

# UC Merced

## Frontiers of Biogeography

### Title

research letter: Species richness, habitable volume, and species densities in freshwater, the sea, and on land

### Permalink

<https://escholarship.org/uc/item/30m4r519>

### Journal

Frontiers of Biogeography, 4(3)

### Author

Dawson, Michael N

### Publication Date

2012

### DOI

10.21425/F5FBG12675

### Copyright Information

Copyright 2012 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

# Species richness, habitable volume, and species densities in freshwater, the sea, and on land

Michael N Dawson

School of Natural Sciences, 5200 North Lake Road, University of California, Merced, CA 95343, USA  
[mdawson@ucmerced.edu](mailto:mdawson@ucmerced.edu); <http://mnd.ucmerced.edu>

**Abstract.** Approximately 0.5–2 million eukaryotic species inhabit the seas, whereas 2–10 million inhabit freshwater or the land. Much has been made of this several-fold difference in species richness but there is little consensus about the causes. Here, I ask a related question: what is the relative density of species in marine and non-marine realms? I use recent estimates of global eukaryotic species richness and published estimates of the areal coverage and depth of habitat for freshwater, marine, and terrestrial biomes. I find that the marine realm harbors ~99.83% of the habitable volume on this planet. Eukaryotic species density of the marine realm is ~3600-fold (i.e., 3–4 orders of magnitude) less than that of non-marine realms. Species–volume relationships (SVRs) help reconcile actinopterygian fish diversity with global primary productivity and emphasize the interacting roles of abiotic and biotic complexity in shaping patterns of biodiversity in freshwater, the sea, and on land. Comparing SVRs of habitats within and across realms may help resolve the factors and interactions that influence species density.

**Keywords.** biogeography, diversity, economy of nature, macroevolution, niche, productivity

## Introduction

Understanding the diversity and distribution of life on Earth has challenged biologists for centuries (e.g., Linnaeus 1758, Wallace 1880). Among the many intriguing questions is: why is species richness so much lower in the sea than on the land (e.g., Hutchinson 1959)? The ocean is more vast than the land, there are more phyla in the sea than on land, and all the phyla but one (Onychophora) have existed far longer as marine than as terrestrial taxa (May 1994). So why are there now only ~0.5–2.0 million eukaryotic species in the sea, yet ~2.0–10 million eukaryotic species on land or in freshwater (Table 1)?

My intent in this paper is not to try to answer this difficult question, nor to sort among the answers that already have been offered. At least, not directly. Rather, I wish to address a related question which common sense suggests to me is important, needs a more transparent and nuanced approach, and is of immediate interest to biogeographers but largely overlooked: what is the relative density of species in marine and non-marine (i.e. freshwater and/or terrestrial) realms? To rephrase the question in terms of a more familiar concept: what is the relative species richness

per unit of habitable volume in marine and non-marine realms?

By most estimates, there are approximately six times as many species in freshwater and on land than there are in the sea (Table 1). The magnitude of the inequality is emphasized by noting that marine habitats constitute ~71% of the Earth's surface area (e.g., May 1994). Averaged per unit area, eukaryotic species richness is approximately 14 times higher in freshwater and on land than it is in the sea. Beyond any debate surrounding estimates of species richness, this is not a contentious ratio (e.g., see May 1994, Vermeij and Grosberg 2010, Carrete Vega and Wiens 2012). In contrast, estimates of species density vary at least 30-fold, irrespective of the number of species, because published estimates of the relative habitable volume of the marine realm range from ~10 to 300 times the habitable volume of the land (Vermeij and Grosberg 2010, Helfman et al. 2009:329, and cited by Carrete Vega and Wiens 2012). Differences in relative species density, incorporating uncertainty in estimates of habitable volume and species richness, may vary ~100-fold or more between marine and non-marine realms.

The substantial uncertainty in estimates of

**Table 1.** Some recent estimates of freshwater, marine, and terrestrial species richness. The percentage of species that are marine is calculated from the numbers provided in the cases that estimates are given in 2 or more columns. The percentage of species that are marine was given in the original publication in the cases that an estimate of species richness is provided in only one column.

	Freshwater	Marine	Terrestrial	Total	Marine as % of total	Reference
<i>Eukaryotes</i>						
Predicted		>1 million		10–30 million (citing others)	3–10%	Winston (1992)
Catalogued				1.4–1.5 million	15%	May (1994)
Predicted		1.4–1.6 million			15%	Bouchet (2006)
Predicted (catalogued)		2.21 ± 0.18 million (193,756)		8.74 ± 1.30 million (1,233,500)	25% (16%)	Mora et al. (2011)
Predicted		300,000		1.8–2.0 million	15–17%	Costello et al. (2011)
Predicted (catalogued)		~0.7 million; range: 0.3–1.0 million (222,000–230,000)		~6 million	12%; 5–17%*	Appeltans et al. (in press)
<i>Some other taxa</i>						
Actinopterygian fishes	15,150	14,740	0		49%	Carrete Vega and Wiens (2012)
Gastropods	~4000	30,000	30,000	80,000–100,000	30–37%	Strong et al. (2008), <sup>1</sup> EB
Hydrozoans	40	3500	0		99%	Daly et al. (2007), Jankowski et al. (2008)

\*Appeltans et al. (in press) updates the estimate of marine diversity given by Costello et al. (2011) but did not update the estimate of total diversity; rather, they cited a global species richness estimate of ~6 million. Pimm and Raven (2000) also estimate ~15% of species are marine.

1. <http://www.britannica.com/EBchecked/topic/226777/gastropod> accessed 20 May 2012.

species density may limit our understanding of how resources are partitioned in the sea versus on land, and in freshwater. Perhaps more importantly, considering how species density compares between realms establishes the need for understanding how species density varies among habitats and among taxa within realms.

