Reefscape genomics: leveraging advances in 3D imaging to assess fine-scale patterns of genomic variation on coral reefs

Pim Bongaerts[1,2*], Caroline E. Dubé[1,3†], Katharine Prata[1,4†], Johanna C. Gijsbers[1,5†], Michelle Achlatis[1,2†], Alejandra Hernandez-Agreda[1]

[1] California Academy of Sciences, San Francisco, CA, USA
[2] Caribbean Research and Management of Biodiversity Foundation, Willemstad, Curaçao
[3] Institut de Biologie Intégrative et des Systèmes, Université Laval, Québec, QC, Canada
[4] School of Biological Sciences, The University of Queensland, St Lucia, QLD, Australia
[5] Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands

Corresponding Author: pbongaerts@calacademy.org
[†] These authors have contributed equally to this work

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Abstract 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, such as (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.

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 important knowledge gaps, their true potential is ultimately dependent on our ability to couple their outputs with environmental and/or phenotypic information at the relevant 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; Selmoni et al., 2020a, b; Fuller et al., 2020). 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 methods generally only allows for limited characterization on a within-reef scale. Lastly, the potential for spatially-explicit, individual-based sampling is hampered as the radio signals used in satellite-based geo-positioning 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 and (geo)referencing of 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 presence of ecological barriers to gene flow and the importance of environment-associated selection. 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. 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 under changing environmental conditions. While advances in omics-based approaches have shown great potential (Riginos et al., 2016; Matz, 2018), our ability to exploit such data have been limited by the lack of tools to gather similar high-resolution data characterizing associated environments and phenotypes.

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 (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 (Iglhaut et al., 2019; Kalacska et al., 2017), 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., 2016; 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 modelling abilities roughly span a grain range of ~0.1-10 mm and spatial extent range of 0.01-1 hectare (Figure 2). Using scale references, a highly accurate local coordinate system of the generated model can be created (mm to cm accuracy; Ledoux et al., 2010), which can then be converted to real-world coordinates based on georeferenced control points, or through integration with acoustic positioning (e.g., ultrashort-baseline or doppler velocity log devices). This enables relative or absolute underwater mapping with unprecedented resolution, efficiency, and repeatability compared to traditional methods using transect tapes, depth gauges, and/or compasses (Foster et al., 2013; Gélin et al., 2017; Williams et al., 2014; Gorospe and Karl, 2013; Dubé et al., 2017, 2020).

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., 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 has the potential to enable fine-scale modelling of further abiotic variables such as 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)

(Edwards et al., 2017; Pedersen et al., 2019). Such large-area characterizations are rapidly providing new insights into coral demographics (Edwards et al., 2017; Brito-Millán et al., 2019; Pedersen et al., 2019), and the simultaneous documentation of the abiotic and biotic reefscape holds particular promise for landscape community genomic approaches (Hand et al., 2015).

