



Reefscape Genomics: Leveraging Advances in 3D Imaging to Assess Fine-Scale Patterns of Genomic Variation on Coral Reefs

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Coral reefs across the world are undergoing rapid deterioration, and understanding the ecological and evolutionary processes that govern these ecosystems is critical to our ability to protect them. Molecular ecological studies have been instrumental in advancing such understanding, and while initially focused primarily on broad-scale patterns, they have gradually uncovered the prevalence of local genetic structuring. Genome-wide sequencing approaches have provided new opportunities to understand both neutral and adaptive contributions to this largely unexplained diversity, but fine-scale assessments have been hampered by challenges associated with aquatic environments, in terms of (geo)referencing, seafloor characterization, and *in situ* phenotyping. Here, we discuss the potential of “reefscape genomics,” leveraging recent advances in underwater imaging to enable spatially explicit genomic studies on coral reefs. More specifically, we consider how (close-range) photogrammetry approaches enable (1) fine-scale spatial mapping of benthic target organisms, (2) repeatable characterization of the abiotic and biotic reefscape, and (3) simultaneous *in situ* mass-phenotyping. The spatially explicit consideration of genomic data –combined with detailed environmental and phenotypic characterization– opens up the opportunity for fine-scale landscape genomic approaches on coral reefs (and other marine ecosystems). Such approaches enable assessment of the spatio-temporal drivers and adaptive potential of the extensive genetic structuring and cryptic diversity encountered in benthic invertebrates, such as reef-building corals. Considering the threats that coral reefs are facing worldwide, we believe that reefscape genomics represents a promising advancement of our molecular ecological toolkit to help inform how we can most effectively conserve and restore coral reef ecosystems into the future.

Keywords: reefscape genomics, seascape genomics, coral reefs, photogrammetry, structure from motion, landscape genomics

INTRODUCTION

Coral reefs are one of the most biodiverse and economically important ecosystems. Yet, they are undergoing an unprecedented decline due to a wide range of anthropogenic stressors (e.g., increasing sea temperatures, ocean acidification, pollution, and overfishing) (Hoegh-Guldberg et al., 2007; McClenachan et al., 2017). Our ability to manage and conserve these vulnerable ecosystems is contingent on our understanding of the fundamental processes underpinning their resilience. Over the past decades, molecular ecology has played a major role in elucidating these processes for reef-building corals (order Scleractinia) (van Oppen and Gates, 2006), by uncovering patterns of dispersal and connectivity (Ayre and Hughes, 2000; van Oppen et al., 2008), contributions of sexual and asexual reproduction (Miller and Ayre, 2004; Foster et al., 2013; Dubé et al., 2017), the prevalence and nature of hybridization (Vollmer and Palumbi, 2002; Combosch et al., 2008), and the endosymbiotic microbial diversity which is critical to their survival (Baums et al., 2014; Boilard et al., 2020). Importantly, the advent of high-throughput genomic approaches (e.g., reduced representation and whole-genome sequencing) has facilitated increasingly sophisticated assessments for non-model organisms (Riginos et al., 2016; Matz, 2018), including the opportunity to study adaptive variation critical to the persistence of coral reefs (Bay and Palumbi, 2014; Dixon et al., 2015). While these genomic advances hold great promise to address knowledge gaps in ecology and evolution, their true potential is ultimately dependent on our ability to couple their outputs with environmental and/or phenotypic information at the relevant spatial scale (Andrew et al., 2013).

Landscape genetics has provided a powerful framework in terrestrial ecosystems to predict population genomic patterns from landscape attributes and processes (Manel et al., 2003; Balkenhol et al., 2016). By extension, landscape genomics is a more recent discipline that queries similar relationships but across both neutral and adaptive parts of the genome (Balkenhol et al., 2017; Li et al., 2017). As its marine counterpart, seascape genomics shares much of the aforesaid theoretical and analytical framework, but is challenged by physical variability of the oceanic environment and the unique life histories of marine organisms (e.g., high dispersal potential and large effective population sizes) (Riginos et al., 2016; Liggins et al., 2019). Recent studies have demonstrated the potential of seascape genomics in the study of reef-building corals, for example by identifying genes associated with thermal adaptation (Jin et al., 2016; Fuller et al., 2020; Selmoni et al., 2020a,b). Nevertheless, there are several major limitations associated with the application of seascape genomics to coral reef environments. Firstly, due to its reliance on remote sensing methods, the environmental characterization mostly focuses on the (upper) ocean surface (i.e., oceanographic features) rather than the benthic landscape (or “benthoscape”). In addition, the spatial resolution (or “grain”) of such remotely sensed methods generally only allows for limited characterization on a within-reef scale. Lastly, spatially explicit, individual-based sampling has been hampered (compared to terrestrial studies) due to the inability

of using satellite-based geo-positioning, as radio signals do not propagate sufficiently underwater.