## Methods

To estimate habitable volume, I surveyed the published literature for estimates of areal coverage of biomes and the depth (height) of the habitable environment therein. Although some remotely sensed data relevant to this question are available, key datasets cover only subsets of habitat types or are in early stages of development (e.g. Lefsky 2010; Los et al. 2012). Rather than take a hybrid approach, I chose instead to use published information alone, so that this paper presents an estimate independent of remotely sensed data. The current estimate may in some years from now be corroborated, modified, or refuted by an estimate using remotely sensed data, but as the latter is unlikely to be perfect (Pfeifer et al. 2012), the difference between the two may itself be useful in suggesting the range of possible estimates. More importantly, notwithstanding some error in source estimates of areas and depths (e.g. that due to topographic complexity), the approach taken here is more explicit and detailed than for previously published estimates (Helfman et al. 2009:329, Vermeij and Grosberg 2010, and cited by Carrete Vega and Wiens 2012) so that the basis of future agreement, disagreement, or reanalysis can be clear.

I excluded the aerial and endolithic realms because of paucity of information and taxonomic focus. The aerial realm is in general poorly sampled but has no known aerial endemics; the multi-generational inhabitants are primarily microbes (Womack et al. 2010; see also Wilkinson et al. 2012) which perhaps may be conceived as highly heterogeneous 'ghost populations' (*sensu* Slatkin 2005) of a coupled terrestrial-atmospheric-aquatic biogeography. The endolithic realm is inhabited principally by archaea and eubacteria and the extent of subsurface and deep-biosphere

habitats is unclear.

The principal sources for estimates of areas are provided in Table 2. Four additional considerations explaining estimates of depth are described in the following paragraphs.

(1) Large-scale geographic variation in habitat depth was incorporated in calculations of habitat volume by recognizing 12 categories of terrestrial habitat closely allied to recognized biomes that are, in part, characterized by reference to their dominant flora (Rosswall and Heal 1975, Campbell et al. 1994:669–676, Purves et al. 1998:1204–1216).

(2) The dominant flora in any habitat generally forms a canopy above which few plants protrude far and in which there are occasional gaps (Whitmore 1990:24–28). Thus, the height of the dominant flora was used to approximate canopy height, and the canopy height was used as the proxy for habitat depth, despite the occurrence of fauna above the canopy and flora and fauna below the ground (e.g. Whitmore 1990:61–62, Risser et al. 1981:203). The justification for this is five-fold:

*i.* There are no known aerial holoplankton. All aerial organisms inevitably must land because all, even those that can feed while airborne (e.g. bats, swallows, and robber flies [Allen 1967:135]), are tied to a terrestrial existence by some part of their life-history or by physics. This is true even of microbes (Womack et al. 2010), of which the vast majority of forms found in the air are better described as (sometimes inter-generational) meroplankton.

*ii.* Tall vertebrates that inhabit short grasslands do not meaningfully exist above the canopy because their nutrition is dependent on the canopy. Moreover, these large animals generally are sufficiently rare that they do not increase by much the habitable volume that is available to their many parasites which, anyway, often have life-stages that are dependent directly upon the vegetation (e.g. Spedding 1971:74). Smaller vertebrates, such as rodents and reptiles, often exist entirely within the canopy (Risser et al. 1981:222).

*iii.* The fraction of the biota that occurs below ground generally is limited to very shallow sub-

surface layers which therefore do not contribute significantly to habitat depth. Analysis of over 200 datasets from field sites distributed globally and covering all major biomes indicates ~50% of roots are  $\leq 0.1$  m deep, and ~85% of roots are  $< 0.5$  m deep (Zeng 2001). The below-ground invertebrate fauna may be diverse and abundant, but similarly is restricted primarily to the shallowest 1–2 decimeters (e.g. Risser et al. 1981:203).

iv. The results of this analysis are reasonably insensitive to modest error in the assumptions. Altering the depth of every terrestrial habitat by 1 m would change the total terrestrial habitable volume by 7.3% and change the terrestrial contribution to global habitable volume by ~0.01%.

v. The habitable volume of marine sediments also was ignored, in part because this generally is a poorly known marine habitat and, in part, because this counterbalances to some extent the exclusion of terrestrial, below-ground, habitable volume. The analyses are reasonably insensitive to this assumption too; altering the mean depth of the ocean by one to two meters changes the marine habitable volume  $\leq 0.05\%$ .

(3) Canopy height (habitat depth) was estimated from the literature, as follows. *Grassland* included highgrass savanna, tallgrass savannah, tallgrass prairie, shortgrass prairie, desert grass savanna, and mountain grassland (Risser et al. 1981:3). Tallgrasses were estimated to reach 2.1–2.4 m tall, midgrasses 0.6–1.2 m tall, and shortgrasses  $\leq 0.4$  m high (Allen 1967:24–48).

*Desert* vegetation includes lichens, annuals, herbaceous perennials, shrubs, succulents, and trees that, if present, usually are low and patchily distributed thus rarely forming a canopy of note (Harris and Campbell 1981, Louw and Seely 1982:1, Thames and Evans 1981:7–8).

*Tundra* describes a variety of habitats ranging from the marginal Fennoscandian sub-alpine birch forest (*Betula pubescens*, 4–6 m high), through willow thicket (mostly *Salix lapponum*, 0.5–1.0 m high), eutrophic forb species such as *Alchemilla vulgaris*, *Geranium silvaticum* (sometimes above 0.30 m high), wet meadow (mostly less than 0.08 m), dry meadow (mostly less than 0.04 m), mires, and exposed lichen heath (rarely more than 0.02

m above the ground) (Berg et al. 1975:105–6, Dahl 1975, Lye 1975, Rosswall and Heal 1975). With the exception of birch forest, tundra is treeless; even in birch forest, trees occupy less than 50% of the area (Sonesson et al. 1975).

