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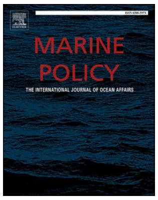

Seascape genomics: Assisting marine biodiversity management by combining genetic knowledge with environmental and ecological information

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ABSTRACT

Biodiversity, including genetic diversity, is the foundation of ecosystems and supports the well-being of all organisms, including humans. Determining how the marine environment shapes genetic diversity and developing best practices to conserve it requires a multi-disciplinary approach that incorporates genomic and environmental information. Seascape genetics and genomics combine spatially resolved ecological, genomic, and environmental data, coupled with modeling to explore past, present, and future patterns of diversity and connectivity. Seascape genetics and genomics provide scientists and managers with a multi-faceted tool that can be applied across a wide range of species and incorporated into marine spatial management. Despite the proven importance of genetic diversity for species resilience, the incorporation of genetic and genomic data is grossly underrepresented in policy, decision-making, and conservation measures. Here, we aim to support the understanding and access to information on seascape genetics and genomics for conservation and environmental management practitioners. We explain how integrating environment, space, traits, and genetics or genomics can advance marine spatial management. We use two advanced case studies to outline methodology and concepts of seascape genomics and the respective policy context, although management uptake is still pending. Lastly, we review the present status of seascape genomics research and discuss challenges, strengths, and future opportunities by providing a road map. We present a successful management uptake case study that could aid the integration of seascape genomics into biodiversity management.

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1. Outline of seascape genomics' scientific and policy context

The conservation of genetic diversity is imperative as anthropogenic pressures [1] and biodiversity loss in our oceans continue to increase [2]. Genetic diversity is essential for adaptive capacity, evolutionary potential, and community functioning, and it plays a significant role in ecosystem services [3]. Despite these challenges, the inclusion of genetic and genomic dimensions (Fig. 1) in conservation policies and management programs remains limited [3]. International efforts have recognized the importance of marine genetic diversity since the 1992 United Nations Convention on Biological Diversity (CBD) highlighted the importance of marine biodiversity and genetic diversity, and launched a conservation program in 1998 (COP 4 Decision IV/5, 1998).

The early CBD intentions are reflected in many current multinational policies such as the EU Habitat and Marine Strategy Framework Directives (Directives 92/42/EEC, 2008/56/EC), as well as the UN Sustainable Development Goal 14, which highlights the need to conserve and sustainably use marine resources (UN, 2022). The maintenance of genetic diversity and adaptive potential are now also specifically mentioned in goal A of the CBD Kunming-Montreal Global Biodiversity Framework (GBF) adopted at COP15 (CBD, 2022). Further, the law on Nature Restoration (European Parliament, 2024) has a strong focus on restoring marine ecosystems and offers the opportunity to establish a framework for fulfilling commitments outlined in the GBF in European countries. Despite the strides taken to address gaps in genetic diversity within policy frameworks, the comprehensive integration of genetic diversity into conservation practices is still lagging, with established goals remaining largely unfulfilled [4,5]. This shortfall is evident not only in the context of marine species diversity [6] and genetic diversity [7,8] in general, but particularly in the specific realm of genetic diversity within marine ecosystems [9].

The research field of seascape genomics uses multidimensional approaches to study how the marine environment influences genetic diversity and connectivity of populations [10]. It is applied in marine spatial management [11]. Seascape genomics is rooted in the principles of population and conservation genetics (Fig. 2) [3,12,13] and landscape ecology [12] (Fig. 3). Environmental and genomic information are combined to explore the impact of environmental factors on genetic diversity, connectivity (Fig. 2), and evolutionary processes of populations and species (Boxs 1 and 2; Fig. 3). In specific instances, the term "seascape genetics" applies when a limited set of genetic markers is used. It contrasts with "seascape genomics", which employs genome-wide marker sets, reference genomes, and/or high-throughput genomic sequencing (Figs. 1, 3) [14,15] (see Box 1).

Seascape ecology [26] and seascape genomic methods are increasingly used in research [17,27]. Multi-faceted applications of seascape genomics (Box 1) make it a valuable tool for various purposes. However, incorporation into spatio-temporal ecosystem management is infrequent. Here we aim to illustrate that the integration of seascape ecology