In this perspective, we discuss the potential for “reefscape genomics,” leveraging advances in underwater imaging to enable fine-scale landscape genomic studies on coral reefs. The term “reefscape” has been used loosely in the coral reef literature, mostly as an underwater equivalent to the term landscape (e.g., Arias-González et al., 2006; Urbina-Barreto et al., 2020). Inherently connected to seascape genomics, we define reefscape genomics as spatially explicit studies focused on a within-reef scale that use reefscape attributes and processes as statistical predictors of genomic variation. This follows a recent call to expand seascape characterization to specifically include the benthic component (Van Wynsberge et al., 2017), but we argue the additional value of doing so at a high spatial resolution. Such fine-scale characterization of the reefscape has recently been made possible due to advances in computer vision, and further facilitated by the increased accessibility of the underwater environment (e.g., through autonomous underwater vehicles, dive propulsion vehicles, and closed-circuit rebreathers). In particular, we believe that close-range photogrammetry has the potential to transform seascape genomics by enabling (1) fine-scale spatial mapping benthic components, (2) repeatable characterization of both abiotic and biotic features of the benthoscape, and (3) simultaneous mass-phenotyping of target organisms. We begin by explaining why a reefscape genomics approach is relevant in terms of major knowledge gaps (focusing mostly on reef-building corals), we then elaborate on the types of relevant (meta)data that can be acquired through photogrammetry, and we conclude by illustrating how such data can be integrated into genomic assessments to address the outlined knowledge gaps.

WHY REEFSCAPE GENOMICS?

The choice of spatial scale in molecular ecology is critical as it defines the ability to identify the processes underlying genetic variation (Hellberg, 2007). Given the biphasic life cycle of most marine organisms (i.e., pelagic larval and benthic adult phase), it has been traditionally assumed that neutral genetic patterns are governed by broad-scale larval dispersal processes (Kinlan et al., 2005; Liggins et al., 2013). However, studies have since demonstrated the prevalence of local genetic differentiation within both species with internal (brooders) and external (broadcasters) fertilization. For brooding species, such fine-scale population structure can be linked to strongly localized sperm and larval dispersal (Underwood et al., 2007; Ledoux et al., 2010; Warner et al., 2016), while such patterns for broadcasting species contradict with their broad dispersal capability and with observations of high gene flow over large distances (Ayre and Hughes, 2000; van Oppen et al., 2008; Cros et al., 2020). These non-intuitive population structures are likely the result of the complex interplay and spatio-temporal variability in species attributes, pelagic conditions, and benthic features (Liggins et al., 2019). The perceived chaos in reef-building corals is—at least in part—due to a mismatch in spatial

resolution (Cros et al., 2020), a predominance of population-level sampling (Riginos and Liggins, 2013; Liggins et al., 2019), and an almost complete lack of temporal assessments (but see Williams et al., 2014; Underwood et al., 2018). Microsatellite-based studies with exhaustive local sampling have demonstrated the critical relevance of fine-scale, individual-based sampling by revealing the important contributions of clonality and inbreeding (Gorospe and Karl, 2013; Dubé et al., 2017), sperm dispersal and self-fertilization (Warner et al., 2016), co-dispersal of siblings, and self-recruitment (Cros et al., 2020; Dubé et al., 2020). Nonetheless, our understanding of reproduction and dispersal processes in benthic reef organisms is still in its infancy given that spatially explicit, individual-based attempts have been incredibly tedious, and have lacked the ability to characterize and integrate the fine-scale composition and configuration of the reefscape.

