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Seascape ecology and landscape ecology: Distinct, related, and synergistic

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Most of ecological theories have been based on terrestrial systems although about 71% of the Earth's surface is covered by water (nearly 96.5% of which is contained in the oceans). Since Darwin, oceanic islands have long been used as "natural laboratories" for developing and testing ecological and evolutionary theories. Yet, terrestrial and marine systems had been 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, Steele 1991a, Levin et al. 1993, Okubo and 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 of this book. Here I compare and contrast this new field with landscape ecology and discuss how they can benefit each other.

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 and Moss 2005, Wu 2006, Wu and Hobbs 2007, Turner and 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): (1) Pattern-process-scale relationships of landscapes; (2) Landscape connectivity and fragmentation; (3) Scale and scaling; (4) Spatial analysis and landscape modeling; (5) Land use and land cover change; (6) Landscape history and legacy effects; (7) Landscape and climate change interactions; (8) Ecosystem services in changing landscapes; (9) Landscape sustainability; and (10) 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).

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 the recent decades (Pittman et al. 2004, Boström et al. 2011, Pittman 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 plays more emphasis on the open and dynamic oceanographic features of marine environments (e.g., Kavanaugh et al. 2014, Kavanaugh et al. 2016). The first view is focused more on coastal seascapes whereas the second more on pelagic seascapes. Thus, these two views are complementary to 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, Steele 1989, 1991b, a, Levin et al. 1993, Okubo and 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.

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 modeling 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 and Paine 1974, Steele 1978, Steele 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 and Paine 1974), and became a widely applied perspective in both terrestrial and marine ecology in the 1980s and 1990s (Pickett and White 1985, Levin et al. 1993, Wu and 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 and 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 28 years ago. 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 – 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, 2004 and as evidenced 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 well-being in changing climate 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.

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