

## 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.

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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.

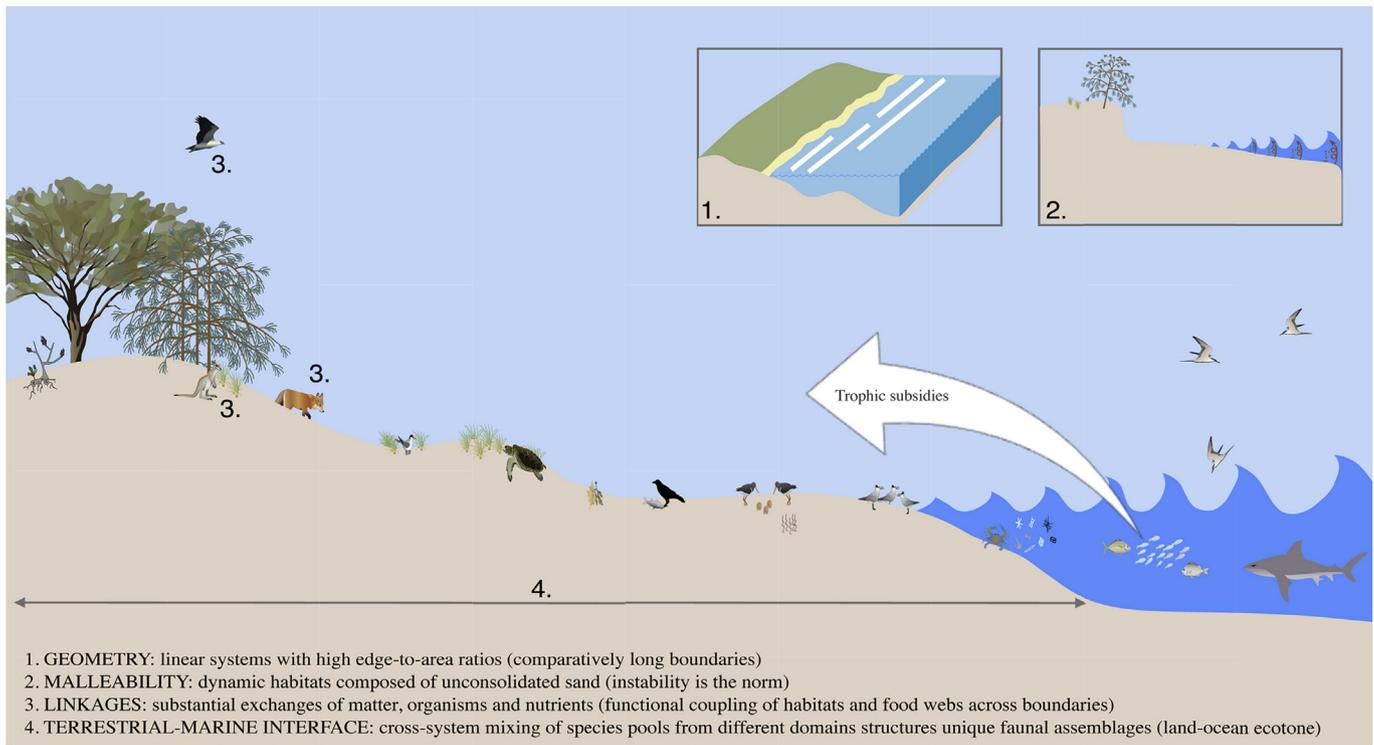
(William Shakespeare, Julius Caesar)

### 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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**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

research framework could be a valuable complement, likely to enhance the explanatory and predictive power of beach ecology models. Processes that drive and control community assembly are central to understanding what determines the architecture of ecological assemblages. Important factors include historical legacies and constraints on species interactions, priority effects, stochastic events, and colonisation rates (Fahimipour and Hein, 2014; Vannette and Fukami, 2014). Invertebrate assemblages on ocean beaches globally show remarkable redundancy in functional and taxonomic guild composition (Schlacher et al., 2008), offering a model system to test central tenets of community assembly theory. It will also be important to answer the related question of whether the same degree of compositional redundancy exists for other taxa, such as fishes of the surf-zones and birds of the dunes on sandy shorelines.

