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Landscape Ecologists' Perspectives on Seascape Ecology

Simon J. Pittman, John A. Wiens, Jianguo Wu and Dean L. Urban

16.1 Introduction

Here we present some thoughts on the emergence of seascape ecology from the perspective of leading ecologists who have been working at the forefront of modern terrestrial landscape ecology in North America since its inception in the 1970s and who continue to play an instrumental role in guiding the discipline into the future. This chapter consists of opinion pieces from three eminent landscape ecologists – John Wiens, Dean Urban and Jianguo Wu – who have profoundly influenced the development of landscape ecology through their prolific and generous written contributions, together with a high level of participation in the US branch of the International Association for Landscape Ecology (USIALE) and the flagship journal, *Landscape Ecology,* established in 1987 (Barrett *et al.* 2015). All three ecologists were influenced, directly or indirectly, by a landmark three-day workshop at Allerton Park, Illinois, in 1983, which is widely regarded as an important catalyst in the formation of landscape ecology in the United States (Wiens 2008; Wu 2013a; Barrett *et al.* 2015). John Wiens and Jianguo Wu are both past recipients (1996 and 2010 respectively) of the award of Distinguished Landscape Ecologist presented by the US-IALE. Dean Urban served as president of USIALE from 2010 to 2012.

This chapter emerged from the recognition that the fledgling discipline of seascape ecology has much to benefit from the experience and lessons learned in terrestrial landscape ecology. Although biophysical differences exist between marine and terrestrial systems, there are sufficient generalities in ecological pattern-process relationships that make landscape ecology applicable. What guidance, concerns and opportunities do landscape ecologists perceive for the future development of the sister discipline of seascape ecology? Are there lessons learned, pitfalls to be aware of and specific focal topics that should receive priority attention?

16.2 From Landscapes to Seascapes (and Back Again)

By John A. Wiens

Terrestrial ecologists, such as myself, sometimes view oceans as undifferentiated masses of water – places where the land ends and we pass the baton to marine ecologists.

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This may be particularly true of landscape ecologists, for whom 'land' is part of their professional identity. Perhaps it is because we are used to looking at the land surface as the template on which ecological dynamics are played out and the ocean's surface seems to us homogeneous and, well, unfathomable.

All it takes is one day at sea to dispel such notions. Mine came on a trip to Cordell Bank, a rocky seamount on the edge of the continental shelf west of San Francisco. Travelling there we saw only an occasional gull but then we were suddenly surrounded by a frenzy of shearwaters, albatrosses, fulmars, auklets and scores of humpback and blue whales. All were feeding on the abundance of krill and fish concentrated about the seamount by the confluence of oceanographic conditions and undersea habitat diversity. Such spatial concentrations of marine life are not unique to Cordell Bank. For millennia, fishermen have realized that some places in the sea support masses of fish while other places are barren. Foraging aggregations of seabirds and whales have been used as indicators for designing marine reserves (Nur *et al.* 2011). On the deeper ocean floor, hydrothermal vents are (literally) hotspots of productivity and biodiversity.

These examples illustrate how the central themes of landscape ecology apply to seascapes as well. Landscapes and seascapes both have spatial *structure*: not every place is the same. Landscapes and seascapes are interconnected mosaics of patches with different environments and inhabitants. The structure of landscapes and seascapes affects how they *function*. The physical structure of Cordell Bank or patches of water of different temperatures produces spatial variations in productivity, feeding relationships and nutrient dynamics. These spatial relationships are not constant; landscapes and seascapes *change*. Feeding aggregations vary in time according to the dynamics of prey populations, which respond to such things as daily tidal cycles or seasonal patterns of upwelling. And the dynamics and patterns of landscapes and seascapes occur over multiple *scales*. Seasonal productivity of Cordell Bank is driven by local factors but the seabirds and whales that feed there may move over thousands of kilometres during a year.

These are general parallels between landscapes and seascapes. How closely they match depends on where one looks. In intertidal and nearshore areas, ecological dynamics are strongly influenced by the relatively stable spatial structure of the substrate close to the surface. In deeper pelagic areas dynamics are largely determined by the water mass, which is fluid on multiple scales of space and time. Boundaries among water masses may shift or disappear over hours to decades. The distributions of organisms and nutrients may also change, but not in the same ways. Consequently, landscape ecologists may be able to get away with giving little attention to the air above the land, but unless they restrict attention to shallow areas, seascape ecologists must focus on spatial patterns and dynamics in the three-dimensional mass of the ocean itself.

