Primer

Biodiversity in water and on land

Richard K. Grosberg[1,*],
Geerat J. Vermeij[2],
and Peter C. Wainwright[3]

Habitats in the sea, in freshwater, and on land differ dramatically in species composition and diversity. Of the roughly 1.5 million known species of macroscopic organisms on earth, the modern ocean — despite its much larger area and volume — supports only about 15% of species, whereas terrestrial environments account for about 80% of species, and freshwater for the remaining 5% (Figure 1). Even when taking into account previously undetected biodiversity in all of the physical realms revealed through molecular techniques, these differences appear to be robust — certainly among multicellular organisms.

A closer look at these differences reveals two striking patterns: first, it's only relatively recently, in the last 100 million years or so, that the number of species on land has come to vastly exceed the diversity in the seas; second, despite some transitions and overlaps in distribution, many major clades of plants, animals, fungi, and microbes occur primarily in only one, or two, of the three realms (Table 1). Although there are exceptions, particularly among fish and some decapod crustaceans (many crabs and shrimp), this observation, together with abundant phylogenetic and fossil evidence, implies that evolutionary transitions among these realms are typically infrequent and apparently difficult.

These contrasts in diversity continue to puzzle both ecologists and evolutionary biologists, and possible explanations must span multiple spatial and temporal scales. There are at least two fundamental questions that must be answered: first, to what extent do the presently observed differences in diversity reflect historical differences in rates of diversification or biases in the rate of transitions between realms?

Second, why are there so few transitions among the great realms?

Given the enormous challenges in estimating speciation and extinction rates, for most groups, it remains unclear whether there are truly differences in rates of diversification across the three realms, and this remains an area of very active research. Nevertheless, we can speculate on some of the major factors that collectively influence diversification.

Amount of productive habitat
As a general rule of thumb, high biodiversity depends on high productivity over the long run (Figure 2A,B). There are exceptions, of course, such as the highly diverse floras of southern Africa (Figure 2C) and western Australia where terrestrial productivity is low, and the diverse faunas of hydrothermal vents and the abyssal plain in the deep sea. And in the world's oceans, there are notable areas in temperate and polar waters that exhibit seasonally high productivity, but low diversity. Nevertheless, deserts notwithstanding, terrestrial environments, for reasons that remain unclear, tend to be far more productive and cover a larger relative area, than marine ones. The most productive marine environments are confined to hydrothermal vents and shallow-water, coastal zones, leaving much of the pelagic zone and the deep sea relatively unproductive. Freshwaters are generally shallower than the oceans, and many lakes and rivers support high productivity of either plankton or bottom-dwelling vegetation.

The high productivity of terrestrial environments is largely due to forests and grasslands and is, geologically speaking, a relatively new state of affairs. Recent evidence from fossil leaves strongly indicates that during the mid-Cretaceous (100 million years ago) there was a dramatic increase in terrestrial productivity, as the land vegetation became dominated by flowering plants, whose photosynthetic capacity far exceeded that of their predecessors. Nevertheless, it remains an important and open question how present-day and historical levels of productivity differ across the
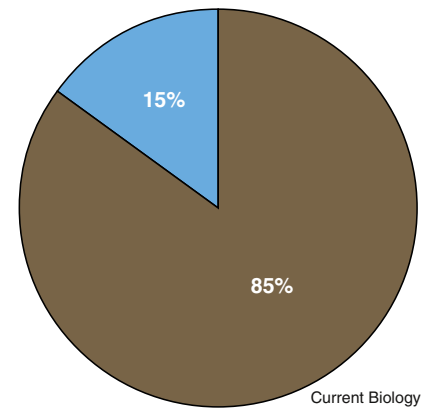

Figure 1. Diversity on land and in the sea. The distribution of macroscopic species diversity in terrestrial (brown) versus marine (blue) realms, according to May (1994).

three physical realms of life and how these patterns relate to the distribution of biodiversity.

Habitat complexity
A three-dimensionally complex, biologically constructed environment is conducive to high diversity (Figure 2A,B). Much of the ocean comprises the relatively homogeneous pelagic zone, which is inhabited by comparatively few macroscopic species. The shallow seafloor, by contrast, can be topographically complex, because of vegetation and reef-builders, including corals, seaweeds, seagrasses, mussels, and oysters, among others. Terrestrial environments are generally far more physically complex, largely because of habitat provided by plants, both above and below ground. Moreover, physical gradients tend to be steeper, and extremes, for instance of temperature, tend to be greater in terrestrial environments. This, in turn, provides far more habitat diversity over smaller spatial scales than exists in most marine environments.

