



Trans-realm biogeography: an immergent inter-face¹

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Introduction

In his influential paper on geographic speciation in sea urchins and jellyfishes, Ernst Mayr (1954:16) concluded that “marine animals agree in [their] pattern of variation and distribution completely with terrestrial animals.” Yet the sentiment that “it is useless to think of [the sea] as we think of the terrestrial world” (Hardy 1962), i.e. that marine and terrestrial realms are fundamentally different, has remained commonplace (e.g. Smetacek and Pollehne 1986, Secord 2003). The persistence of this bipolar abstraction of the natural world is troubling. Aquatic, atmospheric, and terrestrial systems can be tightly coupled such that an almost Gaian perspective is needed to meet the challenges of climate change (Menge et al. 2009) yet perceived irrelevance of research from different realms maintains the barriers to multi-disciplinary understanding that slow scientific progress.

Background

The perception of a vital difference between marine and terrestrial environments, which echoes terrestrial human bias (Smetacek and Pollehne 1986, Hamner 1988, Dawson and Hamner 2008) and ancient Greek natural philosophy, has been propagated in part by the balkanization of 20th century scientific infrastructure (Steele 1995, Sarkar 2005, Stergiou and Browman 2005).

Heaney and Lomolino (2009:1-2), for example, noted during their editorial in the first issue of this magazine that “marine and terrestrial biogeography [have been] discussed in different journals using different terminology”. This lack of meme flow afflicts many relevant disciplines. Menge et al. (2009) bemoaned the lack of cross-referencing between papers in ecological journals serving primarily marine or primarily terrestrial audiences. In journals that do cater to both audiences, such as *Journal of Biogeography*, papers are generally either marine or terrestrial, and rarely link realms². When marine and terrestrial systems have been discussed together, the environments often are contrasted as having “fundamental differences” (e.g. Steele 1985, Smetacek and Pollehne 1986, Hamner 1988, Thomson and Gilligan 2002, Carr et al. 2003, Lourie and Vincent 2004, Halley 2005). Such a radical position, which implies at least two kinds of ecology, two kinds of evolution, etcetera, is not supported by any empirical study nor enshrined in any biological theory. Dawson and Hamner (2008) thus proposed that conceptual integration of marine and terrestrial natural history was awaiting only development of a compelling quantitative comparative framework.

A suitable quantitative comparative framework might be provided by expanding Aleyev's (1977:1) “biohydrodynamic conception of life” in which fluid mechanics provides a suite of tools for comparing the aerial and aqueous fluid environ-

1. ‘*Immergent*’, a play on ideas, is defined in the Oxford English Dictionary as either “Not merging into something else” or “Erroneous spelling of ‘*emergent*’, in sense ‘Unexpectedly arising’, ‘urgent’.”

2. A search of Thompson's Web of Science on 15 November 2009 was conducted for articles containing the topic words ‘marine’, ‘terrestrial’, or ‘marine and terrestrial’ published in the *Journal of Biogeography*. All titles, and the abstract of papers with ambiguous titles, were read before final categorization. Articles categorized as ‘marine’ ($n \approx 119$) or ‘terrestrial’ ($n \approx 139$) outnumbered those that discussed ‘marine and terrestrial’ ($n \approx 4$) issues; a total of 2842 records for the *Journal of Biogeography* were recovered, of which 2558 referred to neither “marine” nor “terrestrial” in the fields included in the topic search.

ments of organisms, whether they fly or float or swim, are rooted in the soil, emerge from sediment, or attach to rock (Dawson and Hamner 2008). This biohydrodynamic approach could be used, for example, to estimate, from basic physical principles, whether propagules might 'drift' as far in the sea or atmosphere depending on their size, shape, and density relative to the surrounding fluid or be able to realize philopatry (Dawson and Hamner 2008). Another quantitative comparative framework might contextualize population dynamics and therefore demographic evolutionary processes in terms of the colors (i.e. frequency spectra) and magnitudes of temporal variation in the respective environments (Vasseur and Yodzis 2004). For example, the rates and extents of change in environmental conditions might be used to standardize comparisons of the wax and wane of populations, responses to climate change, or the duration, net diversification interval, and time for speciation of marine and terrestrial species (Coyne and Orr 2004, Table 12.1) and would compliment the more common geospatial focus on the impact of habitat variation in limiting species' ranges.

