Marine and terrestrial ecology: unifying concepts, revealing differences

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The extent to which similar ecological processes operate on land and in the sea has been much debated, with apparently ‘fundamental’ differences often disappearing when appropriate comparisons are made. However, marine and terrestrial ecology have developed as largely separate intellectual endeavours, which has hampered the search for general patterns and mechanisms. Here, I argue that marine–terrestrial comparative studies can be extremely useful at uncovering mechanisms when they explicitly consider those facets of the environment that are important to a particular hypothesis. Furthermore, the binary ‘marine–terrestrial’ division misses many opportunities for more interesting comparisons, several of which I highlight here. Increasing the flow of concepts, hypotheses, and data between marine and terrestrial ecologists is essential to reveal those differences that really are important.

A tale of two ecologies
Surveying the quest for generality in ecology, Lawton [1] noted that ‘environments are different, organisms are wonderfully different, and the laws, rules and mechanisms we end up with... are contingent’ on the particular system one happens to study. This suggests that untangling the dynamics of any specific community will require a good deal of specialist ecological knowledge. However, the risk is that this knowledge is gained at the expense of a more general view of pattern and process: ecologists specialising in a particular type of system tend to favour particular methods and hypotheses [2], if only through ignorance of those developed in other systems [3]. Thus, although important ecological insights tend eventually to be applied across systems, the search for general patterns in Lawton’s contingencies will typically be restricted to a subset of available case studies, and bounded by system-specific understanding. Forest ecologists will draw on a different empirical and theoretical corpus than will students of grasslands, mangroves, or the deep sea.

A formative decision faced by any ecologist in this respect concerns whether to specialise in marine ecology. Marine ecologists remain, as a rule, largely separate from the ecological mainstream (see Box 1 for a discussion of terminology), working in separate departments or institutes, publishing in (and reading) different journals, and participating in different workshops and meetings [3,4]. The clearest consequences of this separation may be in the policy arena, where marine systems have a much lower profile than do terrestrial systems in discussions of biodiversity and biological responses to climate change [5]. But equally important, these barriers can also reduce the transfer of theory, hypotheses, and methods [3], effectively limiting ‘meme flow’ [6] and leading to unwitting reinvention, duplication of effort, repetition of mistakes, and an overall loss of conceptual coherence (Box 2).

Two decades ago, Steele [7] recognised these problems and championed the idea that communication between marine and terrestrial ecologists could both provide critical tests of theory and lead to more general conclusions. My aim here is to highlight various (still regrettably rare) attempts to meet Steele’s challenge in the fields of community ecology and macroecology, and to suggest areas with high potential for future cross-domain collaborations. My goal is to show that the exchange of concepts, models, and empirical approaches between marine and terrestrial ecologists is usually worth the effort, and is often both enlightening and productive [6,8].

Differences between marine and terrestrial ecosystems: fundamental or incidental?
Before examining where cross-domain collaboration can be most fruitful, it is worth considering why it has not been more common. The physical differences between air and water (summarised in [9,10]), and their consequences for organisms living in these different environments, have led to claims of ‘fundamental’ differences between marine and terrestrial ecology. Certainly, the raw materials upon which biotic and abiotic forces can act are rather different in the two domains. The seas are immensely diverse in terms of higher taxa (most animal phyla have marine members, many exclusively so [11]), yet species-level diversity has been higher on land for some 100 million years (my) [10] and, today, marine species constitute only approximately 15% of all described species and 25% of predicted global species numbers [12]. However, it is not clear whether these stark differences in diversity reflect fundamentally different ecological processes, or whether they are instead an incidental consequence of rather few chance evolutionary events.

In an insightful review [9], Dawson and Hamner argue that to address such questions, one has to acknowledge that reality is far more nuanced than a binary ‘marine–terrestrial’ division allows. Each domain includes its own contrasts, and there is little justification for elevating marine–terrestrial contrasts over and above those between, for example, marine pelagic and marine benthic habitats or between the forest canopy and the rhizosphere.
More specific contrasts are likely to be most revealing, such as comparing invertebrate communities in soil and in marine sediments [13,14], or terrestrial and marine members of a single taxonomic class [15]. Sensible comparisons will depend on the specific question (Figure 1). For example, a food-web ecologist would have little to gain from comparing trees and whales, yet such a comparison makes sense in terms of the carbon cycle [16].

