SYMPOSIUM

The Great Divergence: When Did Diversity on Land Exceed That in the Sea?

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Synopsis Between 85% and 95% of all living macroscopic species are found on land; the rest are mainly marine. We argue that the extraordinary diversity on land is geologically recent, dating from the mid-Cretaceous period, ~110 million years ago. We suggest that the ability and necessity to be rare—that is, to maintain populations at low density—are made possible by the low cost of mobility of consumers on land, and that rarity is critical to the attainment of high-terrestrial diversity. Increasing productivity beginning in the mid-Cretaceous led to an increase in the survival of populations at low density and to an increase in the intensity of selection for that ability as well as for high mobility and habitat specialization. The pre-eminence of terrestrial, as compared to marine, diversity is therefore an historical phenomenon that is best explained by selection-related changes in mobility, dispersibility, and the evolution of partnerships.

In the history of the human economy, the dominance of Europe and North America in terms of wealth and innovation is a very recent phenomenon, dating back to the beginning of the 19th century according to Pomeranz (2000), or perhaps to the age of discovery in the 15th century according to others (Vermeij 2004). Whichever time of origin is correct, there was a great and recent divergence among the economies of the world. Using the same title as Pomeranz did for his landmark book, we explore a similar great divergence in the history of biotic diversity.

It has long been known that there are far more species living on land than in the sea. Although the oceans cover a little >70% of Earth's surface, they account for only a small fraction of nonmicrobial species, estimated at anywhere from 5% (Benton 2009) to 15% (May 1994). Most of the remaining species reside on land. Much of this difference has been attributed to plants, but it is among animals and fungi where the contrast is most marked.

There are ~300,000 living species of land plants compared to ~10,000 red, green, and brown algae and perhaps another 2000 photosymbiotic animals including corals, sponges, and tunicates (Mishler 2000; Draisma et al. 2001; Magallón and Sanderson 2001; Schneider et al., 2004). This 25:1 ratio in favor of macroscopic primary producers on land corresponds to a 1:61.5 ratio (2×10^6 km^2 versus 123×10^6 km^2) for the area available to attached photosynthesizing organisms (data from Likens 1975; Smith 1981). If we include single-celled photosynthesizers, we would add approximately 30,000–40,000 marine species, giving a terrestrial to marine species ratio of very roughly 6:1 and an areal ratio of 0.41:1. Unlike primary producers, which inhabit only the photic zone, macroscopic consumers live throughout the biosphere. Because the ocean has a mean depth of 4 km whereas the terrestrial realm is not >1 km in vertical dimension, the volume of the terrestrial biosphere is only ~1/10 that of the oceanic one; yet the ratio of terrestrial to marine

macroscopic consumer species is on the order of 10 : 1 (also see Dawson and Hamner 2008).

Surprisingly few studies have examined the causes of these striking differences. Speculation has centered on four inter-related factors: (1) the higher per-area net primary productivity on land (May 1994), where vegetation on 29% of Earth's surface fixes about the same amount of biomass available to consumers as do all marine primary producers on 71% of Earth's surface (Field et al. 1997); (2) the generally much narrower specialization of species on land, especially terrestrial plants and the pathogens, parasites, herbivores, dispersers, and gamete vectors associated with them (Hay and Fenical 1988; Hay and Steinberg 1992; May 1994); (3) more effective barriers to dispersal, and therefore the greater opportunities for isolation and speciation, on land (May 1994; but contradicted by Paulay and Meyer 2002; Dawson and Hamner 2008); and (4) the greater 3D complexity of terrestrial ecosystems, and the corresponding diversity of ''niche space'' (May 1994; Briggs 1995). All of these possibilities are ultimately derived from the physical contrasts between the medium of air for life on land and the medium of water for life in the sea (Strathmann 1990; Denny 1993).

Closer inspection of the patterns of diversity shows, however, that the physical and chemical properties of air and water are insufficient by themselves to account for the observed disparity in biodiversity. Not only are some polar terrestrial ecosystems less diverse than their adjacent marine counterparts (Barnes et al. 2009), but fresh-water systems, perhaps with the exceptions of cichlid fish in African rift lakes and fish diversity in the Amazon basin (Roberts 1972), rarely match the wealth of species found in climatically comparable marine habitats. Furthermore, a time traveler to the pre-Devonian realm, >410 million years ago, would have concluded unhesitatingly that macroscopic life in the ocean was far more diverse than that on land. Accordingly, the generally high-modern diversity on land is not only a geologically recent phenomenon, but it is one that hugely amplifies or modifies whatever intrinsic effects the medium of water or air might have in supporting life.