The topics to which landscape ecology has made important contributions are connectivity – fragmentation, boundary dynamics, scale, spatial modelling and statistics, conservation planning, resource management and others (Wiens & Moss 2005) – are also ripe for development in seascape ecology, as the previous chapters illustrate. Applying the approaches and insights of landscape ecology to topographic features such as seamounts or intertidal zones may be (relatively) straightforward. It will be more difficult and require innovative approaches to translate landscape ecology to the seascapes of open pelagic waters where spatial patterns and relationships in the water change with the tides and currents over a vast range of scales (El Niño events are a good example).

The promise of seascape ecology, however, goes beyond adapting the concepts and tools of landscape ecology to the ocean setting. Terrestrial landscapes and oceans are inexorably linked. Even distant uses of the land can affect the ocean environment well out to sea. Overgrazing by cattle in interior Queensland contributes to sedimentation of the Great Barrier Reef and agricultural practices in the corn belt of Iowa promote hypoxia in the Gulf of Mexico (Nassauer *et al.* 2007). The linkages also go in the opposite direction; foraging seabirds or marine mammals can enhance the productivity of terrestrial ecosystems by importing nutrients from marine ecosystems when the animals come ashore (Anderson & Polis 1999). Placing these linkages in a spatially integrated landscape-seascape context will enhance the management of both terrestrial and marine ecosystems, although they will require different approaches. Understanding land-sea linkages rests on knowing how water runs from fields to streams to rivers and thence to and within the sea. Understanding the sea-land linkages rests instead on knowledge of how organisms move between marine areas and the land. Understanding how it all fits together over multiple scales of space and time will require the collaborative efforts of landscape ecologists, hydrologists, oceanographers, animal behaviourists and a new cadre of seascape ecologists. An exciting challenge!

Biography

John Wiens grew up in Oklahoma as an avid birdwatcher. Following degrees from the University of Oklahoma and the University of Wisconsin-Madison (MS, PhD), he joined the faculty of Oregon State University and, subsequently, the University of New Mexico and Colorado State University, where he was a professor of ecology and university distinguished professor. His work has emphasized landscape ecology, conservation and the ecology of birds, leading to over 260 scientific papers and ten books on ecology and landscape ecology. John has chaired several USIALE symposia and in 1996 received the Distinguished Landscape Ecologist award. John left academia in 2002 to join the Nature Conservancy as lead scientist, with the challenge of putting years of classroom teaching and research into conservation practice in the real world. In 2005, John was the recipient of the Cooper Ornithological Society's Loye and Alden Miller Research Award, which is given in recognition of lifetime achievement in ornithological research. In 2008, he joined PRBO Conservation Science as Chief Scientist and since retirement he now divides his time between his home in Corvallis, Oregon and the University of Western Australia where he is a Winthrop Research Professor.

16.3 Seascape Ecology and Landscape Ecology: Distinct, Related and Synergistic

By Jianguo Wu

Most ecological theories have been based on terrestrial systems, despite the fact that about 71% of the Earth's surface is covered by water (nearly 96.5% of which is contained in the oceans). With rare exceptions, terrestrial and marine systems were studied separately with little scholarly communication until the 1980s when scientists began to compare and connect them in order to understand the earth as a whole ecosystem (*e.g.*, Steele 1985, 1991a; Levin *et al.* 1993; Okubo & Levin 2001). The past few decades have witnessed a wave of new research fronts that cut across marine and terrestrial systems. One of these exciting and emerging cross-system fields is seascape ecology, the topic in this book. Here I compare and contrast this new field with landscape ecology and discuss how they can benefit each other.

16.3.1 Landscape Ecology

While the term landscape ecology was coined in 1939, initially as the study of the relationship between biotic communities and their environment in a regional landscape mosaic, modern landscape ecology since the 1980s has become a highly interdisciplinary and comprehensive scientific enterprise, with multiple definitions and interpretations (Forman 1995; Wiens & Moss 2005; Wu 2006; Wu & Hobbs 2007; Turner & Gardner 2015). It is widely accepted that landscape ecology focuses on the relationship between landscape pattern and ecological processes. Landscape pattern refers to spatial heterogeneity, encompassing patchiness and gradients, which is usually neither random nor uniform in reality. Heterogeneity is almost always scale dependent. Thus, landscape ecology is inevitably and fundamentally a science of heterogeneity and scaling. Conceptually, scale multiplicity in pattern and process begets hierarchical thinking.