Comparative analyses will also vary in their focal levels of ecological complexity. At the scale of individual organisms interacting with the environment, physical differences between air and water (e.g., in terms of flow regime) are not as pronounced as one’s intuition might suggest [9], and individual-level allometries may vary predictably across environments [14]. More generally, mechanistic approaches to ecology may suffer less from the marine–terrestrial divide precisely because the physics of the medium is under explicit consideration. Introducing a recent special issue of the Journal of Experimental Biology on ‘Biophysics, bioenergetics and mechanistic approaches to ecology’, Denny [17] boasts: ‘Bacteria, phytoplankton and seaweeds; salmon and jellyfish; vultures, dragonflies, mussels and lizards; we have them all; and although the umbrella term ‘ecomechanics’ [18] retains a largely marine flavour to date, it has great potential to unite workers based on a common methodological approach rather than a specific habitat. However, in this article, I focus on levels of ecological complexity at larger spatial scales: the disciplines of community ecology and macroecology, where comparisons must consider the interactions between multiple individuals of many species and, thus, may be more complicated.

**Community ecology: the messy middle**

The middle ground’, warned Lawton when speaking of the complex interacting communities which sit between single-species population dynamics and regional-scale macroecology, ‘is a mess… do not expect universal rules, even simple contingent general rules, to emerge’ [1]. Nonetheless, it is at the community scale that some of the richest and most revealing comparisons between marine and terrestrial systems can be made, and where new approaches offer the potential to test fundamental hypotheses concerning the structure and diversity of assemblages. As discussed above, marine and terrestrial systems clearly differ in diversity, so any general theory of coexistence ought to be able to explain patterns for both species-rich terrestrial and phylum-rich marine systems, and to predict the conditions under which exceptions occur.

### Box 2. Parallel evolution of diversity measures

The choice of methods, software, and even research questions is governed as much by sociological factors to do with ease of use and tradition within a specific discipline as by any scientific criteria. For example, consider measures of evolutionary diversity. Faith [50] defined phylogenetic diversity (PD) based on the evolutionary history represented by a community of species. Conceptually, this is similar to the measures of taxonomic diversity and distinctness (which I group as TD) later defined by Clarke and Warwick [51]. Although the measures differ in important ways, and each has its advantages and problems, both involve summing (or averaging) the length of the branches on a phylogenetic (or taxonomic) tree linking pairs of species. The important point is that, although both papers were published in similar general applied ecological journals, TD was developed by marine biologists, working in a marine biological institution, and communicating primarily with other marine biologists, whereas PD was developed within the ecological ‘mainstream’ (Box 1). Therefore, although both papers have been well cited (PD: 460 cites, TD: 291 cites, ISI Web of Knowledge, March 2012), their citation patterns differ.

On the basis of their title or abstract, I was able to categorise unambiguously all the papers citing [51] and 432 papers citing [50] according to the focal realm of the study: terrestrial, freshwater, marine, cross-realm, or conceptual (theoretical, methodological, or conceptual discussions of diversity without reference to a specific study system). I found that the measure used to quantify evolutionary diversity was strongly contingent on the system in which the work was done (Figure 1). PD has been widely adopted in empirical studies of terrestrial systems, whereas TD has predominantly been used in marine systems. Equally striking is the contrast in conceptual studies, with only 26 (9%) of citations to TD being conceptual, compared with 142 (31%) for PD. Whether this represents a terrestrial slant to most conceptual studies is unknown.
Explaining diversity