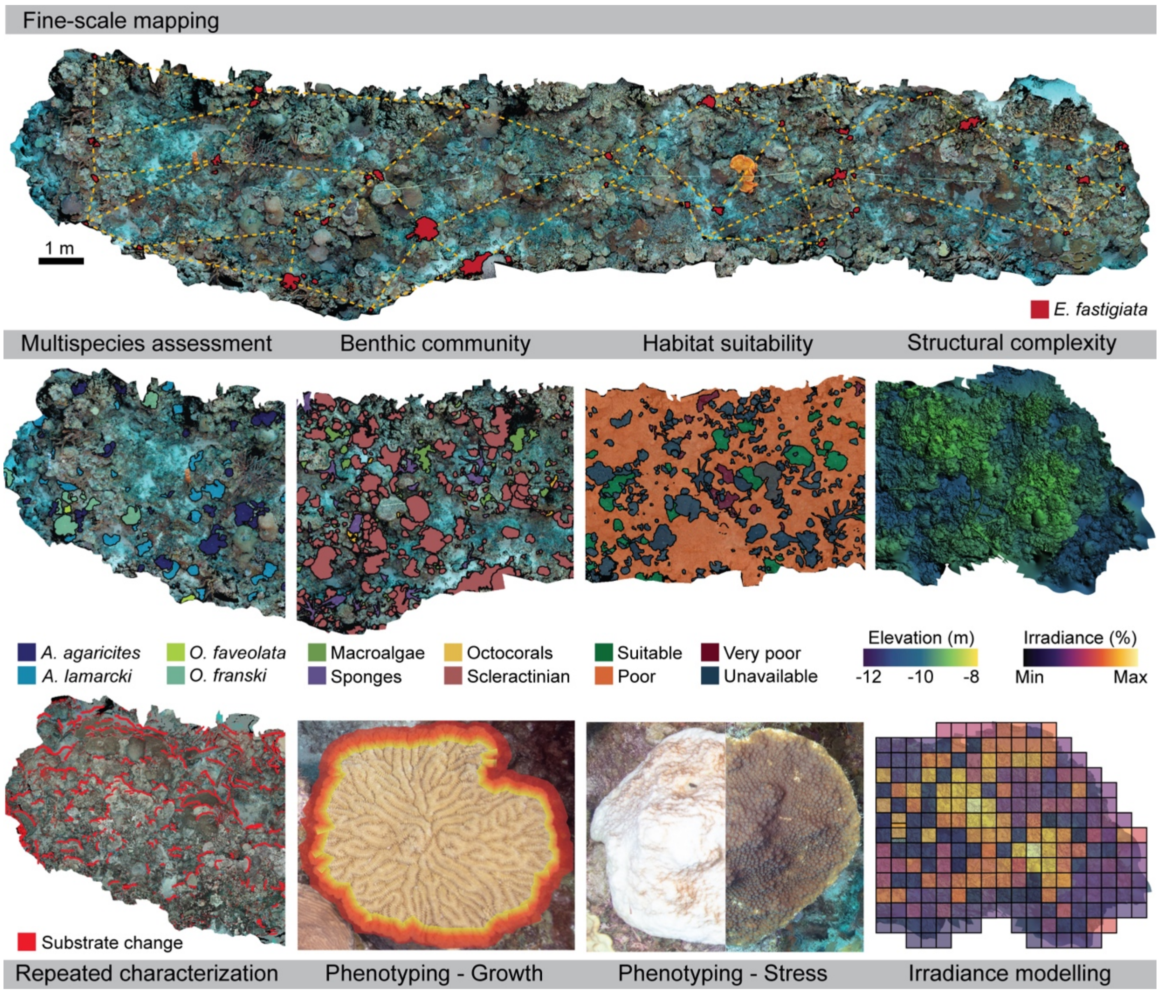

Figure 1. Reefscape genomics: characterizing the underwater landscape. Conceptual diagram summarizing different SfM-enabled characterization examples that can be utilized in reefscape genomic studies. The orthoprojection (25 x 4 m) depicts a Caribbean coral reef community at 20 m depth (from the CoralScape project, Curaçao, Southern Caribbean). Fine-scale mapping allows for accurate positioning of target organisms within the reefscape and *a priori* established sampling designs (depicted here for *Eusmilia fastigiata*). It also enables spatially-explicit, multi-species assessments (e.g., to characterize broader patterns related to life history or the occurrence and consequences of hybridization). Image-based biotic/abiotic characterization of the reefscape can help elucidate the interaction of dispersal, recruitment, and selection processes with the environment (e.g., considering competitive or mutualistic relationships or habitat suitability). Structural complexity or 3D positioning can be similarly considered or used for environmental or biophysical modelling (e.g., incident irradiance, water flow, sedimentation or larval dispersal). Repeated characterization allows for spatio-temporal consideration of the reefscape and target organisms, as well as mass-phenotyping of the latter (e.g., growth rates or stress responses).

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. 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 (Johnston et al., 2019; Chow et al., 2016; Page et al., 2017; Precht et al., 2016; Miller et al., 2016; Gintert et al., 2018). 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; Ferrari et al., 2017; Olinger et al., 2019; Gutiérrez-Heredia et al., 2016), 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.

