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Landscape Ecology in the Rocky Intertidal: Opportunities for Advancing Discovery and Innovation in Intertidal Research

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Abstract

Purpose of Review In this paper, I review the development of landscape-based studies in rocky intertidal communities. The rocky intertidal has served as the site of a number of influential studies in ecology that have helped demonstrate the importance of biological and physical structuring processes in nature. Owing to its ease of access and preponderance of sessile species, the intertidal has also played an important role in studies that monitor the health of coastal systems. Traditional data gathering approaches such as meter tapes and quadrats provide limited capacity to capture data at the spatial and temporal scales across which intertidal systems are currently changing. New approaches and methods are now needed to more efficiently record data across the organizational scales within which ecological processes structure the intertidal.

Recent Findings Recent developments in landscape-based theory have expanded the types of research questions asked by intertidal ecologists. The subsequent incorporation of geospatial technologies into field studies that test the predictions of emerging landscape theory has revealed emergent patterns in intertidal communities and previously unrecognized relationships between species and habitat across multiple scales of ecological organization.

Summary New landscape-based approaches will improve our capacity to collect and analyze data and improve quantitative inferences on how habitat complexity affects patterns of species abundance in the intertidal. The continued integration of landscape ecology into rocky intertidal research can help advance discovery science and provide a platform for bridging basic discovery science with conservation and management efforts centered about this important marine habitat.

Keywords Rocky intertidal · Landscape ecology · Drones · Remote sensing · GIS · Spatial analysis

Introduction

Within the field of ecology, the rocky intertidal has been a habitat of particular importance as it has been the setting for a number of influential studies that helped guide the direction of the discipline. It has served as a model system for ecologists in much the way that *Drosophila* has served as a model system for geneticists. Some of the most influential studies in ecology have been conducted in rocky intertidal systems with two of the most prominent being Connell's [1] studies of competition and Paine's [2, 3] studies of keystone species. These studies not only provided insight into the ecological dynamics of this system but also paved the way for ecologists working in other systems to think about how interspecific competition and predation affected the structure of populations in nature. Other studies within the intertidal have helped provide an understanding of the role that disturbance plays in structuring communities [4] and how population immigration (as measured via larval settlement) can drive the relative rates of ecological processes such as predation and competition [5]. Thus, research conducted in the intertidal has played a critical role in helping advance the broader field of ecology.

Beyond providing insight into the mechanism structuring communities, the rocky intertidal has also played an important role in helping scientists understand how a changing environment can affect marine communities. Some of the earliest studies of the impact of climate change were conducted in the rocky intertidal [6]. These studies have demonstrated the impact of a changing environment on the general structure of

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coastal ecosystems [7], as well as the potential impact on species that have a significant economic value to coastal communities [8, 9]. Monitoring-based studies conducted in the face of climate change have in part led to studies that have helped us understand how marine populations utilize genetic and physiological mechanisms to persist in a changing environment [10, 11]. Monitoring-based studies in the intertidal have helped provide a window into what ecosystems in the future will look like under the influence of climate change and how coastal scientists, resource managers, and society can develop strategies to mitigate potential changes [12].

While previous studies in the intertidal provided valuable information on the potential impacts of a changing environment on marine communities, they relied on research approaches that are labor- and time-intensive and limited in the scales over which they can be employed. Traditional data gathering approaches such as quadrats, meter tapes, and experimental exclosures helped early ecologists elucidate the relationship between process and pattern. However, these approaches have limitations centered about both the temporal and spatial scales across which they can be used to collect data. The rapid shifts that are currently being observed in the coastal environment require new data collection approaches that can rapidly collect data across multiple scales of ecosystem change [13••]. Furthermore, new approaches that can collect data across temporal and spatial scales that were previously inaccessible can be used to detect emergent features in this system that can lead to new avenues of research and improve management strategies centered about the rocky intertidal.

