in spatial conservation prioritization.

METHOD	DESCRIPTION	EXAMPLES
ALLELES (AL)	Alleles are the biodiversity features. Allele presence or frequencies are mapped on the landscape and spatial layers are used as inputs in the prioritization.	[75,90–94]
CONSERVATION UNITS (CU)	Conservation units (management units, evolutionarily significant units or the branches of the phylogenetic tree) are treated as biodiversity features. As intraspecific genetic data are usually spatially sparse, the spatial distribution of individual conservation units is usually not known from observations, but can be predicted using spatial interpolation techniques or **ecological niche models**. In this latter case, each conservation unit is treated as a distinct entity in a model using environmental variables as predictors of its occurrence, with the possibility to include future environmental projections to forecast the response of each conservation unit under different climate change scenarios.	[22,47,84,95–97]
GENETIC METRICS (GM)	Genetic metrics, calculated for each species or conservation unit in each site, are the biodiversity features. Values in unsampled sites are predicted using spatialization techniques. A conceptual and practical difficulty with this method is the need to set representation targets for genetic metrics.	[74,93,98]
SPLIT TAXA (ST)	Taxa (species or conservation units) are the biodiversity features. Each taxon is represented by several spatial layers grouping sites sharing similar genetic characteristics. For example, distinct layers are used to represent sites with low, medium and high allelic richness or areas of low, medium and high genetic differentiation. Each layer has a spatial representation target. A limitation of this approach is that the number of distinct spatial layers and the limits among them are usually arbitrary.	[84,85,99–102]
COSTS (CS)	Costs are calculated as a function of site-specific or between-site genetic metrics. For example, sites with lower allelic richness are given higher protection costs to favor the	[99]

	selection of sites with higher genetic diversity. Pairwise genetic metrics can be integrated through boundary costs cv_{ih}: pairs of sites with lower genetic differentiation are given lower pairwise costs to favor the selection of genetically connected sets of sites. One drawback of this approach is the need to combine information that may be incommensurable, e.g. genetic-based and monetary costs, or when costs are used to define layers of unsuitable habitats.	
ENVIRONMENTAL DIVERSITY (ED)	The ED formulation finds the subset of sites that contain the most representative set of environmental conditions among all candidate sites, subject to a limit on the number of sites that can be selected [50,103]. It uses a dissimilarity matrix to characterize the differences between each pair of sites: thus, it can be adapted to generate prioritizations that ensure a representative sample of genetic diversity among sites, using a genetic distance matrix instead of environmental dissimilarity.	[50,77,78,104]

306

Box 1. Dispersal estimates and their potential usefulness in spatial conservation prioritization

Intraspecific genetic data offer various ways to estimate dispersal in organisms and habitats that are otherwise difficult to study using direct observations, such as tiny fish and invertebrate larvae that have the potential to disperse widely on ocean currents.

Parentage analysis - whereby offspring are assigned to parents based on their DNA - can be used to directly detect dispersal events [78]. In one example, D'Aloia *et al.* [36] genotyped over 7,000 individuals of the neon goby *Elacatinus lori* and used parent-offspring matches to estimate the species' dispersal kernel on the Belize barrier reef (Fig. I-A-B). They found that most larvae dispersed less than 2 km from their parents, despite larvae spending nearly one month dispersing. Like most parentage studies, this was constrained to a relatively small spatial area and required a large amount of sampling that will not be feasible to undertake for all species of interest in SCP. However, follow-up studies have corroborated this strongly limited dispersal pattern. For example, genetic sibship reconstruction revealed that full siblings are spatially arranged as predicted by the parentage dispersal kernel [105] and genetic assignment tests at the scale of the species' range revealed a low frequency of long-distance dispersal events [106]. The congruence between multiple genetic estimates of dispersal in *E. lori* is promising for the application of more feasible genetic-based estimates of dispersal in other species.

