STEVE JONES

TEN THOUSAND WEDGES: BIODIVERSITY, NATURAL SELECTION AND RANDOM CHANGE

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HOW MUCH DO WE KNOW ABOUT BIOLOGICAL DIVERSITY? TO UNDERSTAND WHAT MAINTAINS IT MIGHT HELP IN THE BATTLE TO PRESERVE WHAT REMAINS. STEVE JONES ARGUES THAT ALTHOUGH WE HAVE MORE INFORMATION ABOUT THE GEOGRAPHY OF LIFE THAN IN DARWIN'S TIME, WE LACK A THEORY OF WHY SOME PLACES HAVE LOTS OF CREATURES, WHILE OTHERS HAVE FEW.

In 1859, London – with its two million inhabitants – was the largest city on Earth. It was in addition (and in large part through the activities of the Royal Society) the world centre of geological and biological research, its lasting memorial the publication in that year of *The Origin of Species*, the book that gave birth to modern biology. The capital's people were well aware of its fame, and flocked to public displays in the Zoo, the British Museum and Kew Gardens and – as a more select group (Charles Darwin among them) – to the Linnean, Geological, Royal and Royal Geographic Societies.

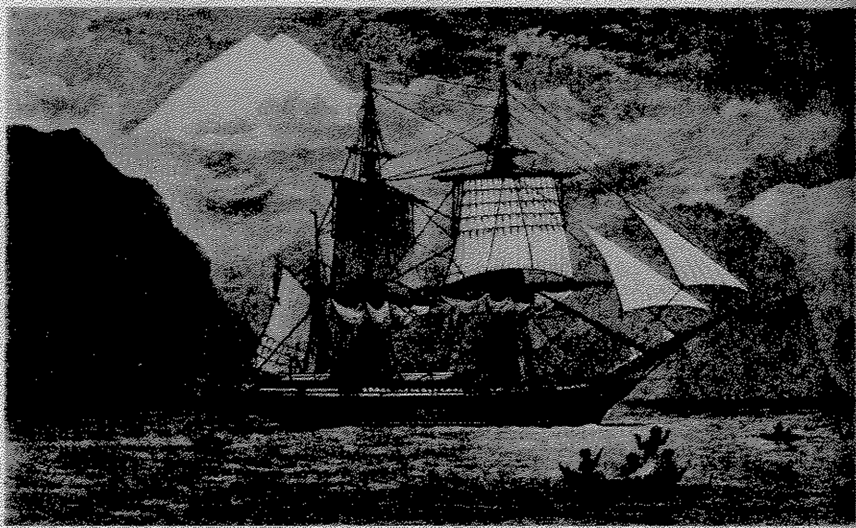
In 2009 Britain's first city has slipped to a global number seventeen in size, but its status as an international centre of gravity of the intertwined sciences of ecology and evolution has not changed. London still represents, by a considerable margin, the world's largest conglomeration of researchers in this field and remains, as it was in Darwin's time, a global hub for the study of biological diversity. The Natural History Museum (in which the great man's statue, once hidden in the tea room, has been promoted to pride of place) has over twenty million specimens of plant and animal, and Kew plans to store tens of thousands of species of plant as seeds. How many kinds of creature there might be altogether is a matter of guesswork; almost two million have been described, but the total may be – some say – twenty times as great (although that figure depends on just how a 'species' is defined).

Charles Darwin founded the modern sciences of evolution and ecology (although neither word appears in *The Origin*). His book was wrong about plenty of things but impressively right about others. He had an uncanny ability to foresee the difficulties that his new science was likely to face. To him, the nature and origin of species was 'the mystery of mysteries' – as it still is. In a prescient hint of disagreements to come, his writings introduce the tension between the power of directed change (natural selection included) and the importance of accident. That argument pervades the history of evolutionary biology and remains unresolved.

Palaeontology, development, genetics, ecology, demography, species diversity and other parts of evolutionary theory share a history of dissent about the role of chance as opposed to directed forces. Since 1859 there have been many reversals of attitude within each of those fields with – no doubt – more to come. Now, the study of biodiversity is revisiting the controversy, with mixed results.

FROM DELIGHT TO DOUBT

In Darwin's early years, Nature seemed bounteous, complicated, and more or less permanent. For the young naturalist on the *Beagle* the main task was to describe, rather than to explain, the world's variety. His joy in life's abundance is clear: as he wrote on his first steps ashore in South America:



HMS *Beagle* in the Straits of Magellan with Mount Sarmiento in the distance.