Dawson and Hamner (2008) suggested these frameworks could be applied, to improve on the existing tendency to intuit the importance of biological differences by qualitatively contrasting organisms in dissimilar physical contexts, in two ways:

1. by quantifying physically dissimilar settings (e.g. marine pelagic with marine coastal benthic) and the respective biological differences in marine and terrestrial realms to establish statistical correlations, and/or
2. to compare marine and terrestrial organisms in environmental settings that were quantitatively similar (e.g. aerial vs. marine plankton with similar Reynolds number, or organisms inhabiting terrestrial vs. marine islands; see also Dawson et al. 2009).

These macro-ecological approaches are yet to be explored empirically. Instead, here, I apply the tradition of thought experiments, testing these

proposals using five papers³ that were unavailable to Dawson and Hamner (2008).

Recent case studies

Latitudinal gradients in diversity (Roy and Goldberg 2007)

In a cogent argument for integrating biogeographic and macro-evolutionary processes when studying latitudinal gradients, Roy and Goldberg (2007) emphasized the potential for dispersal, rather than origination and extinction, to drive patterns of diversity and differences in the mean age of biotas. The potential influence of dispersal, an evolutionary mechanism that has captivated marine biologists for much of the last 30 years (Riddle et al. 2008), led Roy and Goldberg (2007) to pose the question, "are marine and terrestrial diversity gradients driven by different processes?"

Their preliminary answer, based on comparison of avian taxa and marine mollusks which are two of the best studied taxa in their respective environments, was that "the nature of macro-evolutionary and biogeographic processes may differ between terrestrial and marine diversity gradients" (Roy and Goldberg, 2007:S71). For birds, which diversified less rapidly and are on average younger taxa in extratropical latitudes than in the tropics, the primary processes establishing the latitudinal gradient were inferred to be either [1] higher extinction in extratropical regions or [2] time-inhomogenous processes, such as selective extinctions and dispersal of taxa into the extratropics. Both inferences differed from that for marine molluscs: preferential origination in the tropics followed by expansion of geographic ranges into high latitude macroevolutionary sinks. The difference was posited to result from Pleistocene glacial cycles that resulted in "total habitat destruction" and extinction of species restricted to those areas on land but manifested largely as temperature and circulation changes in the ocean that are not strongly linked with global extinction of marine species.

Roy and Goldberg (2007) briefly contrasted terrestrial and marine systems in two additional

3. Publications were located using the Web of Science keyword search "marine AND terrestrial AND freshwater" limited to publications from 2006 to 2009 with additional papers drawn from the citation lists therein.

ways. First, they contrasted the colours of variation, noting that variation in the terrestrial environment is typically 'white' (i.e. random) whereas variation in the marine environment is typically reddened (i.e. auto-correlated). Consequently, for example, population level responses to marine environmental change should include boom-bust cycles of greater magnitude more often resulting in extirpation. Second, they emphasized that "long-distance larval dispersal and recolonization dynamics", considered a key determinant of ecological and biogeographic patterns by marine ecologists, has "virtually no analogue in terrestrial animal ecology". They concluded these "difference[s] in the nature of the [terrestrial and marine] habitats" may explain the "difference between marine and terrestrial groups in the timing, magnitude, and nature of putative extinctions" (Roy and Goldberg 2007:S81) and, therefore, the subsequent sources - origination and/or dispersal - of the modern biotas.

These additional comparisons provide a simple segue to Dawson and Hamner (2008). We showed that although the predominant colours of variation do differ between realms, there is more overlap than generally acknowledged. For example, coastal terrestrial environments are reddened by virtue of their proximity to the sea (Vasseur and Yodzis 2004), and on long time-scales the ocean-atmosphere circulation is tightly coupled (Steele 1995). Similarly, we argued, drawing heavily on data presented by Kinlan and Gaines (2003), that although marine taxa may on average disperse farther than terrestrial taxa, there also are short-dispersing marine taxa and far-dispersing terrestrial taxa; soil-dwelling aerially-dispersed microbes are an example of the latter. Furthermore, from the standpoint of our 'thought experiment', Roy and Goldberg (2007) make three notable caveats. First, Roy and Goldberg (2007) excluded shallow sea basins before stating that marine systems experienced only changes in temperature and circulation with glacial cycles. Yet, like high-latitude intertidal zones scoured by glaciers, the shallow sea basins, continental shelves, and other subtidal areas currently immersed by less than ca. 120 m of ocean, were once inter-

