Estuarine, Coastal and Shelf Science 157 (2015) 1–6

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Golden opportunities: A horizon scan to expand sandy beach ecology

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ARTICLE INFO

Article history:
Received 12 December 2014
Accepted 2 February 2015
Available online 11 February 2015

Keywords:
horizon scan
ecological concepts
cross-system transfer
ecological theories
sandy shorelines
paradigms

ABSTRACT

Robust ecological paradigms and theories should, ideally, hold across several ecosystems. Yet, limited testing of generalities has occurred in some habitats despite these habitats offering unique features to make them good model systems for experiments. We contend this is the case for the ocean-exposed sandy beaches. Beaches have several distinctive traits, including extreme malleability of habitats, strong environmental control of biota, intense cross-boundary exchanges, and food webs highly reliant on imported subsidies. Here we sketch broad topical themes and theoretical concepts of general ecology that are particularly well-suited for ecological studies on sandy shores. These span a broad range: the historical legacies and species traits that determine community assemblages; food-web architectures; novel ecosystems; landscape and spatial ecology and animal movements; invasive species dynamics; ecology of disturbances; ecological thresholds and ecosystem resilience; and habitat restoration and recovery. Collectively, these concepts have the potential to shape the outlook for beach ecology and they should also encourage marine ecologists to embrace, via cross-disciplinary ecological research, exposed sandy beach systems that link the oceans with the land.

There is a tide in the affairs of men.
Which, taken at the flood, leads on to fortune;
Omitted, all the voyage of their life
Is bound in shallows and in miseries.
On such a full sea are we now afloat,
And we must take the current when it serves,
Or lose our ventures.

(William Shakespeare, Julius Caesar)

1. Introduction

Sandy beaches are the most common habitat found at the boundary between the continents and the oceans. Sandy beaches are also amongst the most valuable landforms for humankind, supporting sizeable economies, communities, coastal cities, tourism and allied industries (Houston, 2008). As ecosystems, beaches and their functionally-linked dunes and surf-zones, display several unique traits: 1.) Linear systems characterised by long and open boundaries; 2.) Malleable habitats undergoing frequent and substantial changes in physical extent and environmental conditions; 3.) Intense cross-system exchanges of nutrients, organic matter and organisms; and 4.) Biological communities assembled from both terrestrial and marine species pools (Fig. 1; McLachlan and Brown, 2006). Beaches also provide a suite of ecosystem services to society, ranging from nutrient remineralisation over recreation to fisheries (Schlacher et al., 2008). This combination of large geographic extent, high socio-economic importance, multiple cultural values, and distinctive ecological

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http://dx.doi.org/10.1016/j.ecss.2015.02.002
0272-7714/