> The noise from the insects is so loud, that it may be heard even in a vessel anchored several hundred yards from the shore; yet within the recesses of the forest a universal silence appears to reign. To a person fond of natural history, such a day as this, brings with it a deeper pleasure than he ever can hope again to experience ... The day has passed delightfully. Delight itself, however, is a weak term to express the feelings of a naturalist who, for the first time, has wandered by himself in a Brazilian forest.

To the delighted Darwin, the tropics – unspoiled by man, filled with sunlight and blessed with sufficient products of the bounteous to allow chains of hungry creatures that prey upon each other – were the centre of the world's diversity. Twenty years later *The Origin*, as it transformed a static view of life into a dynamic one, began to ask why. The book begins with chapters on variation and on the struggle for existence and makes the case that an all-pervasive interaction of the two generates new kinds of creature as the result of an ordered process called natural selection: inherited differences in the chances of reproduction. *The Origin* ends in a hymn to its power with the famous tangled bank: 'clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth'. It was a vision of what today we refer to as biodiversity.

The original of the paradisiacal bank is only a few hundred yards from Down House, Darwin's home in Kent for the last forty years of his life. To the patriarch of Downe its inhabitants – like those of the Brazilian forest – made up a crowded system of competitors, each squeezed into its own way of life, any vacancy at once filled by a hungry challenger. So finely tuned were their interactions that natural selection was inevitable. Ancestors were replaced by better-adapted descendants and the world was full with no room for passengers. The directive forces of competition, extinction and replacement were essential parts of his theory. 'The face of Nature', he wrote, 'may be compared to a yielding surface, with ten thousand sharp wedges packed close together and driven inwards by incessant blows, sometimes one wedge being struck, and then another with greater force.' Inevitably, the less successful wedges were squeezed out. That vivid image gave rise in time to the well-known 'Red Queen' model of ecology in which competition is the engine of evolutionary change and in which different creatures must run just to stay in the same place.

That view of Nature is still, as in Victorian times, accompanied by the perception that evolution emerges from a series of rules: 'Throw up a handful of feathers, and all must fall to the ground according to definite laws; but how simple is this problem compared to the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kinds …' Since then, a great variety of laws – definite and less so – has been proposed by ecologists. Many are both linear and prescriptive. Some may have some validity; but most ecologists accept that accident also moulds the diversity of life. As *The Origin* points out, on oceanic islands the number of kinds of inhabitants is scanty and particular groups such as frogs and toads are absent – a result of the hazards of colonisation, denied to creatures that cannot cross the sea and open by chance to only a

genome is now seen as a system, filled with non-linear interactions, and speciation as a side-effect of an incompatibility between intricate organistations. Geneticists sometimes need to remind themselves of the stark simplicity of Mendel for reassurance that their subject has any laws at all. Their confusion has a message for those struggling with the perhaps even more complex issue of how species find their place in Nature.

For a brief and golden period at the end of the last millennium, genetics, ecology and evolution seemed to approach a consensus in which the promise of *The Origin* would be fulfilled. Since then, biologists have been forced once again to face the unpalatable truth that life is less simple than seems reasonable to hope. It is increasingly unclear whether patterns of biodiversity and the extent to which the numbers and the relative abundance of species in a community reflect 'definite laws' *à la* Darwin, rather than a chance assemblage of species, of the kind that might be blown on to an island. We do not know why some communities are diverse and some not, some efficient and others less so, some filled with disease and others plagued by predators, and some resilient but others exceeding fragile. Even the consistency that impressed the young naturalist – the vast variety of the unspoiled and generous tropics – appears less impressive than once it did. Ecology, which once saw ordered communities moving through predictable stages to a more or less stable climax, their structure determined by energy flow or predator pressure, now accepts that many may be little more than a random bunch of functionally equivalent creatures and that changes in space or time may often result from accident.