glacial marine habitat that was totally destroyed during Pleistocene glacial periods. In these cases, both the magnitude and frequency of environmental variation were comparable between marine and high latitude (or altitude) terrestrial environments. Second, Roy and Goldberg (2007) note that evidence for Pleistocene glacial extinctions of terrestrial groups is indirect due to the lack of a well-preserved fossil record; this would also be the case for shallow-water invertebrates that inhabited the aforementioned 0 m to -120 m depth range and had restricted ranges. Thus, the true level of extirpation also is unknown for these taxa, an issue exacerbated by the prevalence of cryptic species (e.g. Bickford et al. 2007, Oliver et al. 2009) and shorter-than-assumed dispersal in marine environments. Third, Roy and Goldberg (2007) acknowledge that differences in macroevolutionary and biogeographic dynamics of terrestrial birds and marine molluscs are phylogenetically incomplete evidence that such dynamics differ in important ways between the land and the sea.

What might constitute good evidence that macroevolutionary and biogeographic dynamics do (or do not) differ between land and sea? Perhaps, studies of the following? The biotas of [a] areas in each realm whose habitats were completely destroyed or [b] areas in each realm whose habitats were modified. For example, perhaps shallow-water tropical basins and high-altitude tropical regions; the biota's of both likely shifted to greater depths or lower altitudes during glacial advance, and vice versa during glacial retreat, but did not necessarily shift many degrees of latitude or longitude near the equator (e.g. Floeter et al. 2008). Another approach would be to compare [c] taxa from each realm whose life-histories are more similar than birds and molluscs. For example, certain categories of terrestrial plants and marine animals (Palumbi 1992).

Roy and Goldberg (2007:S82) concluded that "[s]olving the problem will require using ... information and analytical methods in a consistent manner across different clades within the framework of quantitative models that include both macroevolutionary and biogeographic processes." Moreover, until such comparisons of ter-

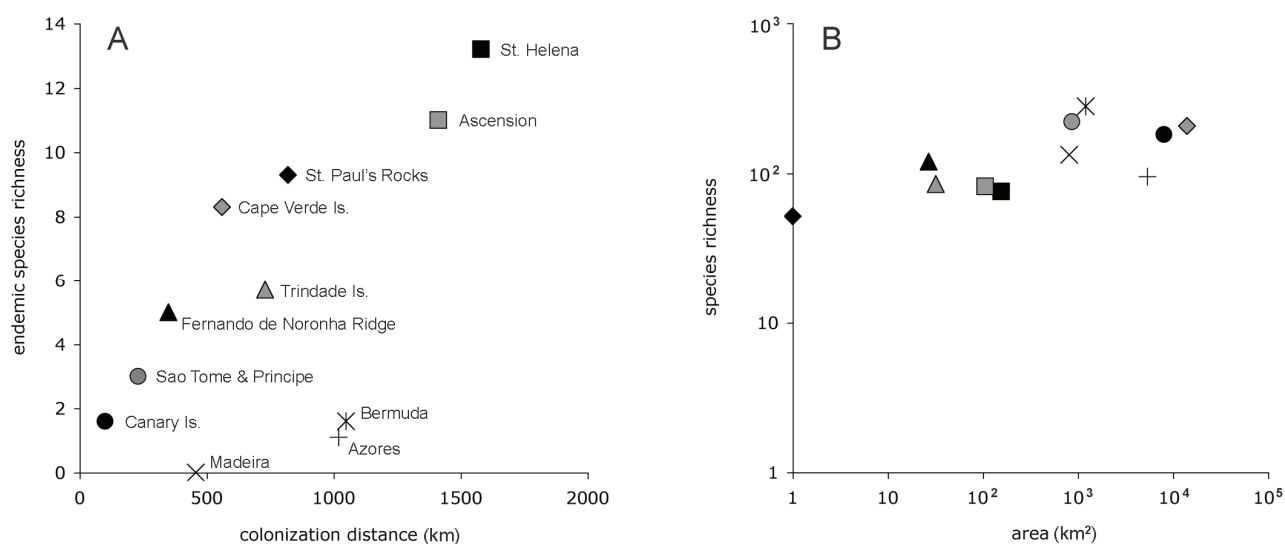


Figure 1. Spatial patterns of species diversity in Atlantic reef fishes inhabiting islands and archipelagoes (data from Floeter et al. 2008, Table 4). **(A)** The number of endemic species plotted against the colonization distance, calculated as the mean distance of an island or archipelago from the nearest mainland and nearest reef habitat. **(B)** The number of species, S , plotted as a function of island or archipelago area, A . $S = 1.755A^{0.1322}$, $R^2 = 0.5167$, $p = 0.013$. Symbols in panel B are as labelled in panel A.

restrial-like with marine-like are done, along with quantifying the biological-environmental differences that may correlate with the impact of different drivers of latitudinal patterns, it is premature to conclude that the nature of macroevolution and biogeographic processes differ between land and sea.