Patterns of adaptive variation in marine environments often occur at local scales, with selection contributing to spatial genetic structuring regardless of the extent of gene flow (Liggins et al., 2019). Habitat-specific sampling has demonstrated how local genetic structure in reef-building corals can reflect divergence across environmentally distinct but spatially adjacent reef habitats (Benzie et al., 1995; Bongaerts et al., 2010, 2011; van Oppen et al., 2018), with parallel patterns observed in coral endosymbionts (Frade et al., 2008; Bongaerts et al., 2010; Pantos et al., 2015; Hernandez-Agreda et al., 2018; van Oppen et al., 2018). Such findings highlight the importance of environment-associated selection and the potential for ecological barriers to gene flow. However, substantial genetic and phenotypic diversity in nominal species is being uncovered within reef habitats (Dubé et al., 2017; Gélin et al., 2017; Forsman et al., 2020), with much of that diversity remaining unexplained. While advances in omics-based approaches have shown great potential (Riginos et al., 2016; Matz, 2018), our ability to understand such diversity has been limited by the difficulty of gathering high-resolution data on the corresponding phenotypes and associated environments. Understanding the adaptive potential of this genetic and phenotypic variation (e.g., tolerance to warming or eutrophication) and its nature or origin (e.g., standing genetic variation, hybridization, somatic mutations, or epigenetic), is becoming increasingly important to predict how corals may persist into the future. It is also critical for coral reef conservation and restoration efforts, to ensure that the adaptive potential of protected, translocated, or restored populations is maximized to promote survival under rapidly changing environmental conditions.