Landscape ecology is both a research field (or a body of knowledge) of how landscape composition and configuration interact with ecological processes on broad scales and a new ecological paradigm that explicitly integrates geographical patterns, ecological processes and spatiotemporal scales. Modern landscape ecology covers a wide range of topics (Wu 2013a): (i) pattern-process-scale relationships of landscapes; (ii) landscape connectivity and fragmentation; (iii) scale and scaling; (iv) spatial analysis and landscape modelling; (v) land use and land cover change; (vi) landscape history and legacy effects; (vii) landscape and climate-change interactions; (viii) ecosystem services in changing landscapes; (ix) landscape sustainability and (x) accuracy assessment and uncertainty analysis. As such, landscape ecology is really an interdisciplinary integration of science and art for studying and improving the relationship between spatial pattern and ecological processes on multiple scales, with landscape sustainability as its ultimate goal (Wu 2006, 2013b).

16.3.2 Seascape Ecology

Seascape ecology is the study of the relationship between spatial pattern and ecological processes in marine environments on a range of spatiotemporal scales. The emergence of seascape ecology was apparently inspired by the rapid development of landscape ecology in recent decades (Pittman *et al.* 2004, 2011; Boström *et al.* 2011; Kavanaugh *et al.* 2016). The current literature indicates that there are different views on seascape ecology in terms of its relationship to landscape ecology. The first view promotes seascape ecology as the application of landscape ecology principles and methods in the study of coastal marine systems (Boström *et al.* 2011; Pittman *et al.* 2011; Olds *et al.* 2016). The second view also acknowledges the relevance and usefulness of landscape ecology but places more emphasis on the open and dynamic oceanographic features of marine environments (*e.g.*, Kavanaugh *et al.* 2014, 2016). The first view is focused more on coastal seascapes whereas the second more on pelagic seascapes. Thus, these two views complement each other, together making seascape ecology more comprehensive in scope and more challenging intellectually.

Fundamentally different from the first two, the third view asserts that, because the 'properties and dynamics of the ocean fluid' differ so much from those of terrestrial landscapes, seascape ecology can benefit little from landscape ecology and that such 'terrestrial analogies' should be 'avoided' (Manderson 2016). While it is true that marine and terrestrial systems are fundamentally different in many ways, both geophysically and biologically (Steele 1985), this fact itself does not suffice the rejection of landscape ecological principles and methods in seascape ecology. On the contrary, interdisciplinary comparisons and fertilization across land and water have been necessary, fruitful and quite promising (Steele 1985, 1989, 1991b; Levin *et al.* 1993; Okubo & Levin 2001). As I discuss below briefly, landscape ecology as a body of knowledge may be of limited use to seascape ecology, but it can be quite relevant as a new ecological paradigm that focuses on pattern-process-scale relations.

16.3.3 How can Landscape and Seascape Ecology Interact with Each Other?

The conceptual similarity between landscape ecology and seascape ecology is apparent although fundamental biophysical differences exist between the two 'scapes'. I see three general ways that seascape ecology can benefit from landscape ecology. The degree of relevance or applicability of the three uses varies with the locations and spatial extents of marine environments, generally decreasing from coastal marine zones to open oceans.

First, the findings of pattern-process-scale relations in terrestrial landscapes should be heuristically useful for seascape ecology, such as the effects of the kinds and amounts of habitat, geometry and connectivity of habitat patches, edges and corridors, matrix (or context) and natural and human disturbances on biodiversity and ecological processes, as well as their scaling relations in space and time. This heuristic value, however, may be quite limited especially for pelagic systems. Second, many spatial analysis and modelling methods used in landscape ecology, such as spatial statistics, categorical and surface pattern metrics and individual-based models, can be used in seascape ecology. Indeed, some of them (*e.g.*, power spectral analysis) were used in marine studies before being introduced into landscape ecology. The Stommel diagram originated in oceanography has had profound influences on the study of scaling and hierarchy in landscape ecology. Of course, remote sensing, GIS and GPS are now frequently used in almost all field-based studies way beyond landscape ecology and geography. The third and most general way is to use landscape ecology as a spatially explicit ecological paradigm that emphasizes spatial heterogeneity, pattern-process relations, scale multiplicity, transient dynamics and holistic human-environmental interactions.