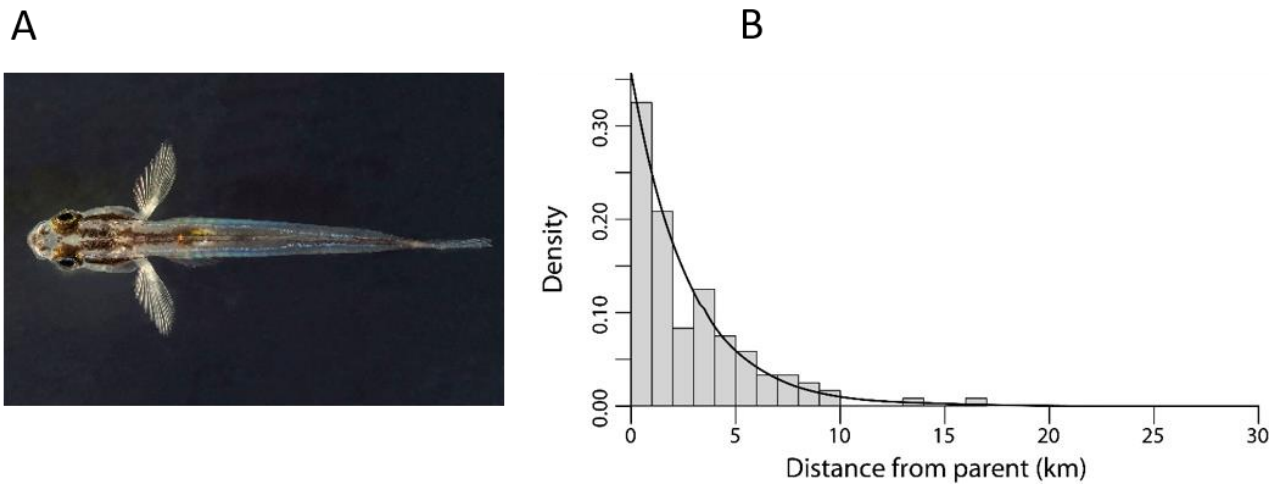

Figure I. Using genetic-based dispersal estimates to inform spatial conservation prioritization. (A) A larva of the neon goby *Elacatinus lori* (photo: J. Majoris); (B) The species' estimated dispersal kernel overlaid on a histogram of dispersal events detected by parentage analysis. Fig. Ib drawn using data from [36].

(end of Box 1)

Box 2. Spatial conservation prioritization as a framework to place new conservation areas

Spatial conservation prioritization (SCP) can be treated as a mathematical problem involving the spatial distribution of biodiversity features (e.g. species, indexed by j = 1, …, S) and conservation costs in a set of sites indexed by i = 1, …, N. r_{ij} indicates the spatial occurrence (binary variable) or abundance (continuous variable) of biodiversity feature j in site i. In one of the several possible types of SCP problems, the minimum set coverage [71], the mathematical formulation involves two equations:

$$min\left(\sum_{i=1}^{N} c_i x_i + b\sum_{i=1}^{N}\sum_{h=1}^{N} x_i(1-x_h)cv_{ih}\right) \quad (1)$$

$$\sum_{i=1}^{N} r_{ij}x_i \geq T_j \;\; \forall j \quad (2)$$

where x_i is the unknown variable indicating whether a site is selected for protection (x_i = 1) or not (x_i = 0). Solving the problem means finding the vector of x_i's that satisfies the two equations.

Equation (1) states that the total cost of protection should be minimized. The total cost is the sum of two terms: the first term is the sum of the site-specific costs of protection, c_i's, which can be defined as the monetary costs required to purchase the sites, as the opportunity costs of other excluded territorial uses or, in the absence of such information, simply as the surface area of the sites. The second term of equation (1) is used to limit the spatial fragmentation of the solution by introducing a boundary costs cv_{ih}, which is typically the length of the physical boundary between site i and h [5]; more simply, when sites have the same shape and size and are placed on a regular grid, cv_{ih} = 1 for adjacent sites and 0 otherwise. For two adjacent sites, the cost is paid when site i is protected but site h is not (x_i = 1 and x_h = 0). The "boundary length modifier" b is set according to the degree of fragmentation that is deemed acceptable (a lower b leads to a more fragmented solution).

Equation (2) constrains the solutions to sets of sites that include a minimum target proportion T_j of the geographical range of each species. T_j is set according to ecological considerations: for example, species with smaller ranges are given higher targets because they might be at higher risk of extinction than species with larger ranges [61].

The SCP problem can be solved using exact or heuristic methods implemented in several software packages [5,107,108]. The solution is a list of priority sites for the creation of new conservation areas (**Figure I**).