Explaining coexistence in diverse communities has taxed ecologists for decades. One hypothesis, the Janzen–Connell (JC) effect, proposes that aggregations of conspecifics are selected against by the actions of specialised natural enemies, which limit recruitment of offspring in the immediate vicinity of reproductive adults [19]. Generally considered only in the context of tropical forests, there is nothing so specific in the formulation of the JC effect; indeed, one of the studies on which it is founded [20] gave as much space to marine case studies (the action of predatory snails on intertidal barnacles) as it did to rainforest trees. Of particular interest, in positing that, on land, the conditions necessary for natural enemies to promote diversity are most likely to occur in the wet tropics, compared with high latitudes where opportunities for specialisation among predators are limited, Connell [20] notes: ‘...the terrestrial high arctic resembles the high intertidal zone where there is too short a time for the predators to feed effectively. At the lower edge of the intertidal zone, the predators can feed almost continuously, as they can in those parts of the terrestrial wet tropics with little seasonal change.’ In other words, not only is the theory explicitly applied to both marine and terrestrial systems, but Connell also suggests that an extensive terrestrial latitudinal gradient is replicated within a few tens of metres on a single seashore. Indeed, Whittaker [21] considered this intertidal gradient to be one of five major global ecosystem gradients (ecoclines), and the suite of opportunities it offers as a tractable analogue to larger-scale gradients is well recognised [22] (although its vastly reduced scale relative to the dispersal distances of the component organisms cautions against pushing the analogy too far).

Connell [20] also identifies coral reefs as being similar to tropical forests, where rarity and wide dispersion of conspecific individuals is favoured by the presence of natural enemies, making an analogy between plants and sessile animals that he further developed in a later influential article [23]. More generally, the environmental conditions (as measured by the typical spatial and temporal scales of environmental variation) that are likely to select for or against the evolution of specialisation are not restricted to either marine or terrestrial systems [6,9,10], suggesting fruitful grounds for testing the role of natural enemies in maintaining diversity within marine communities. Yet, to date, the JC effect has received effectively no attention from marine ecologists: none of the 212 studies that include the term ‘Janzen–Connell’ in their ‘topic’ field, and only 12 (2%) of the 792 studies citing Connell’s original paper [20] are of marine systems (data from ISI Web of Knowledge, April 2012).

Interacting individuals

Framing marine–terrestrial comparisons in terms of the nature of interactions between individuals, rather than simply numbers of species, is useful because it introduces ecological processes (e.g., competition and predation) that are common to all environments. In terms of trophic interactions, there has been debate about whether food webs of fundamentally different character result from differences between aquatic and terrestrial systems in the degree to which feeding is size structured, and in the relative roles of top-down versus bottom-up control (reviewed in [2,24]). A recent promising approach uses body size as a common currency with which to compare interactions from an individual to a network level across ecosystems [14]. The focus on individual size as a structuring property of ecosystems derives primarily from studies of marine communities [4], where size structuring is most obvious and taxonomy is least effective at capturing ecological roles.
in general, size-based analyses have been less common in terrestrial ecology [4]. However, by quantifying statistical variation between communities in the strength of indices of size structure (e.g., various cross-species allometric relationships), one moves from a dichotomy (a community is either size structured or it is not) to a continuum [14], allowing more nuanced comparative analyses and lessening the temptation to enforce a rigid aquatic–terrestrial separation. Another important concept first developed by marine ecologists before being profitably applied more generally concerns the role of large-scale patterns of climate variability on multitrophic ecological interactions and the timing of reproduction and growth [26,27]; climatic indices, such as the North Atlantic Oscillation, are now routinely used by terrestrial ecologists [8].

Common behaviours
One inevitable difference in the study of marine and terrestrial systems concerns the amenability of the two systems to direct observation. As Underwood [28] puts it, terrestrial ecologists usually ‘...can actually see (or hear) [their study] organisms in nature, in groups, in real time and space. That is rarely true for ecologists studying fish or benthic marine invertebrates because of the opacity of the medium. Even when they can be seen, it is usually for very short periods over very small spatial scales.’ Thus, what marine ecologists gain in the ability to sample destructively across entire communities, and so measure, dissect and chemically analyse multiple individuals, they may lose in terms of deep natural historical understanding; a contention supported by the lack of basic biological information for most marine species [29]. Nonetheless, when extensive behavioural observations have been made, commonalities between marine and terrestrial systems emerge [30]. For example, dugongs Dugong dugon respond to the threat of tiger sharks Galeocerdo cuvier across multiple spatial scales, in a fashion surprisingly similar to the responses of elk Cervus elaphus to wolves Canis lupus [30]. Such comparative studies should lead to a more general understanding of how behaviour shapes the dynamics of ecological communities.

