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Opinion

Molecular ecology meets systematic conservation planning

Erica S. Nielsen [1,*,@], Jeffrey O. Hanson [2,@], Silvia B. Carvalho [3,4,@], Maria Beger [5,6,10,@], Romina Henriques [7,10,@], Francine Kershaw [8,10,@], and Sophie von der Heyden [9,10,@]

Integrative and proactive conservation approaches are critical to the long-term persistence of biodiversity. Molecular data can provide important information on evolutionary processes necessary for conserving multiple levels of biodiversity (genes, populations, species, and ecosystems). However, molecular data are rarely used to guide spatial conservation decision-making. Here, we bridge the fields of molecular ecology (ME) and systematic conservation planning (SCP) (the 'why') to build a foundation for the inclusion of molecular data into spatial conservation planning tools (the 'how'), and provide a practical guide for implementing this integrative approach for both conservation planners and molecular ecologists. The proposed framework enhances interdisciplinary capacity, which is crucial to achieving the ambitious global conservation goals envisioned for the next decade.

Highlights

Molecular ecology (ME) and systematic conservation planning (SCP) have seen rapid technological advancements in recent decades, but the use of molecular data to conserve different aspects of biodiversity remains operationally illusive.

Here, the core principles of ME and SCP are combined in a novel way, showcasing how themes and corresponding data types from each field can complement each other.

A framework, including five practical steps, is provided to guide both molecular ecologists and conservation planners to build systematic conservation plans that effectively integrate evolutionary features.

Building a unified approach to conserving the biodiversity spectrum

The world is facing an anthropogenically driven biodiversity crisis [1,2] which must be urgently addressed to restore ecosystem functions, mitigate climate change, and maintain human well-being [3,4]. Protected area establishment is a cornerstone for biodiversity conservation. The global protected area system coverage has been increasing, both in terrestrial and marine ecosystems [5]. However, this system is incomplete and falls short in safeguarding all levels of biodiversity [genes, **populations** (see Glossary), species, and ecosystems] [6]. Consequently, conservation actions are needed in places that will promote biodiversity resilience, **adaptive potential**, and species persistence in a changing world [7].

Over the past 30 years, ecologists and evolutionary scientists have rallied to inform conservation decision-making. **Molecular ecology** (**ME** [8,9]) developed as a field for describing evolutionary processes in non-model/wild species and their populations within an ecological context. Meanwhile, **systematic conservation planning** (**SCP** [10,11]) emerged and provided a transparent, reproducible, and quantitative approach to identifying cost-effective priority areas for conservation. As these fields continue to develop, there is growing acceptance that they should be integrated to inform conservation decisions relevant to evolutionary objectives [12]. Several ME subdisciplines can provide suitable data for SCP, such as extinction probabilities from conservation genetics or landscape **connectivity** from landscape genetics [13]. Recent work has described ME data types most relevant to SCP, highlighting **genetic diversity**, dispersal, and **effective population sizes (N_e)** [14]. However, little guidance exists to enable conservation practitioners and molecular ecologists to navigate when this evolutionary information is needed for conservation management, to implement various genetic/genomic data into conservation planning software, and to assess how well evolutionary objectives are being met [15].

Here, we present a novel, integrative framework that reconciles ME and SCP to identify priority areas that will promote the long-term persistence of biodiversity. Our framework ensures that

[1]Department of Evolution and Ecology, University of California Davis, Davis, CA, USA
[2]Department of Biology, Carleton University, Ottawa, ON, Canada
[3]CIBIO/InBIO, Vairão, Portugal
[4]BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Vairão, Portugal
[5]School of Biology, University of Leeds, Leeds, UK
[6]Centre for Biodiversity and Conservation Science, School of Biological Sciences, University of Queensland, Brisbane, QLD, Australia
[7]Department of Biochemistry, Genetics and Microbiology, University of Pretoria, Pretoria, South Africa
[8]Natural Resources Defense Council, New York, NY, USA
[9]Department of Botany and Zoology, University of Stellenbosch, Stellenbosch, South Africa
[10]These authors contributed equally to this work.

priority areas will be both ecologically and evolutionary driven, and meet criteria for real-world implementation. To achieve this, we bridge concepts, themes, and data used in ME and SCP to build a shared understanding of objectives needed to guide conservation decision-making (the 'why' section). We then outline procedures for: (i) defining **conservation objectives**; and using objectives to (ii) guide ME data collection; (iii) calculate **molecular metrics**; (iii) spatially interpolate metrics; and (iv) integrate them into SCP tools (the 'how' section).

*Correspondence:
esnielsen@ucdavis.edu (E.S. Nielsen).
@Twitter: @erica_at_work (E.S. Nielsen),
@jeff_o_hanson (J.O. Hanson),
@Silviarbc (S.B. Carvalho),
@MariaBeger (M. Beger),
@HenriquesRo (R. Henriques),
@Francine.Kershaw (F. Kershaw), and
@vonderheydenlab (S. von der Heyden).

