

Review

Cite this article: Andreello M, Manel S, Vilcot M, Xuereb A and D'Aloia CC (2023). Benefits of genetic data for spatial conservation planning in coastal habitats. *Cambridge Prisms: Coastal Futures*, 1, e28, 1–13
<https://doi.org/10.1017/cft.2023.16>

Received: 17 January 2023

Revised: 27 April 2023

Accepted: 04 May 2023

Keywords:

Systematic conservation planning; spatial conservation prioritization; marine protected areas; connectivity; eDNA

Corresponding author:

Marco Andreello;

Email: marco.andreello@ias.cnr.it

Benefits of genetic data for spatial conservation planning in coastal habitats

Marco Andreello¹ , Stéphanie Manel^{2,3}, Maurine Vilcot² , Amanda Xuereb⁴ and Cassidy C. D'Aloia⁵

¹Institute for the Study of Anthropogenic Impacts and Sustainability in the Marine Environment, National Research Council, CNR-IAS, Rome, Italy; ²CEFE, University of Montpellier, CNRS, EPHE-PSL University, IRD, Montpellier, France; ³Institut Universitaire de France, Paris, France; ⁴Département de Biologie, Institut de Biologie Intégrative et des Systèmes (IBIS), Université Laval, Québec, QC, Canada and ⁵Department of Biology, University of Toronto Mississauga, Mississauga, ON, Canada

Abstract

Coastal marine environments are subject to a variety of anthropogenic pressures that can negatively impact habitats and the biodiversity they harbor. Conservation actions such as marine protected areas, marine reserves, and other effective area-based conservation measures, are pivotal tools for protecting coastal biodiversity. However, to be effective, conservation area networks must be planned through a systematic conservation planning (SCP) approach. Recently, such approaches have begun to orient their goals toward the conservation of different biodiversity facets and to integrate different types of data. In this review, we illustrate how genetic data and molecular techniques can bring useful knowledge for SCP approaches that are both more comprehensive (sampling the full range of biodiversity) and more adequate (ensuring the long-term persistence of biodiversity). With an emphasis on coastal organisms and habitats, we focus on phylogenetic analysis, the estimation of neutral and adaptive intraspecific genetic diversity at different spatial levels (alpha, beta, and gamma), the study of connectivity and dispersal, and the information obtainable from environmental DNA techniques. For each of these applications, we discuss the benefits of its integration into SCP for coastal systems, its strengths and weaknesses, and the aspects yet to be developed.

Impact statement

Genetic data provide useful information to guide the siting and design of conservation areas in coastal systems, such as marine protected areas. For example, reconstructing the evolutionary relationships between species through a genetic-based phylogenetic tree can inform on the presence of evolutionarily distinct species and orient the creation of marine protected areas toward sites where these species are present. Another useful application of genetic data is parentage analysis, where juveniles can be assigned to their parents and the distance between them can be used to infer the dispersal capacities of these individuals in the larval stage. These data, in turn, can be used to define the spacing between different marine protected areas, so that larvae can disperse between them while minimizing the risk of being transported to areas open to fishing. We review how applications of genetic data (including phylogenetic inference, study of intraspecific genetic variation, estimation of dispersal, and sequencing of environmental DNA) can be fruitfully used to plan networks of marine conservation areas that are more effective, meaning that they protect all facets of biodiversity in the long term. The integration of genetic data into marine spatial conservation planning can thus help reach global goals of biodiversity conservation.

Introduction

The biodiversity of coastal ecosystems is subject to a variety of human pressures, such as water pollution, overfishing, and coastal development (Andreello et al., 2022b; Herbert-Read et al., 2022). Marine conservation areas (MCAs), which include marine protected areas (MPAs), marine reserves, and other effective area-based conservation measures (OECMs), can partially mitigate the impacts of these pressures (Maxwell et al., 2020; Grorud-Colvert et al., 2021; Gurney et al., 2021). The Kunming–Montreal Global Biodiversity Framework of the Convention on Biological Diversity recognizes that conservation areas are pivotal for biodiversity conservation; specifically, the framework prescribes all member states to effectively conserve and manage at least 30% of coastal and marine areas “through ecologically representative, well-connected and equitably governed systems of protected areas and other effective area-based conservation measures” (CBD, 2022).

© The Author(s), 2023. Published by Cambridge University Press. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<http://creativecommons.org/licenses/by/4.0>), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

 Cambridge Prisms

 CAMBRIDGE UNIVERSITY PRESS

To positively impact coastal biodiversity and ecosystems, MCAs should be placed and designed following clear conservation objectives, ideally within a systematic spatial conservation planning framework (Alvarez-Romero *et al.*, 2018; Balbar and Metaxas, 2019). Systematic conservation planning (SCP; here used as a synonym of spatial conservation planning and spatial conservation prioritization) is a process whereby limited resources are allocated to conservation actions (such as the creation of protected areas or ecosystem restoration) that are distributed on the seascape following a criterion of optimality (Margules and Pressey, 2000; Margules and Sarkar, 2007; Moilanen *et al.*, 2009b). The seascape under consideration is subdivided into planning units (PUs) of adequate size, usually dictated by the spatial scale at which the study is conducted. Each PU can be assigned to one or more conservation actions and each conservation action has a cost of implementation. In the case of MCA planning, the conservation actions are the creation of a MCA, or the zoning of a MCA into different statuses (e.g., fully protected or partially protected; Zupan *et al.*, 2018). Costs can be quantified in monetary terms (e.g., direct costs to create and manage a marine reserve or opportunity costs representing loss of previous seascape use) or set proportional to PU size.

The criteria guiding the selection of PUs for protection are usually those of comprehensiveness, adequacy, and efficiency (Kukkala and Moilanen, 2013). Comprehensiveness is the degree to which a set of MCAs samples the full range of biodiversity taking into account different biodiversity facets (e.g., species diversity, phylogenetic diversity, and intraspecific diversity), structure (e.g., habitat types), and functions (e.g., dispersal processes) (Wilson *et al.*, 2009; Pollock *et al.*, 2020). Adequacy means ensuring the long-term preservation of biodiversity: a common approach to address adequacy is to set conservation goals in the form of a minimum portion of species ranges covered by protected areas, but should also consider connectivity and evolutionary processes (Wilson *et al.*, 2009; Andreello *et al.*, 2022a). Efficiency means that comprehensiveness and adequacy should be fulfilled at the minimum possible cost or within a predefined budget. These criteria can be expressed in mathematical terms and formulated as a problem with explicit objectives and constraints, which can be solved using different approaches (Moilanen *et al.*, 2009a). The solution of the SCP problem is a list of PUs chosen for protection, which constitutes the network of MCAs for the region under study.

Molecular ecology techniques provide different types of genetic data that can inform the process of SCP in coastal marine systems (Andreello *et al.*, 2022a; Jeffery *et al.*, 2022; Nielsen *et al.*, 2022; Riginos and Beger, 2022). First, many marine ecosystems are highly biodiverse, making it important, but challenging, to detect and map the distribution of all facets of biodiversity and resolve the evolutionary history of species. Genetic data can help resolve the phylogenetic relationships between marine species and elucidate genetic diversity within species. Second, marine environments are often challenging to sample in, leaving much biodiversity unknown. Sequencing of marine *environmental DNA* (eDNA; terms in italic are defined in the glossary in Table 1) is increasingly employed to complement data on the spatial distribution of species, and has the potential to lead to more comprehensive SCP solutions. Third, genetic data can inform on the existence and distribution of locally adapted populations that can be more resistant to some anthropogenic selective pressures, for example, warming waters created by climate change. Finally, planning well-connected systems of MCAs requires knowledge of dispersal of marine organisms. Genetic data can play an important role in estimating dispersal, where other approaches (such as *biophysical models of larval dispersal*) may fail,

even if their applications to marine organisms must address the additional difficulties posed by high gene flow and large *effective population sizes*. With a focus on the properties of coastal marine systems, we review how four major genetic techniques (phylogenetic inference, estimation of intraspecific genetic diversity, estimation of dispersal, and environmental DNA sequencing) can be fruitfully used in SCP.

Leveraging genetic data for marine spatial conservation planning

Phylogenetic inference

A comprehensive view of biodiversity includes multiple facets (Mace *et al.*, 2003; Purvis *et al.*, 2005), one of which is the evolutionary history or evolutionary change represented by a set of taxa, usually quantified using metrics of *phylogenetic diversity*. Several reasons justify the consideration of evolutionary history in conservation decisions. First, conservation actions that preserve a greater amount of evolutionary history are to be favored because evolutionary history has intrinsic value like all other aspects of biodiversity. In addition, more evolutionary information is lost when a highly differentiated species from an old, species-poor clade becomes extinct than when a weakly differentiated species from a young, species-rich clade becomes extinct: this is often considered a sufficiently strong argument to prioritize phylogenetically distinct or unique species for conservation (Winter *et al.*, 2013). Phylogenetic relationships inferred from genetic data also can help conserve biodiversity when taxonomic status is uncertain (Rosauer *et al.*, 2018). From an anthropocentric point of view, conserving more evolutionary history means conserving more phenotypic diversity, which in turn can translate into enhanced benefits from ecosystem processes and potential future use of biodiversity, increased evolutionary potential, decreased extinction rates, and enhanced human experience due to a preference for nature's variety or novelty (Tucker *et al.*, 2019). A fundamental assumption underlying this point of view is that phylogenetic diversity can be a proxy for *functional diversity*, and is therefore linked to ecosystem functioning and services. However, the strength of the relationship between phylogenetic diversity and functional diversity varies greatly (Mazel *et al.*, 2018, 2019; Owen *et al.*, 2019) and stronger evidence is needed to use phylogenetic diversity as a surrogate for functional diversity in making conservation decisions (Tucker *et al.*, 2019).

High quality species-level phylogenetic trees are available for major groups of coastal organisms, including reef corals (Huang and Roy, 2015), cartilaginous fishes (Stein *et al.*, 2018), ray-finned fishes (Rabosky *et al.*, 2018), and marine mammals (Faurby *et al.*, 2018; Upham *et al.*, 2019), while the phylogenies of other marine taxa remain less known. These unresolved phylogenies will likely benefit from the development of new sequencing technologies that have enabled “phylogenomic” approaches, in which large numbers of sequenced genes in many taxa can be used to infer phylogenetic trees (Kapli *et al.*, 2020). Eventually, data from the EarthBiogenome project will allow estimating the phylogenetic tree of all eukaryotic species (Lewin *et al.*, 2022).

Gap analyses have shown that many existing systems of MCAs do not cover phylogenetic diversity adequately (Mouillot *et al.*, 2011; Guilhaumon *et al.*, 2015; May-Collado *et al.*, 2016; Robuchon *et al.*, 2021; Mouton *et al.*, 2022). For example, Mouillot *et al.* (2016) found that the global MPA system secured only 1.7% of the tree of life for corals, and 17.6% for fishes. Moreover, spatial analyses have shown that areas with high phylogenetic