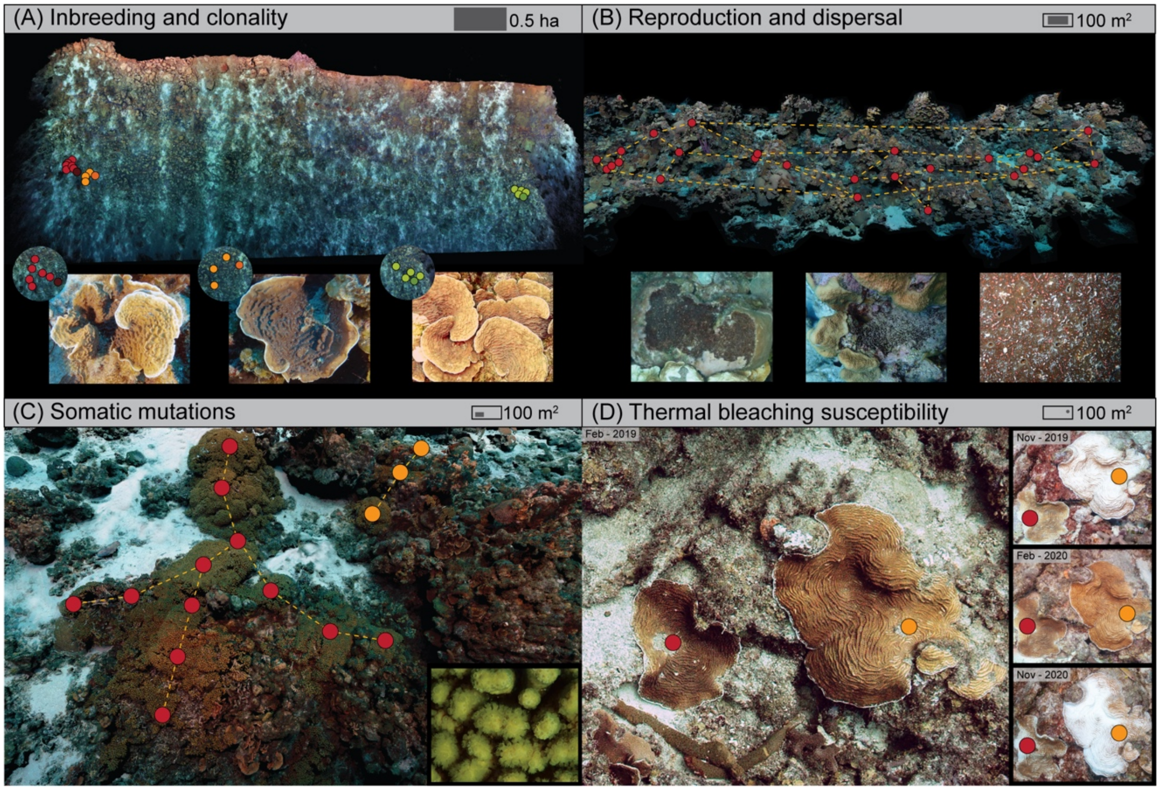

Figure 2. Example applications of reefscape genomics. Four examples of current assessments conducted as part of the CoralScape project on Curaçao (Southern Caribbean). This project monitors large-area plots (0.5-1 ha per plot) and focal plots (100 m^2) covering a range of 5-60 m depth at eight different locations along the leeward shore. These plots are regularly reimaged and incrementally sampled (for different taxa). **A** Broad-scale imaging (>0.5 ha per plot) to exhaustively map, georeference, and sequence the rapidly declining species *Helioseris cucullata* to assess clonality, inbreeding, and local adaptation (Hernandez-Agreda et al., in preparation). **B** Medium-scale imaging (100 m^2 per plot) to track clonal reproduction and assess niche partitioning in coral-eroding sponges of the abundant and fast-expanding species complex *Cliona viridis* (Achlatis et al., in preparation). Inset photographs show different growth forms and a close-up. **C** Medium-scale imaging (100 m^2 per plot) to track the spread of somatic mutations in large monostands of the coral *Madracis mirabilis* (Bongaerts et al., unpublished data). **D** Medium-scale imaging (100 m^2 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 genus *Agaricia* (Prata et al., unpublished). Circles represent samples of target organisms (as depicted in close-up photos) colored by genotype (except for in B).

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 (GEAs); 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, genetic-environment associations 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 the 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, 2015; 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).

Conclusions

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 sponge-dominated 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.

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.

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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References

Agudo-Adriani, E. A., Cappelletto, J., Cavada-Blanco, F., and Cróquer, A. (2019). Structural complexity and benthic cover explain reef-scale variability of fish assemblages in Los Roques National Park, Venezuela. *Front. Mar. Sci.* 6:690. doi: 10.3389/fmars.2019.00690

Alonso, I., Yuval, M., Eyal, G., Treibitz, T., and Murillo, A. C. (2019). CoralSeg: learning coral segmentation from sparse annotations. *J. Field Robot.* 36, 1456–1477. doi: 10.1002/rob.21915

Andrew, R. L., Bernatchez, L., Bonin, A., Buerkle, A. C., Carstens, B. C., Emerson B. C., et al. (2013). A road map for molecular ecology. *Mol. Ecol.* 22, 2605–2626. doi: 10.1111/mec.12319

Arias-González, J., Done, T., Page, C., Cheal, A., Kininmonth, S., and Garza-Pérez, J. (2006). Towards a reefscape ecology: relating biomass and trophic structure of fish assemblages to habitat at Davies Reef, Australia. *Mar. Ecol. Prog. Ser.* 320, 29–41. doi: 10.3354/meps320029

Ayre, D. J., and Hughes, T. P. (2000). Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. *Evolution* 54, 1590–1605. doi: 10.1111/j.0014-3820.2000.tb00704.x

Balkenhol, N., Cushman, S. A., Waits, L. P., and Storfer, A. (2016). "Current status, future opportunities, and remaining challenges in landscape genetics," in Landscape Genetics (John Wiley & Sons, Ltd), 247–256. doi:10.1002/9781118525258.ch14.

Balkenhol, N., Dudaniec, R. Y., Krutovsky, K. V., Johnson, J. S., Cairns, D. M., Segelbacher, G., et al. (2017). "Landscape genomics: understanding relationships between environmental heterogeneity and genomic characteristics of populations," in Population Genomics (Cham, CH: Springer), 261–322. doi: 10.1007/13836_2017_2

Baums, I. B., Devlin-Durante, M. K., and LaJeunesse, T. C. (2014). New insights into the dynamics between reef corals and their associated dinoflagellate endosymbionts from population genetic studies. *Mol. Ecol*. 23, 4203–4215. doi: 10.1111/mec.12788

Baums, I. B., Baker, A. C., Davies, S. W., Grottoli, A. G., Kenkel, C. D., Kitchen, S. A., et al. (2019). Considerations for maximizing the adaptive potential of restored coral populations in the western Atlantic. *Ecol. Appl.* 29:e01978. doi: 10.1002/eap.1978

