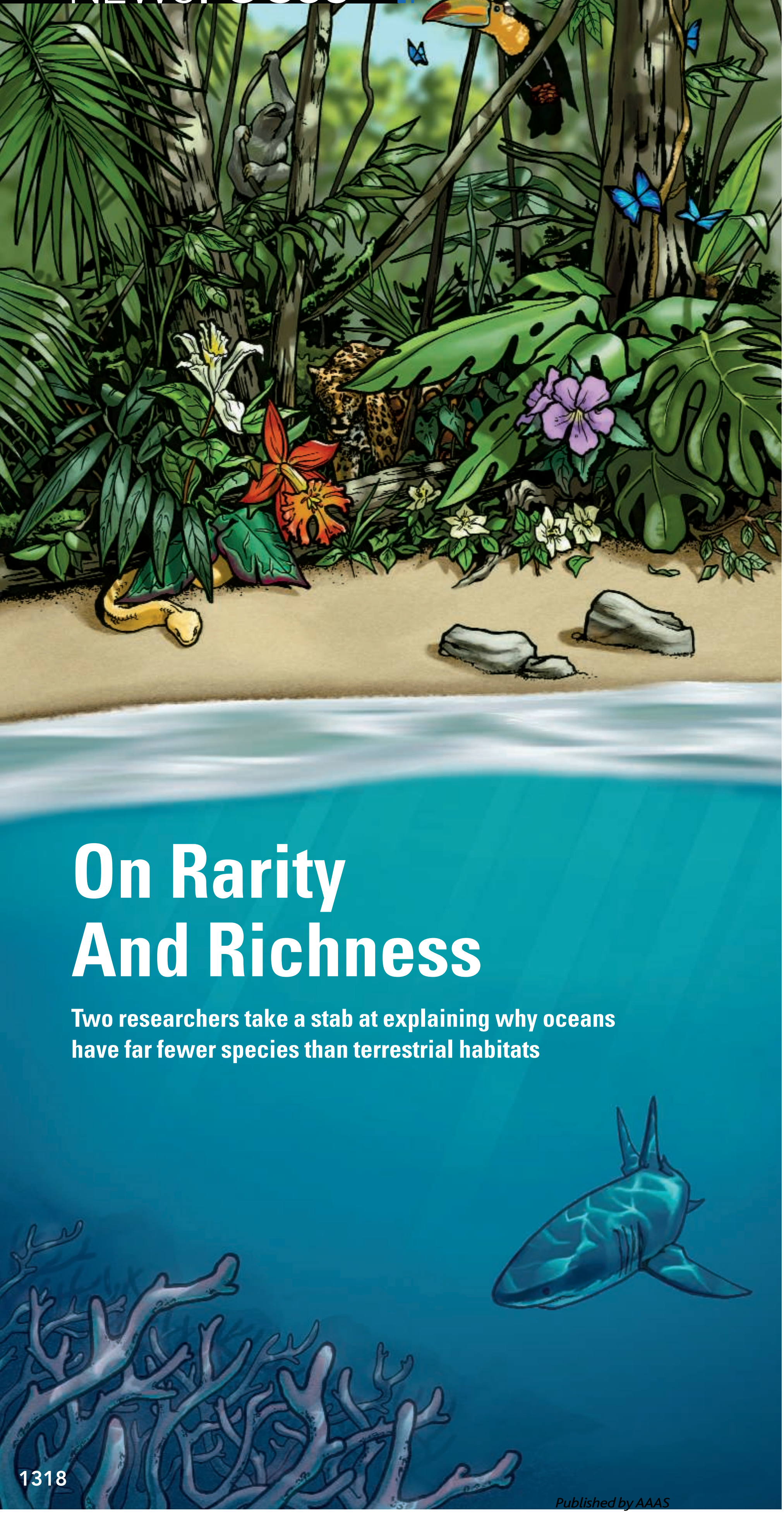

On Rarity And Richness

Two researchers take a stab at explaining why oceans have far fewer species than terrestrial habitats

IF BIODIVERSITY WERE AN OLYMPIC SPORT, life on land would take home the gold and the sea might not even enter a team. Given the vastness of the oceans and the length of time life has thrived there, you might expect marine species to outnumber terrestrial ones. Yet, microbes aside, upward of nine in 10 species crowd into the 30% of Earth's surface that's dry.

It wasn't always that way, say Richard Grosberg and Geerat Vermeij. These researchers from the University of California (UC), Davis, have been studying land and ocean features to understand how evolution proceeds in these two realms. At a recent meeting,* they argued that the difference in diversity is a recent phenomenon.

Back in the Devonian period, 400 million years ago, the seas were home to an abundance of species, perhaps even more than on land. But about 110 million years ago, land plants went through a burst of speciation; so did the pollinators, fungi, and herbivores associated with them. These relationships made "rare" species possible, as plants acquired help in dispersing their pollen and seeds, resulting in relatively low population densities for individual species. Quickly, their numbers left marine biodiversity behind. The trigger for this terrestrial explosion, Grosberg and Vermeij say, was the evolution of a more efficient way in which land plants use water.

"This is an excellent and thoughtful paper addressing an issue in biodiversity that has rarely been tackled," says Michael Benton, a paleontologist at the University of Bristol in the United Kingdom. Jeremy Jackson, a marine ecologist at the Scripps Institution of Oceanography in San Diego, California, calls it "a very big-picture paper. … It's the kind of paper that you think about forever."

A physical phenomenon?

Grosberg started thinking about these issues when he was preparing a series of talks for the 200th anniversary of Charles Darwin's birth. "To me, the interesting question is why are there so many fewer species in the sea than on the land," says Grosberg.