In contrast, the structural complexity of freshwater environments is relatively low, thanks to the short stature of most aquatic plants and the absence of reefs built by animals. (The absence of freshwater shrubs and trees, or large algae, is in itself an intriguing problem. Rooted freshwater plants tend to occur in clear, plankton-poor waters, whereas floating plants and phytoplankton dominate waters of high productivity.) On the other

Figure 2. Features of several major habitat types, and their association with species diversity.
(A) A new world tropical rainforest, typified by high primary productivity, high three-dimensional complexity, and high species diversity (photo: Mary Plage, Getty Images). (B) A tropical coral reef, the marine equivalent of a tropical rainforest (photo: Mark Conlin, Getty Images). (C) The fynbos, a relatively low productivity heathland limited to a coastal swath of the Western Cape region of South Africa, characterized by exceptionally high plant diversity (photo: Richard I'Anson, Getty Images).

hand, freshwater environments are, by nature, more fragmented and thus more island-like than most terrestrial and marine environments, promoting isolation and the potential for diversification across smaller spatial scales.

Physical differences in the media
Water and air differ in viscosity, density, specific heat, diffusibility of gases, concentrations of oxygen and carbon dioxide, conductivity, and transparency. Beyond this, seawater and freshwater also differ in salinity, gas concentration, density, and viscosity. All of these differences are temperature-dependent, and all have significant biological consequences that must affect both ecological and evolutionary processes.

For example, although the per-distance energy outlay of swimming in water at normal speeds is less than the outlay for running on land, attainable speeds and agility are substantially higher on land and in the air, permitting smaller animals to move greater distances at higher speeds when living out of water. As a result, animal-mediated gamete transfer (including pollination) and propagule dispersal are widespread in terrestrial environments but are rare in aquatic ones, especially in the sea.

Higher locomotor performance, faster diffusion of chemical signals, and more effective transmission of visual signals in air imply that species attracting or choosing among mates at a distance can maintain populations at much lower densities than in liquid media. Nevertheless, active suspension

feeding, which is almost unknown on land, but very common in aquatic environments because of the medium's higher density, may enable some internal brooders to capture dilute gametes. This, along with extended sperm storage, potentially allows at least some populations of aquatic sessile species to persist at lower densities than might otherwise be possible.

This effect notwithstanding, visual and chemical signals involved in mate location and recognition will typically operate over shorter distances in water than in air, acoustic signals being a notable exception. Thus, insofar as sexual selection reduces genetic barriers to speciation, terrestrial environments should on the whole be more conducive to both the formation and maintenance of species. Over the last 100 million years, from mid-Cretaceous time onward, sexual selection and other factors permitting rarity have allowed diversity to rise faster on land than in the sea, especially among such very diverse clades as flowering plants, fungi and insects, despite huge radiations among marine molluscs, crustaceans and fishes.

Transitions between domains
These three factors — productivity, habitat complexity, and the physical properties of the media — may also limit the capacity of established taxa to make transitions from one realm to another. The evolutionary challenges and opportunities associated with such transitions reflect the adaptability and potential performance levels of individuals, as organisms compete for resources

in their new surroundings. Not surprisingly, therefore, major evolutionary groups of organisms (i.e., clades) differ dramatically in the frequency of transitions between realms. For example, at least ten independent lineages of mammals (including six with exclusively fossil species) have colonized marine environments from the land, sometimes by way of freshwater (e.g., cetaceans); whereas no terrestrial gastropods, crustaceans, hymenopteran insects, or non-angiosperm vascular plants have become marine.

Cephalopods, echinoderms, tunicates, brachiopods, anthozoans, and hexactinellid (glass) sponges have remained exclusively marine throughout their long evolutionary history; and only one or two clades of demosponges have colonized freshwater (Table 1). Gastropods have made this transition in 33 to 38 independent lineages, and bivalves have done so in at least 20 clades. The only groups in which the reverse transition, from freshwater to the sea, has been at all common are insects and especially fishes. Teleost fishes have moved many times from marine to freshwater habitats, and the reverse, sometimes spurring significant new radiations. Among angiosperms, only five lineages have become truly marine, although the arrival of these plants in coastal marine settings has had profound ecological consequences beginning eighty million years ago.