Several key principles that characterize landscape ecology may also become prominent in seascape ecology, including patch dynamics, scaling, matrix / context, connectivity / fragmentation, ecotones / gradients, ecosystem / landscape services and landscape resilience / sustainability. Patch dynamics and scaling are two science themes transcending the boundaries between physical systems and between academic disciplines, both of which had been explored in the water and on the land before the term seascape ecology existed (Levin & Paine 1974; Steele 1978, 1989; Levin *et al.* 1993). Patch dynamics had its original conceptual roots in terrestrial community ecology in the 1940s (Watt 1947), saw its first mathematical theory developed from intertidal systems in the 1970s (Levin & Paine 1974) and became a widely applied perspective in both terrestrial and marine ecology in the 1980s and 1990s (Pickett & White 1985; Levin *et al.* 1993; Wu & Loucks 1995), epitomizing modern landscape ecology as a unifying framework. Conceptually, landscapes are hierarchically structured land mosaics (Forman 1995) in which patch dynamics take place constantly on multiple scales – *i.e.*, 'hierarchical patch dynamics' in operation (Wu & Loucks 1995).

Pelagic marine environments are open, diffusive and dynamic, with less obvious physical boundaries than terrestrial systems but they also exhibit spatial patchiness and scaling relations in both their physical environment (from eddies to gyres) and ecological organization (from phytoplankton to zooplankton and higher tropic levels). In a seminal paper published in the journal *Landscape Ecology*, the eminent oceanographer John H. Steele (1989) discussed the spatial patterning and scaling of 'ocean landscapes':

> The ocean has a complex physical structure at all scales in space and time, with 'peaks' at certain wave numbers and frequencies. Pelagic ecosystems show regular progressions in size of organisms, life cycle, spatial ambit and tropic status.

These observations remain as relevant and inspiring today as they were when the article was published. Recent studies in seascape ecology have taken the hierarchical patch dynamics and scaling perspectives to a new level, conceptualizing the marine environment as 'a mosaic of distinct seascapes, with unique combinations of biological, chemical, geological and physical processes that define habitats which change over time' and integrating oceanographic and ecological paradigms in studying, managing and protecting marine systems (Kavanaugh *et al.* 2016).

Other key ideas in landscape ecology including matrix / context; connectivity / fragmentation; ecotones / gradients; ecosystem / landscape services; and landscape resilience / sustainability are also relevant, but yet to be fully explored in the context of seascapes. Some pioneering seascape ecological studies utilizing these ideas already exist (Pittman *et al.* 2004 and examples throughout this book). Such studies are crucial to the marine biodiversity conservation, marine resource management and seascape sustainability. By focusing on ecosystems services and human wellbeing in changing climates and marine environments, a seascape sustainability science is expected to occur, in parallel to landscape sustainability science (Wu 2013b). Through integrating ecological studies across land and water, a spatial ecology of landscapes and seascapes is in the making.

Biography

Jianguo (Jingle) Wu is the Dean's Distinguished Professor of Sustainability Science at the School of Life Sciences and School of Sustainability at Arizona State University, Tempe, Arizona, United States. He was awarded his PhD (1991) in ecology from Miami University, Oxford, Ohio, United States and then as a National Science Foundation (NSF) postdoctoral fellow at Cornell University (1991–1992) and Princeton University (1992–1993) working alongside Simon A. Levin. His research focuses on landscape ecology, urban ecology and sustainability science, subjects on which he has authored 14 books and more than 300 journal articles and book chapters. Jianguo has served as editor-in-chief of *Landscape Ecology* since 2005 and serves on the editorial boards of several international journals on ecology and interdisciplinary research. He is the founding director of the Sino-US Center of Conservation, Energy and Sustainability Science (2007–) and the Center for Human-Environment System Sustainability (CHESS), Beijing Normal University (2012). His contributions to landscape ecology have been recognized through several major awards and honours including the American Association for the Advancement of Science (AAAS) Award for International Scientific Cooperation (2006); Leopold Leadership Fellow (2009); Distinguished Landscape Ecologist Award and an Outstanding Scientific Achievements Award and Distinguished Service Award from United States Association for Landscape Ecology (2010, 2011 and 2012).