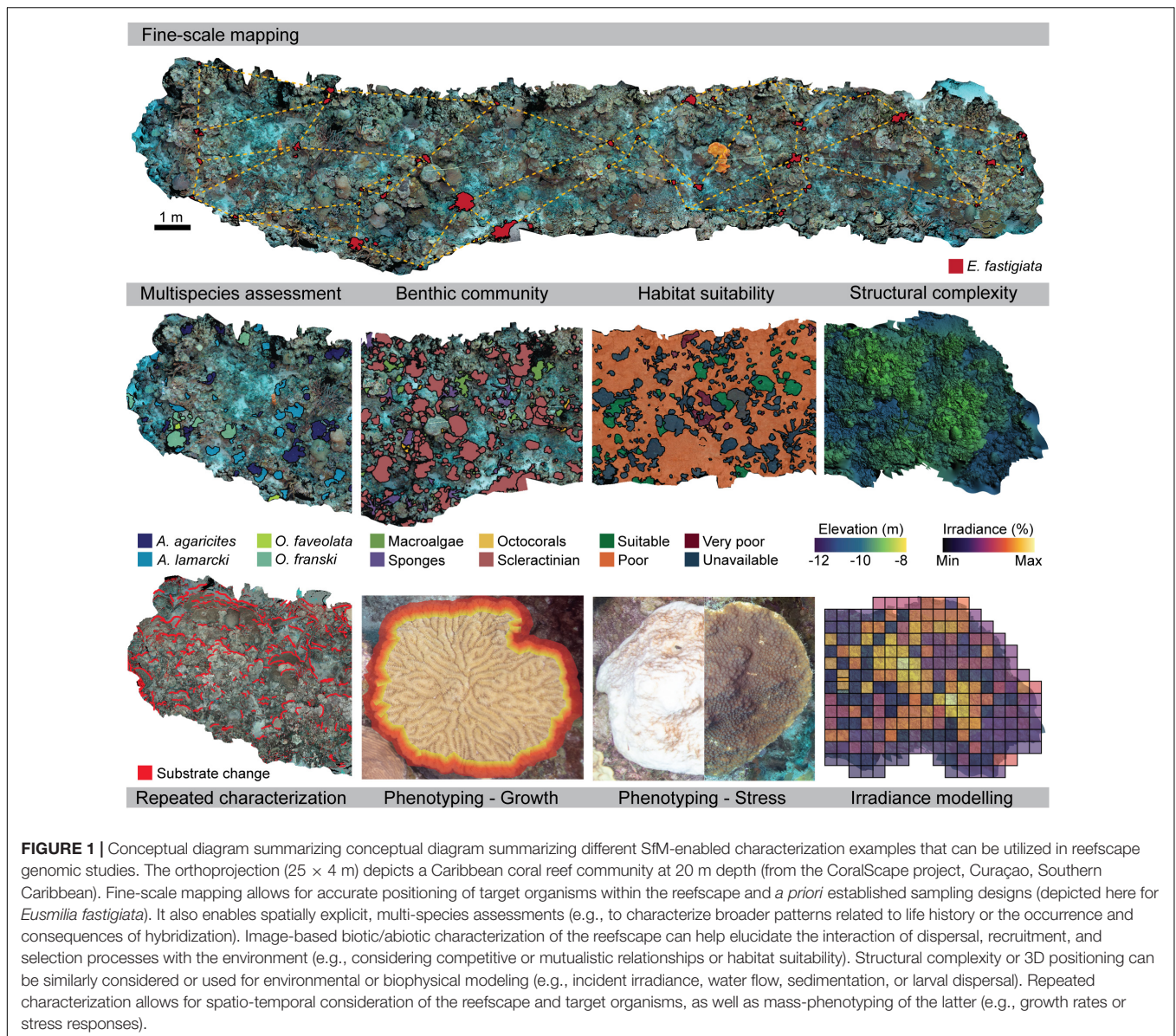
REEFSCAPE CHARACTERIZATION THROUGH CLOSE-RANGE PHOTOGRAMMETRY

The logistical difficulty of fine-scale underwater mapping and (geo)referencing has long hampered spatially explicit coral reef studies and thereby direct coupling of genetic data with environmental, ecological, and phenotypic data. However, recent advances in photogrammetry—in particular Structure from Motion (SfM)—now permit fine-scale 3D characterization based

on consumer-grade cameras and non-expert software (Figueira et al., 2015; Burns and Delparte, 2017; DeBell et al., 2019). In contrast to stereophotogrammetry that usually relies on calibrated image pairs, SfM can approximate camera position and angle from highly overlapping photographs to generate a “sparse point cloud” (Westoby et al., 2012). This can be further processed using multi-view stereo algorithms into a “dense point cloud” (Iglhaut et al., 2019), from which 2D (orthoprojection/mosaic), 2.5D (digital elevation model), or 3D (textured 3D mesh) products can be generated (**Figure 1**). SfM has been widely adopted in geoscience for topographical surveys (Westoby et al., 2012; Fonstad et al., 2013; Smith et al., 2016), including subaerial forest, wetland and coastal characterization (Kalacska et al., 2017; Iglhaut et al., 2019), but its close-range ability overcomes persistent underwater light attenuation and scattering issues, making SfM particularly suited for fine-scale benthoscape characterization.

SfM has rapidly become a critical tool in benthic ecology studies on coral reefs (Burns et al., 2015; Leon et al., 2015; Ferrari et al., 2016b; Edwards et al., 2017; González-Rivero et al., 2017), where the requirement of a static environment (throughout the imaging process) is largely satisfied by the dominance of reef-building corals. Depending on camera resolution and altitude (i.e., distance to seafloor), current modeling abilities roughly span a grain range of ~0.1–10 mm and spatial extent range of 0.01–1 ha (**Figure 2**), with a trade-off between grain size and spatial extent. Using scale references, a highly accurate local coordinate system of the generated model can be created (mm to cm accuracy; Ledoux et al., 2010), enabling underwater mapping with unprecedented resolution, efficiency, and repeatability compared to traditional methods using transect tapes, depth gages, and/or compasses (Foster et al., 2013; Gorospe and Karl, 2013; Williams et al., 2014; Gélin et al., 2017; Dubé et al., 2017, 2020). Such local coordinates can be converted to real-world coordinates by georeferencing the model using, e.g., ground control points (GCPs) or by integrating acoustic positioning and orientation sensors on the imaging platform [e.g., ultrashort-baseline (USBL), Doppler velocity log (DVL), and attitude and heading reference systems (AHRS)]. In both cases, the accuracy of georeferencing will be determined by that of the surface-based global navigation satellite system (GNSS) receiver, and the method used to determine positioning relative to that of the receiver (e.g., a simple vertical upline or sophisticated multisensory navigation system).