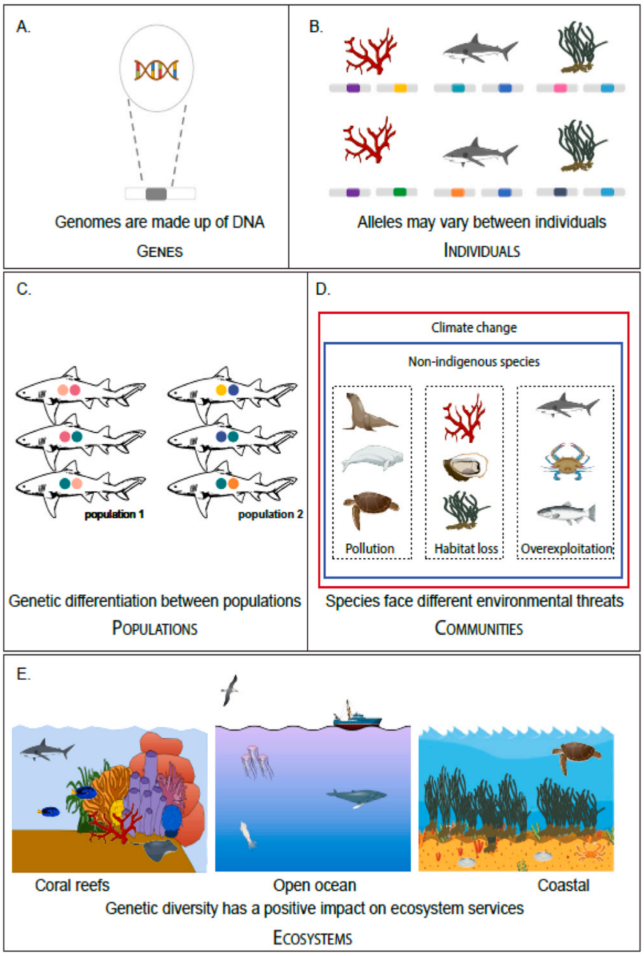
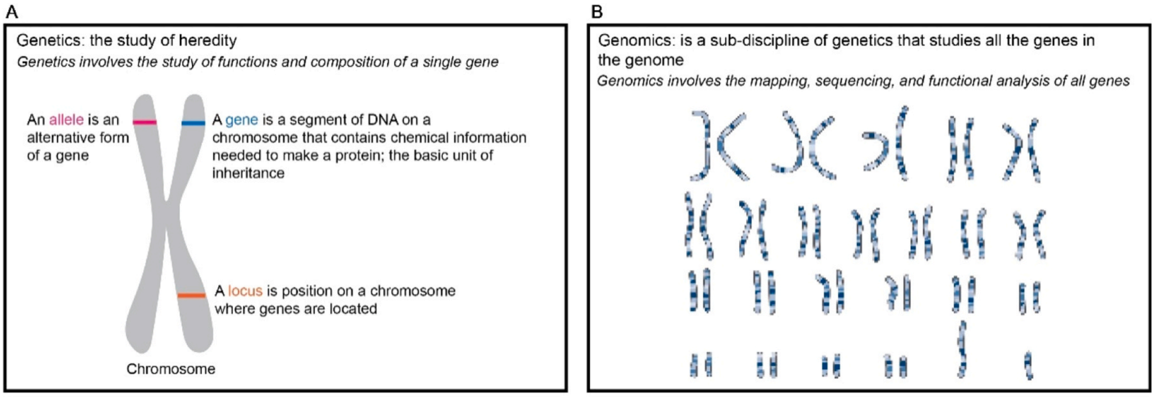


Fig. 2. Genomic assessments analyse the individual genetic codes of thousands of genes (A and B) within populations of wild organisms (C). These populations inhabit communities within a three-dimensional habitat (D), experiencing the influence of diverse physical and biological factors. The emerging insights into population diversity and structure within the context of their habitat (seascape genetics/genomics) enlighten ecosystem services and contribute to the conservation and management of natural populations worldwide (E).



Genetics: the study of heredity

Genetics involves the study of functions and composition of a single gene

An allele is an alternative form of a gene

A gene is a segment of DNA on a chromosome that contains chemical information needed to make a protein; the basic unit of inheritance

A locus is position on a chromosome where genes are located

Genomics: is a sub-discipline of genetics that studies all the genes in the genome

Genomics involves the mapping, sequencing, and functional analysis of all genes

Fig. 1. Definitions and visual illustrations of the scientific disciplines of genetics versus genomics. In concise terms, genetics, as a discipline, involves the examination of individual genes with the aim of comprehending their functions and hereditary traits (A). Whereas genomics encompasses a broader scope, examining the thorough investigation of all genes present on the chromosomes, including mapping, sequencing, and functional analysis (B).

(focused on species and communities) and seascape genomics (focused on diversity within and between populations) (Box 1; Figs. 1, 2 and 3) presents a valuable tool for numerous conservation scenarios. We refer for example to spatial management measures, such as protected areas or fishing regulations (quotas and exclusion zones)[28]. We review the scientific advancements in seascape genomics through exemplification in two case studies, addressing existing challenges, strengths, and future opportunities for its implementation. By using one example that transcends from science to implementation, a road map is provided to facilitate the integration of seascape genomics into management practices.

2. Seascape genomic case studies on their tack to manage global threats

This section outlines two of the five global drivers of biodiversity loss, specifically habitat loss and resource overexploitation. The objective is to illustrate insights that seascape genomics might offer and how it could be integrated into conservation and resource management [29]. The focus is on delineating the current state of the scientific field of seascape genomics and highlighting the advantages of the implementation of seascape genomics information in management and governance.

To illustrate scientific progress, we have selected well-documented cases involving genotyped populations that incorporate spatio-temporal and environmental information. The first example concerns a group of prominent ecosystem engineers, tropical reef-forming corals, whose long-term survival necessitates immediate management interventions. The second case, fisheries, demonstrates how the management of (over)exploited marine living resources could benefit from knowledge derived from spatially structured population genomics. While the majority of the described studies use a single-species approach, future studies are likely to shift towards community-level analyses [30,31] and this will facilitate a more holistic ecosystem-based management approach [32].