16.4 Seascape Ecology

By Dean L. Urban

The emergence of landscape ecology reflected a growing interest in spatial heterogeneity and scale in ecology (*e.g.*, Levin 1992). As the discipline evolved, it has become a multithreaded enterprise with branches to and from a broad range of disciplines. But a few themes are recognizable as hallmarks of the field – how we organize textbooks, how we think about our work. Landscape ecologists think a lot about where pattern comes from, how it scales in space and time and why it matters to populations, communities and ecosystem processes. Marine systems invite the same perspective. (In the landscape ecology laboratory at Duke, we deliberately decided to broach seascape ecology as a new focus and to take advantage of our marine lab. Pat Halpin led that charge. Some later beneficiaries of that decision are contributors to this book.) In general, the principles of landscape ecology translate readily to seascapes.

Agents of pattern include the physical template, biotic processes and disturbance regimes. These apply readily to seascapes, with the notable complication that the physical template is three dimensional and layered and it is dynamic over timescales much faster than most landscapes. For example, landscape ecologists might be concerned with temperature and moisture gradients that reflect the interaction of climate with landform. In the seas, we expect gradients in temperature and chemistry (*e.g.*, salinity) that reflect the interaction of the ocean climate (currents) with bathymetry and the currents change rapidly enough that applications often require data that are resolved on monthly or even finer time scales.

In landscape ecology, patchiness that arises from interacting agents of pattern have often been summarized in 'space-time' diagrams (*e.g.*, Delcourt *et al.* 1983). These diagrams emphasize the characteristic spatiotemporal scaling of various levels of patchiness. Somewhat ironically, these Stommel diagrams came to landscape ecology from marine systems (for an intriguing perspective on these diagrams, see http://rs.resalliance.org/2010/02/24/a-history-of-stommel-diagrams, accessed 6 June 2017). In particular, Steele's (1974) seminal work on the interplay between biophysical dynamics and biotic processes (food web interactions) set a precedent for how to visualize patchiness that has been foundational to landscape ecology.

One implication of pattern is the potential fragmentation of populations into metapopulations. Many landscape ecologists have embraced graph-theoretic models of metapopulations. Ted Ames, a fisherman and historian of fisheries, essentially reinvented graph theory as a conceptual model for the antique cod fisheries of New England because the system just made sense that way (Ames 2004). This underscores the ready translation of terrestrial models to seascapes – again, with the caveat that the model is temporally dynamic while landscape ecologists typically assume the habitat dynamics are very slow relative to the species inhabiting those habitats.

A central challenge in landscape ecology is inferring the relative control of spatial structure (autocorrelation) in species distributions: partitioning beta diversity (Legendre *et al.* 2005). Autocorrelation might be caused by spatially structured environmental constraints such as patterns in temperature or soil moisture; or it might be due to spatial processes such as dispersal or contagious disturbances. The difficulty lies in the reality that spatial processes are often unmeasured and so we would like to make inferences about process from spatial structure that is residual after accounting for environmental constraints. But residual spatial structure might also be due to an unmeasured environmental constraint and so this inference is a challenge. In marine systems, this challenge is further complicated by the fact that the environment moves around with currents. For example, if we observe a marine mammal at a particular location and time, we might wonder whether it is there because it is responding to bathymetry (as distance to shore, or location and experiencing whatever temperature or salinity happens to be there), or responding to temperature (at whatever location that temperature happens to be), or responding to prey species (which might be responding to bathymetry or temperature) (Schick *et al.* 2011). These are complicated questions and the answers likely will require new analytic techniques as well as new data (*e.g.*, from genomics). This work will continue in landscape and seascape ecology, with marine systems perhaps having an advantage precisely because their temporal dynamics might provide more leverage to separate 'environment' from 'location'.

In summary, seascapes might be seen as particularly fast-moving versions of landscapes. The central questions in landscape and seascape ecology are very similar and the analytic approaches overlap substantially. More crossfertilization and interdisciplinary collaboration would seem to be to the benefit of all.