Biodiversity Present and Future

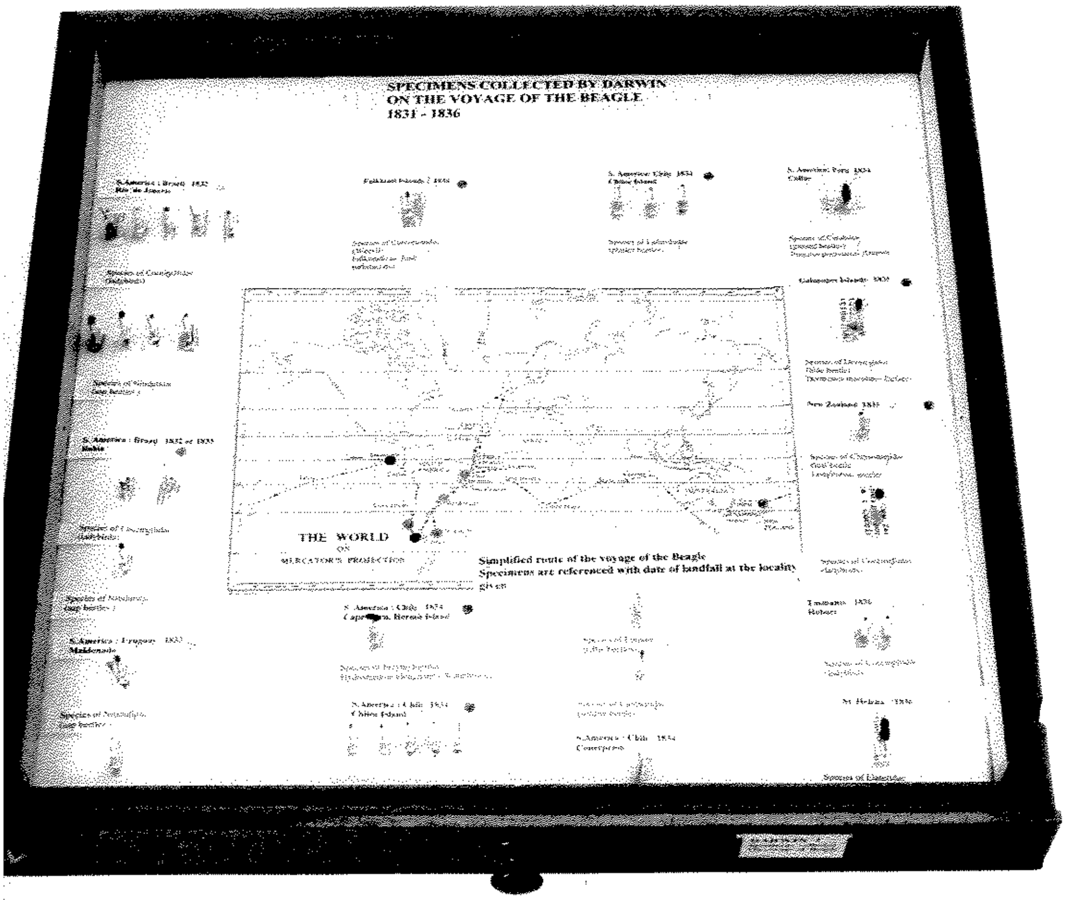
The term 'biodiversity' was invented in the 1960s and came into widespread use in 1988 as the title for a US National Academy of Sciences forum (Wilson & Peter 1988).* It has attracted plenty of interest for the word is usually accompanied by the qualifier 'threatened'. That statement is familiar

* Full references can be found in Further Reading on page 488.

or even banal and few doubt that the worst is yet to come. Even so, the grand extinction that marks the new millennium may present an opportunity to understand diversity. Ecology is often derided as a science without a theory but perhaps the upheavals of the past century may reveal more than did the apparently stable patterns of life seen by the early explorers.

Almost nobody denies the crisis that is upon us. Charles Darwin himself, on the last leg of his voyage, had a vision of what the next century would bring. He landed on St Helena in the South Atlantic. It rose 'like a huge black castle from the ocean', with its scenery having 'English, or rather Welsh, character'. The vegetation, too, was decidedly British, with gorse, blackberries, willows and other imports, supplemented by a variety of species from Australia. Many of its inhabitants were invaders. They had driven the natives to extinction. Darwin found the dead shells of nine species of 'land-shells of a very peculiar form' and noted that specimens of one kind 'differ as a marked variety' from others of the same species picked up a few miles away. All apart from one had been replaced by the common English *Helix aspersa*. As he noted, invasion was rife elsewhere, too. European plants were already 'clothing square leagues of surface almost to the exclusion of all other plants' on the La Plata plains of South America, and American natives were spreading through India 'from Cape Comorin to the Himalaya'.