*Forests* vary with latitude and altitude. Recognized forest types include tropical lowland evergreen rain forest (canopy height = 24–36 m), tropical semi-evergreen rain forest (usually  $\leq 45$  m), montane rainforests (10m), temperate deciduous forest (20 m) (Whitmore 1990:10–36). Koike and Hotta (1996) recognized the Alpine tree limit (approximate canopy height = 10 m), sub-alpine mixed forest (18 m), cool-temperate deciduous broad-leaved forest (30 m), warm-temperate evergreen broad-leaved forest (16 m), coastal wind-swept warm-temperate evergreen broad-leaved forest (12 m), sub-tropical evergreen broad-leaved forest (18 m), and tropical rainforest (60 m). Welden et al. (1991) defined four categories of tree, in moist tropical forest, based on height: shrubs ( $< 4$  m), understory treelets (4 to  $< 10$  m), midstory trees (10 to  $< 20$  m), and canopy trees ( $\geq 20$  m). In general, these forest heights fall in the same range as those estimated more recently using lidar, including temperate conifer forest (Lefsky 2010).

(4) Inevitably, boundaries between the habitats recognized here are somewhat arbitrary. For example, mixed-grass prairie is the intergradation of true prairie and shortgrass prairie (Risser et al. 1981:14). Similarly, birch-forest tundra (Berg et al. 1975) arguably is equivalent to the Alpine tree-limit forest of Koike and Hotta (1996). Resolving these ambiguities is not in the jurisdiction of this analysis. However, these boundaries generally constitute relatively thin transition zones (e.g. Whitmore 1990:15) and, hence, are unlikely to affect significantly these calculations of habitable volume.

Finally, I note that the numbers of species and the areas of habitats change with time (e.g. Whitmore 1990:94–96; Benton 2001; Vermeij and Grosberg 2010). The numbers used here are recent estimates of extant species diversity and of available habitat. Habitat loss, extinction, extirpation from surveyed areas, and extinction debt may bias estimates of natural patterns of species

density. Calculations at the level of realm are not intended to imply anything about the shape of species–area or species–volume relationships within the realm.

## Results

The estimated total habitable volume available to freshwater organisms is 272,605 km<sup>3</sup>. The total habitable volume available to terrestrial organisms is about 2,025,315 km<sup>3</sup>. The total habitable volume available to marine organisms is approximately 1,367,000,000 km<sup>3</sup> (Table 2).

## Discussion

### *Species density*

The marine environment provides approximately 99.83% of the habitable volume on this planet. The terrestrial and freshwater environments together provide the remaining ~0.17% of the habitable volume: ~0.15% terrestrial plus ~0.02% freshwater. This estimate of the terrestrial habitable volume is close to the lower bound (0.33%; Helfman et al. 2009:329) of previously published estimates (see Carrete Vega and Wiens 2012). Thus, eukaryotic species density averaged across the marine realm is, using a ratio of 1 marine to 6 non-marine species (Table 1) in 595 times more habitable marine volume (Table 2), approximately 3600-fold less than the eukaryotic species density of terrestrial and aquatic environments. Given some uncertainty in estimates of species richness and of habitable volume, it seems reasonable to conclude that species density in marine environments is three to four orders of magnitude less than the species density in non-marine environments.

### *Causes of species density are multi-faceted*

Many explanations have been proposed for the differences in species richness of freshwater, land, and sea. For example, the marine realm may be less diverse because it has lower net primary productivity, smaller primary producers (which do not provide cover, and are predated rather than browsed or grazed), less-complex habitats, fewer coevolutionary radiations (particularly no equivalent of angiosperms and insects), slower rates of

evolution, larger population sizes, and less-effective barriers to dispersal, as well as species with less ecological specialization and larger geographical range sizes (Day 1963, Smetacek and Pollehne 1986, Palumbi, 1992, 1994, Angel 1993, May 1994, Benton 2001, Carr et al. 2003, Jablonski and Roy 2003, Vermeij and Grosberg 2010, Costello et al. 2011, Webb et al. 2011, Carrete Vega and Wiens 2012; see also Hamner 1995). However, little resolution has been achieved, in part because this is a challenging problem, the appropriate comparative framework is still developing, and there may be no single answer.

The species richness of marine and terrestrial environments often has been contextualized using area (e.g., Angel 1993, May 1994, Carrete Vega and Wiens 2012) reflecting the descriptive power of terrestrial species–area relationships (SARs; MacArthur and Wilson 1967, Triantis et al. 2012). SARs also may describe patterns in marine biodiversity (e.g., Schopf et al. 1977, Dawson and Hamner 2005, Sandin et al. 2008, Dawson 2009). However, simple binary comparison of marine and terrestrial systems inverts the SAR (May 1994) suggesting that area is a reasonable proxy for the mechanisms that cause diversity differences between locations within the terrestrial realm, whereas the approximation breaks down when also considering the sea (and vice versa). The same may be true of comparisons between an island and a smaller area of mainland, or between an ocean gyre and a smaller area of the sea-floor. Deviations from the SAR, like variations on the SAR itself, must indicate something about variation in the underlying processes (Triantis et al. 2012).