2.1. Rescue from habitat loss - saving the high diversity of coral reefs

Tropical warm-water coral reefs cover only 0.1 % of the oceans, but harbor 25 % of all marine species [33], and approximately 500 million people depend on them for their livelihoods [34]. These biodiverse ecosystems face formidable threats, with warming and ocean acidification standing out as two major challenges [35,36]. Projections indicate that global change will reduce suitable thermal refugia for corals to a fraction of their current expanse even if global warming is contained to 1.5 degrees warmer [37]. Thus, the identification of optimal strategies for local to regional coral reef restoration and conservation management under thermal stress is imperative and can be facilitated through the use [37], as well as estimates on genomic vulnerability [19]. Unfortunately, this responsibility on a global scale often surpasses the jurisdiction of most managers [38]. Consequently, a more robust appeal for international genetic-based biodiversity treaties is warranted, grounded in current scientific data. Tropical reef building coral species and their symbionts exhibit low tolerance to warming, potentially leading to coral bleaching. This phenomenon occurs when the host coral is subjected to overheating, resulting in a substantial decline in the density of symbiotic algae [39]. Nonetheless, specific coral and symbiont genotypes have evolved to endure higher temperatures, thriving in environments like shallow lagoons or warmer regions [40,41]. This suggests that genetic adaptations in certain coral species enable them to acclimate to elevated water temperatures [42].

In a few compelling studies, coral seascape genomics has been applied to assess the impacts of global warming on coral populations by examining connectivity between subpopulations. These studies have incorporated spatially explicit genomic and oceanographic data to identify regions of source populations and identify routes of larval dispersal [43,44]. In theory, as long as these source populations are preserved, the metapopulation is maintained. For example, eco-evolutionary modeling confirmed that the corals of the Great Barrier Reef still maintain high levels of genetic diversity, despite the loss of coral cover in recent years [44], with active Australian legislation and collaborations aiming to conserve and unlock the coding of genetic diversity [45].

Realistically, creating genomic data at spatial scales and resolutions, that are directly applicable for spatial management of coral populations, is likely cost-prohibitive. However, smaller scale efforts can be implemented initially, and then be scaled up when shown (or predicted) to become successful. For example, the first approach could be to use

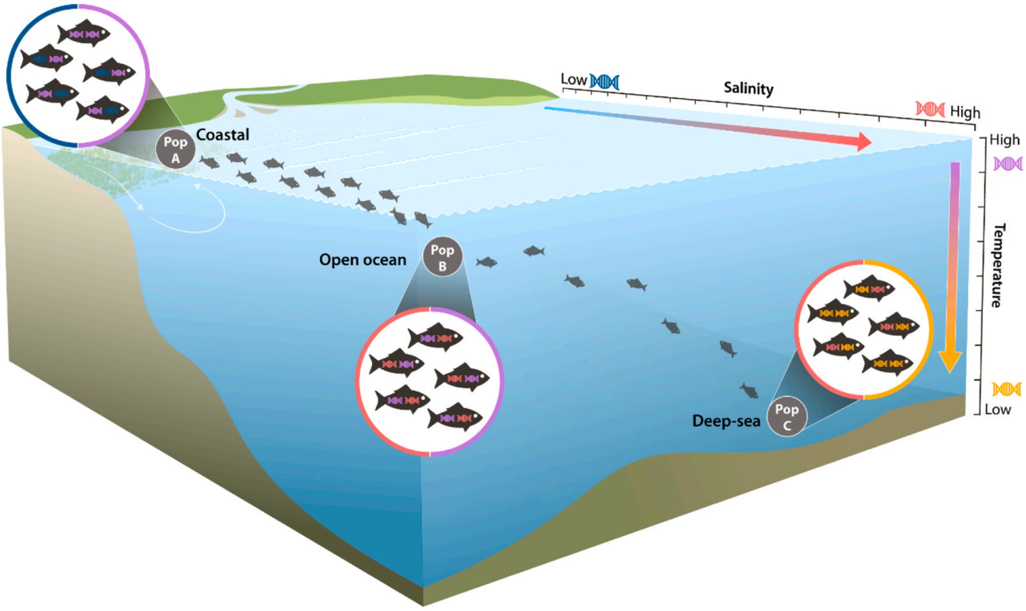


Fig. 3. Seascape genomics incorporates geo-referenced environmental, oceanographic and biophysical data across vertical and horizontal environmental gradients, shown here by temperature and salinity. Evolutionary processes, including genetic connectivity and adaptation, collectively influence the genetic diversity observed within and between populations. Illustration by Jerker Lokrantz/Azote.

predictive modeling to forecast future persistence and adaptive potential [46]. Another approach, is to correlate specific genotypes and environments to pinpoint candidate sites within the genome (and, in some instances, genes) that potentially enable heat resistance. This has been done on small spatial scales by linking distributions of genetic variants to specific environmental conditions, which were first measured in the field and then modeled [47,48]. In the second step, this information can then be used for indexing – based on the present status of a management unit and its predicted health – which allows managers to rank populations according to the urgency of intervention.

Since it is cost-efficient to breed coral in both sea- and land-based farms, the knowledge derived from seascape genomics can also inform selective breeding programs of heat resistant genotypes for rewilding and restoration [49]. The dual approach of integrating population genetic measures within spatial management frameworks and identifying adaptive genotypes for conservation and selective breeding in these areas allows for a more holistic management. Alternatively, one approach can be chosen based on management scope and resources.

2.2. *Future-proof fisheries - empowering living resource management to counteract overexploitation*

Worldwide marine catches have yielded around 80 million tons per year since the 1990s, constituting 17 % of the world population's dietary animal protein intake [50]. However, in 2019, 35.4 % of fish stocks were identified as either overexploited or depleted [50]. Currently, climate change is inducing shifts in the distribution and productivity of numerous commercially valuable species [51,52]. Given the dynamic responses of populations to climate change, ranging from acclimation and adaptation to poleward migration or extinction [53], the continuation of global overfishing poses a high risk of regional ecosystem imbalances. These imbalances could potentially impact population diversity, food web structure, resilience, and overall productivity [54,55]. Therefore, the implementation of effective fisheries management is imperative to address socio-economic concerns, enhance ecosystem resilience, and contribute to conservation objectives.