The power of SfM in resolving 3D structure has enabled the study of structural complexity in relation to species diversity, competition, and coexistence. Structural complexity can be characterized through various metrics: linear and surface rugosity (Dustan et al., 2013; Ferrari et al., 2016a, 2018), fractal dimension (Tokeshi and Arakaki, 2012; Leon et al., 2015; Young et al., 2017), crevice or refuge density (González-Rivero et al., 2017; Agudo-Adriani et al., 2019; Oakley-Cogan et al., 2020), viewshed (González-Rivero et al., 2017; Urbina-Barreto et al., 2020), and surface height range (Torres-Pulliza et al., 2020). Broader-scale environmental parameterization (e.g., through the deployment of sensors) has the potential to enable fine-scale modeling of further abiotic variables that cannot be inferred directly from



the imagery, such as temperature, irradiance, water flow, and sedimentation across the reefscape (Figure 1). As SfM is imagery-based, detailed characterization (2D/3D) of the seafloor can be undertaken through point-based annotation or semantic segmentation, with promising automation potential through machine learning (Alonso et al., 2019; Williams et al., 2019; Pavoni et al., 2020). Species-level identifications and recruit detection can be facilitated by the pairing of individual points to the original photographs (usually having greater resolution than the constructed dense point cloud), with such characterizations rapidly providing new insights into coral demographics (Edwards et al., 2017; Brito-Millán et al., 2019; Pedersen et al., 2019). The simultaneous documentation of the abiotic and biotic reefscape holds particular promise for landscape community genomic approaches focusing on the interaction of environmental and community effects on genomic variation (Hand et al., 2015).

Another major advantage of SfM characterization is its suitability for repeat surveys, describing how target species populations and interfering biotic and abiotic reefscapes change over time. SfM also opens up the opportunity for simultaneous *in situ* phenotyping of focal organisms through the obtained imagery. Although certain morphological (e.g., gross morphology) and ecological (e.g., symbiotic state) aspects can be extracted from a single time-point, repeated characterization allows for the determination of growth rates (surface or linear expansion; Holmes et al., 2008) or susceptibility to stressors (Chow et al., 2016; Miller et al., 2016; Precht et al., 2016; Page et al., 2017; Gintert et al., 2018; Johnston et al., 2019). The third dimension that photogrammetry adds significantly enhances all aspects of phenotyping; for example, growth traits of corals and other invertebrates are more accurately determined from 3D surface areas and volumes (Lavy et al., 2015;