In nearly all cases that have been investigated phylogenetically, secondarily marine lineages with freshwater ancestors have

Table 1. Distribution of biodiversity among the three major physical realms of life.

Taxon	Marine	Freshwater	Terrestrial
Sponges	9,000+	200–250	0
Cnidarians	10,000	<50	0
Bryozoans	5–10,000	<100	0
Mollusks (Gastropods)	50,000	4–5,000	25–30,000
Mollusks (Bivalves)	11,000	1,400+	0
Mollusks (Cephalopods)	800	0	0
Nematodes	35,000	2,000+	10^6(?)
Arthropods (Insects)	1,400 (includes intertidal)	100,000+	5–9×10^6
Arthropods (Arachnids)	1–2,000	5,000 (mostly mites)	10^6+
Arthropods (Crustaceans)	65,000+	12,000	4–5,000
Platyhelminthes	15–20,000	1,000	300–500
Annelids (Polychaetes)	9,000	500+	0
Annelids (Oligochaetes)	<500	1,000+	100
Echinoderms	6–7,000	0	0
Chordates (Mammals)	125	100+	5,000
Chordates (Fish)	15,000	15,000	0
Chordates (Other vertebrates: Amphibians, crocodiles, lizards, snakes, turtles, birds)	<500 (excluding birds)	7,000+	<20,000
Chordates (Tunicates)	3,000	0	0
Fungi	<1,000	<1,000	10^6++(?)
Plants (vascular macrophytes)	<100	2,500+	250,000+
Plants (other macrophytes)	10,000	<500	30,000+ (including mosses)

Rough estimates of species diversity, synthesized from multiple sources, in major groups of multicellular, macroscopic organisms, across marine, freshwater, and terrestrial realms. To the extent possible, we assigned organisms to habitat according to where they breed or spend the majority of their life.

undergone very little diversification in the sea. Vermeij and Dudley (2000) estimated that there are some 1400 insect species that could be considered marine, representing well over 100 separate invasions. Like secondarily marine spiders, mites, scorpions, millipedes, centipedes and land plants, marine insects have undergone little speciation compared to their terrestrial relatives. Even in marine mammals, only four marine clades (cetaceans, sirenian sea cows, pinniped seals, and fossil desmostylians) underwent substantial adaptive radiation.

A singular exception to this pattern has recently been claimed for fishes. In a phylogenetically informed analysis of living species of actinopterygian (ray-finned) fishes, Carrete Vega and Wiens (2012) infer that existing marine clades are derived from freshwater ancestors, and notably, the number of freshwater species is nearly equal to the diversity in the sea. Rates of diversification were estimated to be about the same in freshwater and marine environments, including reefs. There are reasons to be skeptical of some of these inferences. For one, ancestral habitats of fishes are particularly difficult to reconstruct; many fish groups are osmotically highly adaptable and move easily between fresh and salt water. Moreover, all fossil ray-finned fishes from this period are from marine deposits. Finally, even if marine fishes did indeed evolve from freshwater ancestors, they would be the only major group of organisms that attained comparable diversity in the sea as in the habitats from whence they came.

The evolutionary fates of clades making transitions among the great realms depends on the inherent adaptability of their physiological and developmental systems, as well as on the ability of incumbents to exclude competitors that are initially poorly adapted to the new medium. In its new surroundings, a clade may diversify, the extent and ease of which depend on dispersibility and the role of sexual selection and other processes that cause populations to become genetically isolated from one another. Like vertebrates in general, fishes, because of their enhanced homeostatic capacity, seem far more likely to cross ecological hurdles between fresh and salt water than most other organisms, and sexual selection has been a conspicuous driver of speciation of many groups in lakes as well as on reefs. Progress in understanding such transitions must come from studies of how agencies of evolutionary change interact with the physical properties of different media as modified by the species that already occupy target environments.

This problem is especially daunting for microbes, whose scale of interaction is tiny compared to the world of multicellular organisms. For instance, there may be as many as 20,000 'species' of microbes in a liter of seawater. As with all organisms, scaling such samples up to global estimates of diversity remains a major challenge. At this point, however, sampling is far too limited, and we know far too little about diversity, distribution, dispersibility, and speciation of unicellular organisms to predict whether the patterns of transition and diversification across physical realms evident in multicellular organisms apply to microbes.