Table 1. Glossary of terms used in the text

<i>Adaptive genetic diversity.</i> The genetic diversity that is estimated at adaptive genes, that is, those that have an effect on fitness (Holderegger et al., 2006).
<i>Adult spillover.</i> Outward net emigration of adults from marine protected areas (Di Lorenzo et al., 2020).
<i>Assignment test.</i> A statistical approach to match an individual recruit to its source population on the basis of the expected frequency of its multi-locus genotype in alternative putative sources (Manel et al., 2005; Christie et al., 2017).
<i>Biodiversity feature.</i> A component of biodiversity (e.g., species, alleles, and ecosystems) that can be mapped in a seascape.
<i>Biophysical models of larval dispersal.</i> Mathematical models that simulate dispersal of marine larvae by accounting for physical processes (e.g., buoyancy and advection by marine currents, waves, and tides) and biological processes (e.g., swimming, orientation, diel vertical migration, and mortality).
<i>Connectivity.</i> The flow of materials, energy, organisms, genes, etc. among habitat patches or regions of interests (Beger et al., 2022).
<i>Cryptobenthic fishes.</i> Adult fishes of typically <5 cm that are visually and/or behaviorally cryptic, and maintain a close association with the benthos (Depczynski and Bellwood, 2003).
<i>Demographic connectivity.</i> The relative contribution of dispersal to population dynamics.
<i>Effective population size.</i> 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 (Charlesworth, 2009).
<i>Environmental association analysis.</i> A statistical approach to identify genetic variants strongly associated with specific environmental conditions.
<i>Environmental DNA.</i> DNA that can be extracted from environmental samples (such as soil, water, or air), without first isolating any target organisms (Taberlet et al., 2012)
<i>Functional diversity.</i> The diversity of functional forms in a species set (or community) measured by a variety of metrics that use dendrograms or representations in multidimensional space (Pollock et al., 2020).
<i>Gene flow.</i> The transfer of genetic material from one population to another.
<i>Genetic connectivity.</i> The degree to which gene flow affects evolutionary processes within populations (Lowe and Allendorf, 2010).
<i>Genetic rescue.</i> A decrease in population extinction probability owing to gene flow.
<i>Haplotype diversity.</i> Probability that two randomly sampled individuals in a population differ in their haplotypes (i.e., mitochondrial DNA allele types).
<i>Larval export.</i> Outward net emigration of larvae from marine protected areas (Di Lorenzo et al., 2020).
<i>Microsatellite.</i> A set of short repeated DNA sequences at a particular locus on a chromosome, which vary in number in different individuals.
<i>Molecular operational taxonomic unit (MOTU).</i> A group of organisms identified from sequence identity, usually through the use of cluster algorithms and a predefined percentage sequence similarity (Blaxter et al., 2005; Deiner et al., 2017).
<i>Neutral genetic diversity.</i> The genetic diversity estimated at putatively neutral genes, that is, those that do not have any direct effect on fitness. This type of genetic diversity is selectively neutral and is useful to estimate dispersal (Holderegger et al., 2006).
<i>Nucleotide diversity.</i> Average number of nucleotide differences per site between any two DNA sequences chosen randomly from a population.
<i>Outlier test.</i> A statistical approach to identify loci involved in local adaptation by screening for alleles that show unusually high genetic differentiation among populations, that is, outside of the distribution expected under neutrality.
<i>Parentage analysis.</i> A statistical approach to match an individual recruit with a parent or parent-pair from a pool of candidate parents by resolving the Mendelian pattern of shared alleles between the parent and offspring (Christie et al., 2017).
<i>Phylogenetic diversity.</i> A measure of the total evolutionary history represented by a set of taxa, calculated by summing the branch lengths connecting a set of taxa on a phylogeny (Tucker et al., 2019).
<i>Phylogenetic tree.</i> A diagrammatic representation of the evolutionary relationships among various taxa.
<i>Representation target.</i> Minimum portion of a biodiversity feature that must be included in a system of protected areas.
<i>Species distribution model.</i> 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).
<i>Target capture.</i> Targeted capture (or hybridization capture) is a strategy that relies on the development of probes of pre-selected genomic regions used to capture and enrich eDNA by hybridization (Jones and Good, 2016; Sigsgaard et al., 2020).

diversity are also those with high taxonomic richness (Mouillot et al., 2011; Albouy et al., 2017), but do not always overlap with areas with high functional diversity (Mouillot et al., 2011; Mazel et al., 2018; Ng et al., 2022), highlighting the need to consider these biodiversity facets explicitly in SCP (Pollock et al., 2020). A common method to maximize phylogenetic diversity in SCP is to use the branches of the *phylogenetic tree* as *biodiversity features* (Rodrigues and Gaston, 2002).

Finally, although we have emphasized species-level phylogenies, we note that considerable genealogical variation exists within

species, so the phylogenetic approach can also be applied to integrate within-species genetic diversity into SCP (Carvalho et al., 2017).

Estimation of intraspecific genetic diversity

Intraspecific phenotypic diversity, in the form of phenotypic differentiation between individuals and populations, can be an asset allowing species to adapt to novel environmental conditions (Donelson et al., 2019). Such intraspecific phenotypic diversity

emerges from the interaction between environmental variability and genetic diversity. The importance of genetic diversity has now been recognized in applied conservation (Hoban et al., 2020, 2022). For example, the Kunming–Montreal Global Biodiversity Framework commits parties to preserve the genetic diversity of all species (CBD, 2022), including all wild species and not only crops or domestic animals as was prescribed by the Aichi targets (CBD, 2010). This objective is also motivated by mounting evidence of large declines in intraspecific genetic diversity in wild species (Leigh et al., 2019; Exposito-Alonso et al., 2022).

In the context of SCP, intraspecific genetic diversity can be partitioned into an alpha component, measuring genetic diversity within PUs, and a beta component, measuring genetic differentiation between different PUs (Gaggiotti et al., 2018; Jost et al., 2018). This partitioning is relevant to understanding how different populations contribute to the genetic diversity of the species at the seascape scale, the so-called gamma diversity (Donati et al., 2021). When *gene flow* is sufficiently high and *effective population sizes* are large, as in most marine species, PUs will be weakly differentiated and beta diversity will be close to zero, while alpha and gamma diversity will be similar (Donati et al., 2021). In such cases, protecting a relatively small number of PUs could be sufficient for protecting a high level of gamma diversity. In some cases, though, stronger levels of genetic differentiation can persist when oceanographic features act as barriers to gene flow (Pascual et al., 2017; Vilcot et al., 2023), or when life history traits (e.g., lack of a pelagic larval stage) limit species' dispersal capacity (Puritz et al., 2017). In these cases, the beta component of genetic diversity will be of significant consideration in SCP.

Different metrics and approaches can be used to measure the alpha, beta and gamma components of genetic diversity and to prioritize sites for protection. For example, Nielsen et al. (2017) used *haplotype diversity* and *nucleotide diversity* as metrics of alpha diversity in five coastal marine species to build an MCA system encompassing PUs with different levels of local genetic diversity. An alternative approach is to use the spatial distribution of alleles as biodiversity features and to define conservation objectives for the gamma level of genetic diversity. For example, Paz-Vinas et al. (2018) used SCP to reach regional-level targets of representation for different alleles at *microsatellite* loci in six species of freshwater fishes.

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 (Holderegger et al., 2006). Partitioning of genetic diversity into neutral and adaptive components is commonly achieved using *outlier tests* and *environmental association analyses* (Hoban et al., 2016; Manel et al., 2016). These techniques have suggested the existence of genetically based local adaptations to environmental conditions (e.g., water temperature, salinity, and oxygen concentration) despite extensive gene flow and lack of neutral genetic structure (e.g., Sandoval-Castillo et al., 2018; Xuereb et al., 2018; Boulanger et al., 2022; Dorant et al., 2022). Indeed, coastal environmental conditions are expected to change in the future and in many cases have already seen dramatic shifts, including temperature, salinity, and pH, in conjunction with local anthropogenic stressors (He and Silliman, 2019). Consequently, characterizing genetic adaptation is likely to be important for conservation in a climate change context by identifying populations that may harbor pre-adapted genetic variants and that may be able to contribute to the *genetic rescue* of other vulnerable populations (Bay and Palumbi, 2014; Bay et al., 2017; Matz et al., 2020).

Neutral and adaptive loci, and sets of loci associated with different environmental variables, can have markedly different

spatial distributions (Barbosa et al., 2018; Sandoval-Castillo et al., 2018); therefore, spatial protection priorities identified through SCP can vary (Hanson et al., 2020). For example, Xuereb et al. (2021a) identified different sets of priority PUs for protection of genetic diversity for the sea cucumber *Parastichopus californicus* in coastal British Columbia (Canada) depending on whether they considered neutral or putatively adaptive loci. The choice of metrics to measure adaptive genetic diversity also led to different spatial conservation priorities (Xuereb et al., 2021a).

Estimation of dispersal

The importance of connectivity for the conservation and management of marine species has long been recognized and prescribed as an important criterion for siting, sizing, and designing MCAs (Palumbi, 2003; Alvarez-Romero et al., 2018; Balbar and Metaxas, 2019). Indeed, determining whether the set of prioritized MCAs truly represents a connected “network” depends on the strength of connectivity between them. This criterion is emphasized in both the Aichi targets and the Kunming–Montreal Global Biodiversity Framework of the Convention on Biological Diversity, which requires that MCAs form a “well-connected” system (CBD, 2010, 2022).

Networks of MCAs should satisfy different connectivity-related objectives (Beger et al., 2022; Riginos and Beger, 2022). In particular, MCAs should be strategically designed, placed and spaced to protect foraging movements in the home range of species and ontogenetic migrations between habitats for different life cycle stages (Grüss et al., 2011; D'Aloia et al., 2017). Furthermore, MCA networks should ensure *demographic connectivity*, including replenishment of “sink” populations and recolonization of empty habitat patches (Almany et al., 2007; Saenz-Agudelo et al., 2011; Harrison et al., 2020), and *genetic connectivity*, particularly the spread of advantageous genetic variants allowing for *genetic rescue* of imperiled populations (Webster et al., 2017; Bell et al., 2019). Finally, connectivity allows marine reserves to support fisheries outside their borders through *adult spillover* and *larval export* (Andreello et al., 2017; Di Lorenzo et al., 2020; Medoff et al., 2022). Various operational approaches have been developed to integrate these aspects of connectivity into SCP (Daigle et al., 2020; Beger et al., 2022). These methods use node-based or link-based connectivity metrics (Table 2): PUs are represented as nodes (vertices) of a network, and connections (in the form of larval dispersal probabilities, gene flow or spatial distances between pairs of PUs) are the links (edges) between the nodes (Xuereb et al., 2020).

Genetic data can be used to estimate aspects of connectivity through the effects of dispersal (an individual-level process linked to connectivity; Baguette et al., 2013) on population genetics. More precisely, genetic data are used to estimate both noneffective dispersal (where the dispersing agent moves into another habitat regardless of whether it successfully reproduces and transmits its genes) and effective dispersal (when the disperser successfully transmits its genes) (Cayuela et al., 2018).

Noneffective dispersal can be estimated by individual-level genetic approaches such as population *assignment tests* and *parentage analysis* (Broquet and Petit, 2009; Cayuela et al., 2018). Assignment tests can inform on dispersal when individuals are confidently assigned to genetically differentiated groups or populations (Manel et al., 2005; Christie et al., 2017). Given these requirements, assignment tests are impractical for many marine species with large population sizes, high mobility, and weak population structure; however, they have been successfully applied to detect long-

Table 2. Methods to integrate connectivity into spatial conservation planning (SCP)

Method	Description
Connectivity as biodiversity feature (node-based)	Connectivity metrics, calculated for each planning unit (PU) and, possibly, for each species, are used as biodiversity features, possibly in addition to species as biodiversity features, in representation-based SCP (e.g., D'Aloia et al., 2017; Magris et al., 2018). However, setting <i>representation targets</i> for connectivity metrics poses difficulties both conceptually and practically.
Connectivity to split taxa (node-based)	Connectivity metrics are calculated for each PU, and possibly for each species, while species are the biodiversity features. The spatial distribution of each species is then split into several spatial layers grouping PUs sharing similar connectivity attributes (as in Beger et al., 2014). For example, distinct layers are used to represent sites with low, medium, and high local retention. Each layer is then assigned a spatial <i>representation target</i> . A limitation of this approach is that the number of distinct spatial layers and the boundaries between them are usually arbitrary.
Promoting connectivity by adding penalties (node-based)	Species are the biodiversity features and connectivity metrics are calculated for each PU and, possibly, for each species. Penalties are calculated as a function of these PU-specific connectivity metrics (Weeks, 2017). For example, PUs with lower local retention (thus, less likely to be self-persistent) might be given higher penalties to favor the selection of PUs with higher local retention (more likely to be self-persistent). A weight must be chosen to measure the relative importance of connectivity-based penalties and monetary costs.
Promoting connectivity by adding penalties (link-based)	Species are the biodiversity features and connectivity metrics are calculated between each pair of PUs (possibly for each species). Penalties are calculated as functions of pairwise connectivity metrics. One approach is to formulate the SCP problem to penalize solutions that have a high total amount of exposed boundary length by defining connectivity as adjacency between PUs (Ball et al., 2009). Another approach is to formulate the SCP problem to promote the selection of functionally connected PUs by defining connectivity as directional or nondirectional flows of organisms or matter (Beger et al., 2010). In both cases, a weight must be chosen to measure the relative importance of reducing the exposed boundary or promoting connectivity relative to the primary objective of minimizing overall cost.
Promoting connectivity by adding constraints (link-based)	Species are the biodiversity features and connectivity metrics are calculated between each pair of PUs. Various approaches ensure that prioritizations exhibit certain structural characteristics, for example, selected PUs form a contiguous MCA (Önal and Briers, 2006) or each selected PU has a certain number of neighbors surrounding it (Billionnet, 2013). Species-specific functional connectivity metrics can also be integrated to ensure protected area connectivity is achieved for each species (Hanson et al., 2019a). These approaches sometimes lead to formulation of complex SCP problems that require long computation times to be solved.

distance dispersal in a coral reef fish (D'Aloia et al., 2022). In contrast, parentage analysis has been repeatedly used to estimate dispersal in coastal fishes, including studies on dispersal between MPAs and larval supply from marine reserves to fished areas (e.g., Harrison et al., 2012; Almany et al., 2013; Baetscher et al., 2019). With appropriate marker panels, these methods are highly accurate, but usually only assign a small percentage of sampled individuals (Christie et al., 2017): therefore, they require extensive sampling of possible offspring and parents, which can limit their applications to relatively small populations and/or study areas. To date, parentage studies have also been taxonomically biased toward fishes, but there is promise in their application to invertebrates, such as corals (Dubé et al., 2020).