The field of landscape ecology has long examined the role that landscape complexity, defined here as the three-dimensional complex of biogenic and geologic habitat, and multi-scale factors play in driving ecological process and patterns in nature [14]. While their research has primarily been conducted within the terrestrial environment, landscape ecologists have employed spatially explicit theory, data collection, and analysis approaches in their work [15]. Landscape ecologists have also developed metrics that encapsulate the complex interactions that occur between landscape complexity and ecological processes [16]. The large body of landscape ecology research has demonstrated how variation in landscape complexity can affect habitat configuration, the level of connectivity between populations [15, 17], the availability of resources [18], and the maintenance of species diversity [19]. Landscape ecology theory and practice are also key features of current meta-population theory which has informed many modern management strategies including design and implementation of wildlife reserves. Landscape complexity can also impart or enhance disturbance events in a community. For instance, complex patterns of vertical layering in forests and intertidal mussel beds are often cited as playing a role in determining the relative impact of windthrow- and wave-induced disturbance events in these communities [15]. Landscape complexity may also be a key feature in understanding the conservation and management of marine habitats, such as coral reefs [20], which can be highly susceptible to disturbance events.

Marine landscape ecology, sometimes labeled seascape ecology, is a relatively new discipline that employs the theoretical underpinnings and research approaches of landscape ecology to study the role of scale and landscape complexity in driving the ecological dynamics of marine systems. The last two decades have seen an influx of papers which incorporate landscape theory into marine ecological studies, with some of the earliest studies applying these approaches to seagrass communities [21]. One of the earliest compendium of papers on the topic was first published in the journal *Landscape Ecology* [22] and featured studies that described theoretical and applied uses of landscape ecology in marine ecological studies [22]. A special issue in *Marine Ecology Progress Series* [23] shortly followed that focused on the application of spatial approaches to the study of marine systems. The research articles featured within each of these journal issues provided new theoretical and field-based research approaches through which marine ecologists could incorporate considerations of landscape complexity into basic and applied research.

In this review paper, I highlight the development of landscape-based studies in rocky intertidal communities. I first trace the development of landscape-based theory and computational models that would expand the types of research questions asked by intertidal ecologists. This is followed by a discussion of subsequent field studies that employed new data collection approaches to test the predictions of emerging landscape theory developed for the intertidal. I close with a review of emerging approaches for conducting landscape ecological research in the intertidal and the ongoing value of continuing to employ landscape-based approaches in intertidal research.

Landscape-Based Theory in the Rocky Intertidal

In the early 2000s, intertidal ecologist began to develop new research questions in the intertidal by developing a new ecological theory for rocky intertidal systems. Specifically, intertidal researchers began to look towards landscape ecology and its focus on spatial pattern and process to ascertain if the incorporation of spatial heterogeneity in intertidal studies could lead to new avenues of research. This shift in research approaches was in part driven by the emergence of meta-analysis which demonstrated that analyzing large volumes of ecological datasets could help ecologist detect emergent features of ecosystems that were previously unknown. This new focus on spatial process and pattern would help drive a fundamental shift in how intertidal ecologists developed research questions and tested research hypotheses.

One of the earliest efforts to develop a landscape-based model for rocky intertidal systems and subsequent theory can be found in the work of Robles and Desharnais [24] and their use of cellular automate models (a modeling approach that employs a 2-dimensional grid of cells that vary in their spatial and/or environmental state). Their cellular automaton approach describes a 2-dimensional landscape in which intertidal boundaries of prey are set by equilibria between predation and prey production. In their model, predation and prey productivity vary with the underlying environmental gradients and the spatial configuration of prey populations across a theoretical landscape. The 2-D cellular automaton model they developed helped provide an explanation for the distinct patterns of zonation historically observed in rocky intertidal communities. More specifically, their model helped explain abrupt prey boundaries within continuous gradients of predation and converging prey boundaries that are observed in intertidal communities as wave exposure decreases (Fig. 1a). In applying a landscape perspective to a well-studied system, Robles and Desharnais [24] demonstrated that probabilistic processes and prey production and the subsequent effects of predators could be explained by modeling this interaction across environmental gradients that are modified by spatial heterogeneity in the system. Here we have an early theoretical description of how spatial heterogeneity can affect the relative impact of biological process that was long surmised to structure rocky intertidal communities. The theory developed in this early effort would produce new avenues of field research [25, 26] and further refinements of early landscape theory developed for the rocky intertidal [27].