Mechanistic explanations for differences in freshwater, marine, and terrestrial diversity therefore should be sought within a diverse and integrated framework. Such a framework should include, at least, functions of species adaptations and between-species interactions, which are the purview of niche theory, and their rates of dispersal, speciation, and extinction, which are in the realm of island biogeography theory (Hortal et al. 2009). The dimensions of the environment also may be important. For example, the similar spe-

**Table 2.** Habitable volume of aquatic, marine, and terrestrial environments.

Habitat	% Earth's surface <sup>a</sup>	Canopy height or depth (m) <sup>b</sup>	Habitable volume (km <sup>3</sup> )
<i>Freshwater</i>			
Freshwater (swamps, lakes, etc.)	0.8	67 <sup>d</sup>	272,605
		Sub-total	<u>0.3 x 10<sup>6</sup></u>
<i>Marine</i>			
Deep ocean basin	29.8	3,700–5,500	
Ocean ridges	22.1	~3,500–5,500	
Island arcs, trenches, hills, etc.	3.7	3,000–6,000	
Continental shelf	7.4	75 (mean)	
Continental rise and slope	7.8	~150–4,000	
	mean depth	3,796 <sup>e</sup>	1,367x10 <sup>6</sup>
		Sub-total	<u>1,367 x 10<sup>6</sup></u>
<i>Terrestrial</i>			
Extreme desert, rock, sand, and ice	4.7	0.1	2,390
Desert and semi-desert	3.5	0.5	8,900
Tropical rainforest	3.3	60	1,007,011
Savanna	2.9	2	29,498
Cultivated land	2.7	4 <sup>c</sup>	54,928
Boreal forest (Taiga)	2.4	15	183,093
Temperate grassland	1.8	1.5	13,732
Woodland and shrubs	1.7	7	60,522
Tundra	1.6	0.5	4,069
Tropical seasonal forest	1.5	45	343,299
Temperate deciduous forest	1.3	25	165,295
Temperate evergreen forest	1.0	30	152,578
		Sub-total	<u>2.0 x 10<sup>6</sup></u>
		<b>Total</b>	<u><b>1,369 x 10<sup>6</sup></b></u>

<sup>a</sup>Purves et al. (1998:1117, 1207–1216); <sup>b</sup>additional sources, Campbell et al. (1994:670–676), Whitmore (1990:10–36), Raven and Johnson (1992:518–528). <sup>c</sup>estimated as intermediate between midgrass and treelets. <sup>d</sup>Aquatic environments occupy approximately 0.02% of the volume occupied by marine environments (Garrison, 1996:4–6, 2010:4); freshwater as a percentage of marine volume estimated by Gleick (1996)<sup>2</sup> is ~0.01%. <sup>e</sup>Angel (1993), Garrison (1996:4–6, 2010:5) gives ocean volume as 1,370 million km<sup>3</sup>. Surface area of Earth = 5.086x10<sup>8</sup> km<sup>2</sup>, areas of marine environments from Garrison (1996:6, 91–121, 2010:110).

2. <http://ga.water.usgs.gov/edu/waterdistribution.html> accessed 20 May 2012.

cies richness of freshwater and marine actinopterygians (Table 1) has been used to discount primary productivity, which is two orders of magnitude lower in freshwater than in the sea, as an explanation for why there are relatively so few fish in the sea per unit area (Carrete Vega and Wiens 2012). Instead, Carrete Vega and Wiens (2012) favored greater dispersal distances of marine taxa and less physical structure in the seas as providing fewer opportunities for speciation, a long-standing hypothesis (e.g., Palumbi 1992, 1994), although dispersal distances show considerable overlap for freshwater, marine and terrestrial taxa (Kinlan and Gaines 2003, Dawson and Hamner 2008). A more nuanced perspective suggests that, in fact, differences in productivity may play a role. Primary productivity in freshwater systems (0.4 PgC/year, Amthor et al. 1998) subsidized by up to 20% (Lennon 2004, but see Bianchi 2011) of terrestrial productivity (54.5 PgC yr<sup>-1</sup>, Nemani et al. 2003) is approximately one-fifth (i.e. 11.3 PgC yr<sup>-1</sup>) that of marine systems globally (56.4 PgC yr<sup>-1</sup>, Field et al. 1998 [of which ~6–11 PgC yr<sup>-1</sup> is coastal, see Falkowski et al. 1998]). Per unit of habitable volume, available primary productivity is ~1000-fold higher in freshwater than in the sea. Per unit of habitable volume, actinopterygian species density is, in fact, quite similar: ~5000-fold higher in freshwater than in the sea. Thus, differences in productivity—coupled with differences in environmental heterogeneity, habitat complexity, dispersal ability, energetics, rarity and numerous other factors sufficient to generate the remaining five-fold or more opportunities for speciation in freshwater—could explain gross modern differences in actinopterygian species richness between freshwater and the sea. While dispersal ability and the structure of the physical environment probably are relevant (Carrete Vega and Wiens 2012, and many others), the evidence suggests that productivity and other factors are important too (e.g. Vermeij and Grosberg 2010). For example, the costs of moving in different environments (Vermeij & Grosberg 2010) must interact with the distribution and density of resources with consequences for the extent and magnitude of the com-

munity economy (e.g. Polis et al. 1997), its efficiency, and thus species density.

Differences in species density within and among other freshwater, marine and terrestrial taxa also must have multiple causes, the strengths and interactions of which appear to differ from those affecting actinopterygian fish diversity. For example, the ratio of gastropod species richness in freshwater, the sea, and on land is ~4:30:30, close to the respective ratios for primary productivity 11:56:44 (including the aforementioned subsidy) and habitable areas ~1:70:29 (only ~0.1% of gastropods are pelagic, so this ratio also approximates differences in habitable volume for reproductive populations of gastropods). Another example, the high diversity of marine hydrozoans, with catalogued species richness for freshwater:marine:land of ~40:3500:0 (Table 1) could indicate a large effect of habitable volume (freshwater:marine:land = 1:5015:7) mitigated somewhat by primary productivity (11:56:44), but consideration of their biology suggests that functional constraints likely play an important role. Thus, approaches that explore geographical extent and ecological dimensions may improve statistical fits with patterns of, and increase knowledge about causes of, variation in species richness (e.g. Triantis et al. 2003), including deviations from simple correlation with area or evolutionary time (Rabosky et al. 2012; Table 3).