Effective dispersal can be estimated through simple relationships between migration rates and indices of genetic differentiation between populations (e.g., F_{ST}), but the assumptions of these relationships (such as equal size across populations; Whitlock and McCauley, 1999) are rarely met in natural populations, making this approach unreliable. Patterns of isolation-by-distance (IBD), where genetic similarity between individuals or populations decreases with spatial distance, can be used to estimate dispersal distances under the assumption of migration–drift equilibrium and knowledge of effective population density (e.g., Puebla et al., 2012; Benestan et al., 2021). When applied to two coral reef fishes with limited dispersal potential, IBD approaches provided estimates of effective dispersal distances that were very similar to estimates of noneffective dispersal obtained through parentage analysis (Pinsky et al., 2017; Naaykens and D'Aloia, 2022). Future work on other taxa will reveal whether these relationships hold for more dispersive species.

To date, only one marine SCP study has incorporated genetically derived estimates of dispersal rates (Beger et al., 2014). However, in recent years, genetic studies of marine dispersal have increased in number (Xuereb et al., 2020), widened in scope (from single species

to multi species (Benestan et al., 2021); from a single year to multiple years (Catalano et al., 2021); and from the detection of few dispersal events to the estimation of full connectivity matrices (Dedrick et al., 2021)), and seemingly improved in accuracy, as demonstrated by the concordance of dispersal estimates obtained with different approaches (D'Aloia et al., 2015, 2018, 2022; Pinsky et al., 2017; Bode et al., 2019). Moreover, there is potential to gain additional dispersal data from other genetic approaches such as clinal analyses (Gagnaire et al., 2015; Van Wyngaarden et al., 2017), spatial analyses of close kin (Rueger et al., 2020; Benestan et al., 2021; Jasper et al., 2022), and machine learning (e.g., Smith et al., 2023). If these trends continue, more datasets on marine dispersal rates and distances will become available for SCP applications.

Environmental DNA sequencing

Environmental DNA metabarcoding is a recently developed method to detect the presence of species and/or *molecular operational taxonomic units* (MOTUs) from DNA fragments released by organisms into their environment (Taberlet et al., 2018). A genetic marker (metabarcoding) is chosen to target a taxonomic group (e.g., eukaryotes and teleosts), identify MOTUs, and assign MOTUs to known species if the species' metabarcoding is sequenced (Miya, 2022). eDNA metabarcoding is recognized to outperform traditional techniques for detecting elusive species such as *cryptobenthic fishes* (Boulanger et al., 2021; Mathon et al., 2022) and rare species such as nonindigenous (Comtet et al., 2015; Duarte et al., 2021) or threatened species (Weltz et al., 2017; Juhel et al., 2022). For example, eDNA metabarcoding was able to detect 44% more shark species than underwater visual censuses and baited remote underwater video station survey methods, even with a much lower sampling effort (Boussarie et al., 2018).

As SCP requires extensive spatial occurrence data, eDNA is emerging as the method of choice to complete existing occurrence data at large spatial scales (Bani *et al.*, 2020; Table 3). To this end, eDNA metabarcoding has recently been used to improve *species distribution models* of lake fishes (Pukk *et al.*, 2021), deep sea fishes (McClenaghan *et al.*, 2020), and tropical coral reefs (Jaquier *et al.*, [under review](#)). eDNA metabarcoding is also a good method to complement distributional data for multiple biodiversity facets, as shown by the similarities of phylogenetic and functional diversity measurements obtained through eDNA metabarcoding to those obtained through underwater videos (Marques *et al.*, 2021).

eDNA has also started to be used to study intraspecific genetic diversity (Sigsgaard *et al.*, 2020; Table 3). While intraspecific applications of eDNA are currently limited by the nature, number, and length of markers used (see Table S1 in the Supplementary Material), they open important perspectives to the use of eDNA for estimating intraspecific genetic diversity and connectivity when tissue sampling is problematic, as for mobile, cryptobenthic or threatened species (Dugal *et al.*, 2022). The first intraspecific applications of eDNA were based on the metabarcoding of a single mitochondrial sequence (Sigsgaard *et al.*, 2016; Macé *et al.*, 2022). The challenge is now to extend the use of eDNA to multiple markers, including nuclear markers, to obtain more accurate estimates of intraspecific genetic diversity than with one single longer sequence. Andres *et al.* (2021) developed nuclear microsatellites from eDNA and applied it to the estimation of unique genetic contributors in an experimental mesocosm of *Neogobius melanostomus*, showing the potential of this technique to estimate population size. The next step toward obtaining finer spatial genetic structure estimates with eDNA is to get nuclear SNP data. *Target capture* is thus starting to be developed on eDNA for this purpose. In one recent example, Jensen *et al.* (2021) applied target capture of nuclear markers for whale sharks *Rhincodon*

typus on eDNA samples, but they obtained low read coverage of the targeted nuclear regions, and sequences were confounded by the highly abundant mackerel tuna *Euthynnus affinis*.

Successful applications to study interspecific and intraspecific diversity show that analysis of eDNA provides a potentially powerful tool to overcome the lack of spatial biodiversity data for marine SCP (Bani *et al.*, 2020). To the best of our knowledge, only one study has used eDNA metabarcoding in a SCP framework (Mathon *et al.*, [unpublished results](#)): the authors combined marine fish occurrence data from acoustic, video and eDNA metabarcoding to prioritize conservation units in a three-dimensional space across 15 seamounts and deep island slopes in the Coral Sea. eDNA metabarcoding identified almost twice as many families as baited remote underwater video stations, and 596 MOTUs versus 190 species (Mathon *et al.*, [unpublished results](#)).

Conclusions and future perspectives

The studies reviewed here show that genetic data can help meet the overarching goals of comprehensiveness, adequacy, and efficiency that inspire SCP (Nielsen *et al.*, 2022). Inclusion of phylogenetic diversity and intraspecific genetic diversity in addition to taxonomic diversity can increase the comprehensiveness of systems of MCAs, while the characterization of taxonomic diversity, itself, will benefit from the rapid generation of complementary information from eDNA techniques. The integration of connectivity and adaptive genetic diversity can help create networks of MCAs that better satisfy the adequacy criterion, because they ensure greater long-term persistence of biodiversity. In terms of economic efficiency, genetic data has the potential to both generate benefits and incur additional costs. For example, using genetic data to promote connectivity between MCAs and fished areas can increase the

Table 3. Potential use of information gained from eDNA in spatial conservation planning (SCP), and future developments

	Interspecific level	Intraspecific level
Information from eDNA with potential SCP applications	Estimation of species richness (Boulanger <i>et al.</i> , 2021). Estimation of phylogenetic diversity (Marques <i>et al.</i> , 2021). Complete species spatial distributions (Juhel <i>et al.</i> , 2022). Detection of elusive, rare, invasive, or threatened species (Juhel <i>et al.</i> , 2022).	Haplotype detection (Dugal <i>et al.</i> , 2022). Estimation of genetic diversity (Székely <i>et al.</i> , 2021). Estimation of genetic differentiation/connectivity (Parsons <i>et al.</i> , 2018).
Methods	Metabarcoding (e.g., Boulanger <i>et al.</i> , 2021). qPCR or ddPCR (Weltz <i>et al.</i> , 2017; Baker <i>et al.</i> , 2018).	Metabarcoding (Sigsgaard <i>et al.</i> , 2016). Target capture (Jensen <i>et al.</i> , 2021). Shotgun sequencing (Székely <i>et al.</i> , 2021).
Limits and developments	Limited to short sequences because longer sequences are more easily degraded. Shorter sequences only provide limited resolution to distinguish species/individuals. Errors in the amplification and sequencing of eDNA prevent the correct estimation of the number and frequency of haplotypes present in an eDNA sample. Target capture (Jensen <i>et al.</i> , 2021) or the use of unique molecular identifiers (Yoshitake <i>et al.</i> , 2021) shows potential to overcome some of these biases. Need complete reference database to assign MOTUs/sequences to known taxa (Marques <i>et al.</i> , 2021). Obtaining accurate estimates of species biomass and abundance requires further investigations of the relationships between eDNA read abundance and species abundance/biomass (Rourke <i>et al.</i> , 2022).	Need reference database of haplotypes to design taxa-specific primers for sequencing. Estimates of the number of individuals contributing to an eDNA sample are necessary to accurately characterize population-level genetic diversity (Andres <i>et al.</i> , 2021). Currently limited to single mtDNA sequences. In the future, need to extend to multiple markers and to nuclear DNA (Jensen <i>et al.</i> , 2021).
Advantages	Noninvasive. Cost and time efficient. Applicable at large spatial and temporal scales. Better species detection than traditional visual surveys. Multispecies and multi-taxon applications from a single sample. Does not always require taxonomic assignment (use of MOTUs).	

economic efficiency of MCAs thanks to the economic benefits that fisheries derive from increased catches. More generally, however, the integration of new facets and processes may increase the total area required to satisfy additional conservation targets and thus total conservation costs.

There are still few examples of the integration of genetic data in marine SCP, especially with regards to intraspecific genetic data (Table 4). This is mainly due to the low number of species for which spatial genetic data are available. While molecular ecology studies are being carried out on an increasing set of species, it will be

Table 4. List of published spatial conservation planning (SCP) studies for marine and coastal habitats integrating genetic data

Reference	Species, region, and genetic data	Type of analysis ^a	Objectives	Main results
Beger et al., 2014	Boring giant clam <i>Tridacna crocea</i> Coral Triangle 8 microsatellites	<i>Intraspecific genetic diversity</i> : genetic clusters, allelic richness, and local genetic differentiation. <i>Dispersal</i>	Representing 30% to 60% of each genetic feature and ensuring dispersal between conservation units	Inclusion of genetic data and genetic diversity metrics led to selection of planning units (PUs) that were not prioritized using habitat data only. Different metrics of genetic diversity resulted in different spatial conservation priorities.
Nielsen et al., 2017	5 rocky-shore species West coast of South Africa mtDNA	<i>Intraspecific genetic diversity</i> : haplotype diversity, nucleotide diversity, number of private haplotypes, and local genetic differentiation	Representing 30% of each genetic feature for each species individually and across all five species combined	All four genetic metrics selected similar sets of PUs. Single species had different sets of priority PUs and no single species was a good proxy for multispecies genetic patterns.
Mazel et al., 2018	1,536 species of tropical fishes Global Published phylogenetic tree	<i>Phylogenetic inference</i> : maximization of phylogenetic diversity	Maximizing phylogenetic diversity (sum of all branch lengths) for different groups of species and regions	The sets of PUs that maximized phylogenetic diversity did not always ensure a maximization of functional diversity.
Nielsen et al., 2020	5 rocky-shore species West coast of South Africa mtDNA for all species and SNPs for two species	<i>Intraspecific genetic diversity</i> : nucleotide diversity, percent of private alleles, percent of outlier SNPs	Representing 20 to 80% of each genetic feature for different sets of species, marker types (mtDNA vs. SNPs) and genetic diversity metrics (neutral vs. adaptive)	The sets of PUs selected using neutral genetic diversity metrics from mtDNA for the five species were similar to the sets of PUs identified using adaptive genetic diversity metrics from SNPs for the two species with SNPs data.
Xuereb et al., 2021a	California sea cucumber <i>Apostichopus californicus</i> Coast of British Columbia (Canada) 3,699 SNPs	<i>Intraspecific genetic diversity</i> : expected heterozygosity (neutral and adaptive), F_{ST} (neutral and adaptive), population adaptive index (Bonin and Bernatchez, 2009), adaptive score (Manel et al., 2018)	Representing 30% of each genetic feature	Different metrics led to different sets of priority PUs. In particular, adaptive heterozygosity and population adaptive index led to completely nonoverlapping sets of priority PUs.
Phair et al., 2021	Seagrass <i>Zostera capensis</i> Coast of South Africa SNPs	<i>Intraspecific genetic diversity</i> : nucleotide diversity, expected heterozygosity, allelic richness, proportion of shared SNPs, proportion private SNPs, proportion of outlier SNPs	Representing 30 to 50% of each genetic metric	Inclusion of genetic data and genetic diversity metrics led to selection of planning units (PUs) that were not prioritized using habitat data only. Different metrics of genetic diversity led to highly overlapping sets of priority PUs.
Sala et al., 2021	4,242 marine species including fishes, reptiles, birds, mammals, and others Global Published phylogenetic trees	<i>Phylogenetic inference</i> : evolutionary distinctiveness was used to weight species in a multispecies biodiversity benefit function	Maximizing a biodiversity benefit function and comparing it to other benefit functions defined for food provisioning and carbon storage	There were synergies and trade-offs between different objectives. Multi-objective prioritization identified priority areas across the global ocean.
Ng et al., 2022	805 coral species Global Published phylogenetic tree	<i>Phylogenetic inference</i> : maximization of phylogenetic diversity	Maximizing phylogenetic diversity (sum of all branch lengths) for different groups of species and regions	In most regions, the sets of PUs that maximized phylogenetic diversity were highly overlapping with sets of PUs that maximized functional diversity.