### 3. Food-web architectures, complexities, apex predators

Biological transformations of carbon are, arguably, the pivotal ecosystem function. Hence, 'trophic biology' remains a perennially prominent theme in ecology: ecology seeks to understand how ecological systems are configured as carbon transformers, how differences in configurations arise, and how variations in configurations shape the functional efficacy and properties of food webs (Hussey et al., 2014; Ulanowicz et al., 2014). Whilst beach ecology has traditionally measured mainly structural components of the system, there is evidence for an emerging momentum targeting functional properties, including food webs, trophic processes, and ecosystem energetics (e.g. Schlacher and Hartwig, 2013; Morrow et al., 2014). A defining characteristic of beach food-webs is their reliance on imports of marine carbon washed ashore or produced in the abutting surf zone (Spiller et al., 2010; Schlacher et al., 2013a). This feature of beaches (i.e. subsidy-dominated lower trophic levels) may provide a good opportunity to examine causes of variation in fundamental traits of food webs (e.g. connectivity, food-chain length, upper bounds to trophic position, trophic breadth and depth) tested in other ecosystem types. Trophic ecology on ocean beaches has, arguably, been somewhat myopic in its focus on small invertebrates, many of which are buried in the sand (Schlacher and Hartwig, 2013; Schlacher and Thompson, 2013a,b; Lucrezi and Schlacher, 2014). By contrast, the functional role of larger vertebrate carnivores on ocean beaches is less often considered, the exception being limited studies on surf-zone fish, shorebirds, and raptors (Huijbers et al., 2013; Peterson et al., 2013; Schlacher et al., 2013b; Manning et al., 2014; Schlacher et al., 2014d; Huijbers et al., 2015). This contrasts with other ecosystem types where research on apex predators features much more prominently (Heath et al., 2014).

### 4. Novel ecosystems and ecological traps

In a world of rapid human-induced environmental change, animals are faced with novel combinations of ecological features that may not necessarily have been part of their evolutionary history (Sih et al., 2011). In situations where animals show maladaptive behavioural responses to novel conditions, habitats can form ecological or evolutionary traps (Schlaepfer et al., 2002; Sih, 2013). Such is the extent of human utilisation of beaches, that anthropogenic transformation of beaches is common, widespread and often severe (McLachlan et al., 2013), potentially creating evolutionarily novel sets of conditions for beach species (Weston et al., 2014). The existence of such traps and their implications for population viability is generally difficult to demonstrate (Robertson and Hutto, 2006). Because ocean beaches have relatively well-defined conditions to which species respond, and because these conditions are

modified in broadly predictable ways by humans, beach systems may offer good opportunities to investigate the properties and consequences of evolutionary and ecological traps.

### 5. Landscape ecology and interfaces

Ecosystems are rarely isolated: their boundaries are permeable and they exchange energy, material, and organisms with abutting systems. These cross-boundary flows are omnipresent in the biosphere and are major drivers of ecological functioning in many systems (Leroux and Loreau, 2008). Exchanges of matter across boundaries are the mechanistic or theoretical pivots in a number of important conceptual models in modern ecology, including influential advances in the discipline of meta-ecosystems (Gravel et al., 2010), pulsed subsidy effects (Leroux and Loreau, 2012), and spatial ecology (Massol et al., 2011). Ocean beaches are archetypal interface regions, characterised by long and open boundaries across which organisms move and nutrient exchanges couple ecosystems. Surprisingly, though, a relatively small component of beach ecology research has explicitly contextualised its work by drawing on theories from coupled systems and functionally-linked elements of the coastal landscape (Schlacher and Connolly, 2009). These concepts offer an appropriate and fitting framework for beaches as functional interface regions, highlighting an opportunity for closer intellectual linking of beach science with ecology more broadly (Haegeman and Loreau, 2014).