Island evolution (Floeter et al. 2008)

Although many zoogeographic descriptions have reported endemic marine species from oceanic islands (e.g. Randall 1998, Robertson 2001; see also Dawson and Hamner 2005) there has been a long tradition of excluding island theory (e.g. MacArthur and Wilson 1967, Rosenzweig 1995) from marine biogeography and vice versa (see Dawson and Hamner 2008)⁴. The recent phylogenetic analysis of Atlantic fishes by Floeter et al. (2008) provides additional evidence that marine species may evolve on islands and show familiar patterns of increasing endemism in more isolated locations and higher species richness where habitat availability is greater (Fig. 1). The Mid-Atlantic Ridge islands of Ascension and St. Helena, for example,

together harbour 111 reef fish species of which 29 are endemic. Atlantic reef fish species distributions, though, result from the interaction of colonization distances and routes, area (or diversity) of habitat, and island age and history (Floeter et al. 2008). Low endemism on Bermuda, the Canary islands, and other high-latitude islands is inferred to result from Pleistocene glaciation and recent colonization with little time for subsequent speciation (N.B. see discussion of processes influencing bird diversity in Roy and Goldberg [2007]). Intermediate levels of endemism at São Tomé and Príncipe, Fernando de Noronha Ridge and Trindade Island result from close proximity and/or stepping-stone connections to continental margins. High endemism on the Cape Verde islands may be related to isolation from the mainland, high habitat heterogeneity, and maintenance of warm surrounding waters during glacial maxima (Floeter et al. 2008). Exploring the underlying incidence functions may thus enable more explicit quantitative comparison with the adjacent emergent terrestrial habitat.

4. David Starr Jordan, the first President of Stanford University and arguably the father of American Ichthyology, wrote a letter to Robert Evans Snodgrass, before the Hopkins-Stanford Galapagos expedition of 1898-1899 in which he opined that "The archipelago does not appear to offer a good laboratory for researching the impact of isolation, because the barren islands do not harbor many isolated fish pools." Yet 11.7% of the 300 species of reef fishes in the Galapagos are endemic (Allen 2008).

Island ecology (Martins et al. 2008)

With recognition that marine biotas, like terrestrial biotas, of oceanic islands may show endemism, there is growing effort to explore and expand the reach of marine island ecology. Martins et al. (2008) sampled 12 taxa, distributed in the low or middle or high zones of the intertidal rocky shore using an hierarchical sample design in which quadrats were nested within zones, within sites, within islands of the Azorean archipelago. They hypothesized that high dispersal of marine taxa would result in population and community dynamics being influenced more by regional processes than by within-island processes. Indeed, larger-scale (i.e. island-scale) dynamics were evident in the lower-shore (i.e. more marine-influenced) communities, less prevalent in mid-shore communities, and statistically absent from high-shore sites. Martins et al. (2008) concluded that “along the vertical gradient of emersion, there is a trend for a decreasing influence of larger-scale processes with increasing shore height ... [which may be] the result of differences in the dispersal ability between the lower-shore, algal-dominated assemblages ... and the higher-shore, animal-dominated communities” and noted the importance of variance in the immediate environment on population dynamics. These results illustrate two points. [a] In the same way that variation in coastal terrestrial environments is ‘reddened’ by their proximity to the ocean, the reciprocal is also true; variation in marine intertidal environments is ‘whitened’ by their proximity to land. [b] Even over small distances, it is important to quantify variation in both the environment and biota when comparing sea and land. Measurements on the same scale will lead to differences (Gray et al. 2006, Webb et al. 2009) which should be ascribed to the mechanisms directly influencing those differences as opposed to simply ‘marine’ or ‘terrestrial’ categories.