^aThis column indicates which of the four applications of genetic data presented in the main text (phylogenetic inference, intraspecific genetic diversity, dispersal, or eDNA) was used in the study. In the case of intraspecific genetic diversity, the genetic metrics are indicated. Note that there is no published SCP study integrating eDNA data.

important to assess whether environmental variables that are easier to obtain can be used as proxies for intraspecific genetic diversity. The few studies testing such hypotheses have yielded mixed results (Hanson *et al.*, 2017, 2021; Manel *et al.*, 2020) and predictive models relating environmental variables to genetic distance using isolation-by-resistance models (e.g., Boussarie *et al.*, 2022) remain rare in seascape genetics and seldom tested in an SCP setting (Hanson *et al.*, 2019a). eDNA represents a promising alternative, as readily available material could be used to obtain information on intraspecific genetic diversity and connectivity for multiple species from a single sample.

In cases where species-level genetic data already exist, it is important to account for uncertainty when integrating these data into SCP. In particular, uncertainty can arise from (i) genotyping errors (Pompanon *et al.*, 2005), (ii) information content of different molecular markers (D'Aloia *et al.*, 2020), (iii) identification of putatively adaptive and neutral loci (de Mita *et al.*, 2013; Dalongeville *et al.*, 2018), (iv) estimation of seascape genetic parameters from samples of finite size, obtained from a portion of a species' range (parameter uncertainty; Balkenhol and Fortin, 2015; Foster *et al.*, 2021), (v) differences between statistical approaches used to infer seascape genetic parameters and spatial planning algorithms (model uncertainty; Hanson *et al.*, 2019b), (vi) prediction of seascape genetic parameters in unsampled sites (Manel and Holder-egger, 2013), and (vii) availability of only a small number of species with genetic data that are used as a representative surrogate for the genetic biodiversity of all the species present in a region (Nielsen *et al.*, 2020). Recent studies have begun to integrate some of these aspects of uncertainty into genetically informed SCP (Nielsen *et al.*, 2020, 2022; Xuereb *et al.*, 2021a). Moreover, forward-in-time simulations are promising approaches for predicting spatial genetic patterns relevant for SCP and could be used to test the potential impact of conservation actions under complex eco-evolutionary scenarios (Xuereb *et al.*, 2021b), although there remains considerable uncertainty in the estimation of genetic and demographic parameters required for such simulations for the majority of marine species.

In spite of their low number, the published SCP studies in marine and coastal systems show that genetic data provide information that cannot be gained without them. For example, in some taxonomic groups, phylogenetic distances between species are only partially congruent with distances in functional traits, showing that genetic data are necessary to capture and prioritize the evolutionary relationships between species (Mazel *et al.*, 2018). Another important review of marine species showed that genetic-based estimates of larval dispersal can be an order of magnitude smaller than those obtained using *biophysical models* (Manel *et al.*, 2019). Such discrepancies have direct consequences for setting optimal distances between MCAs. More generally, expanding the taxonomic, phylogenetic, geographical, and temporal scope of seascape genetic studies will confirm or refute the generality of these patterns and their consequences on the optimal design of effective MCA networks to protect coastal biodiversity. Given the ongoing increases in molecular data collection across diverse marine taxa and habitats, we anticipate that genetic and genomic data will play an increasingly prominent role in coastal SCP.

Open peer review. To view the open peer review materials for this article, please visit <http://doi.org/10.1017/cft.2023.16>.

Supplementary material. The supplementary material for this article can be found at <http://doi.org/10.1017/cft.2023.16>.

Data availability statement. Data availability is not applicable to this article as no new data were created or analyzed in this study.

Acknowledgments. We thank Richard Schuster, two other anonymous reviewers, and the senior editor Martin Le Tissier for their helpful comments. We also thank the editor Alicia Acosta and the publisher and senior scientific editor Jessica Jones for encouraging us to write this review.

Author contribution. Conceptualization: M.A.; Writing – original draft, and review and editing: M.A., S.M., M.V., A.X., and C.D.

Financial support. This work was supported by Agence Nationale de la Recherche (Grant No. ANR-18-CE02-0016 SEAMOUNTS).

Competing interest. The authors declare no competing interest.

References

- Albouy C, Delattre VL, Mériqot B, Meynard CN and Leprieur F (2017) Multifaceted biodiversity hotspots of marine mammals for conservation priorities. *Diversity and Distributions* 23(6), 615–626. <https://doi.org/10.1111/ddi.12556>
- Almany GR, Berumen ML, Thorrold SR, Planes S and Jones GP (2007) Local replenishment of coral reef fish populations in a marine reserve. *Science* 316 (5825), 742–744. <https://doi.org/10.1126/science.1140597>
- Almany GR, Hamilton RJ, Bode M, Matawai M, Potuku T, Saenz-Agudelo P, Planes S, Berumen ML, Rhodes KL, Thorrold SR, Russ GR and Jones GP (2013) Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. *Current Biology* 23(7), 626–630. <https://doi.org/10.1016/j.cub.2013.03.006>
- Álvarez-Romero JG, Mills M, Adams VM, Gurney GG, Pressey RL, Weeks R, Ban NC, Cheok J, Davies TE, Day JC, Hamel MA, Leslie HM, Magris RA and Storlie CJ (2018) Research advances and gaps in marine planning: Towards a global database in systematic conservation planning. *Biological Conservation* 227, 369–382. <https://doi.org/10.1016/j.biocon.2018.06.027>
- Andreello M, D'Aloia C, Dalongeville A, Escalante MA, Guerrero J, Perrier C, Torres-Florez JP, Xuereb A and Manel S (2022a) Evolving spatial conservation prioritization with intraspecific genetic data. *Trends in Ecology & Evolution* 37(6), 553–564. <https://doi.org/10.1016/j.tree.2022.03.003>
- Andreello M, Darling ES, Wenger A, Suárez-Castro AF, Gelfand S and Ahmadi GN (2022b) A global map of human pressures on tropical coral reefs. *Conservation Letters* 15(1), e12858. <https://doi.org/10.1111/conl.12858>
- Andreello M, Guilhaumon F, Albouy C, Parravicini V, Scholtens J, Verley P, Barange M, Sumaila UR, Manel S and Mouillot D (2017) Global mismatch between fishing dependency and larval supply from marine reserves. *Nature Communications* 8, 16039. <https://doi.org/10.1038/ncomms16039>
- Andres KJ, Sethi SA, Lodge DM and Andrés J (2021) Nuclear eDNA estimates population allele frequencies and abundance in experimental mesocosms and field samples. *Molecular Ecology* 30(3), 685–697. <https://doi.org/10.1111/mec.15765>
- Baetscher DS, Anderson EC, Gilbert-Horvath EA, Malone DP, Saarman ET, Carr MH and Garza JC (2019) Dispersal of a nearshore marine fish connects marine reserves and adjacent fished areas along an open coast. *Molecular Ecology* 28(7), 1611–1623. <https://doi.org/10.1111/mec.15044>
- Baguette M, Blanchet S, Legrand D, Stevens VM and Turlure C (2013) Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews* 88(2), 310–326. <https://doi.org/10.1111/brv.12000>
- Baker CS, Steel D, Nieuirkirk S and Klinck H (2018) Environmental DNA (eDNA) from the wake of the whales: Droplet digital PCR for detection and species identification. *Frontiers in Marine Science* 5, 133. <https://doi.org/10.3389/fmars.2018.00133>
- Balbar AC and Metaxas A (2019) The current application of ecological connectivity in the design of marine protected areas. *Global Ecology and Conservation* 17, e00569. <https://doi.org/10.1016/j.gecco.2019.e00569>
- Balkenhol N and Fortin M-J (2015) Basics of study design: Sampling landscape heterogeneity and genetic variation for landscape genetic studies. In Balkenhol N, Cushman SA, Storfer AT and Waits LP (eds.), *Landscape Genetics*,