Life in many of the other places visited by HMS *Beagle* is now worse than it was. St Helena had, soon after Darwin's time, forty-nine unique flowering plants and thirteen ferns. Seven have been driven to destruction, two survive only in cultivation and many more are on the edge. The island's giant earwig (the world's largest), its giant ground beetle and the St Helena dragonfly, all common at the time of the ship's visit, have not been seen for years. The St Helena petrel is extinct, and the sole remaining endemic feathered creature, the wire bird, is under threat. Nobody needs to be reminded of the equivalent fate of the Australian fauna, or of the dire state of the Galápagos. The Atlantic forest of Brazil – the site of Darwin's



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apotheosis – retains around twenty thousand kinds of plant, one in twelve of the world's known species, over a thousand vertebrates (including such spectacular creatures as the woolly spider monkey and golden tamarind) and huge numbers of insects, many found nowhere else. The habitat has been reduced to one twentieth of its extent at the time of Columbus. Much of the planet's ecosystem is under equal threat.

In 2002 the World Summit for Sustainable Development set out to 'achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level'. The figures are stark. The International Union for the Conservation of Nature publishes an annual

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Red List of species deemed to be in danger. In 2008, 16,928 creatures made it on to that roll of dishonour, six hundred more than in the previous year. The List is biased towards the spectacular and for them the situation is grim. Between 1998 and 2004 (the latest year for which we have figures) the world's birds declined on land, on fresh water and at sea, in the tropics, the temperate zones and the poles. In that brief period, two birds (the Hawaiian crow and Spix's macaw) became extinct. The situation in Europe is also dire (de Heer 2005) with a drop of almost a quarter in the numbers of birds, butterflies and mammals on farmland. One in four of the world's mammals is threatened, with half of the globe's 5,487 species in decline. The numbers of Tasmanian devils have dropped by half over the past decade while whales and dolphins are in almost as bad a shape (Schipper *et al.* 2008). Amphibians are under even greater threat for half of all species face imminent demise. Disease, too, plays a part, for mountain gorillas are under threat from the spread of the virus that causes Ebola fever in humans. The situation is particularly desperate in South East Asia, where almost all species of primate face extinction.

The real danger to diversity in both land and sea is the loss of habitat. The 2005 Millennium Ecosystem Assessment found that almost half of all tropical dry forests and a third of those of the Mediterranean have been replaced by farms and towns, which now cover more than a quarter of the Earth's surface. Asia has lost almost half its forests, even more of its mangroves and its reefs are in a dire state. To balance that, some species are highly invasive. Europe is the source of global threats such as the Austrian pine, the Spanish slug, the German wasp, the Scottish broom and English starling, but its own borders have been crossed by more than ten thousand invaders, among the most troublesome the Canada goose, Argentine ant, Indian strawberry, Chinese mitten crab and New Zealand flatworm.

What drives life's variety and what drives it out? Some extinctions – such as the almost universal loss of island endemics when faced with mainland invaders – do seem to show a certain consistency from place to place.

However, some rules that might seem obvious are not so. Big apes and birds are at more risk than are small ones, but body size has no effect on the fate of carnivores, reptiles, or marine molluscs (Jablonski 2004). And why do some places have many species and others few; and how can some creatures fill the world while others quail before them? Why do some evolve to cope while others give up the ghost? Ecologists have spent years in studying how communities vary in structure and how food, predation, energy flow and sex might change their fate. They have, alas, come to almost no agreement. The problem is that so often revisited by genetics: the difficulty of establishing a reliable scientific framework for an immensely complex system. In ecology, are there any general rules?

The Hidden World of Biodiversity

The 'species concept' has given rise to some of the most sterile debates in biology: but some clear definition is essential to establishing patterns of biodiversity. Is a bird species – such as one of the two thousand or so distinct kinds of island rail claimed once to have lived on the scattered patches of land across the Pacific – as biologically distinct as the mosquitoes of West Africa once classified under the label of '*Anopheles gambiae*' but now known to encompass several distinct insects? Without an objective statement of what the units are, it is hard to establish real levels of natural richness. Around three hundred thousand plants have been described, and four times that number of animals, but some experts claim that there may be as many as twenty million different kinds among the insects alone, to give weight to the familiar claim that, to a first approximation, all animals are insects. Even among mammals numbers have increased by almost a fifth in the past fifteen years, in part because some taxa have been promoted to species status from lower classificatory levels (Schipper 2008).

New technology also hints that some counts may be far less accurate than they appear. DNA probes make it possible to explore realms of life almost unknown a decade ago. Craig Venter, prominent in the project to map the human genome, has set out to classify the microbes of the sea (Gross 2007). Water from the Atlantic, Pacific, Baltic, Mediterranean and Black Seas was passed through filters to capture organisms of a variety of sizes. Already twenty million new genes and thousands of new protein families, some quite novel, have been found. This may indicate the presence of vast numbers of new species in a habitat which comprises 99 per cent of the whole biosphere. The Sargasso Sea alone has at least 1,800 new varieties of bacteria.