Most of the extraordinary diversity on land is due to insects, flowering plants, and fungi, groups with notably few species in the sea. However, one would be mistaken to argue that terrestrial diversity exceeds that in the sea because there are so few flowering plants, insects, and fungi in marine environments. Their marine equivalents—seaweeds, crustaceans, molluscs, nematodes—could, in principle, be just as diverse. The absence of pollinating animals and animal-pollinated plants in the sea likewise is not an explanation for lower marine diversity. This absence is a symptom, not a cause, and must itself be included in any explanation for the enormous contrast in diversity between land and sea.

We propose that (1) the terrestrial domination of diversity today is especially evident in warm regions, and came about only during the past 100 million years, or so; (2) the ability and necessity of most species to be rare—that is, to sustain populations at low density—is critical to the attainment and maintenance of exceptionally high diversity on land; and (3) both persistence of populations at low density and intense individual selection for that ability, imposed by specialized consumers, have increased, particularly in the productive terrestrial tropics.

As discussed at length by Strathmann (1990), Denny (1993), and Dawson and Hamner (2008), air and water differ markedly in physical properties that affect the physiology, behavior, and performance of organisms. Of particular importance to macroscopic organisms are the much lower viscosity, density, and specific heat; and the much more rapid diffusion of gases (and soluble or volatile substances), in air than in water (Table 1). These physical differences have at least five major biological consequences. First, the higher viscosity and density of water make it feasible for many organisms and their food to remain suspended in the medium. Second, the lower diffusion coefficients characteristic of water mean that the detection of diffusively transported chemical cues emanating from food, enemies, and mates is slower and occurs over shorter distances than in air (Denny 1993). Third, the speeds, metabolic rates (especially of invertebrates), and distances achievable by animals moving in air are generally much greater than for animals moving in water, particularly small animals. This is partly because of the huge differences in viscosity of the two media, but also because, all else being equal, of the much higher diffusivity (and effective concentration) of oxygen in

Table 1. Four key physical differences between sea water and air that influence performance and behavior of aquatic versus terrestrial organisms (from Denny 1993)

	Sea water	Air
Density (gm cm^{-3})	1.02	1.2×10^{-3}
Viscosity (gm cm^{-1} sec^{-1})	1.1×10^{-2}	1.8×10^{-4}
Specific heat (J g^{-1}K) @20°C	4.10	1.01
Diffusion coefficient of O$_2$ (m^2 sec^{-1}) @20°C, 1 atm	2.10×10^{-9}	2.03×10^{-5}

air compared to water (Denny 1993, p. 92). Thus, Alexander (1982, p. 126) concluded: "as a general rule, large animals fly, run and swim faster than smaller ones. Also, when animals of similar size are compared, flight is faster than running which in turn tends to be faster than swimming." This is equally true for animals—terrestrial and aquatic—that burrow in sand, a medium in which friction imposes similar effects (Maladen et al. 2009). Fourth, the lower specific heat of air makes it energetically cheaper to operate at higher temperatures in air than in water, expanding the aerobic and performance scope of terrestrial compared to marine animals (Denny 1993). Finally, because light attenuates much more rapidly in water than in air, visual ranges may be more limited. For small macroscopic water-dwellers, life is thus carried on in a much more limited space than in air.

The key to the current extraordinary diversity of species on land is, we suggest, both the ability and the necessity for species to be rare, that is, for populations to persist at low density. In a medium in which mobile ground-dwelling and aerial consumers can range far and wide, the costs in energy or time of making choices among food sources is relatively low; a consumer does not need to accept the first item it encounters. As a result, specialization on scarce, widely scattered food sources and habitats becomes possible. In a highly competitive and enemy-rich environment, the incentive to specialize on toxic or well-defended items for food or shelter is high, not only because such specialization reduces direct competition, but also because the association with dangerous victims can reduce risks to the specialized consumers (Brower 1958; Vermeij 1983, 2004). Moreover, the generally greater distances over which species-specific visual and diffused chemical signals can be transmitted and perceived in air compared to water potentially enable individuals to locate mates and food from farther away. (Acoustic signals are another matter; see Vermeij 2010). For stationary plants that depend on wind or water for fertilization, local population density must be high, so that successful fertilization can take place (Mulcahy 1979; Niklas 1983; Friedman and Barrett 2009); but dense populations are also inviting targets for specialist consumers (Janzen 1970; Regal 1977; Leigh et al. 2004). Consequently, there is a strong incentive for victim species to be rare, and for partnerships to evolve between wide-ranging specialist seed dispersers and pollinators on the one hand, and plants on the other. Intense competition and predation place a premium on specialization and therefore on rarity, especially in air, in which the

potentially high cost of choice that is associated with specialization is reduced.