The question of what causes the observed differences in species density among realms is a coarse version of a more familiar complementary enquiry: what causes differences in species density among locations within (and across) marine and non-marine realms? Integrating these levels has many merits, for example, increasing the number and diversity of samples, enabling comparisons to be chosen to study particular properties, and increasing power to resolve factors and interactions that may affect species diversity (Polis et al. 1997). Whereas there are three recognized realms, there are 26 ecoregions (7 freshwater, 5 marine, 14 terrestrial), 238 major habitat types (53 freshwater, 43 marine, 142 terrestrial)<sup>3</sup>, and thousands of ‘islands’—terrestrial, freshwater,

3. [http://wwf.panda.org/about\\_our\\_earth/ecoregions/about/habitat\\_types/](http://wwf.panda.org/about_our_earth/ecoregions/about/habitat_types/) accessed 08 September 2012.



**Table 3.** A summary of some biodiversity and physical characteristics of freshwater, marine, and terrestrial environments, and their comparison. Estimates of area and volume from Table 2. Estimates of species richness from Table 1. Number (#) of ecoregions and major habitats from WWF (see footnote 2).  $K = \text{choros}$  (see Triantis et al. 2003).

	Freshwater	Terrestrial	Marine	Ratio: non-marine/ marine
Area (km <sup>2</sup> )	4.07 * 10 <sup>6</sup>	144.44 * 10 <sup>6</sup>	360.10 * 10 <sup>6</sup>	0.412
Volume (km <sup>3</sup> )	0.27 * 10 <sup>6</sup>	2.0 * 10 <sup>6</sup>	1,400 * 10 <sup>6</sup>	0.0017
# ecoregions	7	14	5	4.2
# major habitats	53	142	43	4.53
$K_{\text{ecoregions}}$	28 * 10 <sup>6</sup>	2,022 * 10 <sup>6</sup>	1,800 * 10 <sup>6</sup>	1.14
$K_{\text{habitats}}$	216 * 10 <sup>6</sup>	20,511 * 10 <sup>6</sup>	15,484 * 10 <sup>6</sup>	1.34
Species richness	~6–8.7 * 10 <sup>6</sup>		~0.7–2.2 * 10 <sup>6</sup>	3.9–8.6 (mean 6.25)
Species density (species.km <sup>-3</sup> )	~2.61–3.79		~0.0005–0.0016	2,342–5,099 (mean 3,720) i.e. ~10 <sup>3</sup> –10 <sup>4</sup>

and marine—to be compared. The paucity of pelagic marine gastropod species relative to benthic environments is a pattern that also characterizes annelids (Halanych et al. 2007), cnidarians (Daly et al. 2007), foraminifera<sup>4</sup>, microbes (Zinger et al. 2011), and many other marine taxa; it is a pattern paralleled in freshwater lakes (Vander Zanden et al. 2011) and which reaches an extreme when comparing air versus the ground (e.g. Womack et al. 2010, Wilkinson et al. 2012). What is it about benthic habitats, which are smaller than pelagic habitats, that raises or maintains diversity (or, conversely, what is it that inhibits or depletes pelagic diversity)? The open ocean is often likened to a desert, whereas coral reefs surrounded by the ocean are thought of as the rainforests of the sea<sup>5</sup>, although kelp forests are perhaps structurally more similar. By comparing marine and non-marine organisms in environmentally similar settings, and quantifying environmentally dissimilar settings within and among realms (Dawson & Hamner 2008), we might hope to better understand differences in species density.

#### *Improving and using species density estimates*

Estimates of species richness and habitable volume of freshwater, marine, and terrestrial realms remain imprecise, but converging estimates of global species diversity (Table 1) and habitat volume (Helfman et al. 2009, this study) suggest estimates of absolute species densities have a maximum error of several-fold and estimates of relative species densities are accurate to within a few percentage points. While a complete inventory of species richness will take decades or centuries to complete (Bouchet 2006, Costello et al. 2011, Mora et al. 2011, Appeltans et al. in press), improved estimates of habitable volume and physical complexity of terrestrial habitats are tantalizingly close (e.g., Lefsky 2010, Los et al. 2012). Data describing the densities of other attributes, such as the abundance, ecology, energetics, functional biology, and life-history of organisms may provide some of the most important information, but are in shortest supply (e.g. Jetz et al. 2012) and also are among the most difficult to collect.

It is important to recognize that many terrestrial SARs likely provide implicit support for species–volume relationships (SVRs) because terrestrial habitat depth is small relative to areas

4. <http://www.ucmp.berkeley.edu/fosrec/Wetmore.html> accessed 08 September 2012.

5. <http://news.sciencemag.org/sciencenow/2008/01/25-01.html> accessed 08 September 2012.

studied, so areas approximate volumes. Yet SVRs are under-researched and for simplicity often ignored (Scheiner et al. 2011) even though area is commonly acknowledged to be a proxy for habitat diversity and ecological or evolutionary processes (e.g., Hortal et al. 2009, Triantis et al. 2012; see also Sfenthourakis and Panitsa 2012, but see Triantis et al. 2003). This is an oversight because segregation by depth of habitat is known to enhance diversity (e.g. Losos 2009:340; see also e.g. Brusca and Brusca 2003:506), which may be multiplied through species interactions (e.g., Castro and Huber 2003:268, Novotny et al. 2006). To the extent that habitat is engineered by some organisms, and used and modified by others, there seems to be no obvious evolutionary limit to species richness, or density (Vermeij and Grosberg 2010, see also Emerson and Kolm 2005, Hortal et al. 2009).