Effects of species diversity on temporal stability (Jiang and Pu 2009)

As an example of the need to ascribe differences to mechanisms rather than to realm, Jiang and Pu

(2009) showed that aquatic (freshwater and marine) communities and populations generally are more temporally stable than their terrestrial counterparts. The greater stability, however, is not attributable to the physical environment – perhaps because the marine studies included small intertidal rockpools (e.g. Romanuk and Kolasa 2004) in which physical variation is whitened by atmospheric influence – but rather to the multitrophic nature of the aquatic communities versus the unithrophic terrestrial communities considered (Jiang and Pu 2009)⁵.

Microbial community assembly (Horner-Devine et al. 2007, Fuhrman 2009)

Analyses of metagenomic data describing the microbial world hint at ‘universal’ biogeographic patterns. There is growing evidence for microbial taxa-area relationships from aquatic and soil samples with ‘z-values’ (which describe the sensitivity of species richness to area [Whittaker and Fernández-Palacios 2006:81]) similar to those measured in macrobiota, and for microbial distance-decay relationships which indicate mechanisms acting with different relative strengths at different depths in the sea (Fuhrman 2009). Both results support our thought experiment. On the other hand, Fuhrman (2009) concludes that the evidence for microbial latitudinal gradients is mixed between land and sea, perhaps due to different scales of spatial environmental heterogeneity or to the small number (three) of available studies. The largest meta-analysis to date, relevant to our question, is a meta-analysis of 124 microbial datasets (Horner-Devine et al. 2007) that found a majority (56%) of studies describe non-random patterns of species occurrences suggesting assembly ‘rules’. These patterns, which may be due to competitive exclusion, filtering by habitats, or geographic speciation, are trans-realm; the measure of species segregation showed a statistically similar standardized effect size across freshwater, marine, soil, and sediment habitats.

5. Jiang & Pu (2009:657) also note that variation may be polychromatic: “natural communities may oscillate synchronously at one timescale and asynchronously at another timescale, likely a result of the operation of different mechanisms at different scales.”

Box 1. Areas in which a trans-realm perspective may advance biogeography

Reciprocal illumination may occur in several ways, of which some possible examples are provided below, including what a marine perspective may lend to global biogeography (1-3), how marine biogeography may benefit from looking more at terrestrial biogeography (4-6), and synergistic effects at their interface (7-10).

1. Dispersal. Studies of dispersal have preoccupied marine biogeographers for 30 years. Coupled biophysical models are now commonly used to explore larval dispersal (e.g. Cowen et al. 2000, 2006, Dawson et al. 2005, Galindo et al. 2006, Follows et al. 2007). A comparable initiative in atmospheric modeling of aerial (or water-borne) propagules is lacking from studies of terrestrial and freshwater taxa.

2. Cryptic speciation. Studying how cryptic species are distributed has a long history in the seas (e.g. Knowlton et al. 1993). Ten percent of metazoan morphospecies contain cryptic species (Pfenninger and Schwenk 2007) and the proportion may be much higher in marine taxa (Dawson 2004, Bickford et al. 2007, Oliver et al. 2009). Circa 55% of California coastal marine taxa have cryptic north-south phylogeographic lineages (Dawson 2001). Discovering how cryptic species are distributed phylogenetically and geographically is essential for understanding biodiversity and evolutionary mechanisms influencing biogeography and requires comprehensive biogeocoding initiatives (Cunningham 2009).

3. Life-histories. Understanding the influence of life-history, and particularly larval mode, on the ability of organisms to disperse has been a major focus of marine molecular ecology (e.g. Crisp 1978, Palumbi 1992, Bohanek 1999). Terrestrial organisms also have diverse life-histories, for example that influence successional community assembly (Whittaker and Fernández-Palacios 2006), and a full understanding of the effect of life-history on dispersal (or retention) and biogeography demands comparison of the full continuum of life-history strategies across diverse physical environments.

4. Natural selection and local adaptation. The focus of marine ecology on dispersal displaced much attention away from natural selection and local adaptation. Rich theory, and a multitude of examples, developed primarily for terrestrial taxa should be applied increasingly in marine settings.

5. Techniques. Analytical techniques emerge primarily from terrestrial studies. Application and development of analyses for marine taxa will promote better mechanistic understanding across a broader suite of environments (e.g. Roy and Goldberg 2007).

6. Island biogeography. The theory of island biogeography, and extensions thereof, have been absent from studies of marine systems for almost 40 years; their reincorporation is overdue.