### 6. Spatial ecology and animal movement

A defining characteristic of all animal species on ocean shores is mobility: sessile forms cannot persist on the unstable sediments of beaches. The critical role of animal movement is widely recognised for beach invertebrates, reflected in a substantial body of published work on invertebrate movement and orientation (Dugan and McLachlan, 1999; Scapini, 2006; Schlacher and Lucrezi, 2010; Scapini, 2014). Recent advances in tracking technology allow the movement of numerous animal species to be recorded with high resolution over large spatial and temporal scales (Fagan et al., 2013; Benhamou, 2014). Ocean beaches support numerous taxa of larger animals (e.g. shorebirds, raptors, fishes, turtles) that use these linear systems as feeding and breeding sites and which act as important vectors of nutrient transfers (Weston et al., 2014; Schlacher et al., 2014a). As in other ecosystems (Olds et al., 2012), populations of these organisms appear to be distributed in response to spatial heterogeneity and habitat connectivity in coastal landscapes (e.g. beach birds, Meager et al., 2012; Schlacher et al., 2014b) and seascapes (e.g. Ayvazian and Hyndes, 1995; Valesini et al., 2004), but few beach studies have adopted an explicit spatial framework (like that provided by landscape ecology) to examine these questions. Extending modern theoretical advances in animal movement ecology and incorporating new techniques in remote sensing, spatial modelling, and bio-acoustic technology (sensu Fagan et al., 2013; Mansfield et al., 2014) to track these 'maritime vertebrates' of beaches appears a promising research field. A better knowledge of the spatial ecology of beach vertebrates is also critical for improving the conservation of these threatened animals and informing marine spatial planning decisions (Nel et al., 2013).

### 7. Pests and invasive species

There is extensive literature on the ecological, economic and socio-cultural impacts of invasive, predominately non-native, species (Ehrenfeld, 2010). Whilst traditional notions of invasive species effects have, in the vast majority of cases, portrayed large to

catastrophic impacts (Courchamp et al., 2003; Norton, 2009), a more nuanced view has emerged in recent years (Davis et al., 2011; Pysek et al., 2012; Strayer, 2012). Notwithstanding this shift in how society views non-native species, and a more empirical approach to assessing their role in recipient systems, invasive species ecology remains a top science and management priority in many countries (Fleishman et al., 2011), and is highly topical in the ecological literature (Yelenik and D'Antonio, 2013; Moran and Alexander, 2014). Beaches appear to be the exception, however, with few targeted, systematic, and sufficiently-resourced programs focusing on invasive species in beach ecosystems seawards of the dunes. Whilst there are a number of studies documenting impacts of non-native species in coastal dunes (e.g. Maguire et al., 2009; Maslo and Lockwood, 2009; Huijbers et al., 2013), our knowledge of non-native species in other parts of beach ecosystems remains rudimentary and fragmentary, making this a candidate theme for future beach research. This is particularly poignant as beach and dune habitats may be especially prone to species invasions because of their long and open boundaries with abutting systems, favouring routes via sea borne colonisation (e.g. sea spurge) and landward colonisation (e.g. weeds and foxes).

## 8. Disturbance ecology

Disturbance has a rich history in ecology as a putative driver of diversity (Connell, 1978; McCann, 2000; Dornelas, 2010; Fox, 2013). Whilst the immediate consequences of disturbance events are often negative for species populations, positive effects are possible, such as enhancing habitat heterogeneity at landscape scales (Levin and Sibuet, 2012), or the unlocking of resources (Soares et al., 1996). 'Disturbance' is a process regularly attributed to habitats of ocean beaches as they are often described, in physical terms, as 'harsh', 'dynamic', 'unstable', or 'malleable'. Thus, hypothetically, biological assemblages of ocean beaches should be adapted to frequent and widespread disturbance, and there is some empirical evidence to support this notion (e.g. Schoeman et al., 2000; Lucrezi et al., 2009, 2010). It is, however, largely unknown whether disturbance sets upper bounds on diversity or shapes diversity patterns across physical gradients in some other way. Irrespective of the shape of the disturbance–diversity curve, beaches are likely to be good model systems within which to test predictions from disturbance theories developed in other types of ecosystems (Fox, 2013). On beaches, natural (e.g. storms) and opportunistic (e.g. nourishment) ecological disturbances offer replicated, large-scale models to study disturbance to ecosystems (Manning et al., 2014).