Bay, R. A., and Palumbi, S. R. (2014). Multilocus adaptation associated with heat resistance in reef-building corals. *Curr. Bio.* 24, 2952–2956. doi: 10.1016/j.cub.2014.10.044

Benzie, J. A. H., Haskell, A., and Lehman, H. (1995). Variation in the genetic composition of coral (*Pocillopora damicornis* and *Acropora palifera*) populations from different reef habitats. *Mar. Biol.* 121, 731–739. doi: 10.1007/BF00349309

Boilard, A., Dubé, C. E., Gruet, C., Mercière, A., Hernandez-Agreda, A., and Derome, N. (2020). Defining coral bleaching as a microbial dysbiosis within the coral holobiont. *Microorganisms* 8:1682. doi: 10.3390/microorganisms8111682

Bongaerts, P., Riginos, C., Ridgway, T., Sampayo, E. M., van Oppen, M. J. H., Englebert, N., et al. (2010). Genetic divergence across habitats in the widespread coral *Seriatopora hystrix* and its associated *Symbiodinium*. *PLoS One* 5:e10871. doi: 10.1371/journal.pone.0010871

Bongaerts, P., Riginos, C., Hay, K. B., van Oppen, M. J. H., Hoegh-Guldberg, O., and Dove, S. (2011). Adaptive divergence in a scleractinian coral: physiological adaptation of *Seriatopora hystrix* to shallow and deep reef habitats. *BMC Evol. Biol.* 11:303. doi: 10.1186/1471-2148-11-303

Brito-Millán, M., Werner, B. T., Sandin, S. A., and McNamara, D. E. (2019). Influence of aggregation on benthic coral reef spatio-temporal dynamics. *R. Soc. Open Sci*. 6: 181703. doi: 10.1098/rsos.181703

Burns, J., Delparte, D., Gates, R., and Takabayashi, M. (2015). Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. *PeerJ* 3:e1077. doi: 10.7717/peerj.1077

Burns, J. H. R., and Delparte, D. (2017). Comparison of commercial structure-from-motion photogrammetry software used for underwater three-dimensional modeling of coral reef environments. *Int. Arch. Photogramm. Remote Sens. Spatial Inf. Sci*. XLII-2/W3, 127–131. doi: 10.5194/isprs-archives-xlii-2-w3-127-2017

Chow, M. H., Tsang, R. H. L., Lam, E. K. Y., and Ang, P., Jr. (2016). Quantifying the degree of coral bleaching using digital photographic technique. *J. Exp. Mar. Biol. Ecol.* 479, 60–68. doi: 10.1016/j.jembe.2016.03.003

Combosch, D. J., Guzman, H. M., Schuhmacher, H., and Vollmer, S. V. (2008). Interspecific hybridization and restricted trans-Pacific gene flow in the Tropical Eastern Pacific *Pocillopora*. *Mol. Ecol.* 17, 1304–1312. doi: 10.1111/j.1365-294X.2007.03672.x

Cros, A., Toonen, R. J., and Karl, S. A. (2020). Is post-bleaching recovery of *Acropora hyacinthus* on Palau via spread of local kin groups? *Coral Reefs* 39, 687–699. doi: 10.1007/s00338-020-01961-3

DeBell, L., Duffy, J., McKinley, and T., Anderson, K. (2019). Species and habitat mapping in two dimensions and beyond. Structure-from-Motion multi-view stereo photogrammetry for the conservation community. *bioRxiv* [Preprint]. doi: 10.1101/2019.12.16.878033

Dixon, G. B., Davies, S. W., Aglyamova, G. V., Meyer, E., Bay, L. K., and Matz, M. V. (2015). Genomic determinants of coral heat tolerance across latitudes. *Science* 348, 1460–1462. doi: 10.1126/science.1261224

Dray, S., Legendre, P., Peres-Neto, P. R. (2006). Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol. Model*. 196, 483–493. doi: 10.1016/j.ecolmodel.2006.02.015

Dubé, C. E., Boissin, E., Maynard, J. A., and Planes, S. (2017). Fire coral clones demonstrate phenotypic plasticity among reef habitats. *Mol. Ecol.* 26, 3860–3869. doi: 10.1111/mec.14165

Dubé, C. E., 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. *Mol. Ecol.* 29, 1508–1522. doi: 10.1111/mec.15418

Dustan, P., Doherty, O., and Pardede, S. (2013). Digital reef rugosity estimates coral reef habitat complexity. *PLoS One* 8:e57386. doi: 10.1371/journal.pone.0057386

Edwards, C. B., Eynaud, Y., Williams, G. J., Pedersen, N. E., Zgliczynski, B. J., Gleason, A. C., et al. (2017). Large-area imaging reveals biologically driven non-random spatial patterns of corals at a remote reef. *Coral Reefs* 36, 1291–1305. doi: 10.1007/s00338-017-1624-3