Important characteristics of environments and organisms do not sort by realm (Palumbi 1992, Dawson and Hamner 2008, Pawar et al. 2012, Webb 2012) nor necessarily by taxon (Webb et al. 2011) and vary from place to place (Dawson 2009, Vermeij and Grosberg 2010) and through time (Benton 2001, Vermeij and Grosberg 2010, Rabosky et al. 2012). Resolving the relative contributions of factors that do cause differences in species density within and among realms will require carefully designed comparisons (Dawson and Hamner 2008) that take a nuanced perspective of ecological and evolutionary interactions between abiotic and biotic components of ecosystems (Vermeij and Grosberg 2010).

### Acknowledgements

Allen Collins and Peter Schuchert kindly provided guidance on estimates of freshwater and total hydrozoan species richness. Qinghua Guo engaged me in many stimulating discussions about estimating habitable volume. Kostas Triantis, an anonymous reviewer, and Willem Renema provided thoughtful comments that helped improve the manuscript.

### References

- Allen, D.W. (1967) *The life of prairies and plains*. McGraw-Hill, New York.
- Amthor, J.S. and members of the Ecosystems Working Group. (1998) *Terrestrial ecosystem responses to global change: a research strategy*. ORNL Technical Memorandum 1998/27, 37 pp. Oak Ridge National Laboratory, Oak Ridge, TN.
- Angel, M.V. (1993) Biodiversity of the pelagic ocean. *Conservation Biology*, 7, 760–772.
- Appeltans, W., Vanhoorne, B., Decock, W. et al. (in press) The magnitude of global marine species diversity. *Current Biology*.
- Benton, M.J. (2001) Biodiversity on land and in the sea. *Geological Journal*, 36, 211–230.
- Berg, A., Kjølvik, S. & Wielgolaski, F.E. (1975) Measurement of leaf areas and leaf angles of plants at Hardangervidda, Norway. In: *Fennoscandian tundra ecosystems I: plants and microorganisms*, Ecological Studies 16 (ed. by F.E. Wielgolaski), pp. 103–110. Springer-Verlag, New York, NY.
- Bianchi, T.S. (2011) The role of terrestrially derived organic carbon in the coastal ocean: a changing paradigm and the priming effect. *Proceedings of the National Academy of Sciences of the USA*, 108, 19473–19481.
- Bouchet, P. (2006). The magnitude of marine biodiversity. In: *The exploration of marine biodiversity: scientific and technological challenges* (ed. By C.M. Duarte), pp. 31–62. Fundación BBVA, Madrid.
- Brusca, R.C. & Brusca, G.J. (2003) *Invertebrates*, 2<sup>nd</sup> edition. Sinauer, Sunderland, MA.
- Campbell, N.A., Mitchell, L.G. & Reece, J.B. (1994) *Biology: concepts and connections*. Benjamin/Cummings, Redwood City, CA.
- Carr, M.H., Neigel, J.E., Estes, J.A., Andleman, S., Warner, R.R. & Largier, J.L. (2003) Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecological Applications*, 13, S90–S107.
- Carrete Vega, G. & Wiens, J.J. (2012) Why are there so few fish in the sea? *Proceedings of the Royal Society B*, doi: 10.1098/rspb.2012.0075
- Castro, P. & Huber, M.E. (2003) *Marine biology*, 4<sup>th</sup> edition. McGraw-Hill, New York, NY.
- Costello, M.J., Wilson, S. & Houlding, B. (2011) Predicting total global species richness using rates of species description and estimates of taxonomic effort. *Systematic Biology*, doi:10.1093/sysbio/syr080
- Dahl, E. (1975) Flora and plant sociology in Fennoscandian tundra areas. In: *Fennoscandian tundra ecosystems I: plants and microorganisms*, Ecological Studies 16 (ed. by F.E. Wielgolaski), pp.