- Chichester: John Wiley & Sons, Ltd., pp. 58–76. <https://doi.org/10.1002/9781118525258.ch04>
- Ball IR, Possingham HP and Watts M** (2009) Marxan and relatives: Software for spatial conservation prioritisation. In Moilanen A, Wilson KA and Possingham HP (eds.), *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools*. Oxford: Oxford University Press, pp. 185–195.
- Bani A, de Brauwier M, Creer S, Dumbrell AJ, Limmon G, Jompa J, von der Heyden S and Beger M** (2020) Chapter ten – Informing marine spatial planning decisions with environmental DNA. In Dumbrell AJ, Turner EC and Fayle TM (eds.), *Advances in Ecological Research*, Vol. 62. Cambridge, MA: Academic Press, pp. 375–407. <https://doi.org/10.1016/b.s.aacr.2020.01.011>
- Barbosa S, Mestre F, White TA, Paupério J, Alves PC and Searle JB** (2018) Integrative approaches to guide conservation decisions: Using genomics to define conservation units and functional corridors. *Molecular Ecology* 27(17), 3452–3465. <https://doi.org/10.1111/mec.14806>
- Bay RA and Palumbi SR** (2014) Multilocus adaptation associated with heat resistance in reef-building corals. *Current Biology* 24(24), 2952–2956. <https://doi.org/10.1016/j.cub.2014.10.044>
- Bay RA, Rose NH, Logan CA and Palumbi SR** (2017) Genomic models predict successful coral adaptation if future ocean warming rates are reduced. *Science Advances* 3(11), e1701413. <https://doi.org/10.1126/sciadv.1701413>
- Beger M, Linke S, Watts M, Game E, Treml E, Ball I and Possingham HP** (2010) Incorporating asymmetric connectivity into spatial decision making for conservation. *Conservation Letters* 3(5), 359–368. <https://doi.org/10.1111/j.1755-263X.2010.00123.x>
- Beger M, Metaxas A, Balbar AC, McGowan JA, Daigle R, Kuempel CD, Treml EA and Possingham HP** (2022) Demystifying ecological connectivity for actionable spatial conservation planning. *Trends in Ecology & Evolution* 37(12), 1079–1091. <https://doi.org/10.1016/j.tree.2022.09.002>
- Beger M, Selkoe KA, Treml E, Barber PH, von der Heyden S, Crandall ED, Toonen RJ and Riginos C** (2014) Evolving coral reef conservation with genetic information. *Bulletin of Marine Science* 90(1), 159–185. <https://doi.org/10.5343/bms.2012.1106>
- Bell DA, Robinson ZL, Funk WC, Fitzpatrick SW, Allendorf FW, Tallmon DA and Whiteley AR** (2019) The exciting potential and remaining uncertainties of genetic rescue. *Trends in Ecology & Evolution* 34(12), 1070–1079. <https://doi.org/10.1016/j.tree.2019.06.006>
- Benestan L, Fietz K, Loiseau N, Guerin PE, Trofimenko E, Rühs S, Schmidt C, Rath W, Biastoch A, Pérez-Ruzafa A, Baixauli P, Forcada A, Arcas E, Lenfant P, Mallol S, Goñi R, Velez L, Höppner M, Kininmonth S, Mouillot D, Puebla O and Manel S** (2021) Restricted dispersal in a sea of gene flow. *Proceedings of the Royal Society B: Biological Sciences* 288(1951), 20210458. <https://doi.org/10.1098/rspb.2021.0458>
- Billionnet A** (2013) Mathematical optimization ideas for biodiversity conservation. *European Journal of Operational Research* 231(3), 514–534. <https://doi.org/10.1016/j.ejor.2013.03.025>
- Blaxter M, Mann J, Chapman T, Thomas F, Whitton C, Floyd R and Abebe E** (2005) Defining operational taxonomic units using DNA barcode data. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360(1462), 1935–1943. <https://doi.org/10.1098/rstb.2005.1725>
- Bode M, Leis JM, Mason LB, Williamson DH, Harrison HB, Choukroun S and Jones GP** (2019) Successful validation of a larval dispersal model using genetic parentage data. *PLoS Biology* 17(7), e3000380. <https://doi.org/10.1371/journal.pbio.3000380>
- Bonin A and Bernatchez L** (2009) Challenges in assessing adaptive genetic diversity: Overview of methods and empirical illustrations. In Bertorelle G, Bruford MW, Hauffe HC, Rizzoli A and Vernesi C (eds.), *Population Genetics for Animal Conservation*. Cambridge: Cambridge University Press, pp. 123–147. <https://doi.org/10.1017/CBO9780511626920.007>
- Boulanger E, Benestan L, Guerin P-E, Dalongeville A, Mouillot D and Manel S** (2022) Climate differently influences the genomic patterns of two sympatric marine fish species. *Journal of Animal Ecology* 91(6), 1180–1195. <https://doi.org/10.1111/1365-2656.13623>
- Boulanger E, Loiseau N, Valentini A, Arnal V, Boissery P, Dejean T, Deter J, Guellati N, Holon F, Juhel JB, Lenfant P, Manel S and Mouillot D** (2021) Environmental DNA metabarcoding reveals and unpacks a biodiversity conservation paradox in Mediterranean marine reserves. *Proceedings of the Royal Society B: Biological Sciences* 288(1949), 20210112. <https://doi.org/10.1098/rspb.2021.0112>
- Boussarie G, Bakker J, Wangenstein OS, Mariani S, Bonnin L, Juhel JB, Kiszka JJ, Kulbicki M, Manel S, Robbins WD, Vigliola L and Mouillot D** (2018) Environmental DNA illuminates the dark diversity of sharks. *Science Advances* 4(5), eaap9661. <https://doi.org/10.1126/sciadv.aap9661>
- Boussarie G, Momigliano P, Robbins WD, Bonnin L, Cornu JF, Fauvelot C, Kiszka JJ, Manel S, Mouillot D and Vigliola L** (2022) Identifying barriers to gene flow and hierarchical conservation units from seascape genomics: A modelling framework applied to a marine predator. *Ecography* 2022(7), e06158. <https://doi.org/10.1111/ecog.06158>
- Broquet T and Petit EJ** (2009) Molecular estimation of dispersal for ecology and population genetics. *Annual Review of Ecology, Evolution, and Systematics* 40(1), 193–216. <https://doi.org/10.1146/annurev.ecolsys.110308.120324>
- Carvalho SB, Velo-Antón G, Tarroso P, Portela AP, Barata M, Carranza S, Moritz C and Possingham HP** (2017) Spatial conservation prioritization of biodiversity spanning the evolutionary continuum. *Nature Ecology & Evolution* 1(6), 0151. <https://doi.org/10.1038/s41559-017-0151>
- Catalano KA, Dedrick AG, Stuart MR, Puritz JB, Montes HR and Pinsky ML** (2021) Quantifying dispersal variability among nearshore marine populations. *Molecular Ecology* 30(10), 2366–2377. <https://doi.org/10.1111/mec.15732>
- Cayuela H, Rougemont Q, Prunier JG, Moore JS, Clobert J, Besnard A and Bernatchez L** (2018) Demographic and genetic approaches to study dispersal in wild animal populations: A methodological review. *Molecular Ecology* 27(20), 3976–4010. <https://doi.org/10.1111/mec.14848>
- CBD** (2010) The strategic plan for biodiversity 2011–2020 and the Aichi biodiversity targets. COP 10 decision X/2. Available at <https://www.cbd.int/decision/cop/?id=12268> Accessed on 24th May 2023.
- CBD** (2022) Kunming–Montreal Global Biodiversity Framework. CBD/COP/15/L.25. Available at <https://www.cbd.int/doc/decisions/cop-15/cop-15-dec-04-en.pdf> Accessed on 24th May 2023.
- Charlesworth B** (2009) Fundamental concepts in genetics: Effective population size and patterns of molecular evolution and variation. *Nature Reviews. Genetics* 10(3), 195–205. <https://doi.org/10.1038/nrg2526>
- Christie MR, Meirns PG, Gaggiotti OE, Toonen RJ and White C** (2017) Disentangling the relative merits and disadvantages of parentage analysis and assignment tests for inferring population connectivity. *ICES Journal of Marine Science* 74(6), 1749–1762. <https://doi.org/10.1093/icesjms/fsx044>
- Comtet T, Sandionigi A, Viard F and Casiraghi M** (2015) DNA (meta) barcoding of biological invasions: A powerful tool to elucidate invasion processes and help managing aliens. *Biological Invasions* 17(3), 905–922. <https://doi.org/10.1007/s10530-015-0854-y>
- Daigle RM, Metaxas A, Balbar AC, McGowan J, Treml EA, Kuempel CD, Possingham HP and Beger M** (2020) Operationalizing ecological connectivity in spatial conservation planning with Marxan connect. *Methods in Ecology and Evolution* 11(4), 570–579. <https://doi.org/10.1111/2041-210X.13349>
- D’Aloia CC, Andrés JA, Bogdanowicz SM, McCune AR, Harrison RG and Buston PM** (2020) Unraveling hierarchical genetic structure in a marine metapopulation: A comparison of three high-throughput genotyping approaches. *Molecular Ecology* 29(12), 2189–2203. <https://doi.org/10.1111/mec.15405>
- D’Aloia CC, Bogdanowicz SM, Andrés JA and Buston PM** (2022) Population assignment tests uncover rare long-distance marine larval dispersal events. *Ecology* 103(1), e03559. <https://doi.org/10.1002/ecy.3559>
- D’Aloia CC, Bogdanowicz SM, Francis RK, Majoris JE, Harrison RG and Buston PM** (2015) Patterns, causes, and consequences of marine larval dispersal. *Proceedings of the National Academy of Sciences of the United States of America* 112(45), 13940–13945. <https://doi.org/10.1073/pnas.1513754112>
- D’Aloia CC, Daigle RM, Côté IM, Curtis JMR, Guichard F and Fortin M-J** (2017) A multiple-species framework for integrating movement processes across life stages into the design of marine protected areas. *Biological Conservation* 216, 93–100. <https://doi.org/10.1016/j.biocon.2017.10.012>
- D’Aloia CC, Xuereb A, Fortin M-J, Bogdanowicz SM and Buston PM** (2018) Limited dispersal explains the spatial distribution of siblings in a reef fish population. *Marine Ecology Progress Series* 607, 143–154. <https://doi.org/10.3354/meps12792>
- Dalongeville A, Benestan L, Mouillot D, Lobreaux S and Manel S** (2018) Combining six genome scan methods to detect candidate genes to salinity in