Fisheries management often operates on spatio-temporal scales that are not aligned with biological realities [56]. Firstly, spatial management units are not always congruent with genetic units or, in other words, genetic population structure. For example, overexploitation of the smaller of two populations with overlapping management units may lead to their extirpation [57]. Secondly, fisheries assessment models predominantly rely on short-term changes in abundance or biomass, often neglecting long-term evolutionary implications [58]. Conservation of genetic diversity (particularly adaptive genetic variants), increases population resilience during global change [59,60].

Seascape genomics has been proven highly informative on biological boundaries for management and the relation of populations to environmental variables, such as temperature and salinity (e.g., in stripey snapper *Lutjanus carponotatus*[61], common sole *Solea solea* [62] and European hake *Merluccius merluccius* [63]. In the case of Atlantic cod *Gadus morhua*, both low-salinity genetic adaptation and age-specific distribution of coastal and offshore ecotypes are now considered in population-level managed fisheries [64,65]. Seascape genomics has also provided correlative evidence for spatial population structure associated with environmental clines in invertebrate species such as American lobster *Homarus americanus* [66], eastern oyster *Crassostrea virginica* [67], and sea scallop *Placopecten magellanicus* [68], which may eventually benefit the management of these resources (Table 1). Another example is highly migratory fish stocks, which are challenging to manage due to their transboundary nature and knowledge gaps regarding connectivity and population structure. Seascape genomics has rarely been applied to highly migratory fish species, partly because data collection might be challenging. However, with decreasing sequencing costs and increasing availability of large-scale environmental data layers, seascape genomics offers great prospects, for example, to identify migratory "highways," spawning and nursery grounds of migratory species. Spatially resolved seascape and/or population genomics data is starting to become available, for instance, for Atlantic bluefin tuna *Thunnus thynnus* [69,70], Greenland halibut *Reinhardtius hippoglossoides* [71], and grey reef shark *Carcharhinus amblyrhynchos* [72].

Overall, incorporating seascape genomics into fisheries management is poised to yield substantial benefits by providing crucial insights into population structure, connectivity, migration patterns, and potential

Box 1
The art of seascape genomic analysis.

Seascape genomics combines methodologies from diverse scientific disciplines, including evolutionary biology and genetics, ecology, oceanography, climatology, and computational sciences. This approach aims to elucidate the intricate interactions between the marine environment and its inhabitants across various spatial and temporal scales [16] (Fig. 3). The data used in seascape genomics typically fall into two primary categories: (i) biological data encompassing e.g., genomic sequences, and, possibly other auxiliary information such as occurrence data, phenotypes, experimental data; and (ii) environmental data such as spatio-temporally structured seawater temperature and salinity, as well as biophysical modeling of dispersal. Correlation of these data types through statistically informed sampling designs enables the identification of potential locally adapted populations, spatial population structure, or connectivity patterns.

Oceanographic and biophysical modeling further contributes by estimating dispersal probabilities [17,18]. Moreover, predictive modeling offers insights into potential future changes, including genomic vulnerability [19]. However, not all seascape genomic studies follow the same approach and use all available data types and methods. For example, dispersal simulations and predictive modeling are selectively used, even though they arguably yield potent results with implications for management applications. Conceptually, seascape genomics can be thought of as a sophisticated combination of differing data types that illuminate the dynamic interactions between organisms and their environment, showcasing evolutionary trajectories over time.

For a recent review on seascape genomics, see Liggins et al. and Riginos et al. [10,20], and for the broader discipline of population genomics, see Luikart et al. [21]. For an overview of molecular tools and statistical techniques, consult Holliday et al. [22] and Grummer et al. [23]. For knowledge sharing initiatives we refer to the Genomics Observation MetaDatabase (GEOME) which captures metadata of biological samples with associated genomics data [24], the network of researchers and practitioners SEA-UNICORN to advance knowledge and unify concepts and approaches on marine functional connectivity (www.sea-unicorn.com), the G-bike network of researchers and practitioners to enable tools for assessing, monitoring, and managing the genetic resilience and adaptive potential of wild and captive populations (https://g-bikegenetics.eu) [25], the Symphony 2.0 tool for ecosystem-based marine spatial planning (https://www.msp-platform.eu/practices/symphony-tool-ecosystem-based-marine-spatial-planning), the US-based project on cataloging migratory connectivity in the ocean (MiCO) (https://mico.eco/system), and the BaltGene project on Baltic Sea Genetics for managers (https://www.gu.se/en/cemeb-marine-evolutionary-biology/management-conservation/baltgene).

adaptive variation. Utilizing spatial and evolutionary information from seascape genomics in fisheries management policies, including the implementation of quotas and no-take zones, holds the potential to enhance the future-proofing of fisheries management [86].

3. Present challenges, strengths, and future opportunities of seascape genomics

3.1. Obstacles and potential solutions

The integration of seascape genomics into conservation management has been slow. The uptake has been confronted by various challenges including technical knowledge gaps, deficiency in collaborative networks, communication platforms, and knowledge transfer mechanisms among stakeholders [87,88]. The methods used to gather genetic information are complex, and management agencies are often understaffed with personnel trained to analyze and interpret such data. Additionally, the rapid development of technologies contributes to the widening gap between conservation genomics and management [89,90]. For example, the recent introduction of structural variant analysis for population characterization presents challenges in data analysis, but such information can be highly valuable for *in situ* stock discrimination [64,91].