Beyond the modeling approach developed by Robles and Desharnais [24] was the development of other computational models that examined the incorporation of landscape-based factors on process and pattern in intertidal systems. Wootton [28] and Guichard et al. [29] would present landscape-driven models that would further improve our understanding of how landscape processes structure rocky intertidal communities. Employing a cellular automata model, Wootton [28]

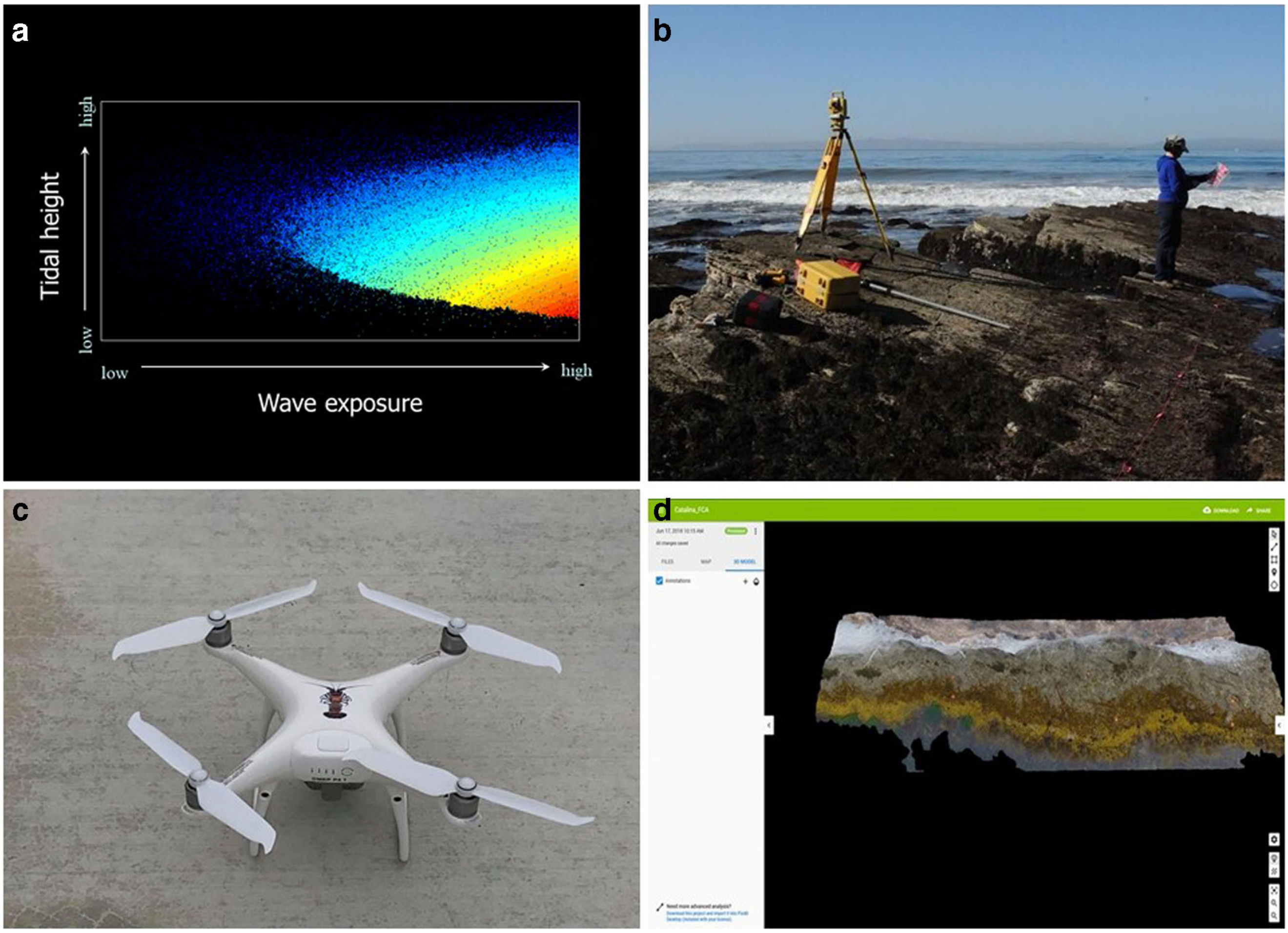

Fig. 1 **a** Cellular automata model output depicting mussel bed formation as a function of variation in wave energy and tidal height. Width of the bed increases with increasing wave energy. Warm colors represent large matrix mussels while cool colors represent small matrix mussels (image courtesy of (**c**). Robles and R. Desharnais). **b** Topcon total station being used to measure mussel bed extent along the California coastline. **c** a DJI Phantom 4 Pro V2 photo survey drone. **d** 3D orthophoto mosaic of rocky intertidal shoreline in Pix4D photogrammetry software

demonstrated that empirically measured rates of species transition and disturbance in intertidal systems produced self-organized patterns. This observation suggested that small-scale self-organizing behavior among conspecifics observed in simulations could explain broad-scale patterns of species distribution in nature [28]. The insight provided by this model suggested that regional-scale patterns observed in intertidal systems could be driven by local-scale self-organizing processes independent of ecological processes long thought to structure intertidal communities [28]. More broadly, these predictions would provide a basis for intertidal ecologists to incorporate considerations of biological self-organization in field-based studies of rocky intertidal communities.

Guichard et al. [29] would employ a lattice model as part of an effort to link small-scale patterns of mussel distribution to large-scale oceanographic influences. Their results suggested that regional scales of disturbance can, in part, affect local-scale disturbance owing to additional interactions between local biotic processes and regional oceanographic regimes. Here we have a theoretical demonstration of scale invariance in the processes that structure intertidal systems at both local and regional scales. The theoretical predictions provided by Guichard et al. [29] provided