Ferrari, R., McKinnon, D., He, H., Smith, R., Corke, P., González-Rivero, M., et al. (2016). Quantifying multiscale habitat structural complexity: a cost-effective framework for underwater 3D modelling. *Remote Sens*. 8:113. doi: 10.3390/rs8020113

Ferrari, R., Figueira, W. F., Pratchett, M. S., Boube, T., Adam, A., Kobelkowsky-Vidrio, T., et al. (2017). 3D photogrammetry quantifies growth and external erosion of individual coral colonies and skeletons. *Sci. Rep.* 7:16737. doi: 10.1038/s41598-017-16408-z

Ferrari, R., Malcolm, H. A., Byrne, M., Friedman, A., Williams, S. B., Schultz, A., et al. (2018). Habitat structural complexity metrics improve predictions of fish abundance and distribution. *Ecography* 41, 1077–1091. doi: 10.1111/ecog.02580

Fonstad, M. A., Dietrich, J. T., Courville, B. C., Jensen, J. L., and Carbonneau, P. E. (2013). Topographic structure from motion: a new development in photogrammetric measurement. *Earth Surf. Process Landf.* 38, 421–430. doi: 10.1002/esp.3366

Forsman, Z. H., Ritson-Williams, R., Tisthammer, K., Knapp, I. S. S., and Toonen, R. J. (2020). Host-symbiont coevolution, cryptic structure, and bleaching susceptibility, in a coral species complex (Scleractinia; Poritidae). *Sci. Rep.* 10:16995. doi: 10.1038/s41598-020-73501-6

Foster, N. L., Baums, I. B., Sanchez, J. A., Paris, C. B., Chollett, I., Agudelo, C. L., et al. (2013). Hurricane-driven patterns of clonality in an ecosystem engineer: the caribbean coral *Montastraea annularis*. *PLoS One* 8:e53283. doi: 10.1371/journal.pone.0053283

Frade, P. R., De Jongh, F., Vermeulen, F., Van Bleijswijk, J., and Bak, R. P. M. (2008). Variation in symbiont distribution between closely related coral species over large depth ranges. *Mol. Ecol.* 17, 691–703. doi: 10.1111/j.1365-294X.2007.03612.x

Fuller, Z., Mocellin, V. J. L., Morris, L. A., Cantin, N., Shepherd, J., Sarre, L., et al. (2020). Population genetics of the coral *Acropora millepora*: toward genomic prediction of bleaching. *Science* 369:6501. doi: 10.1126/science.aba4674

Gélin, P., Fauvelot, C., Bigot, L., Baly, J., and Magalon, H. (2017). From population connectivity to the art of striping Russian dolls: the lessons from *Pocillopora* corals. *Ecol. Evol.* 8, 1411–1426. doi: 10.1002/ece3.3747

Gintert, B. E., Manzello, D. P., Enochs, I. C., Kolodziej, G., Carlton, R., Gleason, A. C. R., et al. (2018). Marked annual coral bleaching resilience of an inshore patch reef in the Florida Keys: a nugget of hope, aberrance, or last man standing? *Coral Reefs* 37, 533–547. doi: 10.1007/s00338-018-1678-x

González-Rivero, M., Harborne, A. R., Herrera-Reveles, A., Bozec, Y.-M., Rogers, A., Friedman, A., et al. (2017). Linking fishes to multiple metrics of coral reef structural complexity using three-dimensional technology. *Sci. Rep.* 7:13965. doi: 10.1038/s41598-017-14272-5

Gorospe, K. D., and Karl, S. A. (2013). Genetic relatedness does not retain spatial pattern across multiple spatial scales: dispersal and colonization in the coral, *Pocillopora damicornis*. *Mol. Ecol.* 22, 3721–3736. doi: 10.1111/mec.12335

Gorospe, K. D., Donahue, M. J., and Karl, S. A. (2015). The importance of sampling design: spatial patterns and clonality in estimating the genetic diversity of coral reefs. *Mar. Biol*. 162, 917–928. doi: 10.1007/s00227-015-2634-8

Gutiérrez-Heredia, L., D'Helft, C., and Reynaud, E. G. (2015). Simple methods for interactive 3D modeling, measurements, and digital databases of coral skeletons. *Limnol. Oceanogr. Methods* 13:e10017. doi: 10.1002/lom3.10017

Gutiérrez-Heredia, L., Benzoni, F., Murphy, E., and Reynaud, E. G. (2016). End to end digitisation and analysis of three-dimensional coral models, from communities to corallites. *PLoS One* 11:e0149641. doi: 10.1371/journal.pone.0149641

Hand, B. K., Lowe, W. H., Kovach, R. P., Muhlfeld, C. C., and Luikart, G. (2015). Landscape community genomics: understanding eco-evolutionary processes in complex environments. *Trends Ecol. Evol.* 30, 161–168. doi: 10.1016/j.tree.2015.01.005

Hellberg, M. E. (2007). Footprints on water: the genetic wake of dispersal among reefs. *Coral Reefs* 26, 463–473. doi: 10.1007/s00338-007-0205-2