By employing managers trained in genomics, molecular assignment techniques have been gradually integrated into salmon management [92]. Such collaborations empower managers who recognize the importance of scientific research in decision-making, providing them with the requisite support and access to genomic data [88]. There are ongoing ambitious efforts to establish connections and platforms between science and management, drawing inspiration from both terrestrial [25] and aquatic contexts [93].

The technical obstacles in the integration of seascape genomic methodologies into management are also not negligible [27]. While high-throughput sequencing has alleviated the genotyping bottlenecks, challenges persist in obtaining high-quality reference genomes, data storage, and analysis [94]. Computational limitations also hinder high-resolution oceanographic modeling, and repositories like GenBank struggle with the processing and storage of vast data volumes. To improve the implementation of seascape genomic findings, scientists need to increase their understanding of the data essential for managerial decision-making [93] and ensure rigorous evaluation and validation of the methodologies.

Additionally, managers face operational challenges that hinder policy implementation and must handle uncertainties and complexities related to vague and sometimes conflicting policy goals. Limited resources for implementation make it challenging to decide on appropriate management measures [87]. Even though it is widely accepted that genetic diversity contributes to healthy and resilient marine ecosystems [95], the significance of genetic diversity is neither always adequately understood, nor is the priority between conflicting conservation goals given [96–98]. Knowledge communication efforts through lectures and deliberative discussions) are effective in increasing managers' perception of genetic diversity [99,100], but need to be continued over time to maintain effects [101].

Furthermore, discrepancies often emerge between the recognition of genetic diversity at higher policy level (e.g., international and national) and its implementation in strategies and actions at regional or local levels. For instance, environmental impact statements of coastal infrastructures, such as wind farms and oil rigs, generally neglect genetic changes (e.g., Belgium: [102,103]; EU, 2020). Nevertheless, these introduced infrastructures may play an important role by acting as novel stepping stones in population spread. As a result of this lack of trickle-down effect, conservation management is not moving forward as fast as desirable, with negative impacts on biodiversity. A potential remedy involves enhancing policy coherence concerning objectives, instruments, and practices [104] and fostering improved communication and collaboration among decision-makers at different levels.

Moreover, while a substantial amount of seascape genomic data exist (Table 1), many applications are still either insufficient or in their infancy. Notably, Sweden has initiated a potentially impactful program for

Box 2
Glossary.

Biodiversity: the diversity of ecosystems, species, populations and genes, and the processes related to the diversity of life.

Dispersal: movements of individuals or propagules that have potential consequences for gene flow within and between populations and across space.

[Fish] stock: a group of individuals (fish) of the same species occupying a well-defined spatial range independent of other groups of the same species. A stock can be regarded as an entity for management or assessment purposes.

Genetic connectivity: transfer of genetic material (via individuals or gametes) between populations.

Genetic diversity: the number of different genetic variants within a population or species.

Genotype: the entire genetic constitution of an organism or the genetic composition at a specific gene locus or set of loci.

Management unit: entity (such as a coastline or fish stock) that has been given the mandate by a State to perform specific management functions

Metapopulation: a group of connected populations of a species.

Migration: the ecological, behavioral and evolutionary implications of the act of moving from one spatial unit to another.

Phenotype: the physical, physiological and behavioral appearance of an organism.

Population: a group of individuals of a given species in a defined area, genetically distinct from other such groups.

Restoration: the process of assisting the recovery of a degraded, damaged, or destroyed ecosystem.

Seascape: spatially heterogeneous and dynamic spaces in the ocean that can be delineated at a wide range of scales in time and space.

Seascape genetics: a research field combining environmental and genetic information to study how environmental factors shape genetic diversity, connectivity, and evolutionary processes of populations and species (see Fig. 3).

Seascape genomics: similar concept to seascape genetics, but by using genome-wide (i.e., thousands) of genetic loci/markers and/or reference genomes and/or high-throughput sequencing technology, seascape genomics often also allows the assessment of adaptive processes (see Fig. 3).

Table 1
Examples of seascape genomics interpreted from a management perspective, driver of global biodiversity change, topic, outcome, organisms, habitat and reference.