a template for field ecologists to incorporate considerations of scale invariance in subsequent studies of the rocky intertidal. These early theory–based papers in intertidal landscape ecology theory would promote the development of new research questions focused on the structure of intertidal systems. However, the multi-scale patterns predicted by these models would require intertidal ecologists to move past traditional methods for measuring ecological patterns and employ new technologies to test the predictions of emerging ecological theory.

Landscape-Based Field Research in the Rocky Intertidal

With the introduction of new landscape-based theory in the rocky intertidal, and its multi-scale predictions, new approaches were needed to test the predictions of emerging intertidal landscape theory. Traditional research tools and approaches such as quadrats, meter tapes, and manipulative experiments could not be easily adapted to capture the multi-scale patterns of species distribution predicted by landscape-based models. Technologies that were relatively new and becoming commercially available at the time such as digital cameras, GPS, and total stations (Fig. 1b) provided ecologists with the tools to measure the multi-scale ecological patterns predicted by emerging intertidal landscape theory [30, 31].

Coupled with the use of new surveying technologies and improvements in computers and software, such as geographic information systems (GIS), provided intertidal ecologists with tools that would improve the visualization and analysis of complex ecological data [32]. Improved computer graphics allowed for clearer visualizations of complex ecosystems data, while advances in computer memory allowed for the long-term storage of increasingly complex ecosystem data. Coupled with improved computer graphics was the introduction of R statistical software as a free alternative for analyzing complex spatial patterns captured within digital imagery. The advances in digital imagery and computing technology allowed for rapid data collection over broad swaths of intertidal habitat and enabled rigorous testing and subsequent analysis of landscape ecological theory that was not previously possible. The integration of multiple technologies into intertidal research provided new avenues of discovery and insights into how landscape complexity drives patterns of species distribution and abundance in the intertidal [31].