Hernandez-Agreda, A., Leggat, W., Bongaerts, P., Herrera, C., Ainsworth, T. D. (2018). Rethinking the coral microbiome: simplicity exists within a diverse microbial biosphere. *mBio* 9:e00812–e00818. doi: 10.1128/ mBio.00812-18

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., et al. (2007). Coral reefs under rapid climate change and ocean acidification. *Science* 318, 1737–1742. doi: 10.1126/science.1152509

Holmes, G., Ortiz, J., Kaniewska, P., and Johnstone, R. (2008). Using three-dimensional surface area to compare the growth of two Pocilloporid coral species. *Mar. Biol.* 155, 421–427. doi: 10.1007/s00227-008-1040-x

Iglhaut, J., Cabo, C., Puliti, S., Piermattei, L., O'Connor, J., and Rosette, J. (2019). Structure from motion photogrammetry in forestry: a review. *Curr. For. Rep.* 5, 155–168. doi: 10.1007/s40725-019-00094-3

Jin, Y. K., Lundgren, P., Lutz, A., Raina, J. B., Howells, E. J., Paley, A. S., et al. (2016). Genetic markers for antioxidant capacity in a reef-building coral. *Sci. Adv.* 2:e1500842. doi: 10.1126/sciadv.1500842

Johnston, M. A., Hickerson, E. L., Nuttall, M. F., Blakeway, R. D., Sterne, T. K., Eckert, R. J., et al. (2019). Coral bleaching and recovery from 2016 to 2017 at East and West Flower Garden Banks, Gulf of Mexico. *Coral Reefs* 38, 787–799. doi: 10.1007/s00338-019-01788-7

Kalacska, M., Chmura, G. L., Lucanus, O., Bérubé, D., and Arroyo-Mora, J. P. (2017). Structure from motion will revolutionize analyses of tidal wetland landscapes. *Remote Sens. Environ.* 199, 14–24. doi: 10.1016/j.rse.2017.06.023

Kinlan, B. P., Gaines, S. D., and Lester, S. E. (2005). Propagule dispersal and the scales of marine community process. *Divers. Distrib.* 11, 139–148. doi: 10.1111/j.1366-9516.2005.00158.x

Korte, A., and Farlow, A. (2013). The advantages and limitations of trait analysis with GWAS: a review. *Plant Methods* 9:29. doi: 10.1186/1746-4811-9-29

Kruszyński, K. J., Kaandorp, J. A., and van Liere, R. (2007). A computational method for quantifying morphological variation in scleractinian corals. *Coral Reefs* 26, 831–840. doi: 10.1007/s00338-007-0270-6

Lavy, A., Eyal, G., Neal, B., Keren, R., Loya, Y., and Ilan, M. (2015). A quick, easy and non-intrusive method for underwater volume and surface area evaluation of benthic organisms by 3D computer modelling. *Methods Ecol. Evol.* 6, 521–531. doi: 10.1111/2041-210x.12331

Ledoux, J.-B., Garrabou, J., Bianchimani, O., Drap, P., Féral, J.-P., and Aurelle, D. (2010). Fine-scale genetic structure and inferences on population biology in the threatened Mediterranean red coral, *Corallium rubrum*. *Mol. Ecol.* 19, 4204–4216. doi: 10.1111/j.1365-294x.2010.04814.x

Leon, J. X., Roelfsema, C. M., Saunders, M. I., and Phinn, S. R. (2015). Measuring coral reef terrain roughness using 'Structure-from-Motion' close-range photogrammetry. *Geomorphology (Amst.)* 242, 21–28. doi: 10.1016/j.geomorph.2015.01.030

Li, Y., Zhang, X.-X., Mao, R.-L., Yang, J., Miao, C.-Y., Li, Z., et al. (2017). Ten years of landscape genomics: challenges and opportunities. *Front. Plant Sci*. 8:2138. doi: 10.3389/fpls.2017.02136

Liggins, L., Treml, E. A., and Riginos, C. (2013). Taking the plunge: an introduction to undertaking seascape genetic studies and using biophysical models. *Geogr. Compass* 7, 173–196. doi: 10.1111/gec3.12031

Liggins, L., Treml, E. A., and Riginos, C. (2019). "Seascape genomics: contextualizing adaptive and neutral genomic variation in the ocean environment," in Population Genomics (Cham, CH: Springer), 171–218. doi: 10.1007/13836_2019_68

Manel, S., Schwartz, M. K., Luikart, G., and Taberlet, P. (2003). Landscape genetics: combining landscape ecology and population genetics. *Trends Ecol. Evol.* 18, 189–197. doi: 10.1016/s0169-5347(03)00008-9

Matz, M. V. (2018). Fantastic beasts and how to sequence them: ecological genomics for obscure model organisms. *Trends Genet.* 34, 121–132. doi: 10.1016/j.tig.2017.11.002

McClenachan, L., O'Connor, G., Neal, B.P., Pandolfi, J.M., and Jackson, J.B. (2017). Ghost reefs: nautical charts document large spatial scale of coral reef loss over 240 years. *Sci. Adv.* 3:e1603155. doi: 10.1126/sciadv.1603155

McRae, B. H. (2006). Isolation by resistance. *Evol*. 60, 1551–1561. doi: 10.1554/05-321.1

Meuwissen, T. H., Hayes, B. J., and Goddard, M. E. (2001). Prediction of total genetic value using genome-wide dense marker maps. *Genetics* 157, 1819–1829.