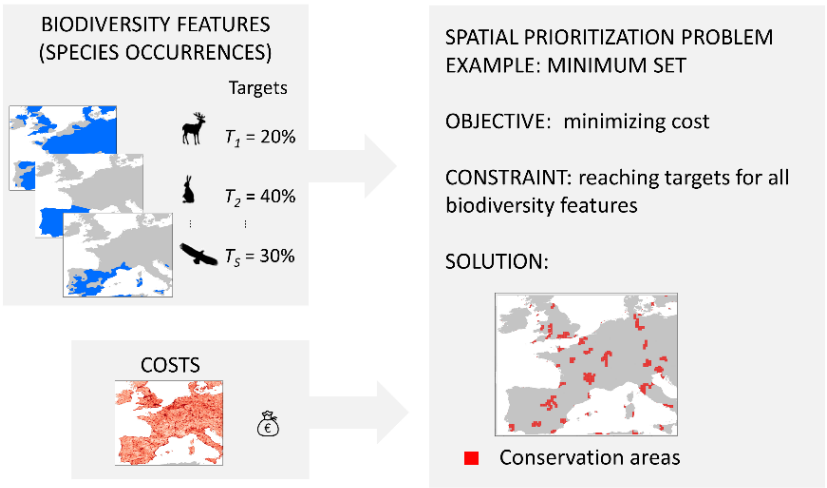

Figure I

(end of Box 2)

Box 3. Retaining adaptive genetic diversity to foster persistence under uncertain future conditions

Prioritizing portfolios of genetic combinations increases the probability that "winning" combinations can persist during periods of environmental change [71]. Depending on the genetic structure of the species, targeting sites with high within-site adaptive genetic diversity or sites with populations adapted to different local conditions will help build conservation area networks that retain the genetic diversity of species.

An example of prioritizing within-site diversity is given by Xuereb *et al.* [74]. They used environmental association analysis to identify 51 SNPs associated with mean bottom temperature in the California sea cucumber *Parastichopus californicus* living in the coastal seas of British Columbia (Canada). Then, they used within-site heterozygosity at these putatively adaptive SNPs as a biodiversity feature in spatial conservation prioritization (SCP), which led to the selection of sites in the northern region of the study area. In a second prioritization exercise, they used the frequency of warm-temperature-associated alleles as a biodiversity feature, which led to the selection of sites in the southern region. These results illustrate a trade-off between prioritizing specific alleles versus prioritizing genetic diversity.

The second option is protecting a portfolio of sites with a diverse set of adaptations. Hanson *et al.* [84] genotyped three amphibian species living in the Iberian peninsula at several thousand SNPs. Using outlier detection and environmental association analyses with climatic and soil variables, they identified several putatively adaptive loci in each species. They then identified sets of populations sharing similar adaptations (adaptive units [24]) by applying genetic clustering techniques to these putatively adaptive loci and used them as distinct biodiversity features in SCP. This allowed them to identify a set of complementary priority areas for the conservation of adaptive genetic diversity at the species level.

When selecting different sites, it is important that the genetic variants that may be favorable under future conditions will be able to spread to the other sites. For this reason, it is advisable to combine the

prioritization of genetically diverse sites with estimates of dispersal to build adaptation networks capable of exchanging favorable genetic variants when needed [71]. Various approaches are available to integrate this type of information in SCP (see main text). It should be noted, however, that prioritizing portfolios of genetic combinations is still subject to the difficulties of correctly characterizing adaptive genetic diversity.

(end of Box 3)

GLOSSARY

Adaptive genetic diversity. The genetic diversity that is estimated at adaptive genes, i.e. those that have an effect on fitness [27]

Biodiversity feature. A component of biodiversity (e.g. species, alleles, ecosystems) that can be mapped in a landscape.

Census population size. The count of individuals in a population, often restricted to adult individuals.

Comprehensiveness. The degree to which a set of conservation areas includes all elements of biodiversity features [51].

Demographic connectivity. The relative contribution of dispersal to population dynamics.

Demographic rescue. A decrease in population extinction probability owing to the simple addition of immigrants.

Dispersal kernel. The statistical distribution of dispersal distances in a population.