Among the first field studies to integrate these emerging technologies in the rocky intertidal can be found in the work of Robles et al. [26]. They employed digital imagery and total station theodolites in order to test the predictions of one of the first cellular automaton models developed for a rocky intertidal community [24]. Robles et al. [26] tested the hypothesis that positive interactions (i.e., self-organization) among mussels within a mussel bed could produce landscape patterns in boundary intensity. This hypothesis represented a shift from traditional ecological paradigms of boundaries being driven by strong interspecific interactions such as predation and competition [1, 33]. They also proposed that the sharpness of species boundaries could be driven, in part, by an increasing complex intertidal landscape of biogenic and geologic structure and its interaction with the surrounding environment. The proposed mechanism for any observed variation in boundary distribution and sharpness was due to individual mussels aggregating in the face of a potential limiting factor such as wave stress.

The field test of this hypothesis involved the construction of photo mosaics of entire mussel beds, composed of the mussel *Mytilus californianus*, at 12 mussel beds along the rocky shoreline of British Columbia, Canada. Each of their sites varied in wave exposure and topographic complexity. Digital cameras were used to create the photo mosaics while a total station allowed component photos within the larger mosaic at each site to be geotagged with a position measured relative to mean lower low water (MLLW). Geotagging each individual photo allowed any organisms present within an individual photo to also be assigned an individual position relative to MLLW. Their analysis involved GIS interpolation of boundary locations and estimation of the corresponding boundary intensities using a contagion index [26]. Similarities between predicted and real trends in boundary intensity (sharp vs. diffuse) over a field measured wave energy gradient supported the hypothesis that spatially varying neighborhood processes determined variation in mussel bed boundary intensity. Discrepancies from spatial trends predicted in their model suggested that increasing landscape complexity disrupted the neighborhood interactions which resulted in an increasingly diffuse population boundary [26]. This early integration of digital technologies and spatial analysis provided a new approach for predicting and detecting previously unknown landscape-derived structuring processes in the intertidal.

Beyond testing landscape ecological theory, these new approaches have been used in other studies to help improve our understanding of rocky intertidal communities. Meager and colleagues [34, 35] have applied digital photogrammetry and fractal dimension to disentangle the relationship between topographic complexity and patterns of species abundance in intertidal communities. Their work has provided new metrics for measuring species richness in the intertidal as well as an approach for using microscale measurements to predict macroscale patterns of species richness. Coastal monitoring programs along the US West Coast have recently employed the use of terrestrial laser scanners (TLS) to measure species diversity in rocky intertidal systems that are part of ongoing monitoring efforts. The data provided by TLS not only produces digital orthophotos of intertidal communities but also allows for measurements of the underlying landscape to improve our understanding of how coastal geology may play a role in affecting intertidal species diversity.

Beyond providing estimates of species richness in the intertidal, marine landscape approaches have also been used to understand how landscape complexity can affect the thermal regimes that impact intertidal communities [36]. Whethey et al. [36] have employed land surface models to model thermal regimes and the variation in temperature that invertebrates experience across an intertidal landscape. This work has broad implications for helping us predict communities that may be susceptible to increasing thermal stress as a result of climate change. In management-based studies, Windell [37] has used digital imagery as part of efforts to understand how key intertidal foraging habitat inside and outside of marine protected areas changes over time. This type of information can provide resource managers with information on the efficacy of MPA design and allow managers to rapidly adapt existing conservation approaches in the face of a changing environment. Looking forward, the integration of landscape technologies and theory should continue to help ecologists improve our understanding of the processes that structure rocky intertidal ecosystems.