Miller, K. J., and Ayre, D. J. (2004). The role of sexual and asexual reproduction in structuring high latitude populations of the reef coral *Pocillopora damicornis*. *Heredity* 92, 557–568. doi: 10.1038/sj.hdy.6800459

Miller, M. W., Karazsia, J., Groves, C. E., Griffin, S., Moore, T., Wilber, P., et al. (2016). Detecting sedimentation impacts to coral reefs resulting from dredging the Port of Miami, Florida USA. *PeerJ* 4:e2711. doi: 10.7717/peerj.2711

Oakley-Cogan, A., Tebbett, S. B., and Bellwood, D. R. (2020). Habitat zonation on coral reefs: structural complexity, nutritional resources and herbivorous fish distributions. *PLoS One* 15:e0233498. doi: 10.1371/journal.pone.0233498

Olinger, L. K., Scott, A. R., McMurray, S. E., and Pawlik, J. R. (2019). Growth estimates of Caribbean reef sponges on a shipwreck using 3D photogrammetry. *Sci. Rep.* 9:18398. doi: 10.1038/s41598-019-54681-2

Page, C. A., Field, S. N., Pollock, F. J., Lamb, J. B., Shedrawi, G., and Wilson, S. K. (2017). Assessing coral health and disease from digital photographs and in situ surveys. *Environ. Monit. Assess.* 189:18. doi: 10.1007/s10661-016-5743-z

Pantos, O., Bongaerts, P., Dennis, P. G., Tyson, G. W., and Hoegh-Guldberg, O. (2015). Habitat-specific environmental conditions primarily control the microbiomes of the coral *Seriatopora hystrix*. *ISME J.* 9:1916. doi: 10.1038/ismej. 2015.3

Pavoni, G., Corsini, M., and Cignoni, P. (2020). A state of the art technology in large scale underwater monitoring. *ERCIM News* 2020:121.

Pedersen, N. E., Edwards, C. B., Eynaud, Y., Gleason, A. C., Smith, J. E., and Sandin, S. A. (2019). The influence of habitat and adults on the spatial distribution of juvenile corals. *Ecography* 42, 1703–1713. doi: 10.1111/ecog.04520

Petkova, D., Novembre, J., and Stephens, M. (2016). Visualizing spatial population structure with estimated effective migration surfaces. *Nat. Genet.* 48, 94–100. doi: 10.1038/ng.3464

Precht, W. F., Gintert, B. E., Robbart, M. L., Fura, R., and van Woesik, R. (2016). Unprecedented disease-related coral mortality in Southeastern Florida. *Sci. Rep.* 6:31374. doi: 10.1038/srep31374

Rellstab, C., Gugerli, F., Eckert, A. J., Hancock, A. M., Holderegger, R. (2015). A practical guide to environmental association analysis in landscape genomics. *Mol. Ecol.* 24, 4348–4370. doi: 10.1111/mec.13322

Riginos, C., and Liggins, L. (2013). Seascape genetics: populations, individuals, and genes marooned and adrift. *Geogr. Compass* 7, 197–216. doi: 10.1111/gec3.12032

Riginos, C. (2015). Clones in space—how sampling can bias genetic diversity estimates in corals: editorial comment on the feature article by Gorospe et al. *Mar. Biol.* 162, 913–915. doi: 10.1007/s00227-015-2638-4

Riginos, C., Crandall, E. D., Liggins, L., Bongaerts, P., and Treml, E. A. (2016). Navigating the currents of seascape genomics: how spatial analyses can augment population genomic studies. *Curr. Zool.* 62, 581–601. doi: 10.1093/cz/zow067

Selmoni, O., Rochat, E., Lecellier, G., Berteaux-Lecellier, V., and Joost, S. (2020a). Seascape genomics as a new tool to empower coral reef conservation strategies: an example on north-western Pacific *Acropora digitifera*. *Evol. Appl.* 13, 1923–1938. doi: 10.1111/eva.12944

Selmoni, O., Lecellier, G., Magalon, H., Vigliola, L., Benzoni, F., Peignon, C., et al. (2020b). Seascape genomics reveals candidate molecular targets of heat stress adaptation in three coral species. *bioRxiv* [Preprint]. doi: 10.1101/2020.05.12.090050

Smith, M. W., Carrivick, J. L., and Quincey, D. J. (2015). Structure from motion photogrammetry in physical geography. *Prog. Phys. Geogr.* 40, 247–75. doi: 10.1177/0309133315615805