The 'why': bridging themes in molecular ecology and systematic conservation planning

ME is grounded in understanding spatiotemporal genetic variation of natural populations, and offers multiple evolutionary metrics fundamental to assessing, and conserving, genetic diversity [16]. Major evolutionary themes have a strong focus on connectivity, adaptive potential, diversity, differentiation, and demography (hereafter, 'CADDD'). Connectivity describes the level of **gene flow** between populations across their distributional range, including source/sink dynamics; adaptive potential refers to the genetic variance potentially derived from local selective pressures and can pertain to the **genomic vulnerability** of a species or its resilience to environmental changes (here we restrict this definition to relate to the amounts/frequencies of genes assumed to have adaptive functions); diversity represents all extant genetic variation in a population or species (putatively neutral or adaptive); differentiation refers to the relative degree of the isolation as measured by differences in allele frequencies among individuals or genetic clusters (populations); and demography includes inbreeding levels and N_e, as well as historical changes in both. Thus, CADDD encompasses data across putatively neutral and adaptive **loci** fundamental for assuring the long-term persistence of intraspecific biodiversity [12,17,18]. We propose that understanding how metrics of CADDD integrate into the defining themes of SCP can offer more clarity about whether molecular metrics are needed for conservation objectives.

SCP is a transparent, reproducible, and quantitative approach concerned with the optimal application of spatially explicit conservation **management actions** to promote the representation and persistence of biodiversity [10,19]. It involves generating **prioritizations** of sites to achieve conservation objectives, while accounting for social, economic, and political constraints efficiently. Conservation objective examples include safeguarding habitat of threatened species, restoring connectivity between isolated populations, or securing a comprehensive range of ecosystems [10]. Achieving such objectives requires clear and quantitative choices of the evolutionary levels (genes, populations, species, and ecosystems) and facets (taxonomic, phylogenetic, and functional) of biodiversity that are to be included [20,21]. SCP involves dividing the planning region into **planning units**, calculating the amount of each **conservation feature** in each one, and identifying sets of planning units that meet conservation goals. To ensure that prioritizations are feasible for implementation, SCP accounts for economic and opportunity costs, and resource-use requirements (e.g., ensuring sufficient areas for agricultural production or recreational fishing [22]). To maximize the efficiency of SCP, different algorithms and tools have been developed, including Marxan [23], Zonation [24], and the prioritizr R package [25] (Box 1). SCP has a set of principles to guide effective decision-making, which can be easily integrated with CADDD (Figure 1 and Table 1). Comprehensiveness refers to a system of conservation areas that sample the main components of biodiversity within a region of interest (e.g., ecoregions, habitat types, or species). Molecular data can provide insights into comprehensiveness at the species level using phylogenetic diversity as a conservation feature [26] or to find areas that best represent species, lineages, and populations [27]. Adequacy refers to the ability of a protected area network to promote long-term persistence of biodiversity and to ensure the viability of populations, species, and habitats. Molecular data can provide important insights into adequacy, by identifying **evolutionary significant units (ESUs)**, measuring differentiation, quantifying genetic diversity

Box 1. Conservation planning decision support tools

Currently, the most commonly used **decision support tools** for conservation planning are Marxan, Zonation, and the prioritizr R package [23–25]. These tools frame conservation planning as mathematical optimization problems and solve them to generate prioritizations. Both prioritizr and Zonation can import spatially explicit data formats (e.g., ESRI Shapefile or GeoTIFF). Additional software, such as CLUZ and QMarxan [88][ii], are available to assist with spatial processing for Marxan (step 4 of 'The how' section). In addition, Marxan Connect [70] is a general-purpose tool that enables inputting measures of connectivity, such as demographic (i.e., animal tracking/dispersal data), genetic, or structural connectivity (i.e., landscape resistance) as conservation features in Marxan prioritizations.

Each of the tools uses different mathematical formulations to express optimization problems. For example, Marxan uses the minimum set formulation wherein the goal is to identify the 'cheapest' set of planning units for implementing management actions, while ensuring that the expected amount of each feature meets a minimum threshold (termed 'representation target'). Zonation uses a budget-limited formulation in which the goal is to maximize the overall amount of each feature, while ensuring that the total cost of implementing management actions does not exceed a budget threshold. Finally, prioritizr allows users to create custom-built problem formulations (including both minimum set and budget-limited formulations). Additionally, these tools, except for Marxan (but see Marxan with Zones [89]), can accommodate multiple management actions and zones.

These tools also use different algorithms to generate prioritizations. Zonation uses a backward heuristic algorithm to iteratively rank planning units [24]. As such, thresholds are often imposed to identify planning units for prioritization (e.g., top 20% ranked planning units). Marxan uses the simulated annealing algorithm, which can identify prioritizations that are more cost-effective compared with heuristic algorithms [23]. Although both of these algorithms could identify cost-effective prioritizations, they do not guarantee optimality [90]. Non-optimal solutions can misdirect conservation resources and lead to inefficiencies. To overcome this limitation, prioritizr uses exact algorithms, which guarantee optimality [25], while Marxan and Zonation offer flexibility to quickly generate multiple solutions for stakeholder negotiations [23,24].

and adaptive potential, and estimating N_e [28]. Representativeness refers to the need to capture the full variety of biodiversity within conservation areas, ideally within each level of biological organization. Molecular data are imperative to assure that the diversity within each species is suitably represented, for instance, by prioritizing areas to capture each ESU or private alleles [29,30]. We distinguish interspecific data as applying to comprehensiveness, and intraspecific measures (e.g., number of populations) as applying to representativeness. Efficiency highlights the need to consider the economic and opportunity costs of foregone commercial and recreational activities [31]. While molecular data are unlikely to contribute directly to reserve efficiency, it can facilitate it by providing cost-effective data to guide SCP procedures. Connectivity relates to conservation plans that counteract landscape fragmentation and protect ecological corridors that underpin biodiversity persistence and ecosystem functioning [32]. Molecular connectivity can inform the objective of establishing connected reserve areas, within which the flow of genes can lead to demographic and genetic benefits in metapopulations [33].