Management practice	Global change	Topic	Outcome	Organism [Classification]	Habitat	Ref.
Conservation management and spatial planning	Climate change	Identification of adaptive potential based on environmental characteristics and genotype frequencies, combined with connectivity analysis	Identification of reefs carrying potential heat stress adaptation and dispersal potential to neighboring reefs	Coral [Cnidaria]	Coastal	[47]
Conservation management	Climate change	Future proofing’ efforts rely on predicting how neutral and adaptive genomic patterns will change under future climate scenarios	Range-edge populations harbor beneficial adaptations	Crayweed [Macroalgae]	Coastal - Benthos	[73]
Conservation and living resource management	Climate change	The viability of remnant populations could be impacted by continued fishing, by-catch pressure, and climate change	Climate change could inflict a strong selective force upon remnant populations	Blue skate [Fish]	Open ocean - Pelagic	[74]
Conservation management	Habitat loss	Environmental factors may influence the evolutionary potential of populations and species	Species-specific habitat requirements and responses to environmental stresses may be better predictors of evolutionary patterns than strong environmental gradients	Crab [Crustacea], Sea urchin [Echinodermata], Limpet [Mollusca]	Coastal	[30]
Living resource management	Habitat loss/ resource overexploitation	Study of fine-scale spatial genetic structure and comparison to environmental variables and current-mediated larval dispersal within a modelling framework	Oceanographic currents and geographic proximity explain over 20 % of the variance observed at neutral loci, while genetic variance at outlier loci was explained by sea surface temperature extremes.	Cockle [Mollusca]	Coastal - Plankton	[75]
Conservation management	Habitat loss	Artificial structures function as stepping stone connectivity to suitable habitats	The marine steppingstone effect is obviously important for the distribution of sessile taxa	Mussel [Mollusca]	Coastal	[76]
Conservation management	Non-indigenous species and populations	Species introductions promote secondary contacts between taxa with long histories of geographically separate divergence	The outcomes of species introductions are diverse, from introgression swamping to strong barriers to gene flow; lead to local containment or widespread invasion	Sea squirt [Tunicata] and Mussel [Mollusca]	Coastal	[77]
Conservation management	Non-indigenous species and populations	During range expansions, strong random sampling effects caused by small population sizes, may decrease genetic diversity with increased distance from the point of invasion or the center of the historic range	Patterns of genetic diversity correlate with invasion pathway	Lionfish [Fish]	Coastal	[78]
Conservation management	Non-indigenous species and populations	Rapid climate-driven evolution might shift biogeographic distributions in response to global change	Rapid evolutionary adaptation has played a pivotal role in enabling the successful invasion of a wide range of habitats	Mussel [Mollusca]	Coastal	[79]
Environmental management	Pollution	Specific evolutionary circumstances and mechanisms might rescue species at risk of decline from lethal levels of pollution	High nucleotide diversity might have been a crucial substrate for selective sweeps to stimulate rapid adaptation	Killifish [Fish]	Estuary	[80, 81]
Conservation management	Pollution	Two types of point sources of aquatic environmental pollution affect gene diversity, genetic differentiation, and adaptation differently	Genetic effects are associated with exposure to sewage treatment plant effluents on wild populations	Mussel [Mollusca]	Baltic Sea; Coastal	[82]
Living resource management and spatial planning	Resource overexploitation	Investigation of the influence of environment, geographic isolation, and larval dispersal on the variation in allele frequencies	Important to consider spatial scale in the design of a protected area network	Mullet [Fish]	Coastal	[83]
Living resource management	Resource overexploitation	Testing for the presence of genetic discontinuities and spatial processes influencing spatial structure	Depletion of one population also affects recruitment of other populations	Sea cucumber [Echinodermata]	Benthos	[84]
Living resource management	Resource overexploitation	Environmental association analysis to identify bioclimatic variables correlated with putatively adaptive genetic variation	Environmental variables play a role as drivers of spatially varying selection	Sea cucumber [Echinodermata]	Benthos	[85]

monitoring genetic diversity over time in aquatic species, including several marine ones (currently Atlantic herring *Clupea harengus*, Atlantic cod, eelgrass *Zostera marina* [105] and bladder wrack *Fucus vesiculosus*). Indicators have been developed and applied to freshwater species [106, 107], and are applied to the other species as temporal data becomes available. Indicator values are planned to be reported in the context of the CBD and its new monitoring framework linked to the Kunming-Montreal Global Biodiversity Framework adopted in December 2022 (www.cbd.int/gbf). Other integration of the genetic information in management is currently explored in research-management collaborations [108].

3.2. Strengths and future opportunities of seascape genomics

The findings of seascape genomics translate well into management processes and offer a valuable perspective on the global biodiversity challenges (see Table 1 for examples). Recent years have witnessed notable technological advancements that have propelled seascape genomics forward, enabled by access to high-quality spatio-temporally structured digital repositories. Noteworthy contributors to this progress include the European Union's Earth observation program Copernicus (copernicus.eu), the British Oceanographic Data Centre (BODC), the ICES data portal, data archiving repositories such as Dryad, the Microbe Atlas Project (microbeatlas.org), the European Nucleotide Archive, and GEOME [24]. These repositories collectively provide the necessary genetic, environmental, and oceanographic data required for conducting correlation and association studies [10].

Furthermore, the integration of automated high-throughput data collection, the growing applicability of "genetic nets" facilitated by environmental DNA (eDNA), and developments with in-situ automation presents new opportunities for continuous sampling and the establishment of remote observatories [109,110].

3.2.1. *Roadmap to integrate seascape genomics into management*

Recent developments in genomics and modeling have provided scientists with a versatile and powerful toolbox for monitoring marine populations, offering insights into their demographic and adaptive history [15,111]. Examples span diverse habitats, ranging from the inshore dispersal of cockle larvae in the Irish Sea (Table 1) to unraveling the genetic connectivity of adult reef sharks across the tropical Indo-Pacific Ocean [72]. Other applications include the implementation of a Marine Protected Area (MPA) in Scotland to safeguard the critically endangered flapper skate *Dipturus intermedius* [112] (Marine Scotland, 2020), real-time monitoring of the Northeast Atlantic cod fishery in a marine protected area [113], and the adaptive management of eelgrass meadows along the Swedish west coast (details below). Despite the considerable number of published seascape genomics studies (Table 1), the implementation of research outcomes into management practices remains limited. To address this, we highlight a series of roadmap-style steps (Fig. 4) to depict a successful update of seascape genomics into management, drawing on the case of Swedish seagrass, in which several authors of this paper are involved.