## 9. Ecological thresholds, resilience, critical transitions

Many ocean beaches worldwide have undergone significant modifications by humans, often on an intensive and massive scale, resulting in widespread expansions of urbanised sectors of the coast. Moreover, future changes in storm intensities and direction, and sea-level rise, mean that beaches and their ecologies are likely to change greatly (Pilkey and Cooper, 2014). Management and conservation responses to these human pressures routinely focus on maintaining shoreline position and sand volumes, but rarely include the maintenance of biological assets or ecological function (Schlacher et al., 2007; Harris et al., 2014). This failure can be attributed partly to a lack of data on how the *function* of beach systems changes with increasing levels of human modifications (Schlacher et al., 2014c). From a conservation perspective, a critically important question is whether beach systems lose function suddenly beyond a threshold or tipping point, switching to a different functional domain (sensu Jaramillo et al., 2012; Veraart et al., 2012; Hubbard et al., 2014; Lever et al., 2014). Resilience

theory also highlights the role of ecological processes acting as feedback mechanisms between environmental impacts and ecosystem state (Nyström et al., 2012). We contend that testing predictions of theories on critical transitions, regime shifts and feedback loops (Scheffer et al., 2012) is a priority for sandy beach ecology (see also Engel and Gupta, 2014). The incorporation of beaches into this discipline will also benefit resilience research. Theoretically, a model of more rapid recovery after disturbance on beaches (Schoeman et al., 2000) means that beaches can provide a useful test case at the extreme end of malleability of ecosystems. Moreover, because research on regime shifts (and recovery) has been developed almost exclusively in structured habitats (e.g. coral reefs and vegetated habitats such as seagrass meadows), metrics capable of assessing shifts and recovery in non-structured habitats are poorly developed.

## 10. Restoration and recovery

Society generally has strong expectations of beaches, surf-zones, and dunes, to provide ecosystem services primarily associated with recreation, real estate values, and the protection of human assets (Maguire et al., 2011). On coastlines where human modifications have diminished the capacity of beach and other coastal systems to deliver these services, restoration is widely practiced (Elliott et al., 2007). Restoration of dunes is a long-established and widespread practice on sedimentary shorelines (Nordstrom, 2008; Nordstrom et al., 2011). In a broader context, ecosystem restoration can be a controversial issue that involves complex social, economic and environmental decisions (Elliott et al., 2007; Ritchie et al., 2012; Lampert and Hastings, 2014). Moreover, recovery trajectories can be highly variable and it is often uncertain to which extent 'recovered' systems resemble, in functional and structural terms, systems not significantly altered by human stressors (Duarte et al., 2013). Leaving aside ethical issues regarding ecological restoration, if we accept that the practice is likely to continue, it offers opportunities for beach ecology: arguably, restoration projects can be viewed as 'experiments' (sensu Peterson et al., 2006). These interventions also occur at spatial or economic scales much larger than is practicable for purely academic research, and can be used to examine a multitude of questions, such as community assembly, habitat controls on functional and structural recovery trajectories, patch-mosaic dynamics and phylogenetic constraints to recovery. Importantly, ecological knowledge may be leveraged to optimise the planning and engineering components in restoration practice to improve ecological (and perhaps even engineered) outcomes.

## 11. Conclusions and outlook

Beaches possess several attributes that make them useful ecological model systems to address the types of questions we have sketched here, and many others (Fig. 1). Four broad attributes seem particularly relevant to us in this context: 1.) Beach systems have an essentially linear geometry, with long ecosystem boundaries (high edge-to-area ratios), 2.) Functional coupling of food webs is frequent and strong through the exchange of matter, organisms and nutrients; 3.) The physical matrix of beaches is of an unconsolidated nature, meaning that they are malleable habitats that can be unstable, highly dynamic and prone to disturbance (induced changes in extent and shape); and 4.) Beaches constitute interfaces between the oceans and the land, meaning that the biota represent a melange from terrestrial and marine species pools.

Beaches also offer some practical advantages to ecologists: they are relatively easy to access and work on (compared with permanently wet ecosystems); opportunities exist for spatial replication across continents, climates, and biogeographies; control sites can

be defined (albeit this possibility is being increasingly undermined by increasing human uses and coastal development (Schlacher et al., 2007)); and they contain relatively well-defined (at least conceptually) food webs composed of species with broadly predictable habitat requirements.

Beaches also represent one of the largest socio-ecological systems. Because they span diverse human cultures and communities, cross-disciplinary study of beaches holds much promise with respect to addressing broadly applicable questions of anthropogenic utilisation of, and impact on, ecosystems. Indeed, ecological conservation of beaches will increasingly require integration of biophysical, economic, and social considerations (Bodin et al., 2014; Scyphers et al., 2014).

On the planet's ocean beaches, there is indeed “*a tide in the affairs of men*” (William Shakespeare, 1599) in more than a metaphorical sense: research opportunities abound for those with sand between their toes.

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