The soil, too, is a hotbed of life. Two shovelfuls of earth taken a metre apart may possess entirely distinct communities. The number of species per gram of soil has been estimated, on the basis of molecular taxonomy, to be between 2,000 and 800,000 depending on what criteria are used (Dance 2008). Two sites in Alaska, one in tundra and one in taiga forest, shared only eighteen kinds of invertebrates (microbes excluded) out of a total of some 1,300. Until our ability to identify the evolutionary units is more dependable the many claims of regular geographic patterns of diversity may be overstated.

Biodiversity and Where to Find It

However it is measured (from species richness, to listings based on information theory, or on weighting the index towards rarer or endemic creatures, or by including data from different ecosystems within a region) there appears at first sight to be a clear tendency for tropical landscapes to be more diverse than those to the north or the south. For terrestrial creatures, part of the global pattern comes from geography: there is relatively more land – and hence more habitat – near the equator than the poles (although the effect does remain when that is corrected for). Sampling effort is also in part to blame: in Darwin's day Britain would have scored top of any biodiversity index – but that was simply because so much was known of the natural history of that undistinguished group of islands. Even on a smaller scale, incomplete sampling confuses real patterns. In mountain ranges, frequently taken as a microcosm of the contrast between the warm tropics and colder poles, species diversity is often claimed to decrease with altitude. However, a survey of more than 400,000 records of 3,000 flower species in the Pyrenees shows that simply by varying the distance between samples almost any pattern of diversity change with height, positive, negative, or hump-shaped, can be generated (Nogues-Bravo 2008).

Recent historical accidents may also have a large influence upon ecological trends. In the Pyrenees altitudinal changes in floral richness are much confused by the fact that farmers have modified lowland habitats more than they have those far above them. One surprise has been to find that what seem to be pristine habitats have long been modified by man: itself a complication when trying to establish natural patterns of variability. Even Darwin's Atlantic forest of Brazil, together with the vast biological storehouse of the Amazon jungle, are partly human constructs, for their structure has been much disturbed by the large indigenous population that lived there in pre-Columbian times and turned parts of it into parkland (Heckenberger *et al.* 2008).

A century and a half of research has improved our knowledge of ecosystems, but many regions of the globe and – more important – many habitats remain relatively unexplored. Sometimes, detailed sampling reveals astonishing patterns of diversity: a single bay on the island of Flores, in the East Indies, has more species of fish than does the entire tropical Atlantic (Briggs 2005). As a result, the geography of diversity has begun to look more complicated than it did. The Conservation International organisation names 34 patches of land as 'hotspots' that contain almost half the world's known plant species and a third of its vertebrates. Together, they represent less than 2 per cent of the terrestrial world. The hottest spots of all are indeed in the tropics – Sundaland, Madagascar, Brazil's Atlantic forest and the Caribbean. Together, in one two-hundredth of the total land surface, they boast a fifth of known plants and a sixth of vertebrates (Sodhi 2008). For mammals, in contrast, the high points of variation include the Andes and the Hengduan Mountains of south-western China (Schipper 2008).

Mediterranean ecosystems such as those of South Africa, of Western Australia, or of the Mediterranean itself, also contain large numbers of creatures although they are well away from the equator. Hotspots are important in conservation, but (Grenyer 2006) there is often little congruence in the distribution of threatened species, particularly when the rarest creatures with the smallest ranges are considered – indeed, if anything they tend to be found in different places. A study of large-scale spatial change in amphibia, birds and mammals across the Western hemisphere suggests that there is some congruence of pattern for birds and amphibians (but much less for all three groups considered together) when areas of high local differentiation are considered. However, the opposite is not true – the three have large regions of relative homogeneity in quite different places (McKnight 2007). In the deep sea, too, there are few consistent associations of biological diversity with depth, latitude, sediment type, or water quality.

What Drives Biodiversity?

Many rules of diversity have been proposed. Food, predators, climate, efficiency of energy transfer and complexity of the habitat have all been appealed to as agents underlying community structure. Some cases are convincing, but a closer look reveals a disappointing lack of consistency from one ecosystem to another. Some are under top-down control through the action of predators, while others respond to forces that well upwards from the primary producers and yet more depend on an interaction between the two. It might seem obvious that a complicated place like a rainforest is more productive and more diverse than a peat bog, and a survey of dozens of habitats suggests that the most connected communities may be more efficient. Even that evidence is not always persuasive, for experiments in which particular species have been removed one by one from grassland or pond to see how well the remainder survive give results that are ambiguous at best. A search for order behind local or global patterns of ecological change has not always been a success.