The first four of these principles have long been known within the SCP literature as the CARE principles [34,35], and here we build on them to include connectivity (CARE-C). Understanding and integrating the connections between CADDD and CARE-C are essential for performing transdisciplinary analyses in which both ME and SCP tools are used to create novel conservation strategies (Figure 1 and Table 1). These connections are the foundation for integrating the two fields: we use them to explain and supplement a review of recent studies working at this interface (Table S1 in the supplemental information online).

The 'how': a practical guide to incorporating molecular data into spatial plans

We propose a five-step framework to achieve integration across ME and SCP, and highlight a case study in which the framework is used to prioritize CADDD-CARE dynamics (Box 2).

1. Define objectives

Conservation objectives should be defined following the CARE-C and CADDD principles. Following the CARE-C principles, objectives could be defined to ensure adequate coverage of different ecosystem types, provide habitat for threatened species, and minimize fragmentation of priority areas to

Glossary

Adaptive potential: capacity of populations to evolve genetically based changes in response to selection [87].
Connectivity: flow of genes, organisms, matter, and energy between and among locations.
Conservation features: biotic and abiotic elements for which long-term persistence is desirable.
Conservation objectives: quantifiable measure of success for a conservation planning exercise. Common examples include safeguarding an adequate amount of habitat for different species, or a suitable level of coverage for different ecosystems, or rare alleles, within a prioritization plan.
Conservation planning cost: any costs associated with implementing a conservation plan, including land acquisition, management, transaction, damage, and opportunity costs, or any surrogate, such as land area and human footprint.
Decision support tool: software that narrows the field of choice to support determinations, judgments, and courses of action, by providing management recommendations, foresight into potential outcomes of candidate management actions, or synthesizing available information.
Effective population size (N_e): number of individuals in a theoretical population that would generate the same value of a statistic of interest as observed in a real population.
Evolutionary significant unit (ESU): population that has substantial reproductive isolation, representing a distinct evolutionary component of the species.
Gene flow: exchange of alleles between populations due to migration with reproduction.
Genetic diversity: total number of genetic variants contained in a population/species. Example metrics include haplotype and nucleotide diversity, heterozygosity, or allelic richness.
Genomic vulnerability: measure of the genotypic change needed in a population to retain genotype–environment relationships under future environmental conditions.
Heterozygosity (He): proportion of individuals in a population that have more than one type of allele at a particular locus. Expected He is the proportion of heterozygous genotypes

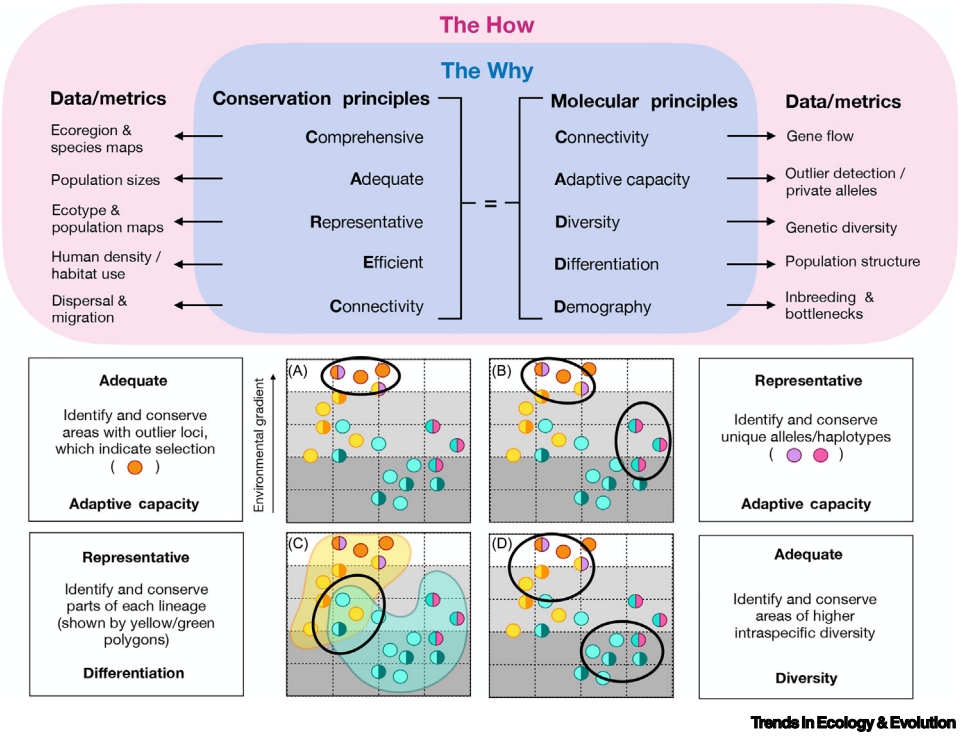

Figure 1. Integrating molecular ecology and systematic conservation planning. Theoretical integration of molecular ecology and systematic conservation planning. We show how the CARE-C principles of conservation planning (comprehensive, adequate, representative, efficient, connected) align with the prevalent topics in molecular ecology, here termed CADDD (connectivity, adaptive capacity, diversity, differentiation, demography), and highlight some example data/metrics used to capture each theoretical component. Spatial examples are also shown for prioritizations with objectives pertaining to the following principles: (A) adequate and adaptive capacity, (B) representative and adaptive capacity, (C) representative and differentiation, (D) adequate and diversity. Here, the spatial domains depict an environmental gradient (shown in gray scale) that is split into equal-size planning units. Individuals are shown by colored circles, with colors representing different genotypes. Theoretical conservation priority areas to maximize each combination of CARE-C and CADDD principles [using a minimum set formulation (Box 1)] are encircled by a black line.

support connectivity. Objectives could also emphasize cost efficiency, such as minimizing land acquisition costs, accounting for existing protected areas, and avoiding places designated for other resource use [36]. Objectives based on the CADDD principles could include securing an adequate amount of adaptive variants for particular species to enhance their persistence under global change (Table 1, cell g), protecting populations with different evolutionary histories to retain the breadth of molecular variation (Table 1, cell n), or maximizing gene flow between reserves (Table 1, cell p).