- the Mediterranean striped red mullet (*Mullus surmuletus*). *BMC Genomics* **19** (1), 217. <https://doi.org/10.1186/s12864-018-4579-z>
- de Mita S, Thuillet A-C, Gay L, Ahmadi N, Manel S, Ronfort J and Vigouroux Y (2013) Detecting selection along environmental gradients: Analysis of eight methods and their effectiveness for outbreeding and selfing populations. *Molecular Ecology* **22**(5), 1383–1399. <https://doi.org/10.1111/mec.12182>
- Dedrick AG, Catalano KA, Stuart MR, White JW, Montes Jr. HR and Pinsky ML (2021) Persistence of a reef fish metapopulation via network connectivity: Theory and data. *Ecology Letters* **24**(6), 1121–1132. <https://doi.org/10.1111/ele.13721>
- Deiner K, Bik HM, Mächler E, Seymour M, Lacoursière-Roussel A, Altermatt F, Creer S, Bista I, Lodge DM, Vere N, Pfrender ME and Bernatchez L (2017) Environmental DNA metabarcoding: Transforming how we survey animal and plant communities. *Molecular Ecology* **26**(21), 5872–5895. <https://doi.org/10.1111/mec.14350>
- Depczynski M and Bellwood DR (2003) The role of cryptobenthic reef fishes in coral reef trophodynamics. *Marine Ecology Progress Series* **256**, 183–191. <https://doi.org/10.3354/meps256183>
- Di Lorenzo M, Guidetti P, Di Franco A, Calò A and Claudet J (2020) Assessing spillover from marine protected areas and its drivers: A meta-analytical approach. *Fish and Fisheries* **21**(5), 906–915. <https://doi.org/10.1111/faf.12469>
- Donati GFA, Zemp N, Manel S, Poirier M, Claverie T, Ferraton F, Gaboriau T, Govinden R, Hagen O, Ibrahim S, Mouillot D, Leblond J, Julius P, Velez L, Zareer I, Ziyad A, Leprieur F, Albouy C and Pellissier L (2021) Species ecology explains the spatial components of genetic diversity in tropical reef fishes. *Proceedings of the Royal Society B: Biological Sciences* **288**(1959), 20211574. <https://doi.org/10.1098/rspb.2021.1574>
- Donelson JM, Sunday JM, Figueira WF, Gaitán-Espitia JD, Hobday AJ, Johnson CR, Leis JM, Ling SD, Marshall D, Pandolfi JM, Pecl G, Rodgers GG, Booth DJ and Munday PL (2019) Understanding interactions between plasticity, adaptation and range shifts in response to marine environmental change. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**(1768), 20180186. <https://doi.org/10.1098/rstb.2018.0186>
- Dorant Y, Laporte M, Rougemont Q, Cayuela H, Rochette R and Bernatchez L (2022) Landscape genomics of the American lobster (*Homarus americanus*). *Molecular Ecology* **31**(20), 5182–5200. <https://doi.org/10.1111/mec.16653>
- Duarte S, Vieira PE, Lavrador AS and Costa FO (2021) Status and prospects of marine NIS detection and monitoring through (e)DNA metabarcoding. *Science of the Total Environment* **751**, 141729. <https://doi.org/10.1016/j.scitotenv.2020.141729>
- Dubé CE, Boissin E, Mercière A and Planes S (2020) Parentage analyses identify local dispersal events and sibling aggregations in a natural population of millepora hydrocorals, a free-spawning marine invertebrate. *Molecular Ecology* **29**(8), 1508–1522. <https://doi.org/10.1111/mec.15418>
- Dugal L, Thomas L, Jensen MR, Sigsgaard EE, Simpson T, Jarman S, Thomsen PF and Meekan M (2022) Individual haplotyping of whale sharks from seawater environmental DNA. *Molecular Ecology Resources* **22**(1), 56–65. <https://doi.org/10.1111/1755-0998.13451>
- Exposito-Alonso M, Booker TR, Czech L, Gillespie L, Hateley S, Kyriazis CC, Lang PLM, Leventhal L, Nogues-Bravo D, Pagowski V, Ruffley M, Spence JP, Toro Arana SE, Weiß CL and Zess E (2022) Genetic diversity loss in the Anthropocene. *Science* **377**(6613), 1431–1435. <https://doi.org/10.1126/science.abn5642>
- Faurby S, Davis M, Pedersen RØ, Schowanek SD, Antonelli A and Svenning J-C (2018) PHYLACINE 1.2: The phylogenetic atlas of mammal macroecology. *Ecology* **99**(11), 2626–2626. <https://doi.org/10.1002/ecy.2443>
- Foster SD, Feutry P, Grewe P and Davies C (2021) Sample size requirements for genetic studies on yellowfin tuna. *PLoS One* **16**(11), e0259113. <https://doi.org/10.1371/journal.pone.0259113>
- Gaggiotti OE, Chao A, Peres-Neto P, Chiu CH, Edwards C, Fortin MJ, Jost L, Richards CM and Selkoe KA (2018) Diversity from genes to ecosystems: A unifying framework to study variation across biological metrics and scales. *Evolutionary Applications* **11**(7), 1176–1193. <https://doi.org/10.1111/eva.12593>
- Gagnaire P, Broquet T, Aurelle D, Viard F, Souissi A, Bonhomme F, Arnaud-Haond S and Bierne N (2015) Using neutral, selected, and hitchhiker loci to assess connectivity of marine populations in the genomic era. *Evolutionary Applications* **8**(8), 769–786. <https://doi.org/10.1111/eva.12288>
- Grorud-Colvert K, Sullivan-Stack J, Roberts C, Constant V, Horta e Costa B, Pike EP, Kingston N, Laffoley D, Sala E, Claudet J, Friedlander AM, Gill DA, Lester SE, Day JC, Gonçalves EJ, Ahmadi GN, Rand M, Villagomez A, Ban NC, Gurney GG, Spalding AK, Bennett NJ, Briggs J, Morgan LE, Moffitt R, Deguignet M, Pikitch EK, Darling ES, Jessen S, Hameed SO, di Carlo G, Guidetti P, Harris JM, Torre J, Kizilkaya Z, Agardy T, Cury P, Shah NJ, Sack K, Cao L, Fernandez M and Lubchenco J (2021) The MPA guide: A framework to achieve global goals for the ocean. *Science* **373**(6560), eabf0861. <https://doi.org/10.1126/science.abf0861>
- Grüss A, Kaplan DM, Guenette S, Roberts CM and Botsford LW (2011) Consequences of adult and juvenile movement for marine protected areas. *Biological Conservation* **144**(2), 692–702. <https://doi.org/10.1016/j.biocon.2010.12.015>
- Guilhaumon F, Albouy C, Claudet J, Velez L, Ben Rais Lasram F, Tomasini JA, Douzery EJP, Meynard CN, Mouquet N, Troussellier M, Araújo MB and Mouillot D (2015) Representing taxonomic, phylogenetic and functional diversity: New challenges for Mediterranean marine-protected areas. *Diversity and Distributions* **21**(2), 175–187. <https://doi.org/10.1111/ddi.12280>
- Gurney GG, Darling ES, Ahmadi GN, Agostini VN, Ban NC, Blythe J, Claudet J, Epstein G, Estradivari, Himes-Cornell A, Jonas HD, Armitage D, Campbell SJ, Cox C, Friedman WR, Gill D, Lestari P, Mangubhai S, McLeod E, Muthiga NA, Naggea J, Ranaivoson R, Wenger A, Yulianto I and Jupiter SD (2021) Biodiversity needs every tool in the box: Use OECMs. *Nature* **595**(7869), 646–649. <https://doi.org/10.1038/d41586-021-02041-4>
- Hanson JO, Fuller RA and Rhodes JR (2019a) Conventional methods for enhancing connectivity in conservation planning do not always maintain gene flow. *Journal of Applied Ecology* **56**(4), 913–922. <https://doi.org/10.1111/1365-2664.13315>
- Hanson JO, Marques A, Veríssimo A, Camacho-Sanchez M, Velo-Antón G, Martínez-Solano Í and Carvalho SB (2020) Conservation planning for adaptive and neutral evolutionary processes. *Journal of Applied Ecology* **57** (11), 2159–2169. <https://doi.org/10.1111/1365-2664.13718>
- Hanson JO, Rhodes JR, Riginos C and Fuller RA (2017) Environmental and geographic variables are effective surrogates for genetic variation in conservation planning. *Proceedings of the National Academy of Sciences of the United States of America* **114**(48), 12755–12760. <https://doi.org/10.1073/pnas.1711009114>
- Hanson JO, Schuster R, Strimas-Mackey M and Bennett JR (2019b) Optimality in prioritizing conservation projects. *Methods in Ecology and Evolution* **10** (10), 1655–1663. <https://doi.org/10.1111/2041-210X.13264>
- Hanson JO, Veríssimo A, Velo-Antón G, Marques A, Camacho-Sanchez M, Martínez-Solano Í, Gonçalves H, Sequeira F, Possingham HP and Carvalho SB (2021) Evaluating surrogates of genetic diversity for conservation planning. *Conservation Biology* **35**(2), 634–642. <https://doi.org/10.1111/cobi.13602>
- Harrison HB, Bode M, Williamson DH, Berumen ML and Jones GP (2020) A connectivity portfolio effect stabilizes marine reserve performance. *Proceedings of the National Academy of Sciences* **117**(41), 25595–25600. <https://doi.org/10.1073/pnas.1920580117>
- Harrison HB, Williamson DH, Evans RD, Almany GR, Thorrold SR, Russ GR, Feldheim KA, van Herwerden L, Planes S, Srinivasan M, Berumen ML and Jones GP (2012) Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Current Biology* **22**(11), 1023–1028.
- He Q and Silliman BR (2019) Climate change, human impacts, and coastal ecosystems in the Anthropocene. *Current Biology* **29**(19), R1021–R1035. <https://doi.org/10.1016/j.cub.2019.08.042>
- Herbert-Read JE, Thornton A, Amon DJ, Birchenough SNR, Côté IM, Dias MP, Godley BJ, Keith SA, McKinley E, Peck LS, Calado R, Defeo O, Degraer S, Johnston EL, Kaartokallio H, Macreadie PI, Metaxas A, Muthumbi AWN, Obura DO, Paterson DM, Piola AR, Richardson AJ, Schloss IR, Snelgrove PVR, Stewart BD, Thompson PM, Watson GJ, Worthington TA, Yasuhara M and Sutherland WJ (2022) A global horizon scan of issues impacting marine and coastal biodiversity conservation. *Nature Ecology & Evolution* **6**(9), 1262–1270. <https://doi.org/10.1038/s41559-022-01812-0>
- Hoban S, Archer FI, Bertola LD, Bragg JG, Breed MF, Bruford MW, Coleman MA, Ekblom R, Funk WC, Grueber CE, Hand BK, Jaffé R, Jensen E,

- Johnson JS, Kershaw F, Liggins L, MacDonald AJ, Mergeay J, Miller JM, Muller-Karger F, O'Brien D, Paz-Vinas I, Potter KM, Razgour O, Vernesi C and Hunter ME (2022) Global genetic diversity status and trends: Towards a suite of essential biodiversity variables (EBVs) for genetic composition. *Biological Reviews* 97(4), 1511–1538. <https://doi.org/10.1111/brv.12852>
- Hoban S, Bruford M, D'Urban Jackson J, Lopes-Fernandes M, Heuertz M, Hohenlohe PA, Paz-Vinas I, Sjögren-Gulve P, Segelbacher G, Vernesi C, Aitken S, Bertola LD, Bloomer P, Breed M, Rodriguez-Correa H, Funk WC, Grueber CE, Hunter ME, Jaffe R, Liggins L, Mergeay J, Moharrek F, O'Brien D, Ogden R, Palma-Silva C, Pierson J, Ramakrishnan U, Simondroissart M, Tani N, Waits L and Laikre L (2020) Genetic diversity targets and indicators in the CBD post-2020 global biodiversity framework must be improved. *Biological Conservation* 248, 108654. <https://doi.org/10.1016/j.biocon.2020.108654>
- Hoban S, Kelley JL, Lotterhos KE, Antolin MF, Bradburd G, Lowry DB, Poss ML, Reed LK, Storfer A and Whitlock MC (2016) Finding the genomic basis of local adaptation: Pitfalls, practical solutions, and future directions. *American Naturalist* 188(4), 379–397. <https://doi.org/10.1086/688018>
- Holderegger R, Kamm U and Gugerli F (2006) Adaptive vs. neutral genetic diversity: Implications for landscape genetics. *Landscape Ecology* 21(6), 797–807. <https://doi.org/10.1007/s10980-005-5245-9>
- Huang D and Roy K (2015) The future of evolutionary diversity in reef corals. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370 (1662), 20140010. <https://doi.org/10.1098/rstb.2014.0010>
- Jaquier M, Albouy C, Bach W, Waldock C, Marques V, Maire E, Juhel J-B, Andreollo M, Valentini A, Manel S, Dejean T, Mouillot D, Pellissier L (under review) eDNA recovers fish composition turnover of the coral reefs of West Indian Ocean Islands. *Environmental DNA*.
- Jasper ME, Hoffmann AA and Schmidt TL (2022) Estimating dispersal using close kin dyads: The kindisperse R package. *Molecular Ecology Resources* 22(3), 1200–1212. <https://doi.org/10.1111/1755-0998.13520>
- Jeffery NW, Lehnert SJ, Kess T, Layton KKS, Wringe BF and Stanley RRE (2022) Application of omics tools in designing and monitoring marine protected areas for a sustainable blue economy. *Frontiers in Genetics* 13, 886494. <https://doi.org/10.3389/fgene.2022.886494>
- Jensen MR, Sigsgaard EE, Liu S, Manica A, Bach SS, Hansen MM, Møller PR and Thomsen PF (2021) Genome-scale target capture of mitochondrial and nuclear environmental DNA from water samples. *Molecular Ecology Resources* 21(3), 690–702. <https://doi.org/10.1111/1755-0998.13293>
- Jones MR and Good JM (2016) Targeted capture in evolutionary and ecological genomics. *Molecular Ecology* 25(1), 185–202. <https://doi.org/10.1111/mec.13304>
- Jost L, Archer F, Flanagan S, Gaggiotti O, Hoban S and Latch E (2018) Differentiation measures for conservation genetics. *Evolutionary Applications* 11(7), 1139–1148. <https://doi.org/10.1111/eva.12590>
- Juhel J-B, Marques V, Utama RS, Vimono IB, Sugeha HY, Kadarusman K, Cochet C, Dejean T, Hoey A, Mouillot D, Hocdé R and Pouyaud L (2022) Estimating the extended and hidden species diversity from environmental DNA in hyper-diverse regions. *Ecography* 2022(10), e06299. <https://doi.org/10.1111/ecog.06299>
- Kapli P, Yang Z and Telford MJ (2020) Phylogenetic tree building in the genomic age. *Nature Reviews Genetics* 21(7), 428–444. <https://doi.org/10.1038/s41576-020-0233-0>
- Kukkala AS and Moilanen A (2013) Core concepts of spatial prioritisation in systematic conservation planning. *Biological Reviews* 88(2), 443–464. <https://doi.org/10.1111/brv.12008>
- Leigh DM, Hendry AP, Vázquez-Domínguez E and Friesen VL (2019) Estimated six per cent loss of genetic variation in wild populations since the industrial revolution. *Evolutionary Applications* 12(8), 1505–1512. <https://doi.org/10.1111/eva.12810>
- Lewin HA, Richards S, Lieberman Aiden E, Allende ML, Archibald JM, Bálint M, Barker KB, Baumgartner B, Belov K, Bertorelle G, Blaxter ML, Cai J, Caporale ND, Carlson K, Castilla-Rubio JC, Chaw SM, Chen L, Childers AK, Coddington JA, Conde DA, Corominas M, Crandall KA, Crawford AJ, DiPalma F, Durbin R, Ebenezzer TGE, Edwards SV, Fedrigo O, Flicke P, Formenti G, Gibbs RA, Gilbert MTP, Goldstein MM, Graves JM, Greely HT, Grigoriev IV, Hackett KJ, Hall N, Haussler D, Helgen KM, Hogg CJ, Isobe S, Jakobsen KS, Janke A, Jarvis ED, Johnson WE, Jones SJM, Karlsson EK, Kersey PJ, Kim JH, Kress WJ, Kuraku S, Lawnczak MKN, Leebens-Mack JH, Li X, Lindblad-Toh K, Liu X, Lopez JV, Marques-Bonet T, Mazard S, Mazet JAK, Mazzoni CJ, Myers EW, O'Neill RJ, Paez S, Park H, Robinson GE, Roquet C, Ryder OA, Sabir JSM, Shaffer HB, Shank TM, Sherkow JS, Soltis PS, Tang B, Tedersoo L, Uliano-Silva M, Wang K, Wei X, Wetzer R, Wilson JL, Xu X, Yang H, Yoder AD and Zhang G (2022) The earth BioGenome project 2020: Starting the clock. *Proceedings of the National Academy of Sciences of the United States of America* 119(4), e2115635118. <https://doi.org/10.1073/pnas.2115635118>
- Lowe WH and Allendorf FW (2010) What can genetics tell us about population connectivity? *Molecular Ecology* 19(15), 3038–3051. <https://doi.org/10.1111/j.1365-294X.2010.04688.x>
- Macé B, Hocdé R, Marques V, Guerin PE, Valentini A, Arnal V, Pellissier L and Manel S (2022) Evaluating bioinformatics pipelines for population-level inference using environmental DNA. *Environmental DNA* 4(3), 674–686. <https://doi.org/10.1002/edn3.269>
- Mace GM, Gittleman JL and Purvis A (2003) Preserving the tree of life. *Science* 300(5626), 1707–1709. <https://doi.org/10.1126/science.1085510>
- Magris RA, Andreollo M, Pressey RL, Mouillot D, Dalongeville A, Jacobi MN and Manel S (2018) Biologically representative and well-connected marine reserves enhance biodiversity persistence in conservation planning. *Conservation Letters* 11(4), e12439. <https://doi.org/10.1111/conl.12439>
- Manel S, Andreollo M, Henry K, Verdet D, Darracq A, Guerin PE, Desprez B and Devaux P (2018) Predicting genotype environmental range from genome-environment associations. *Molecular Ecology* 27(13), 2823–2833. <https://doi.org/10.1111/mec.14723>
- Manel S, Gaggiotti O and Waples R (2005) Assignment methods: Matching biological questions with appropriate techniques. *Trends in Ecology & Evolution* 20(3), 136–142. <https://doi.org/10.1016/j.tree.2004.12.004>
- Manel S, Guerin P-E, Mouillot D, Blanchet S, Velez L, Albouy C and Pellissier L (2020) Global determinants of freshwater and marine fish genetic diversity. *Nature Communications* 11(1), 1–9. <https://doi.org/10.1038/s41467-020-14409-7>
- Manel S and Holderegger R (2013) Ten years of landscape genetics. *Trends in Ecology & Evolution* 28(10), 614–621. <https://doi.org/10.1016/j.tree.2013.05.012>
- Manel S, Loiseau N, Andreollo M, Fietz K, Goñi R, Forcada A, Lenfant P, Kininmonth S, Marcos C, Marques V, Mallol S, Pérez-Ruzafa A, Breusing C, Puebla O and Mouillot D (2019) Long-distance benefits of marine reserves: Myth or reality? *Trends in Ecology & Evolution* 34(4), 342–354. <https://doi.org/10.1016/j.tree.2019.01.002>
- Manel S, Perrier C, Pralong M, Abi-Rached L, Paganini J, Pontarotti P and Aurelle D (2016) Genomic resources and their influence on the detection of the signal of positive selection in genome scans. *Molecular Ecology* 25(1), 170–184. <https://doi.org/10.1111/mec.13468>
- Margules C and Sarkar S (2007) *Systematic Conservation Planning*, Cambridge: Cambridge University Press.
- Margules CR and Pressey RL (2000) Systematic conservation planning. *Nature* 405(6783), 243. <https://doi.org/10.1038/35012251>
- Marques V, Castagné P, Polanco Fernández A, Borrero-Pérez GH, Hocdé R, Guérin PÉ, Juhel JB, Velez L, Loiseau N, Letessier TB, Bessudo S, Valentini A, Dejean T, Mouillot D, Pellissier L and Villéger S (2021) Use of environmental DNA in assessment of fish functional and phylogenetic diversity. *Conservation Biology* 35(6), 1944–1956. <https://doi.org/10.1111/cobi.13802>
- Mathon L, Baletaud F, Lebourges-Dhaussy A, Lecellier G, Menkes C, Bachelier C, Bonneville C, Dejean T, Dumas M, Fiat S, Grelet J, Habasque J, Manel S, Mannocci L, Mouillot D, Peran M, Roudaut G, Sidobre C, Varillon D, Vigliola L (unpublished results) 3D conservation planning of multiple biodiversity metrics reveals deep-sea 30x30 CBD target. Unpublished results.
- Mathon L, Marques V, Mouillot D, Albouy C, Andreollo M, Baletaud F, Borrero-Pérez GH, Dejean T, Edgar GJ, Grondin J, Guerin PE, Hocdé R, Juhel JB, Kadarusman, Maire E, Mariani G, McLean M, Polanco F. A, Pouyaud L, Stuart-Smith RD, Sugeha HY, Valentini A, Vigliola L, Vimono IB, Pellissier L and Manel S (2022) Cross-ocean patterns and processes in fish biodiversity on coral reefs through the lens of eDNA metabarcoding. *Proceedings of the Royal Society B: Biological Sciences* 289(1973), 20220162. <https://doi.org/10.1098/rspb.2022.0162>