Future of Landscape Ecology in the Intertidal

Advances in computing software, processing, and data collection technologies now allow intertidal ecologists to ask questions and conduct studies that had not been possible in previous decades of intertidal research. Emerging technologies such as aerial unmanned vehicles, aka drones, and approaches that incorporate stable isotope data into GIS platforms can enhance the ability to understand multi-scale relationships between ecological patterns and landscape complexity in marine systems. These technological advances can improve our understanding of how trophic relationships in managed marine populations vary as a function of landscape complexity in the marine environment. Furthermore, they can provide data, collected over vast spatial scales, that can be used to assist the ongoing development of management strategies focused on rocky intertidal communities.

Aerial drones (Fig. 1c) have seen increased use in ecological studies due to their ability to rapidly capture multi-scale data on landscape complexity at a relatively low cost [38, 39, 40••]. Intertidal ecologists have traditionally relied on quadrat surveys or manipulative experiments that can capture fine-scale patterns and elucidate ecological mechanisms, but may preclude investigations of how rocky intertidal populations interact with their environment across larger spatial scales [19, 39]. This limitation in traditional intertidal research methods can impede rigorous quantitative assessments on how landscape complexity drives the ecological dynamics of rocky intertidal communities over multiple scales of organization. Modern drones, outfitted with high-resolution digital cameras, provide a method for capturing multi-scale data on landscape complexity and community composition in rocky intertidal systems at scales of a few centimeters up to hundreds of meters (Fig. 1d). Beyond their capacity to capture high-resolution image data, drones come with a number of other advantages that provide ecologists with new ways to study the environmental factors that structure rocky intertidal systems across multiple spatial and temporal scales. These include but are not limited to (1) carrying various imaging (e.g., hyperspectral cameras) payloads to collect spatial datasets; (2) increased frequency in survey intervals; (3) low altitude, autonomous flight that allows sensors to collect fine spatial resolution data; and (4) low operating costs [39, 40••].

In addition to recent improvements in mapping technologies, recent advances in the ability to incorporate stable isotope data into GIS databases (isoscapes) also have the potential to change the ways in which ecologists study the rocky intertidal. Compared with traditional methods used to assess diet in field studies, such as gut content analysis, stable isotope analysis (SIA) supports estimates of prey preference across long temporal scales [41]. Isotope-based trophic studies rely on the assumption that consumers incorporate the isotopic signature of their prey into their tissues in a predictable manner, creating a long-term record of their main prey sources [42]. For intertidal studies focusing on the role of keystone predators, such as *Pisaster ochraceus*, SIA-based studies can provide insight into how the diet of key species may change in the face of changing prey communities. A primary advantage of stable isotope analyses is that they are low cost and can be contracted out to stable isotope facilities. Investigators simply need only to prepare their samples in the manner provided by a contract laboratory, thereby avoiding having to invest resources in procuring and operating stable isotope analytical equipment.

Stable isotope analysis has historically been used to assess connectivity and trophic positioning in terrestrial populations. However, SIA is also being used to assess connectivity among oceanic species, some that are often the focus of many fisheries agencies [43, 44]. Isoscapes can allow researchers to visualize how complex marine landscapes affect population connectivity and to quantify the probability that a given landscape will affect connectivity between or the trophic positioning of managed species [45, 46•]. Examples of this type of approach have been used for fisheries-related species such as tuna [44] and marine mammals [47]. More recent applications have also been applied to fisheries, such as the Pacific spiny lobster *Panulirus interruptus*, which occupy the rocky intertidal [48]. The results of this recent work reveal fine-scale coupling of lobster foraging preferences to sub-meter variation in the complexity of rocky intertidal habitat. In the future, isoscapes may be able to provide a cost-effective method for answering population-level questions (i.e., population discrimination) and provide a complementary approach to genetic analysis. Recent data from Southern California demonstrate that stable isotopes can discriminate between connected lobster populations on a scale of 10s of meters within rocky intertidal habitats, whereas traditional genetic approaches have typically distinguished unique populations on the scale of 1000s of meters in the Southern California Bight [49]. Isoscape approaches, when coupled with high-resolution habitat mapping data in marine systems, can enhance the ability of intertidal researchers to understand multi-scale relationships between process and pattern in the rocky intertidal.