The contrasts we highlight here show that, although major principles of ecological organization cut across systems inhabiting different media, differences in the physical properties of the media, the steepness of environmental gradients, and the relationship

between the geographic distribution of favorable habitats and dispersibility nonetheless greatly influence how species interact with each other, how and to what extent speciation occurs, and the kinds of adaptations that are likely to evolve. Biodiversity is more than counting species; it is about understanding interactions, phenotypes, and evolutionary processes in a heterogeneous biosphere.

Further reading

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[1]Department of Evolution and Ecology University of California, Davis, One Shields Avenue, Davis, CA 95616, USA. [2]Department of Geology, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA. [3]Department of Evolution and Ecology, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA.
*E-mail: rkgrosberg@ucdavis.edu

Spontaneous innovation in tool manufacture and use in a Goffin's cockatoo

Alice M.I. Auersperg[1], Birgit Szabo[1], Auguste M.P. von Bayern[2,3], and Alex Kacelnik[2]

Accounts of complex tool innovations in animals, particularly in species not adaptively specialized for doing so, are exceedingly rare and often linked to advanced cognitive abilities in the physical domain [1], even though the relation between such capabilities and intelligence is poorly understood [2]. For this reason, discoveries of such capabilities transcend anecdotal value and contribute significantly to comparative cognition [3–5]. Among birds, there are several reports of tool innovations in corvids, but very few documented records in other families (for example [1,3–7]). Here, we report a case of spontaneous tool innovation in the Goffin's cockatoo (*Cacatua goffini*), a species endemic to the Tanimbar archipelago in Indonesia. Like most corellas, they live in social groups (~10–100) in tropical dry forests, roost in simple tree holes, and feed mainly on a seed based diet (which occasionally causes interference with agriculture) [8]. There are no records of tool-related behavior in the wild. We report how a captive male named Figaro successfully, reliably and repeatedly made and used stick-type tools to rake in food, manufacturing them from two different materials and displaying different steps and techniques.

During apparently playful explorations, Figaro inserted a stone pebble through the aviary wire mesh, where it fell on a structural wooden beam. After attempting to reach the pebble with his claw, he went away, fetched a piece of bamboo, returned, and used it to fish (unsuccessfully) for the stone, adjusting the movement of the functional tool-end to the movement of the pebble. To follow this serendipitous observation we placed cashew nuts where the pebble had been, in 10 trials over three days. Testing took place in visual isolation from the group, but (to avoid the stress of isolation) in the company of Heidi, a submissive female.

In the first test, after trying an undersized stick from the aviary's floor, Figaro started breaking a large splinter off the beam (European larch, which had previously been left untouched by the animals), using his beak through the wire mesh. Heidi joined in for the last cut, but Figaro chased her away and finally got hold of the splinter by threading it in through the mesh. He immediately started to use it to rake in the nut. Occasionally the nut fell off the distal side of the beam, and we repositioned it. The curved bill forced the bird to work diagonally downwards to see the movement of the reward (see Supplemental Movie S1). Figaro combined straight pulls (placing the tool's end behind the nut and pulling it towards him) and sideward levering movements against the grid. He used 10 tools in 10 trials, nine of which were manufactured and one ready-made (Figure 1A).

Time for manufacture improved across trials, indicative of learning, but, notably, improvement was not gradual: the first attempt took nearly 25 minutes, but afterwards the mean time for manufacture was short and stable (excluding the first test, $X \pm SE = 2:27\pm0:34$; Figure 1B). Except for tool T6, which was initially too long (Figaro halved it following one ineffective raking attempt), the splinters were cut off at their final, suitable length (Figure S1 in the Supplemental Information). T9 was a piece of bamboo from the aviary's floor. T10's manufacturing was complex, involving four cuts to a branching twig on the aviary floor (Figure 1C). The first cut (cut 1) was discarded; he then (cut 2) removed a large side arm from near the twig's stem by stepping on the stem whilst twisting off the sidearm with his beak. Figaro tried the entire side arm first, but after an unsuccessful insertion attempt shortened the remaining first by a third (cut 3) and finally cut the remaining part in half (cut 4). He used the resulting distal piece successfully to retrieve the food.

We tested another male, Pipin, and Heidi in the same situation. Pipin did not try to use tools, but Heidi,