On land, gamete transfer by animal vectors is mainly through pollination of stationary plants, although gamete transfer by collembolans has been documented for mosses (Cronberg et al. 2006), and may well occur much more widely in other groups, including fungi. In the sea, gamete transfer by animal vectors could, in principle, have evolved in many stationary suspension-feeding animals, as well as in seaweeds (Strathmann 1990). That this has not happened (as far as we know) represents part of the puzzle of the current marine–terrestrial contrast in species diversity.

That animal-mediated dispersal of propagules such as seeds, fertilized eggs, and larvae are likewise known primarily in terrestrial and freshwater environments is another part of the puzzle (Strathmann 1990). Exceptions are freshwater unionoidean bivalves, whose larvae (glochidia and lasidia) are dispersed (and protected) in a fish host; and many parasitic trematodes, which have complex life cycles involving more than one host. In perhaps the majority of aquatic parasites with complex life cycles, however, one of the hosts is typically a terrestrial or aerial animal such as a mammal, bird, or insect. Kano's (2009) case of juvenile fresh-water neritid gastropods being carried upstream by crawling adults of other neritid species is one of the very few documented examples of animal-mediated dispersal involving fully aquatic species.

This extreme rarity is surprising, because some marine animals would surely benefit from mobile animal helpers that bring about fertilization or dispersal. Barnacles, for example, despite their inability to move as adults, practice internal fertilization with an extremely long penis. Penis length itself may be constrained by damage from waves or predators (Strathmann 1990; Hoch 2008; Neufeld and Palmer, 2008). Thus, their mating success and the persistence of their populations depend on locally high densities.

The rarity of animal-mediated transfer and dispersal of gametes in the sea is unlikely to be due to intrinsic limitations on the capacity of sessile marine organisms to provide appropriate rewards to potential vectors. For example, the scleractinian coral *Pocillipora damicornis* facultatively produces lipid-rich structures that are fed upon by obligately commensal xanthid crabs, which, in turn, defend host corals against a variety of predators (Stimson 1990). This study makes it clear that marine invertebrates can induce the production of rewards, but

we know of no examples of rewards being produced that specifically target particular helpers from afar.

Why, then, are there no known animal vectors in the sea? Strathmann (1990) offered three explanations. First, the gain in fertilization efficiency that could be realized by attracting gamete vectors (and rewarding them) would be less than the costs of simply investing in more gametes that passively disperse. This may well be true; however, to our knowledge there is no decisive evidence that water-mediated fertilization would be less efficient than other possible mechanisms, especially since gametes can remain viable in seawater for a surprisingly long time (Johnson and Yund 2004, 2007; Bishop and Permberton, 2006). Indeed, in the case of terrestrial plants, Friedman and Barrett (2009) argued that wind pollination is as efficient as animal-mediated pollination, at least over short distances and at high-population densities. Second, the physical challenges of locating hosts in water, "may limit the effectiveness of advertised rewards to pollinators" (Strathmann 1990, p. 200). And third, "if prospective pollinators have access to better alternative sources of food in aquatic habitats, higher rewards to pollinators might be required in aquatic habitats" (Strathmann 1990, p. 200). Strathmann (1990) does not elaborate on this third explanation, but we believe it is the most plausible: in contrast to air, where there is little suspended food, potential vectors in water generally have abundant food available while they are moving from place to place. Therefore the rewards that would constitute a sufficient nutritional incentive to offset the costs of locomotion and risks of predation in transit may well be higher in water than in air.