Community phylogenetics
A final example of the potential of cross-system collaboration in community ecology concerns the emerging field of community phylogenetics [31,32], analysing together the evolutionary history, biological characteristics, and patterns of occurrence of species. Empirical community phylogenetics has to date focused almost exclusively on terrestrial systems [32]. Given that most terrestrial studies tend to be ‘taxocenic’ (i.e., they focus on specific taxonomic groups, such as birds or butterflies, in isolation to other organisms using the same resources [28]), this means that the phylogenetic diversity encompassed in community phylogenetic studies has tended to be rather low. Contrast this with the tradition (indeed necessity) of considering transphylectic interactions in marine studies [28] and it becomes clear that applying community phylogenetic methods to marine systems may allow for more direct tests of specific hypotheses. For example, the prediction that phylogenetic community structure will depend on the relative importance of physiological tolerances versus competition [32] could be tested using the gradient in the intertidal zone from the highly competitive lower shore to the physiologically stressful upper shore. In addition, there appear to be no a priori predictions about whether high phyllum or species richness would lead to greater competition [28]; thus, testing whether competition intensity varies with average relatedness within a community would be of great interest.

A frequently cited obstacle to the application of phylogenetic ecology to marine systems is the lack of comprehensive phylogenies for marine taxa. One possibility is to use taxonomy as a surrogate for phylogeny [33,34]; however, more exciting is the potential of new methods directly to address the phylogeny gap. For example, although DNA barcodes were originally devised as an identification tool, they can also provide a bridge between taxonomy and phylogenetics [35]. The major animal barcode (cytochrome c oxidase subunit I; COI) contains at least some phylogenetic signal [36] and, when paired with other initiatives to resolve deeper nodes in the animal tree [37], could provide a route to resolving evolutionary relationships across entire communities (see [38] for an example of what has already been achieved in a plant community). This is important because DNA barcoding does not have the traditional bias towards large-bodied, charismatic groups: of approximately 170 000 barcoded animal species, from 23 phyla, >90% are invertebrates and approximately 10–15% are marine (T.J.W., unpublished analysis of data obtained from the Barcode of Life Data System [39], April 2012), a figure rather similar to the 18% of recorded animal species that are marine [12]. Such advances mean that we may soon enter a new era in the availability of comprehensive phylogenies for marine assemblages.

Macroecology: statistical order from the scrum
Lawton [1] felt that the best chance of finding simple ecological rules lay in stepping back from the ‘mind-bogging details’ of community ecology to see the bigger picture; that statistical order and manageable contingency emerge from the scrum at large spatial scales. Likewise, it is at such macroecological scales that the broadest similarities (and possibly the most revealing differences) between marine and terrestrial systems may lie [4,9] (see [6] for a trans-realm discussion of the related discipline of biogeography). In particular, the statistical tools of macroecology offer a means to test some of the hypotheses outlined above.

Although most macroecology to date has concerned terrestrial systems [4], sufficient evidence now exists to state that general macroecological patterns and relationships also appear to hold in the sea. For instance, most marine species are rare, whether one measures numbers of individuals (species–abundance distributions, SADs [40]) or spatial distribution (species–range size distributions [41]), and the relationship between local abundance and regional distribution (the abundance–occupancy relationship, AOR) is typically positive [25]. Likewise, both the latitudinal gradient in species richness and the species–area relationship (SAR) appear to have general support across marine and terrestrial systems [42,43].
From pattern to process: the role of environmental variation