Dispersal matrix. A dispersal matrix describes the probability of dispersal between a set of sites in the landscape. Each element of the dispersal matrix is the dispersal probability from site *j* to site *i*, which may be different from the dispersal probability from site *i* to site *j* (asymmetric dispersal).

Ecological niche model. A statistical model linking the spatial occurrence of a biodiversity feature to a set of environmental variables. It is often used to predict species occurrences in places where no data are available (spatial prediction) or in the future (forecasting).

Effective population size. The size of an ideal population experiencing the same rate of genetic drift or inbreeding as the population under study. The ideal population is usually a closed population of constant size with discrete generations and a Poisson variance in reproductive success between individuals.

Environmental association analysis. A statistical approach to identify genetic variants strongly associated with specific environmental conditions.

Genetic rescue. A decrease in population extinction probability owing to gene flow.

Inbreeding depression. Reduced fitness of offspring with related parents, often due to deleterious recessive alleles that become expressed in homozygous state.

Outlier test. A statistical approach to identify loci involved in local adaptation by screening for alleles that show unusually high genetic differentiation among populations, i.e. outside of the distribution expected under neutrality.

Neutral genetic diversity. The genetic diversity estimated at putatively neutral genes, I.e. those that do not have any direct effect on fitness. This type of genetic diversity is selectively neutral and is useful to estimate dispersal and population size [27].

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639

Outstanding questions

What is the risk of disregarding intraspecific genetic data in spatial conservation prioritization (SCP) for biodiversity persistence? Conservation decisions have been and will be made in the absence of intraspecific genetic data, especially when they are too demanding to be collected. In what cases is it worth spending more time and money to collect genetic data?

As intraspecific genetic data are still lacking for many species, to what extent can they be replaced by surrogate information such as environmental variables in setting spatial conservation priorities?

What is the best method to spatialize genetic data to obtain information for unsampled sites?

How much more land and sea surface area will have to be protected to represent intraspecific genetic diversity? Previous studies showed that moderate extension of the current global system of conservation areas (CAs) would be sufficient to represent phylogenetic and functional diversity, but would this be true for intraspecific genetic diversity?

What is the impact of uncertainty in genetic data on the outcome of SCP? When uncertain genetic data are used in conjunction with other types of information to represent additional constraints to prioritization, the results risk being economically inefficient or unfavorable for conservation.

What is the risk of integrating intraspecific genetic data for some species only? Maximizing genetic diversity of one species can lower diversity of others. How would one select the species to collect genetic data on?

Table S1. List of published studies integrating intraspecific genetic data in spatial conservation prioritization

Ref	Citation	Number of species	Molecular markers[a]	Integration of genetic data[b]	SCP method[c]	Genetic metrics[d]	Inference of information in unsampled sites
[1]	Moritz (2002)	10	mtDNA	ED	Environmental diversity	Nei's [26] genetic distance averaged across species	Not performed. Only sampled sites were included in the prioritization.
[2]	Bonin et al. (2007)	2	AFLP	GM	Exhaustive search	Proportion of polymorphic loci Population adaptive index [2]	Not performed. Only sampled sites were included in the prioritization.
[3]	Thomassen et al. (2011)	7	AFLP, msat, nuDNA	ST	RESNET	Nei's [26] genetic distance F_{ST} ϕ_{ST}	Generalized dissimilarity modelling [27]
[4]	Diniz-Filho et al. (2012)	1	msat	AL	Simulated annealing		Not performed. Only sampled sites were included in the prioritization.
[5]	Taberlet et al. (2012)	39	AFLP	AL	ZONATION		Not needed. Sampling was performed using a regular grid
[6]	Vasconcelos et al. (2012)	30	None[e]	CU	ZONATION		Ecological niche model with MAXENT [28]
[7]	Beger et al. (2014)	1	msat	ST, CM	MARXAN	Genetic clusters identified with STRUCTURE [29] Allelic richness Local F_{ST} estimated with GESTE [30] Asymmetric recent migration rates estimated with BAYESASS+ [31]	Allelic richness and local F_{ST} were interpolated in ARCGIS. Asymmetric migration rates were applied to proximate neighborhood identified using Thiessen polygons
[8]	Schlottfeldt et al. (2015)	1	msat	AL, GM	Multi-objective Evolutionary	Expected heterozygosity	Not performed. Only sampled sites were included in the prioritization.