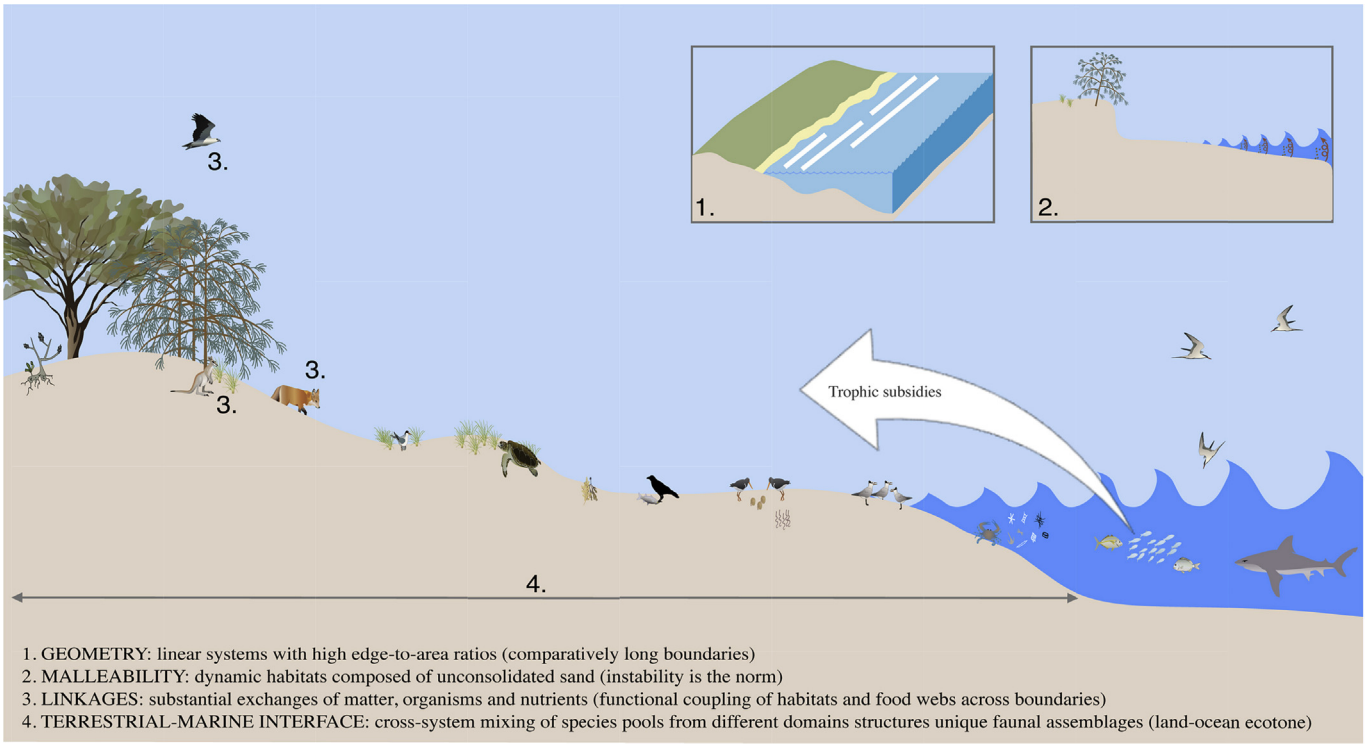

Fig. 1. Conceptual diagram of a dune-beach-surf ecosystems, illustrating prominent biota and four key features and processes that define these habitats and their ecological assemblages: i) *linear geometry*, meaning long and open boundaries, ii) *malleable habitats*, meaning frequent changes and instability; iii) *cross-boundary exchanges*, meaning close functional linkages between abutting components; and iv) *ocean-land interfaces*, meaning unique faunas assembled from both terrestrial and marine species pools.

properties makes sandy beaches multi-faceted and significant systems to study.

Scientifically, sandy-beach ecology – as a sub-discipline of ecology – has made significant progress over the last decades in broadening its scope, embracing novel techniques, building stronger conceptual and theoretical frameworks, and linking fundamental research to applications in conservation and management (Nel et al., 2014). For example, one of sandy-beach ecology's most important conceptual contributions to ecology is the quasi-paradigmatic thesis of persistent and dominant habitat and physical controls on invertebrate assemblages (McLachlan, 1990; Defeo and McLachlan, 2005; Schlacher and Thompson, 2013a,b). In this 'environmental control model', predictions of compound community descriptors (e.g. taxonomic richness, total biomass) based on equally simple habitat attributes (e.g. slope, grain size) are remarkably strong (Defeo and McLachlan, 2013). This existing model therefore provides a good starting point from which beach ecology can branch out to address wider ecological questions relating to the role of environmental heterogeneity (e.g. species–diversity relationships, the role of refugia, niche diversity).

Progress in science, in the field of ecology and elsewhere, pivots on the continual renewal and critical testing of existing theories (Popper, 1935), and the creation of new knowledge (Feyerabend, 2010). Equally, all branches of ecology stand to benefit greatly from critically examining paradigms that define their field (e.g. Rowden et al., 2010; Schlacher et al., 2010; Elliott and Whitfield, 2011; McClain and Schlacher, in press). Thus, ecology must continually evolve as a field to remain relevant, and beach ecology, especially, stands to make rapid and substantial gains through the transfer of theories and concepts developed in other ecosystems. Those broader concepts, too, would benefit from being more fully tested on beach systems, with their unique properties (Fig. 1). Such transfers and adoptions of theories from allied disciplines are critical for intellectual renewal, for maintaining currency, and for improving the attractiveness of beaches as model systems to test broader ecological theories and emerging ideas (Schoeman et al., 2014).

Here we outline several thematic areas that represent important developments and ideas in the modern ecological research literature beyond ocean beaches; these ideas have generally not been transferred to ecological studies on ocean beaches to any significant extent. This is not intended to be a canonical list, but merely represents a set of examples of the types of broader ecological theory that can fruitfully be tested on ocean beaches. These questions are poorly represented in the sandy-shore literature.

The overarching intent of this paper is to stimulate debate and to encourage scientists working in other habitats to include ocean beaches as test systems to address both applied and theoretical questions in ecology. Whereas broad research directions have been put forward for other habitats (Sánchez-Azofeifa et al., 2005; Graham et al., 2014), and more generally for ecology (Sutherland et al., 2013), this process has yet to take place for beach and dune ecology – we put this paper forward as a catalyst to achieve this.

2. Community assembly: historical legacies, phylogenetic constraints, species traits

All biological elements of ecological systems carry strong evolutionary signatures, with modern structures and processes reflecting evolutionary histories, phylogenetic constraints, and adaptive opportunities. For example, modern distributions and habitat associations of species likely reflect the net outcome of niche conservatism and niche evolution (Hopkins et al., 2014). Beach ecology has illustrated these evolutionary signals by emphasising species traits that confer plasticity (e.g. Soares et al., 1999), but a broader recognition of evolutionary pasts in its