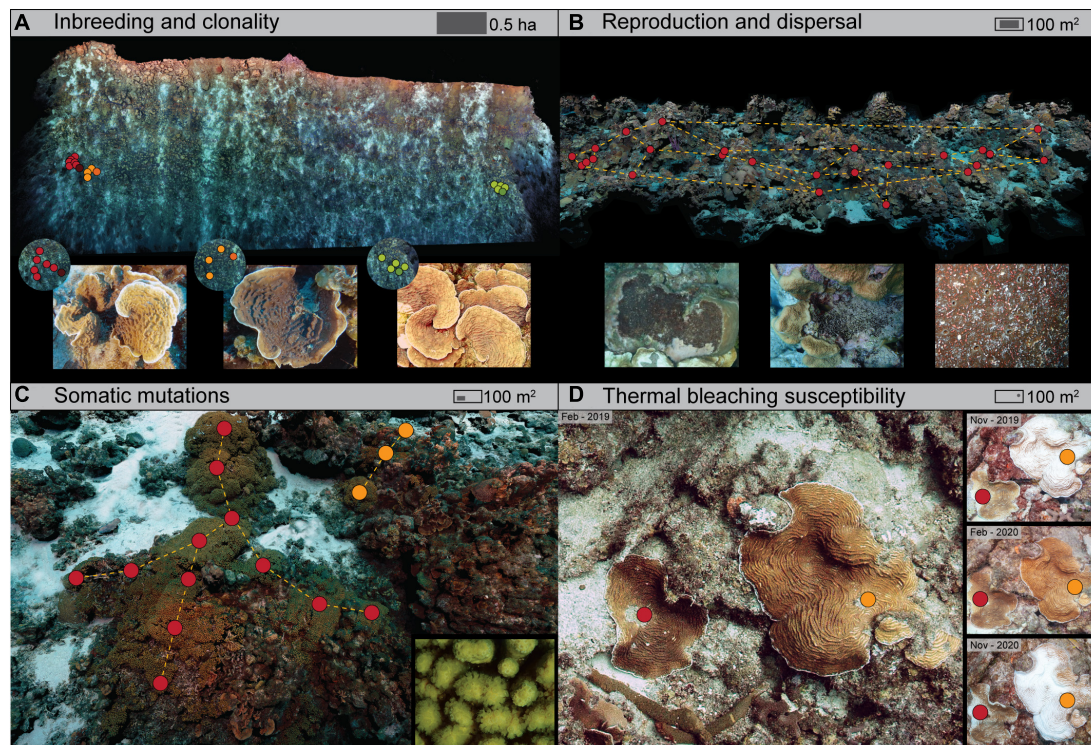


FIGURE 2 | Four example applications of reefscape genomics, conducted as part of the CoralScape project in Curaçao (Southern Caribbean). This project monitors large-area plots (0.5–1 ha per plot) and focal plots (100 m²) covering a range of 5–60 m depth at eight different locations along the leeward shore. The focal plots are reimaged twice a year (using a Canon 5DsR with an EF 24 mm f/1.4 prime lens and four Inon Z330 strobes) and incrementally sampled (for different taxa). Collected samples are referenced to the 3D model using video from a head-mounted camera, with the diver carrying a 96-well rack with numbered 0.5 mL tubes bungee-mounted to their forearm. **(A)** Broad-scale imaging (>0.5 ha per plot) to assess the impact of rapid population decline on the reproduction and genomic variation in the coral *Helioseris cucullata*, and to evaluate extinction risk and appropriate conservation strategies (Hernandez-Agreda et al., unpublished data). **(B)** Medium-scale imaging (100 m² per plot) to understand the roles of niche partitioning and asexual reproduction in the fast expansion of coral-eroding sponges in the *Cliona viridis* species complex (Achlati et al., unpublished data). Inset photographs show different growth forms and a close-up. **(C)** Medium-scale imaging (100 m² per plot) to track the spread of somatic mutations in the coral *Madracis mirabilis*, and assess their contributions to genetic diversity in large monospecific stands (Bongaerts et al., unpublished data). **(D)** Medium-scale imaging (100 m² per plot) to disentangle the role of environment and genotype in bleaching response and the overall effect of bleaching on population genetic diversity within the coral genus *Agaricia* (Prata et al., unpublished data). Circles represent samples of target organisms (as depicted in close-up photos) colored by genotype (except for in **B**).

Gutiérrez-Heredia et al., 2016; Ferrari et al., 2017; Olinger et al., 2019), as are other colony-level and polyp-level morphological traits (Kruszyński et al., 2007; Gutiérrez-Heredia et al., 2015).

OPPORTUNITIES ENABLED BY REEFSCAPE GENOMICS

Photogrammetric approaches uniquely enable both fine-scale mapping and simultaneous characterization of the focal organism and surrounding reefscape, and will provide a step change in our ability to conduct landscape genomic assessments in marine environments. Such approaches have the potential to overcome pervasive sampling biases associated with underwater population genetic studies (Gorospe et al., 2015; Riginos, 2015) in that rigorous sampling designs can be established based on *a priori* characterized positioning, micro-environment, and phenotypes of organisms across the reefscape (Figure 1). As the spatial extent and grain of the reefscape characterization

can vary per imaging platform (diver-based or autonomous underwater vehicle) and strategy (low or high altitude), reefscape genomic approaches allow for spatially explicit assessments from fine-scale (e.g., assessing the spread of somatic mutations or distribution of endosymbiotic associations within/between colonies), to medium-scale (e.g., patterns of genetic variation, kinship, and clonality within/across reef habitats), and broad-scale (e.g., in conservation genomics assessments of rare and threatened species at the scale of hectares) (Figure 2). Currently, these assessments can be conducted across multiple locations to enable parallel comparisons, or they can be incorporated within a hierarchical seascape genomics framework. Ultimately, they may converge with broader seascape-scale assessments as technologies advance. The explicit consideration of the benthoscape opens up the novel opportunity to assess the effect of the fine-scale biotic and abiotic composition, configuration, and traversability of the underwater landscape on gene flow and dispersal through the use of spatial correlation analyses (e.g., Moran's Eigenvector Maps; Dray et al., 2006) and analyses that identify gene flow

pathways (e.g., resistance-based; McRae, 2006; Petkova et al., 2016). Overall, by enabling repeatable surveys and eliminating constraints on grain size (previously imposed through shipboard, aerial, or orbital characterization), we can now effectively assess the fine-scale spatiotemporal drivers of the extensive unexplained diversity and the hierarchical genetic structuring on coral reefs.