Although examples of using both CADDD and CARE-C principles to define objectives are rare, previous studies have shown that this can strengthen analyses. For example, Diniz-Filho *et al.* [37] defined objectives based on CADDD to represent a proportion of neutral genetic diversity of the Brazilian tree *Eugenia dysenterica* (Table 1, cell m), and objectives based on CARE-C to avoid regions where deforestation and demand for anthropogenic land-use were forecasted to increase. Defining conservation objectives is imperative because they have a critical role in each of the following steps.

2. Obtain molecular data

Molecular data need to be obtained so that they can inform conservation decisions. Field samples can be collected and genotyped, or previously published data can be collated from data

expected under Hardy–Weinberg equilibrium, which is often compared with the observed He.
Hybridization: interbreeding of two divergent lineages with independent evolutionary histories.
Inbreeding coefficient: measure of relative excess of homozygous individuals in a population, relative to the expectations under Hardy–Weinberg equilibrium; can result from reproduction between related individuals.
Interpolation: process of creating spatial surface data based on a set of sampled points.
Locus/loci: region/position in the genome.
Management actions: activities or interventions that can be implemented to achieve conservation goals (e.g., the establishment of a protected area, habitat restoration, or invasive species eradication).
Molecular ecology (ME): use of molecular tools to study ecological questions.
Molecular marker: specific regions of DNA that can be identified within the genome and allow detection of variations or polymorphisms that exist among individuals in the population.
Molecular metrics: statistical measures describing the state of variation in a molecular marker.
Planning units: discrete spatial areas that can be managed independently (e.g., grid cells, property boundaries, river segments, or coral reefs).
Population: group of individuals that coexist in time and space, utilize the same resources and habitat, and are more likely to interbreed.
Prioritization: priority areas identified as a result of the systematic conservation planning process.
Systematic conservation planning (SCP): structured process of locating, configuring, and designating areas to promote the representation and persistence of biodiversity and other natural values in a cost-effective way.

Table 1. Matching objectives and metrics across fields[a]

Conservation principles	Molecular principles				
	Connectivity (gene flow)	Adaptive capacity	Diversity	Differentiation	Demography
Comprehensive : PA system should contain broad range of biotic elements (e.g., species, ecoregions, etc.)	(a)	(b)	(c) OBJECTIVE: PA network to include all species present in system METRICS: Phylogenetic endemism Phylogenetic diversity	(d) OBJECTIVE: PA network to include all species present in system METRICS: Phylogenetic trees based on genetic differences Phylogeographic maps Phylogenetic distinctiveness	(e)
Adequate: PA system should contain a sufficient sample of each biotic element (e.g., amount of habitat) to achieve its long-term persistence	(f)	(g) OBJECTIVE: PA system to include a sufficient sample of a range of adaptive diversity to maximize probability of persistence under different disturbances METRICS: Genomic vulnerability Outlier allele frequency Rare/private alleles Population adaptive index (PAI) Adaptive score (Sadapt)	(h) OBJECTIVE: PA system to include areas that contain genetically diverse populations to ensure long-term persistence (e.g., low inbreeding, high heterozygosity) METRICS: Proportion of genetic 'unit' (species, population, deme) required to maximize genetic diversity Nucleotide and haplotype diversity Heterozygosity Allelic richness	(i) OBJECTIVE: PA system to include unique populations METRICS: Population structure (admixture plots) F_{ST}-based metrics Genetic distances (i.e., Nei's genetic distance)	(j) OBJECTIVE: PA systems that maintain adequate N_e (e.g., prioritizing management of populations with high N_e, or past demographic stability) METRICS: N_e **Inbreeding coefficients** Demographic history simulations
Representative: PA system should capture a sample of each biotic element that reflects diversity within that element (e.g., different ecotypes, etc.)	(k)	(l) OBJECTIVE: PA system to include a sufficient sample of a range of adaptive diversity and selective genotypes METRICS: Allele frequencies of candidate loci pertaining to different environmental features Adaptive genetic diversity Differently adapted lineages	(m) OBJECTIVE: PA system to include a sufficient sample of a range of neutral diversity, including rare alleles METRICS: Haplotype networks Rare/private alleles Neutral genetic clustering	(n) OBJECTIVE: Represent evolutionarily unique populations/lineages METRICS: Population structure (admixture plots/PCAs) F_{ST}-based metrics Genetic distances Lineage delineations	(o) OBJECTIVE: PA system to include a range of populations dynamics (e.g., to maintain metapopulation processes, such as adaptation, gene flow and divergence) METRICS: Measures of hybridization and inbreeding N_e and population growth rates Simulated eco-evolutionary range dynamics
Efficient: PA system should be cost-effective					
Connectivity: PA system should capture linkages that underpin persistence among sites	(p) OBJECTIVE: Maintain and/or enhance connectivity between populations METRICS: Migration rates (m) Effective number of migrants Slatkin's psi	(q) OBJECTIVE: Ensure that populations with potentially beneficial adaptations that export individuals are represented by a PA system (e.g., genetic rescue) METRICS: Allele frequencies of candidate loci or rare/private alleles	(r) OBJECTIVE: Ensure connectivity between places with high diversity is prioritized over others METRICS: Connectivity measures in combination with: Nucleotide or haplotype diversity Heterozygosity Allelic richness	(s)	(t) OBJECTIVE: Maintain and/or enhance connectivity between source and sink populations (i.e., ensure effective number of migrants between populations) METRICS: Effective number of migrants Connectivity and N_e measures Migration and resistance surfaces