- 62–67. Springer–Verlag, New York, NY.
- Daly, M., Brugler, M.R., Cartwright, P. et al. (2007) The phylum Cnidaria: a review of phylogenetic patterns and diversity 300 years after Linnaeus. *Zootaxa*, 1668, 127–182.
- Dawson, M.N. (2009) Trans-realm biogeography: an immergent interface. *Frontiers of Biogeography*, 1, 62–70.
- Dawson, M.N. & Hamner, W.M. (2005) Rapid evolutionary radiation of marine zooplankton in peripheral environments. *Proceedings of the National Academy of Sciences of the USA*, 102, 9235–9240.
- Dawson, M.N. & Hamner, W.M. (2008) A biophysical perspective on dispersal and the geography of evolution in marine and terrestrial systems. *Journal of the Royal Society – Interface*, 5, 135–150.
- Day, J.H. (1963) The complexity of the biotic environment. In: *Speciation in the Sea*, Systematics Association Publication No. 5 (ed. by J.P. Harding & N. Tebble), pp. 31–49. Systematics Association, London.
- Emerson, B.C. & Kolm, N. (2005) Species diversity can drive speciation. *Nature*, 434, 1015–1017.
- Falkowski, P.G., Barber, R.T. & Smetacek, V. (1998). Biogeochemical controls and feedbacks on ocean primary production. *Science*, 281, 200–206.
- Field, C.B., Behrenfeld, M.J., Randerson, J.T. & Falkowski, P. (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, 281, 237–240.
- Garrison, T. (1996) *Oceanography – an invitation to marine science*, 2<sup>nd</sup> edition. Wadsworth, Belmont, CA
- Garrison, T. (2010) *Oceanography – an invitation to marine science*, 7<sup>th</sup> edition. Brooks/Cole, Belmont, CA.
- Gleick, P.H. (1996) Water resources, volume 2. In: *Encyclopedia of Climate and Weather* (ed. by S.H. Schneider), pp. 817–823. Oxford University Press, New York, NY.
- Halanych, K.M., Cox, L.N. & Struck, T.H. (2007) A brief review of holopelagic annelids. *Integrative and Comparative Biology*, 47, 872–879.
- Hamner, W.M. (1995) Predation, cover, and convergent evolution in epipelagic oceans. *Marine and Freshwater Behaviour and Physiology*, 26, 71–89.
- Harris, G.A. & Campbell, G.S. (1981) Morphological and physiological characteristics of desert plants. In: *Water in desert ecosystems*, US/IBP Synthesis Series 11 (ed. by D.D. Evans & J.L. Thames), pp. 1–12. Dowden, Hutchinson, and Ross, Stroudsburg, PA.
- Helfman, G.S., Collette, B.B., Facey, D.E. & Bowen, B.W. (2009) *The diversity of fishes: biology, evolution, and ecology*, 2<sup>nd</sup> edition. Wiley–Blackwell, Sunderland, MA.
- Hortal, J., Triantis, K.A., Meiri, S., Thébault, E. & Sfenthourakis, S. (2009) Island species richness increases with habitat diversity. *American Naturalist*, 174, E205–E217.
- Hutchinson, G.E. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist*, 93, 145–159.
- Jablonski, D. & Roy, K. (2003) Geographical range and speciation in fossil and living mollusks. *Proceedings of the Royal Society of London B*, 270, 401–406.
- Jankowski, T., Collins, A.G. & Campbell, R. (2008) Global diversity of inland water cnidarians. *Hydrobiologia*, 595, 35–40.
- Jetz, W., McPherson, J.M. & Guralnick, R.P. (2012) Integrating biodiversity distribution knowledge: toward a global map of life. *Trends in Ecology and Evolution*, 27, 151–159.
- Kinlan, B.P. & Gaines, S.D. (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology*, 84, 2007–2020.
- Koike, F. & Hotta, M. (1996) Foliage canopy structure and height distribution of woody species in climax forests. *Journal of Plant Research*, 109, 53–60.
- Lefsky, M.A. (2010) A global forest canopy height map from the Moderate Resolution Imaging Spectroradiometer and the Geoscience Laser Altimeter System. *Geophysical Research Letters*, 37, L15401, doi:10.1029/2010GL043622.
- Lennon, J.T. (2004) Experimental evidence that terrestrial carbon subsidies increase CO<sub>2</sub> flux from lake ecosystems. *Oecologia*, 138, 584–591.
- Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. Holmiae, Laurentii Salvii.
- Los, S.O., Rosette, J.A.B., Kljun, N. et al. (2012) Vegetation height and cover fraction between 60°S and 60°N from ICESat GLAS data. *Geoscientific Model Development*, 5, 413–432.
- Losos, J.B. (2009) *Lizards in an evolutionary tree – ecology and adaptive radiation of anoles*. University of California Press, Berkeley, CA.
- Louw, G.N. & Seely, M.K. (1982) *Ecology of desert organisms*. Longman, London.
- Lye, K.A. (1975) Survey of the main plant communities on Hardangervidda. In: *Fennoscandian tundra ecosystems I: plants and microorganisms*, Ecological Studies 16 (ed. by F.E. Wielgolaski), pp. 68–73. Springer–Verlag, New York, NY.