					Algorithms (MOEA, [36])	p-value of χ^2 test for Hardy-Weinberg equilibrium	
[9]	Diniz-Filho et al. (2016)	1	msat	AL	Exhaustive search		Not performed. Only sampled sites were included in the prioritization.
[10]	Hermoso et al. (2016)	4	Msat, mtDNA	CU	MARXAN		Generalized dissimilarity modelling [27]
[11]	Carvalho et al. (2017)	33	mtDNA	CU	ZONATION, MARXAN		Phylogeographical interpolation with PHYLIN [32]
[12]	Hanson et al. (2017)	27	AFLP	ED	RAPTR	Gower's [33] distance	Not needed. Sampling was performed using a regular grid
[13]	Nielsen et al. (2017)	5	mtDNA	ST	MARXAN	Haplotype diversity Nucleotide diversity Number of private haplotypes Local genetic differentiation	Inverse distance-weighting
[14]	Hanson et al. (2018)	1	AFLP	ED	RAPTR	Gower's [33] distance	Not needed. Sampling was performed using a regular grid
[15]	Vasconcelos et al. (2018)	23	mtDNA	CU	ZONATION		Ecological niche model with MAXENT [28]
[16]	Paz-Vinas et al. (2018)	6	msat	AL	MARXAN	Allelic richness Private allelic richness Jost's [34] differentiation	Generalized linear models for spatial stream networks [35,36]
[17]	Rosauer et al. (2018)	11	None[e]	CU	MARXAN		Lineage distribution model [37]
[18]	Hanson et al. (2019)	9	AFLP	CM	PRIORITIZR	Landscape resistance estimated from Nei's [26] genetic distance between sites	Not needed. Sampling was performed using a regular grid

[19]	Diniz-Filho et al. (2020)	1	msat	AL	Exhaustive search		Not performed. Only sampled sites were included in the prioritization.
[20]	Hanson et al. (2020)	3	SNP	CU, ST	PRIORITIZR	Mean individual heterozygosity	Thin plate splines; phylogenetic interpolation with PHYLIN [32]
[21]	Nielsen et al. (2020)	5	mtDNA, SNP	ST	MARXAN	Nucleotide diversity Percentage of private alleles Percent of outlier SNPs	Inverse distance-weighting
[22]	Hanson et al. (2021)	10	msat	ED	Environmental diversity	Jost's [34] genetic differentiation	Not performed. Only sampled sites were included in the prioritization.
[23]	Phair et al. (2021)	1	SNP	ST	MARXAN	Nucleotide diversity Expected heterozygosity Allelic richness Number of shared SNPs and private SNPs Proportion of outlier SNPs	Inverse distance-weighting
[24]	von Takach et al. (2021)	1	SNP	AL	PRIORITIZR		Not performed. Only sampled sites were included in the prioritization.
[25]	Xuereb et al. (2021)	1	SNP	GM	PRIORITIZR	Expected heterozygosity Local F_{ST} Adaptive score [38] Population adaptive index [39].	Inverse distance-weighting

Notes

The table includes only papers using intraspecific genetic data to obtain information that is used to define the input of a spatial conservation prioritization problem. The table was prepared starting from papers known to the authors and searching within the literature cited in them.

[a] Type of molecular marker used: mitochondrial DNA (mtDNA), nuclear DNA (nuDNA), amplified fragment length polymorphisms (AFLP), microsatellites (msat), single nucleotide polymorphisms (SNP)

[b] Methods used to integrate intraspecific genetic data in spatial conservation prioritization: alleles (AL), conservation units (CU), genetic metrics (GM), split taxa (ST), environmental diversity (ED). See **Table 1** in the main text for description of the methods

[c] Method or software package used to perform spatial conservation prioritization (SCP): environmental diversity [40], MARXAN [41], ZONATION [42], PRIORITIZR [43], RAPTR [14], RESNET [44], MOEA (multi-objective evolutionary algorithms, [45]). Exhaustive search means that all the possible combinations of sites were considered.

[d] Genetic metrics used in the prioritization either as biodiversity features (GM method), to split taxa layers (ST methods), as a distance or dissimilarity metric in the environmental diversity method (ED) or to integrate information on connectivity.

[e] ESUs had been identified in other studies

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