[a]This table highlights the specific ways in which different components of conservation and molecular fields intersect, including examples of how different data types can be used to meet the respective objectives for protected area (PA) systems.

repositories (e.g., NCBI GenBank[i] and GeOMe[ii] [38]). In both cases, molecular data must contain spatial information (e.g., GPS coordinates) [39]. It is critical that the spatial locations where molecular data were collected are well suited to the objectives underpinning a conservation planning exercise. Taberlet *et al.* [40] aimed to generate a prioritization to secure broad-scale patterns of intraspecific neutral genetic variation for multiple plant species, and collected samples for each species across a spatial grid. Sampling design tools, such as SPOTG [41], are available to determine optimal sampling strategies to meet different ME objectives.

Deciding which **molecular marker**(s) to characterize molecular data from should be informed by conservation objectives. Multiple molecular markers are available [42], each with its advantages and disadvantages for particular conservation applications (see [43] for details). Traditionally, common markers were mitochondrial DNA (mtDNA) and microsatellites, while genome-wide SNPs are steadily gaining popularity as the dominant marker choice [28]. These markers are often used to detect spatial structure and historical processes, and can also be used to prioritize areas that capture an adequate amount of intraspecific adaptive variation (Table 1, cell g). Xuereb *et al.* [44] identified loci under selection in the giant California sea cucumber, *Parastichopus californicus,* using a redundancy analysis approach. When these SNPs, mainly associated with seafloor temperature gradient, were input into SCP, they gave higher priority to sites further south compared with non-adaptive genomic data sets.

SNPs offer more precise genomic inference, yet how SNP data are generated and analyzed requires careful consideration (reviewed in [45]). For example, estimates of population differentiation (F_{ST} metrics) were found to differ between genomic sequencing types [46], and putatively adaptive candidate loci have been shown to differ between outlier detection methods [47]. There is limited research on how different markers, sequencing types, and genomic analyses influence conservation planning outcomes, but Nielsen *et al.* [43] found that genetic markers (such as mtDNA) can capture the adaptive patterns of genomic SNPs when combined across multiple species. There are reports of SNPs offering minor changes to population structure originally identified by mtDNA or microsatellites (often with higher levels of substructuring [48,49]), but it remains unclear as to whether this degree of genetic structure is essential to meet conservation objectives.

3. Calculate molecular metrics

Molecular metrics are used to describe genetic characteristics of individuals, populations, or species. Given the diversity of metrics available (Table 1), they must be relevant to the conservation objectives. Species- and lineage-level analyses can inform about incipient speciation, phylogenetic diversity, and evolutionary distinctiveness [50]. Henriques *et al.* [51] assessed the efficacy of established marine protected areas in protecting a comprehensive array of evolutionary diversity in sparid fishes based on phylogenetic diversity (Table 1, cell d). Population-level analyses provide data about spatiotemporal patterns of intraspecific structure and diversity, and can provide evidence for selective pressures and local adaptation. Hanson *et al.* [52] used SNPs to characterize adaptive population clusters within amphibian species to prioritize management across the selection gradient, highlighting how metrics of population adaptive potential can create a representative reserve system (Table 1, cell l; and Box 2). Several tools exist to identify lineages and populations, such as general mixed Yule-coalescent models [53] and Bayesian clustering algorithms [54], respectively. Individual-level analyses can inform population membership, gene flow, and **hybridization** (Figure 1). Parker *et al.* [55] combined mitochondrial and nuclear genes to measure hybridization and introgression of introduced and native catfishes to identify areas where inbreeding was less likely to occur, using a demographic genetic metric for reserve design (Table 1, cell j) and preserving an adequate amount of nonhybridized areas. While these examples portray analyses within discrete taxonomic units, defining such units from the species to population continuum is often challenging.

Genomic data provide advantages to delineate species, populations, lineages, and ESUs (reviewed in [56]).

4. Prepare spatial features for prioritizations

SCP requires spatially explicit data for conservation features, **conservation planning costs**, and connectivity. Data must be available for all planning units considered within the planning region. Molecular metrics often pertain to point localities, such that many planning units lack measurements. Such point data need to be transformed into spatial data layers [57] and predicted over the planning domain. There are two main methodologies for predicting molecular data across space: geostatistics (using tools such as inverse distance weighting, kriging, and thin-plate splines [58,59]) and statistical models (using tools such as random forest, genetic dissimilarity, and eco-evolutionary models [60,61]). Phair *et al.* [62] used the geostatistic tool of inverse distance weighting to interpolate genomic neutral and adaptive diversity metrics of the seagrass, *Zostera capensis*, across South African estuaries to identify unique conservation priority areas compared with scenarios only targeting habitat type. By comparison, Bay *et al.* [63] used a statistical model (Gradient Forest), originally developed to model spatial variation in community composition [61], to predict changes in genetic variation under different climate scenarios for the American yellow warbler, *Setophaga petechia*, in North America. Machine learning techniques can simulate changes in the spatial patterns of the genetic diversity of a species over time in response to threatening processes, and future studies may be able to identify priority areas that are robust or maladapted to anticipated climatic threats [64]. The full range of intraspecific lineages can be predicted using models assuming that the lineage occurring at a given location is

Box 2. Case study

The five-step framework described in the main text was used to identify conservation areas for three frog species in the Iberian Peninsula (Figure I). Methodological details can be found in [52].