- MacArthur, R.H. & Wilson, E.O. (1967) The theory of island biogeography. Princeton, Princeton University Press, NJ.
- May, R.M. (1994) Biological diversity: differences between land and sea. *Philosophical Transactions of the Royal Society of London B*, 343, 105–111.
- Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. & Worm, B. (2011) How many species are there on Earth and in the ocean? *PLoS Biology*, 9, e1001127. doi:10.1371/journal.pbio.1001127
- Nemani, R.R., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J., Myneni, R.B. & Running, S.W. (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science*, 300, 1560–1563.
- Novotny, V., Drozd, P., Miller, S.E., Kulfan, M., Janda, M., Basset, Y. & Weiblen, G.D. (2006). Why are there so many species of herbivorous insects in tropical rainforests? *Science*, 313, 1115–1118.
- Palumbi, S.R. (1992) Marine speciation on a small planet. *Trends in Ecology and Evolution*, 7, 114–118.
- Palumbi, S.R. (1994) Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics*, 25, 547–572.
- Pawar, S., Dell, A.I. & Savage, V.M. (2012) Dimensionality of consumer search space drives trophic interaction strengths. *Nature*, doi:10.1038/nature11131.
- Pfeifer, M., Disney, M., Quaife, T. & Marchant, R. (2012) Terrestrial ecosystems from space: a review of earth observation products for macroecology applications. *Global Ecology and Biogeography*, 21, 603–624.
- Pimm, S.L. & P. Raven (2000). Extinction by numbers. *Nature*, 403, 843–845.
- Polis, G.A., Anderson, W.B. & Holt, R.D. (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, 28, 289–316.
- Purves, W.K., Orians, G.H., Heller, H.C. & Sadava, D. (1998) *Life: the science of biology*, 5<sup>th</sup> edition. Sinauer Associates/W.H. Freeman, Sunderland, MA / Salt Lake City, UT.
- Rabosky, D.L., Slater, G.J. & Alfaro, M.E. (2012) Clade age and species richness are decoupled across the eukaryotic tree of life. *PLoS Biol* 10(8): e1001381. doi:10.1371/journal.pbio.1001381
- Raven, P.H. & Johnson, G.B. (1992) *Biology*. Mosby Year Book, St. Louis, MO.
- Risser, P.G., Birney, E.C., Blocker, H.D., May, S.W., Parton, W.J. & Wiens, J.A. (1981) The true prairie ecosystem. *US/IBP synthesis series 16*. Hutchinson Ross, Stroudsburg, PA.
- Rosswall, T. & Heal, O.W. (1975). The IBP tundra biome – an introduction. In: *Structure and function of tundra ecosystems*, *Ecological Bulletins 20* (ed. by T. Rosswall & O.W. Heal), pp. 7–16. Swedish Natural Science Research Council, Stockholm.
- Sandin, S.A., Vermeij, M.J.A. & Hurlbert, A.H. (2008) Island biogeography of Caribbean coral reef fish. *Global Ecology and Biogeography*, 17, 770–777.
- Scheiner, S.M., Chiarucci, A., Fox, G.A., Helmus, M.R., McGlenn, D.J. & Willig, M.R. (2011) The underpinnings of the relationship of species richness with space and time. *Ecological Monographs*, 81, 195–213.
- Schopf, T.J.M., Fisher, J.B. & Smith, C.A.F. Jr (1977) Is the marine latitudinal diversity gradient merely another example of the species–area curve? In: *Marine organisms, genetics, ecology, and evolution* (ed. by B. Battaglia & J.A. Beardmore), pp. 365–386. Plenum, New York, NY.
- Sfenthourakis, S. & Pantis, M. (2012) From plots to islands: species diversity at different scales. *Journal of Biogeography*, 39, 750–759.
- Slatkin, M. (2005) Seeing ghosts: the effect of unsampled populations on migration rates estimated for sampled populations. *Molecular Ecology*, 14, 67–73.
- Smetacek, V. & Pollehne, F. (1986) Nutrient cycling in pelagic systems: a reappraisal of the conceptual framework. *Ophelia*, 26, 401–428.
- Sonesson, M., Wielgolaski, F.E. & Kallio, P. (1975). Description of Fennoscandian tundra ecosystems. In: *Fennoscandian tundra ecosystems I: plants and microorganisms*, *Ecological Studies 16* (ed. by F.E. Wielgolaski), pp. 3–28. Springer-Verlag, New York, NY.
- Spedding, C.R.W. (1971). *Grassland ecology*. Clarendon Press, Oxford.
- Strong E.E., Gargominy, O., Ponder, W.F. & Bouchet, P. (2008). Global diversity of gastropods (Gastropoda; Mollusca) in freshwater. *Hydrobiologia*, 595, 149–166.
- Thames, J.L. & Evans, D.D. (1981). Desert systems: an overview. In: *Water in desert ecosystems*, *US/IBP Synthesis Series 11* (ed. by D.D. Evans & J.L. Thames), pp. 1–12. Dowden, Hutchinson, and Ross, Stroudsburg, PA.
- Triantis, K.A., Mylonas, M., Lika, K. & Vardinoyannis, K. (2003) A model for the species–area–habitat relationship. *Journal of Biogeography*, 30, 19–27.
- Triantis, K.A., Guilhaumon, F. & Whittaker, R.J. (2012) The island species–area relationship: biology and statistics. *Journal of Biogeography*, 39, 215–231.

- Vander Zanden, M.J., Vadeboncoeur, Y. & Chandra, S. (2011) Fish reliance on littoral-benthic resources and the distribution of primary production in lakes. *Ecosystems*, 14, 894–903.
- Vermeij, G. & Grosberg, R.K. (2010) The Great Divergence: when did diversity on land exceed that in the sea? *Integrative and Comparative Biology*, 50, 675–682.
- Wallace, A.R. (1880) *Island life; or, the phenomena and causes of insular faunas and floras, including a revision and attempted solution of the problem of geological climates*. Macmillan & Company, London.
- Webb, T.J. (2012) Marine and terrestrial ecology: unifying concepts, revealing differences. *Trends in Ecology and Evolution*, 27, 535–541.
- Webb, T.J., Dulvy, N.K., Jennings, S. & Polunin, N.V.C. (2011) The birds and the seas: body size reconciles differences in the abundance–occupancy relationship across marine and terrestrial vertebrates. *Oikos*, 120, 537–549.
- Welden, C.W., Hewett, S.W., Hubbell, S.P. & Foster, R.B. (1991) Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology*, 72, 35–50.
- Whitmore, T.C. (1990) *An introduction to tropical rainforests*. Clarendon Press, Oxford.
- Wilkinson, D.M., Koumoutsaris, S., Mitchell, E.A.D. & Bey, I. (2012) Modelling the effect of size on the aerial dispersal of microorganisms. *Journal of Biogeography*, 39, 89–97.
- Winston, J.E. (1992) Systematics and marine conservation. In: *Systematics, ecology and the biodiversity crisis* (ed. by N. Eldredge), pp. 144–168. Columbia University Press, New York, NY.
- Womack, A.M., Bohannon, B.J.M. & Green, J.L. (2010) Biodiversity and biogeography of the atmosphere. *Philosophical Transactions of the Royal Society B*, 365, 3645–3653.
- Zeng, X. (2001) Global vegetation root distribution for land modeling. *Journal of Hydrometeorology*, 2, 525–530.
- Zinger, L., Amaral-Zettler, L.A., Fuhrman, J.A., Horner-Devine, M.C., Huse, S.M., Welch, D.B.M., Martiny, J.B.H., Sogin, M., Boetius, A. & Ramette, A. (2011) Global patterns of bacterial beta-diversity in seafloor and seawater ecosystems. *PLoS ONE* 6, e24570. doi:10.1371/journal.pone.0024570

Edited by Willem Renema