Animal-mediated pollination and dispersal of plants are likely to be very old, but probably did not become globally important until Late Cretaceous time. Transfer of gametes and dispersal of spores by low-mobility collembolans, other arthropods, and snails are known in mosses and fungi (Cronberg et al. 2006), and could have arisen during the very earliest phases of animal evolution on land in the Silurian period, some 420 million years ago (Shear and Selden 2001; Labandeira 2006a, 2006b). Although pollination by insects may already have been present in medullosan seed ferns during the Carboniferous period (Labandeira 2000), and pollinators of early diverging Cretaceous angiosperms have ancestors among insects associated with Jurassic gymnosperms (Labandeira 1998; Ren et al. 2009), highly specialized pollination and pollinators evolved during the Cretaceous. Angiosperms,

which are now thought to be plesiomorphically insect-pollinated (Hu et al. 2008), originated ∼140 million years ago during the Early Cretaceous; but they greatly expanded, beginning ∼110 million years ago during mid-Cretaceous time with the explosive diversification of the eudicots (Heimhofer et al., 2005; Boyce et al. 2009; Wang et al. 2009; Brodribb and Feild 2010). Moreover, the pollinators of Jurassic gymnosperms—scorpionflies of three extinct families—and the different pollinators of Early Cretaceous angiosperms were relatively slow animals with limited mobility (Ren et al. 2009) compared to the major pollinators of the past one hundred million years, including bees, butterflies, birds, and bats.

The expansion of angiosperms was paralleled by huge radiations in insects, especially among Coleoptera, Hymenoptera, and Lepidoptera, as well as in the fungi, many of whose species are associated with plants (James et al. 2006; Lloyd et al. 2008; McKenna et al. 2009). Earlier denials of this parallel diversification of angiosperms and insects (Labandeira and Sepkoski 1993; Hunt et al. 2007) are founded either on family-level diversity or on the observation that many beetle families originated before the Cretaceous. The family-level analysis ignores the vast size of many insect families, such as the Curculionidae (40,000 species of weevils); whereas the pre-Cretaceous origins of most beetle clades indicates nothing about the subsequent radiation within these clades.

Low-population density, which is associated with such factors as rarity, large body size, and specialization, is well known to expose a population to the risk of extinction (see e.g., Davidson et al. 2009). Partnerships between mobile consumers and stationary producers reduce this risk, and therefore allow for the accumulation of rare species as well as for the establishment of new small isolates that in time can become distinct species. Mobility, specialization, and rarity are thus components of a positive diversity feedback, which operates most strongly in those environments in which locomotion and resource location are least-constrained and where selection for specialization is most intense. Due to the differences in the physical properties of air and water, those environments are primarily terrestrial.

If species can more easily persist with increasing rarity, and if their risk of extinction decreases through time as rarity becomes more feasible, diversity should generally rise over time on land as well as in the sea, but more so on, the land. A literal reading of the marine fossil record indicates a general global step-wise rise in diversity at the generic level in the

sea (Sepkoski et al. 1981), whereas on land the emerging consensus is a pattern of exponential rise (Benton 1995, 2009; Kalmar and Currie 2010). Problems of unequal and inconsistent sampling and of preservation of fossils have led many analysts to massage the raw data statistically by standardizing sampling protocols. The resulting consensus holds that, although marine global diversity rose during the Early Paleozoic, it fluctuated around a plateau for hundreds of millions of years, and did not rise substantially even after the Jurassic period (Alroy et al. 2008; Rabosky 2009).

In our view, the manipulations required to reach this consensus distort the underlying signal. In the analysis of Alroy et al. (2008), for example, all marine taxa with aragonitic calcified skeletons were discarded because they are not always preserved; yet these taxa comprise the majority of calcified organisms during the Cenozoic era. Eliminating them thus underestimates expansion during the Cenozoic. Alroy et al. (2008) employed time slices (or bins) of equal length, which often cut across extinction boundaries, and constrained samples on which species counts were based to contain equal numbers of individuals. This latter attempt to reduce sampling artifacts means that large samples representing abundant sites with many species were reduced in order to make them equal in size to samples with less adequate preservation from less fossiliferous localities. If the abundance of fossils generally increased through time, as the increasing thickness of shell beds through time and the decreasing number of sedimentary formations without fossils indicate (Kidwell and Brenchley 1996; Peters 2007; but for a contrary view see Smith and McGowan 2008), a systematic bias against Cretaceous and Cenozoic taxa is introduced, because rare species in large samples are under-represented.