1. Define conservation objectives

The aim was to identify areas representing an adequate amount of neutral and adaptive features for three frog species (*Pelobates cultripes*, *Hyla molleri*, and *Rana iberica*), while limiting conflicts with existing land-use and accounting for existing protected areas.

2. Obtain molecular data

Stratified sampling was conducted, ensuring collection from representative climatic conditions across the ranges of the species. Non-gray colors in Figure I represent different climatic regions identified within the range of each species, whereas black dots represent sampling sites. Tissue samples were genotyped by Diversity Arrays Technology [91] generating SNPs.

3. Calculating molecular metrics

Molecular metrics were calculated for the three species (only shown in Figure I for *P. cultripes*). Lineages were identified using STRUCTURE [92], CLUMPP [93], and Evanno's K method [94]. Two lineages were identified (Figure I, represented by dots and triangles, respectively). Average **heterozygosity (He)** of each sampling locality was computed using inbreedR ([95] (3A), and outlier loci were identified using three outlier loci detection techniques. Within each lineage, individuals were further assigned to neutral (3B) and adaptive (3C) genetic clusters, using neutral and putative adaptive loci, respectively, using Gaussian mixture model-based cluster analyses [96] (Figure I; represented by distinct colors labeled 1–10).

4. Prepare spatial features for prioritization

Geostatistical models were used to predict molecular metrics across the range of each species. Predictions of He were made using thin-plate splines (4A) and predictions of major neutral lineages (Figure I; delimited by black lines) and neutral (4B) and adaptive (4C) clusters (Figure I; indicated by colors 1–10) were made with interpolation using phylin [66]. Maps of contemporary and potential future habitat suitability were computed using Maximum Entropy modeling, and combined to compute scores of long-term habitat suitability (4D). The human footprint index (HPI) was used to describe anthropogenic impact (4E). Data delineating the boundaries of existing protected areas were compiled (4F).

5. Spatial prioritization

The prioritizr R package was applied with the minimum set formulation of the reserve selection problem. HPI was used as a surrogate for opportunity costs. Representation targets were specified to secure neutral and adaptive processes for each species. Constraints were specified to avoid areas with high anthropogenic impact (per HPI), and keep existing protected areas. Results identified priority areas (5A).