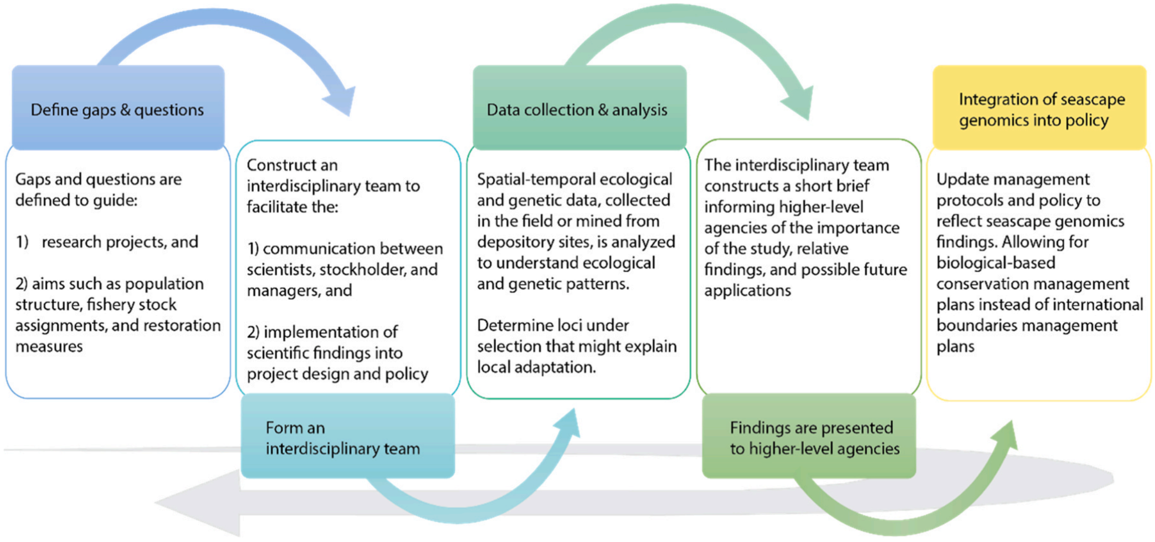
3.2.1.1. Co-creation to define gaps and questions. Initiating a collaborative science-management project begins by identifying initial gaps and questions. These initial discussions will determine if the project aligns with the goals of both researchers and managers. The establishment of common ground may encounter challenges due to diverse partners being mandated to fulfill distinct aims. For example, researchers are constrained by academic objectives, encompassing the necessity to publish and develop projects that align with grant application goals, while managers' responsibilities are delineated by state or federal objectives. Additionally, management scales frequently exhibit more localized dimensions than at a broader seascape scale (e.g., MPA management [114].

Despite these limitations, the identification of shared objectives remains possible through co-creation within an interdisciplinary team consisting of, but not limited to, researchers, conservation practitioners, stakeholders, and governmental agencies. Once the interdisciplinary team is established, the refinement of specific objectives and project planning can begin.

In the context of implementing seascape genomics for the management and restoration of eelgrass meadows along the Swedish coast, the collaborative effort involves the research group ZORRO (gu.se/en/research/zorro) at the University of Gothenburg and conservation practitioners at the County Administrative Board (CAB) of Västra Götaland and other regions, along with the Swedish Agency of Marine and Water Management (SwAM). These entities converge with the shared objective of mitigating seagrass loss and enhancing seagrass conservation. All parties acknowledged the vital ecosystem services provided by these meadows, including erosion mitigation, water quality improvement, and their role as carbon and nitrogen sinks [115,116]. Furthermore, there is a collective acknowledgement of the pivotal role played by the underlying genetic diversity in the conservation and restoration of these meadows. A key factor for the success of this collaboration venture lies in maintaining open and frequent communication, fostering discussion on implementation strategies, and addressing the specific needs of the groups involved.

3.2.1.2. Data collection and analysis. Following the definition of objectives, the next step involves the essential process of collecting and integrating data into spatially referenced datasets, a crucial component of seascape genomics assessments (Fig. 3, Box 1). This process may encompass various methods, including field studies or mining data from repository sites, or a combination of both approaches.

In the eelgrass case study, a comprehensive set of seascape genetic, biophysical, and environmental data was gathered and analyzed. This information was then used to identify valuable and vulnerable meadows



Gaps and questions are defined to guide:
1) research projects, and
2) aims such as population structure, fishery stock assignments, and restoration measures

Construct an interdisciplinary team to facilitate the:
1) communication between scientists, stockholder, and managers, and
2) implementation of scientific findings into project design and policy

Spatial-temporal ecological and genetic data, collected in the field or mined from depository sites, is analyzed to understand ecological and genetic patterns.

Determine loci under selection that might explain local adaptation.

The interdisciplinary team constructs a short brief informing higher-level agencies of the importance of the study, relative findings, and possible future applications

Update management protocols and policy to reflect seascape genomics findings. Allowing for biological-based conservation management plans instead of international boundaries management plans

Fig. 4. Seascape genomics can be embedded in the management cycle of biodiversity protection. Initially, an interdisciplinary team collaborates to identify gaps and formulate relevant questions. Upon reaching a consensus on specific aims, data retrieval and collection begin, followed by the preparation of analyses and the design of models aimed at integrating the results. This process facilitates the incorporation of novel insights derived from seascape genomics into policy frameworks. Subsequently, as new gaps emerge, additional questions are generated, affording opportunities to update management practices and policies to accommodate the incorporation of these findings.

along the Swedish west coast, allowing for the prioritization of intervention based on urgency and cost-effectiveness [117]. The findings indicated that, despite recent declines, the genetic diversity within these populations remained relatively high. Consequently, after establishing that genetic differentiation exists on small spatial scales, local populations with high genetic diversity, similar genetic background, and limited isolation from the recipient population were identified as potential donor material for future restoration efforts [118]. Moreover, biophysical modeling was used to identify candidate restoration sites where the entire eelgrass metapopulation would benefit the most from increased dispersal [117].