- Matz MV, Trembl EA and Haller BC (2020) Estimating the potential for coral adaptation to global warming across the Indo-West Pacific. *Global Change Biology* 26(6), 3473–3481. <https://doi.org/10.1111/gcb.15060>
- Maxwell SL, Cazalis V, Dudley N, Hoffmann M, Rodrigues ASL, Stolton S, Visconti P, Woodley S, Kingston N, Lewis E, Maron M, Strassburg BBN, Wenger A, Jonas HD, Venter O and Watson JEM (2020) Area-based conservation in the twenty-first century. *Nature* 586(7828), 217–227. <https://doi.org/10.1038/s41586-020-2773-z>
- May-Collado LJ, Zambrana-Torrelío C and Agnarsson I (2016) Global spatial analyses of phylogenetic conservation priorities for aquatic mammals. In Pellens R and Grandcolas P (eds.), *Biodiversity Conservation and Phylogenetic Systematics*. Cham: Springer, pp. 305–318.
- Mazel F, Pennell MW, Cadotte MW, Diaz S, Dalla Riva GV, Grenyer R, Leprieur F, Mooers AO, Mouillot D, Tucker CM and Pearse WD (2018) Prioritizing phylogenetic diversity captures functional diversity unreliably. *Nature Communications* 9(1), 2888. <https://doi.org/10.1038/s41467-018-05126-3>
- Mazel F, Pennell MW, Cadotte MW, Diaz S, Riva GVD, Grenyer R, Leprieur F, Mooers AO, Mouillot D, Tucker CM and Pearse WD (2019) Reply to: “Global conservation of phylogenetic diversity captures more than just functional diversity.” *Nature Communications* 10(1), 858. <https://doi.org/10.1038/s41467-019-08603-5>
- McClenaghan B, Compson ZG and Hajibabaei M (2020) Validating metabarcoding-based biodiversity assessments with multi-species occupancy models: A case study using coastal marine eDNA. *PLoS One* 15(3), e0224119. <https://doi.org/10.1371/journal.pone.0224119>
- Medoff S, Lynham J and Raynor J (2022) Spillover benefits from the world’s largest fully protected MPA. *Science* 378(6617), 313–316. <https://doi.org/10.1126/science.abn0098>
- Miya M (2022) Environmental DNA metabarcoding: A novel method for biodiversity monitoring of marine fish communities. *Annual Review of Marine Science* 14(1), 161–185. <https://doi.org/10.1146/annurev-marine-041421-082251>
- Moilanen A, Possingham HP and Polasky S (2009a) A mathematical classification of conservation prioritization problems. In Moilanen A, Wilson KA and Possingham HP (eds.), *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools*. Oxford: Oxford University Press, pp. 28–42.
- Moilanen A, Wilson KA and Possingham H (eds.) (2009b) *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools*, Oxford: Oxford University Press.
- Mouillot D, Albouy C, Guilhaumon F, Ben Rais Lasram F, Coll M, Devictor V, Meynard CN, Pauly D, Tomasini JA, Troussellier M, Velez L, Watson R, Douzery EJP and Mouquet N (2011) Protected and threatened components of fish biodiversity in the Mediterranean Sea. *Current Biology* 21(12), 1044–1050. <https://doi.org/10.1016/j.cub.2011.05.005>
- Mouillot D, Parravicini V, Bellwood DR, Leprieur F, Huang D, Cowman PF, Albouy C, Hughes TP, Thuiller W and Guilhaumon F (2016) Global marine protected areas do not secure the evolutionary history of tropical corals and fishes. *Nature Communications* 7, 10359. <https://doi.org/10.1038/ncomms10359>
- Mouton TL, Stephenson F, Torres LG, Rayment W, Brough T, McLean M, Tonkin JD, Albouy C and Leprieur F (2022) Spatial mismatch in diversity facets reveals contrasting protection for New Zealand’s cetacean biodiversity. *Biological Conservation* 267, 109484. <https://doi.org/10.1016/j.biocon.2022.109484>
- Naaykens T and D’Aloia CC (2022) Isolation-by-distance and genetic parentage analysis provide similar larval dispersal estimates. *Molecular Ecology* 31(11), 3072–3082. <https://doi.org/10.1111/mec.16465>
- Ng LWK, Chisholm C, Carrasco LR, Darling ES, Guilhaumon F, Mooers AO, Tucker CM, Winter M and Huang D (2022) Prioritizing phylogenetic diversity to protect functional diversity of reef corals. *Diversity and Distributions* 28(8), 1721–1734. <https://doi.org/10.1111/ddi.13526>
- Nielsen ES, Beger M, Henriques R, Selkoe KA and von der Heyden S (2017) Multispecies genetic objectives in spatial conservation planning. *Conservation Biology* 31(4), 872–882. <https://doi.org/10.1111/cobi.12875>
- Nielsen ES, Beger M, Henriques R and von der Heyden S (2020) A comparison of genetic and genomic approaches to represent evolutionary potential in conservation planning. *Biological Conservation* 251, 108770. <https://doi.org/10.1016/j.biocon.2020.108770>
- Nielsen ES, Hanson JO, Carvalho SB, Beger M, Henriques R, Kershaw F and von der Heyden S (2023) Molecular ecology meets systematic conservation planning. *Trends in Ecology & Evolution* 38(2), 143–155. <https://doi.org/10.1016/j.tree.2022.09.006>
- Önal H and Briers RA (2006) Optimal selection of a connected reserve network. *Operations Research* 54(2), 379–388. <https://doi.org/10.1287/opre.1060.0272>
- Owen NR, Gumbs R, Gray CL and Faith DP (2019) Global conservation of phylogenetic diversity captures more than just functional diversity. *Nature Communications* 10(1), 859. <https://doi.org/10.1038/s41467-019-08600-8>
- Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications* 13(sp1), 146–158. [https://doi.org/10.1890/1051-0761\(2003\)013\(0146:pgdcat\)2.0.co;2](https://doi.org/10.1890/1051-0761(2003)013(0146:pgdcat)2.0.co;2)
- Parsons KM, Everett M, Dahlheim M and Park L (2018) Water, water everywhere: Environmental DNA can unlock population structure in elusive marine species. *Royal Society Open Science* 5(8), 180537. <https://doi.org/10.1098/rsos.180537>
- Pascual M, Rives B, Schunter C and Macpherson E (2017) Impact of life history traits on gene flow: A multispecies systematic review across oceanographic barriers in the Mediterranean Sea. *PLoS One* 12(5), e0176419. <https://doi.org/10.1371/journal.pone.0176419>
- Paz-Vinas I, Loot G, Hermoso V, Veysière C, Poulet N, Grenouillet G and Blanchet S (2018) Systematic conservation planning for intraspecific genetic diversity. *Proceedings of the Royal Society B: Biological Sciences* 285(1877), 20172746. <https://doi.org/10.1098/rspb.2017.2746>
- Phair NL, Nielsen ES and von der Heyden S (2021) Applying genomic data to seagrass conservation. *Biodiversity and Conservation* 30(7), 2079–2096. <https://doi.org/10.1007/s10531-021-02184-w>
- Pinsky ML, Saenz-Agudelo P, Salles OC, Almany GR, Bode M, Berumen ML, Andréfouët S, Thorrold SR, Jones GP and Planes S (2017) Marine dispersal scales are congruent over evolutionary and ecological time. *Current Biology* 27(1), 149–154. <https://doi.org/10.1016/j.cub.2016.10.053>
- Pollock LJ, O’Connor LMJ, Mokany K, Rosauer DF, Talluto MV and Thuiller W (2020) Protecting biodiversity (in all its complexity): New models and methods. *Trends in Ecology & Evolution* 35(12), 1119–1128. <https://doi.org/10.1016/j.tree.2020.08.015>
- Pompanon F, Bonin A, Bellemain E and Taberlet P (2005) Genotyping errors: Causes, consequences and solutions. *Nature Reviews Genetics* 6(11), 847–859. <https://doi.org/10.1038/nrg1707>
- Puebla O, Bermingham E and McMillan WO (2012) On the spatial scale of dispersal in coral reef fishes. *Molecular Ecology* 21(23), 5675–5688. <https://doi.org/10.1111/j.1365-294X.2012.05734.x>
- Pukk L, Kanefsky J, Heathman AL, Weise EM, Nathan LR, Herbst SJ, Sard NM, Scribner KT and Robinson JD (2021) eDNA metabarcoding in lakes to quantify influences of landscape features and human activity on aquatic invasive species prevalence and fish community diversity. *Diversity and Distributions* 27(10), 2016–2031. <https://doi.org/10.1111/ddi.13370>
- Puritz JB, Keever CC, Addison JA, Barbosa SS, Byrne M, Hart MW, Grosberg RK and Toonen RJ (2017) Life-history predicts past and present population connectivity in two sympatric sea stars. *Ecology and Evolution* 7(11), 3916–3930. <https://doi.org/10.1002/ece3.2938>
- Purvis A, Gittleman JL and Brooks T (2005) *Phylogeny and Conservation*. Oxford: Blackwell Pub. Ltd. <https://doi.org/10.1017/CBO9780511614927>
- Rabosky DL, Chang J, Title PO, Cowman PF, Sallan L, Friedman M, Kaschner K, Garilao C, Near TJ, Coll M and Alfaro ME (2018) An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* 559(7714), 392–395. <https://doi.org/10.1038/s41586-018-0273-1>
- Riginos C and Beger M (2022) Incorporating genetic measures of connectivity and adaptation in marine spatial planning for corals. In van Oppen MJH and Aranda Lastra M (eds.), *Coral Reef Conservation and Restoration in the Omics Age*. Cham: Springer International Publishing, pp. 7–33. https://doi.org/10.1007/978-3-031-07055-6_2
- Robuchon M, Pavoine S, Véron S, Delli G, Faith DP, Mandrici A, Pellens R, Dubois G and Leroy B (2021) Revisiting species and areas of interest for conserving global mammalian phylogenetic diversity. *Nature Communications* 12(1), 1–11. <https://doi.org/10.1038/s41467-021-23861-y>