Selection is expected to play a dominant role in shaping the genetic variation of coral reef inhabitants due to the marked environmental heterogeneity occurring between and within reef habitats. Existing approaches investigating adaptive variation can be divided into those that identify genetic signatures of selection resulting from environmental conditions [e.g., outlier tests and genetic-environment association (GEA); Rellstab et al., 2015] and those that identify associations between genotypes and phenotypic traits [e.g., quantitative trait loci (QTL mapping); Stinchcombe and Hoekstra, 2008, genome-wide association studies (GWAS); Korte and Farlow, 2013, and genome-wide selection (GS); Meuwissen et al., 2001]. However, in coral reef invertebrates, GEAs have almost exclusively been explored in relation to either broad-scale oceanographic settings or discrete reef habitats. Characterization of the reefscape now opens the opportunity to investigate the role of fine-scale and biotic selective pressures in population genetic structuring (Gorospe and Karl, 2013), and to explore whether the “sympatric” distribution of morphologically cryptic lineages (Warner et al., 2015) may have overlooked niche partitioning across micro-environments. Moreover, the difficulty of conducting large-scale phenotypic characterization through aquarium-based (due to collection impact concerns) or natural experiments (due to challenges of the underwater environment) has hindered the ability to detect genetic-phenotypic associations. As photogrammetry offers the opportunity of repeated characterization of target organisms, it has the potential to scale up phenotyping efforts of critical traits. Large sample sizes are particularly important for the detection of polygenic signals (i.e., where the phenotype is influenced by more than one locus), such as those identified in relation to thermal bleaching susceptibility (Bay and Palumbi, 2014; Jin et al., 2016; Fuller et al., 2020). Overall, the most promising advance of reefscape genomics is the ability to simultaneously consider the interaction of genotype, (micro-)environment, and phenotype. Disentangling this interaction could elucidate fundamental but poorly understood processes affecting natural evolutionary trajectories, such as cryptic diversification, hybridization, and heritable changes in gene expression (epigenetics). Considering this interaction would also have substantial benefits in terms of restoration and assisted evolution efforts, through more informed identification of resilient natural genotypes and selection of suitable outplanting/transplantation environments (as described in van Oppen et al., 2015; Baums et al., 2019).

CONCLUSION

As advances in genomics have offered the opportunity to transition from few neutral markers to genome-wide

assessments, advances in underwater imaging now unlock the full potential of these assessments in benthic marine ecosystems by enabling spatially explicit (individual-based) sampling integrated with fine-scale biotic and abiotic characterization. As discussed in this perspective, this provides the unprecedented potential to apply fine-scale landscape genomics approaches to coral reef environments, allowing us to address fundamental knowledge gaps regarding the role of neutral and adaptive processes in the structuring of coral reef biodiversity. Additional methodological advantages are the opportunities for simultaneous mass-phenotyping (e.g., growth and thermal susceptibility), repeatable surveys (e.g., explaining how demographic changes contribute to changing allele frequencies), cumulative data gathering (e.g., revisit and expand sampling to additional individuals or species), efficient characterization of difficult-to-access environments (e.g., mesophotic habitats), and robust sampling design planning (e.g., based on *a priori* mapped individuals). Although close-range photogrammetry is uniquely suited to document the static structures of reef-building corals, a “benthoscape genomics” approach (to use a more inclusive term) is equally applicable to other marine benthic habitats (e.g., deep-sea bioherms, mangroves, or rocky reefs) where the requirement of a largely static environment can be met. Studying fine-scale patterns and processes in marine ecosystems will be critical in advancing our understanding of contradictory metapopulation structures, our ability to accurately analyze and interpret broader-scale patterns, and ultimately, our capacity to effectively conserve these ecosystems into the future.

AUTHOR CONTRIBUTIONS

PB conceived of the presented idea with input from the other authors. JG created the figures. All authors helped develop the concepts and contributed equally to the writing of the manuscript.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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