Stinchcombe, J. R., and Hoekstra, H. E. (2008). Combining population genomics and quantitative genetics: finding the genes underlying ecologically important traits. *Heredity* 100, 158–170. doi: 10.1038/sj.hdy.6800937

Tokeshi, M., and Arakaki, S. (2012). Habitat complexity in aquatic systems: fractals and beyond. *Hydrobiologia* 685, 27–47. doi: 10.1007/s10750-011-0832-z

Torres-Pulliza, D., Dornelas, M. A., Pizarro, O., Bewley, M., Blowes, S. A., Boutros, N., et al. (2020). A geometric basis for surface habitat complexity and biodiversity. *Nat. Ecol. Evol*. 4, 1495–1501. doi: 10.1038/s41559-020-1281-8

Underwood, J. N., Smith, L. D., van Oppen, M. J. H., and Gilmour, J. P. (2007). Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. *Mol. Ecol*. 16, 771–784. doi: 10.1111/j.1365-294X.2006.03187.x

Underwood, J. N., Richards, Z. T., Miller, K. J., Puotinen, M. L., and Gilmour, J. P. (2018). Genetic signatures through space, time and multiple disturbances in a ubiquitous brooding coral. *Mol. Ecol*. 27, 1586–1602. doi: 10.1111/mec.14559

Urbina-Barreto, I., Chiroleu, F., Pinel, R., Fréchon, L., Mahamadaly, V., Elise, S., et al. (2020). Quantifying the shelter capacity of coral reefs using photogrammetric 3D modeling: from colonies to reefscapes. *Ecol. Indic.* 107151. doi: 10.1016/j.ecolind.2020.107151

van Oppen, M. J. H., and Gates, R. D. (2006). Conservation genetics and the resilience of reef-building corals. *Mol. Ecol*. 15, 3863–3883. doi: 10.1111/j.1365-294x.2006.03026.x

van Oppen, M. J. H., Lutz, A., De'ath, G., Peplow, L., and Kininmonth, S. (2008). Genetic traces of recent long-distance dispersal in a predominantly self-recruiting coral. *PLoS One* 3:e3401. doi: 0.1371/journal.pone.0003401

van Oppen, M. J. H., Oliver, J. K., Putnam, H. M., and Gates, R. D. (2015). Building coral reef resilience through assisted evolution. *Proc. Natl. Acad. Sci. U.S.A* 112, 2307–2313. doi: 0.1073/pnas.1422301112

van Oppen, M. J. H, Bongaerts, P., Frade, P., Peplow, L. M., Boyd, S. E., Nim, H. T., et al. (2018). Adaptation to reef habitats through selection on the coral animal and its associated microbiome. *Mol. Ecol.* 27, 2956–2971. doi: 10.1111/mec.14763

Van Wynsberge, S., Andréfouët, S., Gaertner-Mazouni, N., Tiavouane, J., Grulois, D., Lefèvre, J., et al. (2017). Considering reefscape configuration and composition in biophysical models advance seascape genetics. *PLoS One* 12:e0178239. doi: 10.1371/journal.pone.0178239

Vollmer, S. V., and Palumbi, S. R. (2002). Hybridization and the evolution of reef coral diversity. *Science* 296, 2023–2025. doi: 10.1126/science.1069524

Warner, P. A., van Oppen, M. J. H., and Willis, B. L. (2015). Unexpected cryptic species diversity in the widespread coral *Seriatopora hystrix* masks spatial-genetic patterns of connectivity. *Mol. Ecol.* 24, 2993–3008. doi: 10.1111/mec.13225

Warner, P. A., Willis, B. L., and van Oppen, M. J. H. (2016). Sperm dispersal distances estimated by parentage analysis in a brooding scleractinian coral. *Mol. Ecol.* 25, 1398–1415. doi: 10.1111/mec.13553

Westoby, M. J., Brasington, J., Glasser, N. F., Hambrey, M. J., and Reynolds, J. M. (2012). 'Structure-from-Motion' photogrammetry: a low-cost, effective tool for geoscience applications. *Geomorphology* 179, 300–314. doi: 10.1016/j.geomorph.2012.08.021

Williams, D. E., Miller, M. W., and Baums, I. B. (2014). Cryptic changes in the genetic structure of a highly clonal coral population and the relationship with ecological performance. *Coral Reefs* 33, 595–606. doi: 10.1007/s00338-014-1157-y

Williams, I. D., Couch, C. S., Beijbom, O., Oliver, T. A., Vargas-Angel, B., Schumacher, B.D., et al. (2019). Leveraging automated image analysis tools to transform our capacity to assess status and trends of coral reefs. *Front. Mar. Sci.* 6:222. doi: 10.3389/fmars.2019.00222

Young, G. C., Dey, S., Rogers, A. D., and Exton, D. (2017). Cost and time-effective method for multi-scale measures of rugosity, fractal dimension, and vector dispersion from coral reef 3D models. *PLoS One* 12:e0175341. doi: 10.1371/journal.pone.0175341