- Rodrigues ASL and Gaston KJ (2002) Maximising phylogenetic diversity in the selection of networks of conservation areas. *Biological Conservation* 105(1), 103–111. [https://doi.org/10.1016/S0006-3207\(01\)00208-7](https://doi.org/10.1016/S0006-3207(01)00208-7)
- Rosauer DF, Byrne M, Blom MPK, Coates DJ, Donnellan S, Doughty P, Keogh JS, Kinloch J, Laver RJ, Myers C, Oliver PM, Potter S, Rabosky DL, Afonso Silva AC, Smith J and Moritz C (2018) Real-world conservation planning for evolutionary diversity in the Kimberley, Australia, sidesteps uncertain taxonomy. *Conservation Letters* 11(4), e12438. <https://doi.org/10.1111/conl.12438>
- Rourke ML, Fowler AM, Hughes JM, Broadhurst MK, DiBattista JD, Fielder S, Wilkes Walburn J and Furlan EM (2022) Environmental DNA (eDNA) as a tool for assessing fish biomass: A review of approaches and future considerations for resource surveys. *Environmental DNA* 4(1), 9–33. <https://doi.org/10.1002/edn3.185>
- Rueger T, Harrison HB, Buston PM, Gardiner NM, Berumen ML and Jones GP (2020) Natal philopatry increases relatedness within groups of coral reef cardinalfish. *Proceedings of the Royal Society B: Biological Sciences* 287(1930), 20201133. <https://doi.org/10.1098/rspb.2020.1133>
- Saenz-Agudelo P, Jones GP, Thorrold SR and Planes S (2011) Connectivity dominates larval replenishment in a coastal reef fish metapopulation. *Proceedings of the Royal Society B-Biological Sciences* 278(1720), 2954–2961. <https://doi.org/10.1098/rspb.2010.2780>
- Sala E, Mayorga J, Bradley D, Cabral RB, Atwood TB, Auber A, Cheung W, Costello C, Ferretti F, Friedlander AM, Gaines SD, Garilao C, Goodell W, Halpern BS, Hinson A, Kaschner K, Kesner-Reyes K, Leprieur F, McGowan J, Morgan LE, Mouillot D, Palacios-Abrantes J, Possingham HP, Rechberger KD, Worm B and Lubchenco J (2021) Protecting the global ocean for biodiversity, food and climate. *Nature* 592(7854), 397–402. <https://doi.org/10.1038/s41586-021-03371-z>
- Sandoval-Castillo J, Robinson NA, Hart AM, Strain LWS and Beheregaray LB (2018) Seascape genomics reveals adaptive divergence in a connected and commercially important mollusc, the greenlip abalone (*Haliotis laevigata*), along a longitudinal environmental gradient. *Molecular Ecology* 27(7), 1603–1620. <https://doi.org/10.1111/mec.14526>
- Sigsgaard EE, Jensen MR, Winkelmann IE, Møller PR, Hansen MM and Thomsen PF (2020) Population-level inferences from environmental DNA—Current status and future perspectives. *Evolutionary Applications* 13(2), 245–262. <https://doi.org/10.1111/eva.12882>
- Sigsgaard EE, Nielsen IB, Bach SS, Lorenzen ED, Robinson DP, Knudsen SW, Pedersen MW, Jaidah MA, Orlando L, Willerslev E, Møller PR and Thomsen PF (2016) Population characteristics of a large whale shark aggregation inferred from seawater environmental DNA. *Nature Ecology & Evolution* 1(1), 1–5. <https://doi.org/10.1038/s41559-016-0004>
- Smith CCR, Tittes S, Ralph PL and Kern AD (2023) Dispersal inference from population genetic variation using a convolutional neural network. *Genetics* 224(2), iyad068. <https://doi.org/10.1093/genetics/iyad068>
- Stein RW, Mull CG, Kuhn TS, Aschliman NC, Davidson LNK, Joy JB, Smith GJ, Dulvy NK and Mooers AO (2018) Global priorities for conserving the evolutionary history of sharks, rays and chimaeras. *Nature Ecology & Evolution* 2(2), 288–298. <https://doi.org/10.1038/s41559-017-0448-4>
- Székely D, Corfixen NL, Morch LL, Knudsen SW, McCarthy ML, Teilmann J, Heide-Jørgensen MP and Olsen MT (2021) Environmental DNA captures the genetic diversity of bowhead whales (*Balaena mysticetus*) in West Greenland. *Environmental DNA* 3(1), 248–260. <https://doi.org/10.1002/edn3.176>
- Taberlet P, Bonin A, Zinger L and Coissac E (2018) *Environmental DNA: For Biodiversity Research and Monitoring*. Oxford: Oxford University Press.
- Taberlet P, Coissac E, Hajibabaei M and Rieseberg LH (2012) Environmental DNA. *Molecular Ecology* 21(8), 1789–1793. <https://doi.org/10.1111/j.1365-294X.2012.05542.x>
- Tucker CM, Aze T, Cadotte MW, Cantalapiedra JL, Chisholm C, Díaz S, Grenyer R, Huang D, Mazel F, Pearse WD, Pennell MW, Winter M and Mooers AO (2019) Assessing the utility of conserving evolutionary history. *Biological Reviews* 94(5), 1740–1760. <https://doi.org/10.1111/brv.12526>
- Upham NS, Esselstyn JA and Jetz W (2019) Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biology* 17(12), e3000494. <https://doi.org/10.1371/journal.pbio.3000494>
- van Wyngaarden M, Snelgrove PVR, DiBacco C, Hamilton LC, Rodríguez-Ezpeleta N, Jeffery NW, Stanley RRE and Bradbury IR (2017) Identifying patterns of dispersal, connectivity and selection in the sea scallop, *Placopecten magellanicus*, using RADseq-derived SNPs. *Evolutionary Applications* 10(1), 102–117. <https://doi.org/10.1111/eva.12432>
- Vilcot M, Albouy C, Donati GFA, Claverie T, Julius P, Manel S, Pellissier L and Leprieur F (2023) Spatial genetic differentiation correlates with species assemblage turnover across tropical reef fish lineages. *Global Ecology and Biogeography* 32(4), 535–547. <https://doi.org/10.1111/geb.13637>
- Webster MS, Colton MA, Darling ES, Armstrong J, Pinsky ML, Knowlton N, Schindler DE (2017) Who should pick the winners of climate change? *Trends in Ecology & Evolution* 32(3), 167–173. <https://doi.org/10.1016/j.tree.2016.12.007>
- Weeks R (2017) Incorporating seascape connectivity in conservation prioritisation. *PLoS One* 12(7), e0182396. <https://doi.org/10.1371/journal.pone.0182396>
- Weltz K, Lyle JM, Ovenden J, Morgan JAT, Moreno DA and Semmens JM (2017) Application of environmental DNA to detect an endangered marine skate species in the wild. *PLoS One* 12(6), e0178124. <https://doi.org/10.1371/journal.pone.0178124>
- Whitlock MC and McCauley DE (1999) Indirect measures of gene flow and migration: $F_{ST} \approx 1/(4Nm+1)$. *Heredity* 82(2), 117–125. <https://doi.org/10.1038/sj.hdy.6884960>
- Wilson KA, Cabeza M and Klein CJ (2009) Fundamental concepts of spatial conservation prioritization. In Moilanen A, Wilson KA and Possingham HP (eds.), *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools*. Oxford: Oxford University Press, pp. 16–27.
- Winter M, Devictor V and Schweiger O (2013) Phylogenetic diversity and nature conservation: Where are we? *Trends in Ecology & Evolution* 28(4), 199–204. <https://doi.org/10.1016/j.tree.2012.10.015>
- Xuereb A, D'Aloia CC, Andreollo M, Bernatchez L and Fortin M (2021a) Incorporating putatively neutral and adaptive genomic data into marine conservation planning. *Conservation Biology* 35(3), 909–920. <https://doi.org/10.1111/cobi.13609>
- Xuereb A, D'Aloia CC, Daigle RM, Andreollo M, Dalongeville A, Manel S, Mouillot D, Guichard F, Côté IM, Curtis JMR, Bernatchez L and Fortin M-J (2020) Marine conservation and marine protected areas. In Oleksiak MF and Rajora OP (eds.), *Population Genomics: Marine Organisms*. Cham: Springer International Publishing, pp. 423–446. https://doi.org/10.1007/13836_2018_63
- Xuereb A, Kimber CM, Curtis JMR, Bernatchez L and Fortin M-J (2018) Putatively adaptive genetic variation in the giant California Sea cucumber (*Parastichopus californicus*) as revealed by environmental association analysis of restriction-site associated DNA sequencing data. *Molecular Ecology* 27(24), 5035–5048. <https://doi.org/10.1111/mec.14942>
- Xuereb A, Rougemont Q, Tiffin P, Xue H and Phifer-Rixey M (2021b) Individual-based eco-evolutionary models for understanding adaptation in changing seas. *Proceedings of the Royal Society B: Biological Sciences* 288(1962), 20212006. <https://doi.org/10.1098/rspb.2021.2006>
- Yoshitake K, Fujiwara A, Matsuura A, Sekino M, Yasuike M, Nakamura Y, Nakamichi R, Kodama M, Takahama Y, Takasuka A, Asakawa S, Nishikiori K, Kobayashi T and Watabe S (2021) Estimation of tuna population by the improved analytical pipeline of unique molecular identifier-assisted HaCeD-Seq (haplotype count from eDNA). *Scientific Reports* 11(1), 7031. <https://doi.org/10.1038/s41598-021-86190-6>
- Zupan M, Fragkopoulou E, Claudet J, Erzinci K, Horta e Costa B and Gonçalves EJ (2018) Marine partially protected areas: Drivers of ecological effectiveness. *Frontiers in Ecology and the Environment* 16(7), 381–387. <https://doi.org/10.1002/fee.1934>