Beyond assessing shifts in intertidal population structure, landscape approaches can also be employed to understand the eco-physiological responses of organisms to changes in their surrounding environment. Infrared thermography is increasingly being used by ecologists and physiologists to understand how thermal stress and small-scale temperature variability affect the abundance and distribution of species [50•]. On rocky intertidal shores, infrared thermography is being used to assess thermoregulatory processes in gastropods, mussels, and sea stars and the effect of heat stress on barnacle recruitment [50•]. Though ground-truthing and calibration challenges still remain with this technique, it has the potential to provide a reliable and rapid tool for measuring environmental and biological temperature variability. This feature of thermography will become increasingly important as shifting global climates and thermal stresses begin to impart ever-increasing impacts on rocky intertidal communities. Additionally, ongoing improvements in the tools used to log data in the rocky intertidal [51•] coupled with new approaches in eco-forecasting [13••] will drastically help the capacity of intertidal researchers to record and estimate the potential impacts of climate change on marine communities.

Conclusions

The field of landscape ecology offers new opportunities to advance our knowledge of spatial patterns and process in rocky intertidal systems. Emerging landscape theory has provided new insights into the role of landscape complexity in driving population structure in rocky intertidal systems. This theory has, in turn, changed the types of hypotheses developed around intertidal systems and the types of research conducted in this system. More specifically, the landscape-based theory has served as the basis for studies that have illuminated previously unknown forcing mechanisms in intertidal communities [24–26].

New landscape-based technologies have improved our capacity to collect and analyze data and improve quantitative inferences on how structural complexity affects patterns of species distribution and abundance in the intertidal. These technologies will allow ecologists to supplement approaches such as quadrat surveys and manipulative experiments in order to improve our basic understanding of the processes that structure these systems. Current advances in GIS modeling, computer graphics, and spatial statistics provide clearer visualizations of ecosystem dynamics across complex marine landscapes and the ability to make statistical inferences on these dynamics. Improvement in data collection techniques such as digital and multi-spectral imagery and LIDAR has enhanced the ability of coastal ecologists to resolve landscape features critical to understanding the ecological dynamics of the intertidal down to a scale of a few meters. Meanwhile, advances in drone and stable isotope approaches now provide low-cost approaches for capturing landscape data and quantifying linkages between intertidal populations as a function of landscape complexity. The overall synthesis of these and future landscape-based approaches can offer new insights and approaches for studying the rocky intertidal.

Beyond the advancement of basic knowledge, the inclusion of landscape approaches in intertidal research can also support coastal survey programs that monitor the rocky intertidal in order to estimate the health and status of coastal environments. While traditional survey methods such as meter tapes and quadrats helped identify early climate-driven shifts in intertidal habitat, the current extent and rate at which coastal habitat is changing will require new approaches for measuring ongoing habitat shifts. Aerial drones coupled with digital imagery and machine-based photo classification can provide intertidal ecologists with advanced technological approaches for detecting the ongoing impacts of climate change on intertidal habitat. Having the capacity to rapidly detect climate-driven changes will allow ecologists to work with coastal managers to develop mitigation strategies that can potentially offset any deleterious shifts in intertidal habitat. The continued integration of landscape ecology into rocky intertidal research can help advance discovery science in this ecosystem and provide a platform for bridging basic discovery science with conservation and management efforts centered about this important marine habitat.

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Compliance with Ethical Standards

Conflict of Interest Dr. Garza has no conflicts of interests to declare.

Human and Animal Rights and Informed Consent

This article contains no studies with human or animal subjects performed by the author.

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