These and other problems with analyses of global diversity through time (Vermeij and Leighton 2003) persuade us that the unmanipulated data reveal a more credible pattern of diversity than do the filtered data. This pattern is one of increasing genus-level (and likely species-level) diversity through time in terrestrial as well as in marine environments (Bambach 1977; Benton 2009). The rise in diversity, both regionally and globally, was faster on land than among benthic marine taxa (Knoll et al. 1979; Kalmar and Currie 2010), especially from Cretaceous time onward. It is no accident that all the hyper-diverse terrestrial clades of plants, insects, and fungi diversified in the last 100 million years, and that no comparable increases occurred in pre-Cretaceous time. Moreover, terrestrial animals with high-mobility and high-metabolic rates, including flying insects and endothermic birds and mammals, belong mainly to clades that originated during the Cretaceous and Cenozoic. The evolution of these animals promoted rarity not only among their own ranks, but also among the plants and animals they help to disperse.

G. J. Retallack (personal communication) has suggested to us that the apparent surge in terrestrial diversity during the Cretaceous and the apparent low diversity of terrestrial ecosystems during the Paleozoic era are artifacts of preservation. This suggestion is difficult to evaluate, but we do not believe artifacts account for the observed pattern. The terrestrial fossil record is much less complete than is the marine record, particularly for the Paleozoic, but the phylogenetic evidence that the hyper-diverse terrestrial groups originated or radiated during the Cretaceous seems to us a compelling argument that terrestrial systems have undergone enormous diversification during the past 100 million years.

Why was the mid-Cretaceous the temporal turning point of disproportionate growth in terrestrial diversity? After all, the necessary physical differences between air and water, and their potential biological consequences, existed long before the mid-Cretaceous. We suggest that an increase in productivity, begun on land with the evolution of more derived angiosperms, stimulated the positive feedbacks among mobility, specialization, and competition that led to huge increases in the number of species on land. The most direct evidence for increased primary productivity on land comes from analyses of leaf-vein densities in land plants (Boyce et al., 2009; Brodribb and Feild 2010). With a higher density of veins, the rate of transpiration of the leaf rises, and the rate of fixation of biomass increases correspondingly. All known land plants living before 100–110 million years ago had low vein densities, averaging ~2-mm vein length per square millimeter of leaf area, and rarely exceeding 5-mm vein length per square millimeter. Flowering plants, especially those in the derived eudicot clade, have average vein densities of 8 mm per square millimeter, some four times higher than in their predecessors and in living nonangiosperms. These increases correspond to a 3- to 4-fold rise in the per-leaf rate of transpiration and of biomass production beginning ~100 million years ago (Boyce et al. 2009; Brodribb and Feild 2010). These high rates were rendered even higher by increases in the number of leaves covering an area of ground (Boyce et al. 2009).

The rise in terrestrial productivity led to an increase in marine productivity and diversity as well (Bambach 1999; Vermeij 2004). It also led to higher rates of consumption by herbivores and predators. What triggered this increased biological activity is not entirely clear. The release of vast quantities of nutrients from the crust and mantle during large-scale episodes of flood-basalt (including submarine) volcanism in the Cretaceous may have played a role (Vermeij 1995), but intense selection from competitors and predators would surely have amplified this stimulus (Vermeij 2004), especially on land. There are the same number of constraints on locomotion in air as in the water, but the magnitude of each of these constraints is generally less in air. These effects would be strongest in warm climates. Indeed, the interval of explosive radiation of angiosperms and their consumers in the mid to Late Cretaceous was globally warm, as were subsequent episodes of world-wide diversification during the Late Paleocene to Early Eocene, the Early to Middle Miocene, and to a lesser extent the Early Pliocene.

Contrary to Rabosky's (2009) assertion that diversity has reached an upper limit imposed by competition, we see no evidence for an insuperable upper bound. An upper limit may indeed exist for large-bodied, highly metabolizing consumers, but for plants, small animals (especially parasites), and species with low metabolic rates, potential diversity is likely to be limited only by opportunities for speciation, that is, by circumstances permitting genetic isolation of viable populations. With rarity being more easily achieved and increasingly necessary, both the persistence and formation of species likely rose in the post-Jurassic world, especially on land.

Our interpretation of diversity on land and in the sea points to the conclusion that the number of species present locally, regionally, and globally cannot be fully explained without an understanding of both the physical and biotic interactions and feedbacks that govern the economy of life. Species do not evolve, live, or disappear in isolation; they interact with each other. It is the interactions among species, set in the context of the cost of doing business in the physical and chemical environment, that determine how many species can live in air and water. These costs and benefits are not static: they vary in space and change over time, and it is this variation and change that together determine the history of biotic diversity on Earth. What remains to be seen is whether these spatial and temporal scales differ between land and sea, and how they further contribute to the present disparity in diversity (Dawson and Hamner 2008).

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