Such generality is encouraging, but common patterns need not imply common mechanisms and comparative studies of marine and terrestrial ecosystems are likely to be revealing as macroecology seeks to become more mechanistic in its approach. For instance, the physiological characteristics of a group of species must surely influence how extensively they are distributed. Thus, the finding that latitudinal trends in thermal tolerance and niche filling differ predictably between marine and terrestrial systems [44,45] has important implications when using macroecological ‘rules’ to predict the responses of species in different systems to a changing climate. If the pace and scale of human activities leads to a convergence of marine and terrestrial environmental dynamics [7], then studying the macroecology of a variety of systems offers the best chance of predicting responses to environmental change.

Differences in environmental variability present a major opportunity for theoretical advances in macroecology. For instance, seasonal variation in temperature, already dampened at the sea surface compared with on land [44,46], almost disappears in the deep sea whether one considers a single site [47] or an entire ocean (Figure 2). Of course, even at depth, there is considerable spatial variation in temperature and other environmental variables (such as energy availability), which are important in structuring deep-sea communities [34]. However, the key point is that, by studying the considerable variation in biological diversity in the deep sea, it may be possible to isolate the effects of differences in mean environmental conditions from differences in environmental variability in a way that is seldom achievable on land. Other widely distributed deep-sea habitats, for instance chemosynthetic ecosystems [48,49], offer similar comparative opportunities.

The role of biology: towards a trait-based macroecology

Another opportunity for the marine macroecologist derives from the tendency for marine sampling programmes to target entire multi-phylum communities, such that comparable data on the key macroecological variables of abundance and distribution are often available across taxa varying considerably in their biological traits [33]. Again, this opens up novel comparative possibilities, for instance comparing the distributions of related species with differing dispersal modes (e.g., sessile benthic species with or without a planktonic larval phase, or holo- and meroplanktonic species [9,33]). Clearly, the availability of biological trait data will be a limiting factor here [29]; however, where suitable data are available, interesting comparisons between purely taxonomic and purely trait-based macroecology are possible; for instance, the contrast between species-based and size-structured AORs in marine fish [25].

![Figure 2](image_url) Figure 2. Latitudinal variation in sea-water temperature in the Atlantic Ocean at the sea surface and in the deep sea. Data are from The World Ocean Atlas 2009 [52], for longitudes between 0° and 30° W, and for both ‘winter’ (January–March) and ‘summer’ (July–September) to reflect annual variation in both hemispheres. The World Ocean Atlas uses all available observations to derive temperatures at standard depths, and presents them as means of five decadal periods at a 1° resolution. Full details of the quality control and interpolation algorithms used are given in [52], as are limitations of the data (e.g., a general decline in the number of observations with depth). The general pattern shown here, of far less latitudinal and seasonal variation in temperature in the deep sea compared with the sea surface, is robust to such limitations.
Concluding remarks
The physical differences between marine and terrestrial systems clearly impact the way in which organisms interact with each other and their environment. However, rather than assuming that these differences have resulted in fundamentally different ecological processes in the two domains, carefully construed cross-system comparisons in which physical differences are either eliminated as much as possible (e.g., by comparing marine and terrestrial sediment communities [13]) or are explicitly accounted for in the analysis (e.g., relating biological attributes such as body size or range size to metrics of the biophysical environment [9]) offer an effective route to understanding how the environment determines ecological process. The fact that structural barriers exist to such cross-system collaboration, in terms of the institutional and intellectual separation of marine from ‘mainstream’ ecology [3,4,7], perhaps explains why such efforts have historically been rather thin on the ground. However, exploring when ecological theory can cross the land–sea boundary and, equally importantly, when it cannot, can be revealing. As Underwood [28] puts it, ‘Reflecting on differences – even if they are not real, or if real, intractable – at least gives one pause for thought about what might actually matter.’ If one embraces the variability within and among ecosystems, is it possible to tease out generalities in the way that putative ecological ‘rules’ are contingent on specific biotic and abiotic settings? We must hope so, because predicting how communities will respond to environmental change will depend on it.

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