Beyond eelgrass, studies on marine species with more complex life histories, involving drifting larval stages and actively moving (sub) adults, can benefit from biophysical dispersal modeling. Even complicated life histories might become better understood through statistical models, such as correlational genetic niche and dynamic energy budgets (DEB) [119]. Seascape genomics is also valuable in revealing the spatio-temporal dynamics of rare species [74], as well as emblematic communities such as coral reefs (see above; Table 1). The applicability of seascape genomics extends across a broad-life history spectrum, from short-lived microbes [120] to millenary seagrass clones [121].

3.2.1.3. Integration of seascape genomics into policy. The least developed yet fundamentally crucial phase in the management cycle involves integrating seascape genomic findings into management protocols and policies (Fig. 4). Urgent expansion of adaptive management strategies to address future challenges is imperative [122], and the development of scenarios that enhance the capacity to handle uncertainties or unlikely but possible events is vital for realistic forecasting. Stakeholder involvement is essential in developing these scenarios, thereby guiding scientists and managers in the development of forecasting models. The ability to assess various spatial and temporal scales in seascape genomics enables advising on management-relevant spatial scales and designing adaptive plans that consider anticipated future changes (see also Table 1).

In the seagrass case, eco-evolutionary modeling was used to predict the impact of halting eelgrass decline on the future genetic diversity and persistence of these meadows [117]. Ongoing efforts focus on integrating eelgrass seascape genetic data into management practices related to protection, restoration, and monitoring [105,123]. Priority areas with high genetic diversity and connectivity, identified in [105, 117,123], have been communicated to the County Administrative Board. Additionally, the European Commission recognizes and advocates for the importance of the approach in assessing the efficiency of the EU network of MPAs and defining management units [124]. Test planting for eelgrass restoration has been conducted at several sites recommended in the same study [117]. Ecological monitoring efforts, under various policies like the European Water Framework Directive (WFD), Marine Strategy Framework Directive (MSFD), and Habitat Directive are ongoing for eelgrass. Also incorporating genetic diversity monitoring would be beneficial, and is likely becoming a requirement under the new EU Nature Restoration Law. To establish a baseline, SwAM has financed large-spatial scale genetic assessments for eelgrass [105] and other species [108]. Attempts are underway to spatially align monitoring sites from different directives, such as the EU Habitat Directive, EU MSFD, and EU WFD, to integrate data from various monitoring initiatives into a seascape genomics framework [123]. Adopting a similar approach to the eelgrass case and drawing parallels to global CO_2 emissions [125], scenarios are being developed for fisheries management [126], marine ecology under climate change [127], coral reef resilience [128], future-proofing underwater forests [73], and the expansion of MPAs [129].

4. Conclusions

The multi-disciplinary combination of environmental and genomic data using diverse modeling approaches represents a powerful approach for generating relevant knowledge to support biodiversity conservation (Box 1, Table 1). Assessing various spatio-temporal scales facilitates the development of management plans at spatially relevant scales, considering genetic adaptability in the face of future environmental changes.

Seascape genomics approaches align with an ecosystem-based policy perspective, aiming to integrate the management of land, water, and living resources (e.g., EU MSFD) [130]. Applications encompass the design of protected areas, coastal zoning, habitat restoration, predicting species invasions, and living resource stock assessment. Notably, advanced applications are observed in coral reefs, seagrass meadows, and commercial fish stocks in coastal environments. The potential for applications in the deep-sea, offshore pelagic seas, polar seas, poorly studied oceans, and highly migratory species holds promise. While current applications of seascape genomics in MPAs and ocean zoning focus on source-sink metapopulation dynamics and connectivity, these can be extended with global change scenarios affecting ecosystem services. Recent living resource management applications emphasize connectivity, matching fish stocks and populations, and the impact of fishing (Table 1). Scenarios demonstrating effects of climate and habitat change on fisheries-related biodiversity will be promising for ecosystem-based climate adaptation.

To fully leverage the integration and implementation of seascape genomic information in marine ecosystem and resource management, collaboration among scientists, policymakers, and managers is essential to ensure that:

- International and national policies are translated into practical guidance for implementation;
- The best available scientific knowledge and methodology on seascape genomics is used;
- New knowledge is continuously incorporated into biodiversity management;
- The audience and users of seascape genomic studies are expanded.

Seascape genomics combines essential genomic insights with spatial, temporal and environmental information required for biodiversity management. However, improved integration into marine conservation and resource management is crucial to preserve genetic diversity and prevent the ongoing loss of biodiversity, providing future generations with a more sustainable planet.

Author contributions

FAMV launched the idea; JR, MJ, CA, HC, PRDW, EF, LG, PRJ, ATL, MR, MT and FAMV developed the concept, mined the literature, and wrote the first draft; LL and AS provided major input on end-users; JR, MJ and FAMV reviewed and edited with the help of all co-authors.

Ethics statement

Ethical approval was not required for this research.

Declaration of Competing Interests

The authors declare no competing interests.

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Data availability

No data was used for the research described in the article.

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