7. Marine and terrestrial (and freshwater) environments interact at the coast. Many taxa live at, or cross, this margin (e.g. anadromous and catadromous organisms, mangroves, shorebirds). These taxa may tell us about differences and commonalities between freshwater, marine, and terrestrial biogeography.

8. Generation-corrected frequency spectra. Frequency spectra are presented in terms of absolute time (e.g. months, Vasseur and Yodzis 2004), but organisms' life-spans differ dramatically. Demographic and evolutionary effects of environmental variation depend on their duration relative to generation time. Frequency spectra measured in generation times will promote appropriate biophysical comparison of marine and terrestrial systems.

9. Constraints. Comparison of physically similar environments in different realms may reveal vacant niches and evolutionary constraints that influence biogeographic patterns.

10. Trans-realm comparative phylogeography. Statistical and comparative phylogeography (e.g. Knowles 2004, Hickerson et al. 2007) have become mainstays of biogeography, revealing shared biogeographic histories including glacial refugia (Maggs et al. 2008), post-glacial recolonization routes (e.g. Taberlet et al. 1998), cryptic historical filters (Riddle et al. 2000), and elucidating evolutionary mechanisms (Hickerson and Meyer 2008) within realms. Few studies have integrated across realms (but see Riginos 2005), although statistical comparative techniques would similarly enable quantitative comparisons, or contrasts, of biogeographic patterns and mechanisms among clades with shared evolutionary histories where they are co-distributed (e.g. across Pacific islands) or interdigitated (e.g. marine and terrestrial taxa in Beringia). Difficulties of mounting inter-realm biogeographic analyses are substantial, beginning with acquiring the necessary geographically large-scale and densely sampled biotic inventories, particularly from marine habitats. Maritime regions where existing marine and terrestrial phylogeographic and biogeographic studies might easily be enriched include southeast and southwest USA, Baja California, southeast Australia, and the North Atlantic (e.g. Avise 1992, O'Hara and Poore 2000, Wares & Cunningham 2002, Blanchette et al. 2008, Ayre et al. 2009, Pelc et al. 2009).

Prospective

These five studies provide a surprisingly consistent picture of the state of comparative inter-realm biogeography. Studies often make a priori divisions between marine and terrestrial environments (e.g. Horner-Devine et al. 2007, Roy and Goldberg 2007, Jiang and Pu 2009). Oftentimes, the comparisons involve multiple potential sources of variation, only some of which are ascribed to the marine and terrestrial experimental groups (e.g. Roy and Goldberg 2007). Yet, differences between the realms are not supported (e.g. Horner-Devine et al. 2007) or can be explained by trophic, biogeographic, macroevolutionary, or life-history traits that are not necessarily realm-specific (e.g. Roy and Goldberg 2007, Floeter et al. 2008, Jiang and Pu 2009). The results of our thought experiment therefore generally support the contention that “marine and terrestrial biogeography ... have a great deal in common and will provide reciprocal illumination in many respects” (Heaney and Lomolino 2009, see also Dawson and Hamner 2008; Box 1).

To achieve reciprocal illumination, we must break down the boundaries currently separating sub-disciplines of biogeography (Lomolino and Heaney 2004) practised by different people using almost entirely different scientific infrastructure (Steele 1995, Sarkar 2005; see also Stergiou and Browman 2005). When inventing derivative terms such as ‘riverscape’ and ‘seascape’ that superficially equate environments, we might also imagine a truly inclusive vocabulary that is applicable trans-realm. While supporting detailed within-realm studies as chapters in books (e.g. Lomolino and Heaney 2004), articles in journals (see footnote 1), sections in articles (e.g. Riddle et al. 2008), and symposia at conferences (e.g. the 3rd Biennial meeting of the International Biogeography Society), we should increasingly foster cross-realm multi-disciplinary treatments (e.g. Briggs 1995, Lomolino et al. 2006, Dawson and Hamner 2008; Box 1). The degree to which integration of freshwater, marine, and terrestrial biogeography gives way to their assimilation will depend on the extent to which a ‘seagrass roots’ community-up approach can align with a new or re-organized

scientific infrastructure (see Menge et al. 2009). For the first time in over 50 years, we – biogeographers, *Frontiers of Biogeography*, and the International Biogeography Society – may have the potential to cross this major frontier.

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