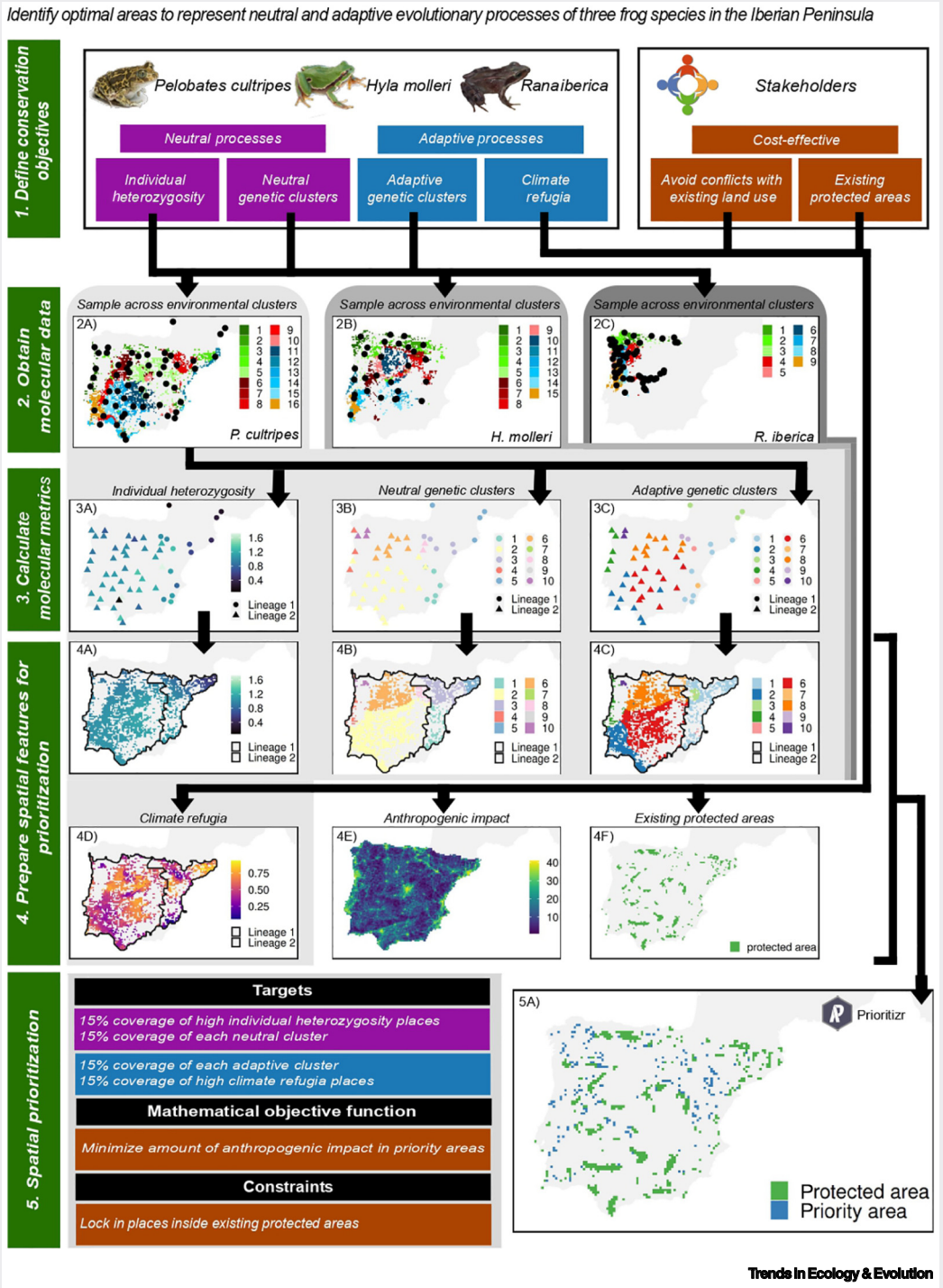

Figure I. Case study using five-step framework for integrating ME and SCP. Each row represents a step in the process, with boxes/maps representing data utilized within each step. Boxes within a light gray background highlight data inputs for our example species, *P. cultripes*, with the darker gray backgrounds representing data for the other two species which are not shown. The final step combines the data as conservation features, sets targets for each feature, and is input into a spatial planning tool to generate conservation priorities.

more likely to be a member of the closest known lineage [65]. For instance, the R package phylin uses kriging and inverse distance weighting to predict the probability of occurrence of each lineage in each location, informed by its 'distance' to all other localities, where 'distance' may be geographical, a measure of landscape resistance, or a measure of environmental differentiation [66]. Spatial sampling biases may influence the accuracy and confidence of **interpolations**. Sampling that is not fully representative of the region may result in poorly fitted models, and kriging does not apply to data sets without a spatial autocorrelation structure. Ideally, sampling sites should be distributed across the planning area, either following a systematic approach or stratified by ecological gradients. Importantly, ME conservation features should be prepared along with other features, such as land-use, habitat type, and/or existing protected areas, before being input in SCP tools (Box 3).

5. Spatial prioritization

5a. Set conservation constraints and targets

To help meet objectives, conservation planning frequently involves setting quantifiable targets for conservation features. Targets often specify a minimum level of spatial coverage of each feature that prioritizations should secure. Conventionally, targets have been set for ecological objectives, such as the percentage of the geographic range of a species [67], but they can also be used to meet evolutionary objectives, such as representing genetic diversity, ESUs, gene flow, and the adaptive potential of species [68] (Table 1). To maximize phylogenetic diversity (Table 1, cell c), Rosauer *et al.* [27] used targets of 15% of the spatial range of each branch of a phylogenetic tree containing 11 lizard genera, representing both inter- and intraspecific diversity. At the intraspecific level, population divergence/structure can be used to delineate conservation areas (Table 1, cell i) by securing a percentage of areas with low estimates of population differentiation (i.e., F_{ST}-based measures [29,69]), or a percentage of each lineage [52]. While they allow for quantifiable measures of effectiveness, targets are not always necessary to meet conservation goals. For example, prioritizations can be weighted by genetic connectivity matrices to promote connectivity (Table 1, cell p). Alternatively, specific planning regions can be 'locked-in' or secured within a reserve *a priori* (often due to socioeconomic constraints), and prioritizations can be used to identify the best areas to expand reserves to meet evolutionary objectives (Box 2 [70]).

5b. Choose a prioritization tool and run scenarios

SCP tools use mathematical algorithms to generate prioritizations that represent conservation features for the lowest cost (Box 1). Once spatial data have been collated and prepared, several scenarios are often considered to compare trade-offs in meeting targets for different features, and are useful to pinpoint areas where molecular and traditional objectives differ/overlap in their spatial priorities. Scenario comparisons are an essential part of SCP in that they can explore contradictions between different conservation features. In their goal to conserve the mammalian tree of life (Table 1, cell c), Rosauer *et al.* [71] found that many areas prioritized for high levels of phylogenetic diversity (molecular objective) substantially differed from areas prioritized for high species diversity (traditional objective). Features can also be weighted according to their importance, which is a built-in function of the prioritization tool Zonation, in which the computational strategy is to prioritize meeting targets of highly weighted features [24]. Carvalho *et al.* [20] considered alternate scenarios of prioritizing species distributions, where all species were weighted equally, or maximizing phylogenetic diversity, where the weight of each feature was relative to phylogenetic branch lengths. Comparing scenarios from traditional conservation and molecular features is a powerful approach to meeting objectives such as enhancing both species and lineage persistence.

Box 3. Conservation features

The final preparation of molecular features for SCP input requires converting spatial data into conservation features. Molecular conservation features can be defined as three types: (i) a measure of variation, in which areas will have a range of values (i.e., genetic diversity, allelic richness); (ii) a measure of demarcation, in which areas will be categorized into genetic entities (i.e., lineages or ESUs); or (iii) a measure of connectivity, in which connections between localities will have a range of values (i.e., gene flow or landscape resistance). Diversity metrics can either be retained as continuous metrics or categorized into discrete groups. For example, Nielsen *et al.* [29] categorized genetic diversity from mtDNA into low, medium, and high classes to ensure that each category was represented. Alternatively, Xuereb *et al.* [44] used continuous molecular metrics and targeted to protect 30% of the total number of planning units instead of a percentage of each molecular class. Whether to categorize molecular metrics should be driven by the data and question. If the objective is to have an adequate amount of genetic diversity (see Table 1, cell h in main text), and there is only a small geographical area with high diversity, then binning genetic diversity and conserving 20% of the high-ranking areas may not be as suitable as using a continuous metric and protecting a percentage of the entire area. If one wants to create a reserve system representative of genetic diversity (see Table 1, cell m in main text), then categorizing molecular diversity by similarity (e.g., by identifying genetic clusters or evolutionary lineages) and protecting a percentage of each category is likely the most appropriate solution.