The difference is striking. In 1994, Robert May of the University of Oxford in the United Kingdom concluded that 85% of the world's macroscopic species lived on land, based on the existing record of species across the globe. A 2009 study by Benton found landlubbers to be even more common, accounting for 95% to 98% of the world's multicelled species. "Both recognized that the estimates were ballparks, simply because we don't actually know how

*The Society for Integrative and Comparative Biology meeting was held 3 to 7 January in Seattle, Washington.

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many species there really are," says Grosberg.

The land-sea disparity occurs even in diversity hot spots. A single hectare in a tropical rainforest may contain some 475 tree species and more than 25,000 insect species. But a hectare of coral reef, often called the sea's "rainforest," might be home to at most 300 coral, 600 fish, and about 200 algal species.

Grosberg wasn't the first to wonder what lies behind these numbers. In 1990, Richard Strathmann, a marine biologist at the University of Washington, Seattle, wrote an influential paper pointing to physical characteristics of water that could slow down speciation in the seas. Denser and much more viscous than air, water makes travel more challenging. Gases diffuse more slowly. The much higher specific heat of water means aquatic organisms must work harder to stay functional. Organisms can usually detect food, mates, or enemies by sight or smell over longer distances in air than in water. Strathmann; Mark Denny of Hopkins Marine Station of Stanford University in Pacific Grove, California; and Grosberg have all noted that these differences help make terrestrial environments more hospitable and, most likely, more conducive to the evolution of new species.

Grosberg recognized, however, that physical differences couldn't be the whole explanation. Some polar terrestrial ecosystems are less diverse than nearby marine environments, and freshwater habitats tend to be species-poor compared with similar marine habitats. But he was stumped as to what else might be a factor.

Then Vermeij heard Grosberg give his talk at UC Davis. "He said to me, 'You've missed the point,' " says Grosberg.

Rarity a boon to biodiversity

A paleontologist, Vermeij tends to see events in a long perspective. "It struck me that this enormous difference can't be very old," Vermeij recalls.

Vermeij pointed out that the degree of diversity in the two realms was pretty much equal until about 110 million years ago. About that time, flowering plants took off, as did insects that pollinated them, with species tending to become ever more specialized. Plants came to prefer certain microclimate and soil regimes. Insects pollinated only particular plants; parasites became quite picky about their hosts, and so on. Many kinds of fungi became associated with a favorite host plant. The rise in potential biotic interactions, coupled with more complex habitats than available in the sea, created many more opportunities for new species to form, particularly in the tropics.

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Leaf power. Grosberg (*left*) and Vermeij think the evolution of denser leaf veins (*above*) helped boost terrestrial biodiversity.

Along with increased specialization, terrestrial evolution led to dispersed communities. "The medium of air permits … extensive and rapid locomotion," Vermeij notes. Mobile organisms can locate mates over long distances and easily travel to them. And many stationary plants have gotten animals to do the work of finding mates, transferring pollen, and spreading seeds. The strategy works well: Today, more than 200,000 species are pollinators. In such a system, Vermeij points out, mobile pollinators and dispersers can maintain populations of rare individuals.

With few exceptions, animal-mediated transfer of gametes, fertilized eggs or larvae, or seeds occurs only on land. Grosberg and Vermeij note that arrying such loads is too challenging under water because of water's viscosity. Instead, marine organisms tend to live in higher-density communities and sometimes employ extraordinary measures for fertilization. Consider barnacles, which have penises that are 10 times the diameter of the barnacle in order to reach a potential mate.

The development of dispersed communities "is the key to the current extraordinary diversity of species on land," Grosberg says: High-density populations are at increased risk of being eaten or wiped out by disease, while dispersed communities face reduced competition and predation.

The missing trigger

Yet even with this scenario worked out, Grosberg and Vermeij still lacked an explanation for why the gap in diversity between land and sea began to widen when it did. Then, they heard about a February 2009 paper on the evolution of leaf-vein density in flowering plants. C. Kevin Boyce of the University of Chicago in Illinois and his colleagues had measured the densities of leaf veins in many kinds of plants. They also gathered fossil leaf-vein measurements from the published literature. They found that ferns, conifers, and early flowering plants had relatively low leaf-vein densities. But flowering plants that evolved later sometimes squeezed in three to 10 times as many veins per millimeter. Those extra veins correlated with increased photosynthetic capacity, Boyce and his colleagues reported online on 25 February 2009 in the *Proceedings of the Royal Society B.*

"That paper was the bridge that Vermeij and I crossed in understanding why the disparity gap happened when it did," Grosberg recalls. About 110 million years ago, higher leaf-vein densities—and increases in the number of leaves—resulted in greater biomass production. All this added energy set in motion a positive feedback loop that encouraged more specialization. Speciation took off, particularly in the tropics.

"The idea of key innovations in plant and animal evolution [such as denser leaf veins] is a very old one," says Michael Hart of Simon Fraser University in Burnaby, Canada, "but connecting it to the land-sea difference in species diversity is important and new."

However, the explanation Vermeij and Grosberg propose has some critics. Evolutionary biologist A. Richard Palmer of the University of Alberta in Edmonton, Canada, says so much terrestrial diversity is due to insects and flowering plants that they may overwhelm the real biodiversity picture. And while he calls Grosberg and Vermeij's case for extreme rarity being more feasible on land "a novel contribution," he points out that some deep-ocean species are also quite rare. "Rarity doesn't seem unique to land," he says. And Strathmann points out that the difference in the number of species on land versus the number in the sea may be exaggerated because many marine species have gone unrecognized.

Nevertheless, Grosberg and Vermeij's ideas are attracting attention. "Every step of the way [in their argument] is to some degree conjectural," says Jackson. "But every step of the way makes sense." **–ELIZABETH PENNISI**