Biography

Dean Urban is professor of landscape ecology and senior associate dean for academic initiatives in the Nicholas School of the Environment at Duke University. He received his PhD in ecology from the University of Tennessee (1986), working at Oak Ridge National Laboratory in the formative years of landscape ecology. A hallmark of his work is integrated studies that extrapolate our fine-scale empirical understanding of environmental issues to the larger space and time scales of management and policy. Specific research interests include the implications of climate change for forest ecosystems and the consequences of land use pattern on forest habitat connectivity and watershed function in developed landscapes. He has been named a Distinguished Landscape Ecologist but is especially proud to have placed more than a hundred masters students into positions in governmental and nongovernmental environmental organizations, where they are having a direct impact on landscape management.

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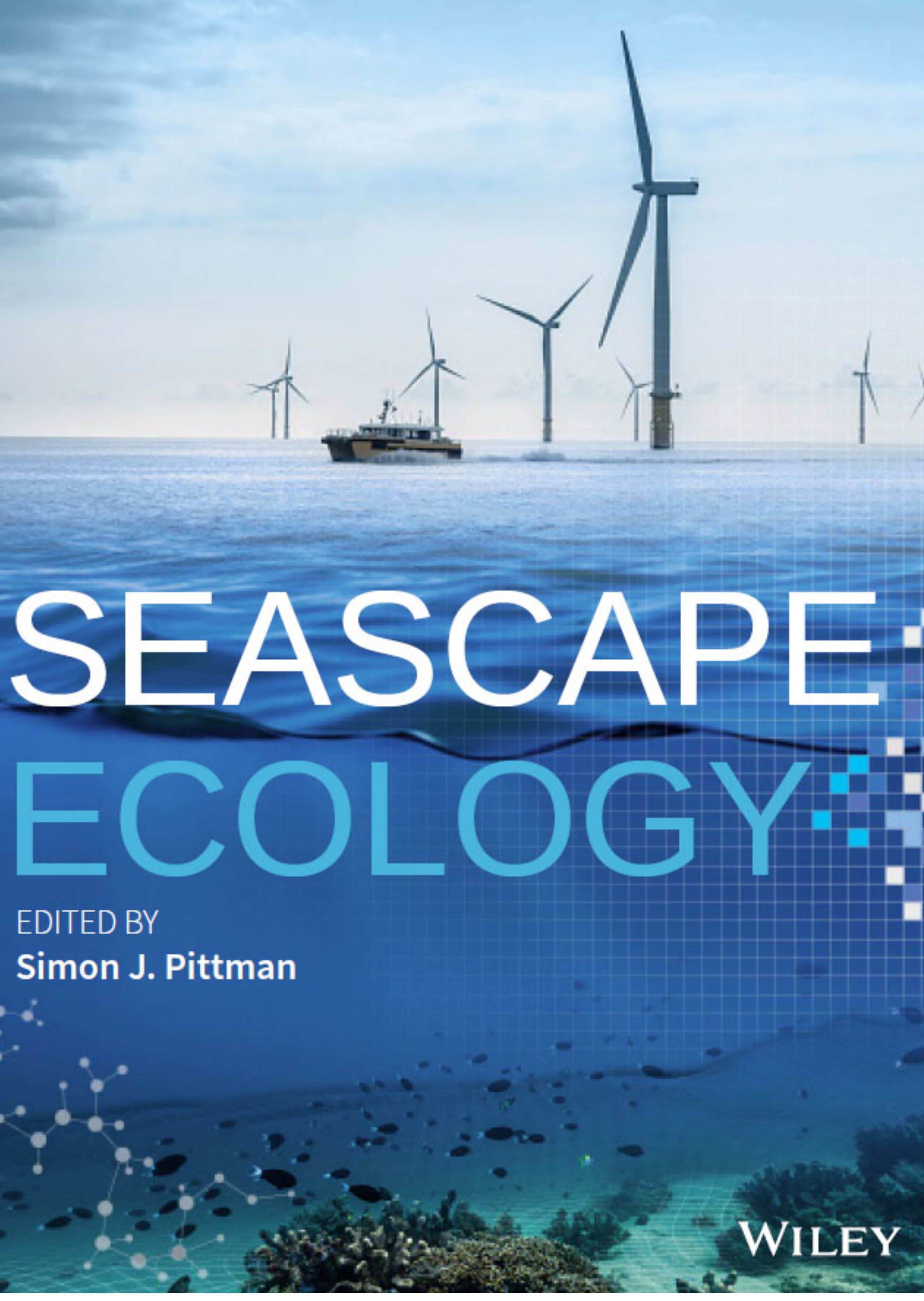
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