Evolutionary features should then be combined with more traditional conservation features needed to meet conservation objectives, such as species ranges, habitat types, and land-use spatial layers. Hermoso *et al.* [97] had conservation planning scenarios, including species distributions of 46 freshwater fish species along with genetic lineages of four fish species, with a river disturbance index as a surrogate of potential conservation costs. Scenarios can be run with different objectives and their related features, such as ensuring high phylogenetic diversity, but additionally prioritizing: (i) fully protected national parks; (ii) national parks open for development; or (iii) areas immediately outside of national parks [98]. For species that are of conservation concern, EDGE scores can be calculated using phylogenetic diversity and Red List category weights [99], combining them into a single conservation feature.

Challenges and ways forward

Bridging ME and SCP provides unique and timely opportunities to tackle the biodiversity crisis, but is not without challenges (see Outstanding questions). Although molecular data have the potential to enhance conservation decision-making, their use should be pondered against the conservation objectives. For example, delaying conservation actions to produce molecular data may lead to poorer biodiversity outcomes when urgent intervention is required [72]. Molecular data are rarely available for all species considered in conservation planning, and are often limited by molecular marker types. Despite the growth of available genomic data sets, the number of species genotyped across their range is still relatively low compared with less informative genetic markers (such as mtDNA). Although many of the examples provided in this review use molecular data produced through older sequencing techniques (e.g., mtDNA and microsatellites), we emphasize that overall methodology and rationale for integrating molecular data into conservation planning remain similar when using more recent techniques. For example, both Beger *et al.* [69] and Hanson *et al.* [52] incorporate differentiation into prioritizations by subdividing the distributions of a species into evolutionary lineages, and conserving a proportion of each lineage, using microsatellites and genome-wide SNPs, respectively.

Increasingly, conservation planners may rely on genomic data for a set of keystone species [62], umbrella species ([73], but see [74]), or use other cost-effective surrogates of molecular metrics ([75], but see [76]). While high-throughput sequencing is invaluable to identify the adaptive potential of natural populations, there is still much uncertainty around the physiological aspects of adaptive potential and how to best map it across space and time [77]. We suggest further exploration of ME–SCP integration comparing multiple marker types, sampling designs, interpolation techniques, and spatial planning algorithms to further develop best practice guidelines. Finally, we found that certain ME–SCP links were extensively studied (such as Table 1, cells c, d, and m), but others require further inquiry, such as ways in which molecular diversity and differentiation can be used to enhance connectivity in reserves (Table S1 in the supplemental information online).

Despite these challenges, exciting recent developments within each field are likely to facilitate greater integration. The development of sequencing approaches and their applicability, such as the innovation of environmental DNA (eDNA) metabarcoding, may provide near real-time data on species diversity, and potentially within-species diversity [78], for conservation planning [79]. This, in addition to big data sets generated with other technologies, including remote sensing, citizen science, and internet ecology [80,81], will revolutionize the amount of data that can be used in conservation planning. In parallel, the sophistication and accuracy of climate models and ecological modeling to predict the distribution and abundance of different biodiversity dimensions across space and time are rapidly increasing [21,77,82,83]. The accompanying development of automated processes can leverage big data sets and prediction models to account for multiple biodiversity facets. This type of data will be invaluable to conserving biodiversity while attempting to protect or manage dynamic ecological, evolutionary, and socioeconomic processes [84] including planning under changing climates [85].

Concluding remarks

Ultimately, integrating ME and SCP concepts will pivot on co-creation between policymakers, planners, and molecular ecologists from the onset [15,86]. Bridging these fields is essential for achieving the recently proposed global conservation commitments for 2030 [3], such as expanding protected area systems, enhancing multispecies connectivity, meeting socioeconomic goals, promoting ecosystem services, and safeguarding genetic diversity. Only with an integrated approach can we design optimal conservation solutions able to revert biodiversity loss and achieve the ambitious vision of a sustainable future over the next decades.

Outstanding questions

When will spatial conservation planning benefit from molecular data, and when is more than one molecular data type needed? When are molecular data needed from multiple time points to meet conservation objectives?

How should we interpret molecular data across a wide range of taxa to meet conservation objectives and/or set conservation targets across multiple species and molecular metrics?

How can molecular data be used to inform multispecies conservation plans when such data are scarce or not available for all relevant species? Can ecological keystone and umbrella species serve as surrogates for multispecies evolutionary protection?

What is the best way to evaluate the effectiveness of, and adaptively manage, a conservation plan that aims to conserve evolutionary potential?

How can studies integrating ME into SCP better incorporate socioeconomic conservation features to understand the costs and effects of conserving evolutionary potential while meeting other objectives, such as development or tourism?

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Declaration of interests

None declared by authors.

Supplemental information

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Resources

[i]www.ncbi.nlm.nih.gov/genbank/

[ii]https://geome-db.org/

[iii]https://aproposinfosystems.com/

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