The most productive parts of the world are, it is often said, the most blessed with unique forms of life, perhaps because they have more energy input from sunshine. Whales and dolphins also tend to be most diverse and most abundant in middle latitudes such as the southern Indian Ocean; and although these are not close to the equator they are regions of high productivity (Schipper *et al.* 2008). Metabolic rate may be the main driver, with small or relatively warm-blooded creatures living more speedy lives and generating more species than do their opposites (although the shared geographic patterns of change in warm- and cold-blooded creatures does not fit this notion).

An alternative view emphasises the importance of predators in maintaining community structure and a whole science of food webs attempts to analyse the patterns of eating and being eaten among species in a search for regularity. The re-introduction of wolves to Yellowstone National Park led to more corpses being scattered across the landscape and to increased opportunities for a variety of scavengers, while browsers increase the plant diversity of the pastures upon which they feed. Conservation biologists often believe that large predators help maintain the structure of a community and much effort is devoted to ensuring the survival of such creatures (Sergio *et al.* 2008). Once again a wider look at the dozens of claims made for the importance of predators reveals a depressing lack of consistency. Although the trophic effects of a large predator may be important in some places they do not seem to be important general agents as many creatures seem to live lives rather detached from those of most other species around them. A meta-analysis of twenty food webs (Vermaat *et al.* 2009) hints that they might fall into two classes, highly interconnected or more linear, with fewer links; but the tie between predation, energy flow and community structure is not clear, and may involve further attributes of each species such as how easy they are to eat.

Randomness and the Diversity of Life

In the past few years, a new notion has emerged: that community structure can best be explained with a radical and at first sight absurd assumption that, in effect, all the species involved are equivalent and that their abundance turns on random fluctuations in survival and in reproduction (reviewed in Leigh 2007). This 'neutral model' of ecology has parallels with its equivalent in genetics, in which levels of inherited variation emerge from a balance between random mutation and the accidents of genetic drift. That model has been tested against the real world, and although it sometimes fails, at the level of DNA sequence it retains considerable explanatory power (Clark 2009). In ecology, too, a random model of communities may carry more general conviction than does a series of special cases that explain some patterns in some places but have little predictive power overall.

Darwin accepted random change when he noted that islands contain fewer species than do nearby tracts of mainland and the claim that island life is driven by the accidents of migration and extinction has held up well. The same is true in other populations, on a variety of timescales. Thus, when cataclysms strike, as in the five great extinctions of the past five hundred million years (most associated with comets or great geological upheavals), huge numbers of species of many kinds disappear through mere ill luck, and rules that might help predict their ability to withstand everyday pressures do not much apply (Jablonski 2004). Other geological events quite unrelated to the biological universe such as continental drift also have persistent effects on the diversity of communities. In the same way, the last ice age stripped Northern Europe of most life and the glaciated regions are still depauperate as the result of an ancient historical accident rather than as a response to modern conditions.

The peak of coastal marine species variety is in Indonesia and on the northern coasts of Australia (Renema *et al.* 2008). There, coral reefs flourish. Such places are often appealed to as an epitome of undisturbed and productive nature, in which new kinds of creature can evolve to add to the treasury of life. A closer look at the fossils and the genes shows that in fact the occupants of the reefs have moved across the globe as conditions changed. During the Eocene, marine diversity found its peak in south-west Europe and North Africa, along the Arabian Peninsula and in what is now Pakistan. As these lands were raised from the sea when Arabia crashed into Asia, many of their inhabitants migrated to more congenial places, the present Indo-Australian region included. Most of the animals supposed to have originated there have in fact an ancient and dispersed history. Global disasters of fifty million years ago have done more to shape the geography of today's teeming reefs than have climate, food or sunlight. Evolution, that reminds us, works on a far longer timescale than does ecology.

As in genetics, there are many non-linear interactions in ecology (Andersen *et al.* 2009) and, as in the weather and the stock market, a small disturbance can lead to a sudden and unpredictable change in state. An attempt to shoot foxes to increase the numbers of red grouse prey backfired, for the predators normally caught only the birds most filled with parasites and once they were removed disease spread and killed many more birds than before. In a related case, an attack by one insect herbivore on a leaf often alters its attractiveness to other grazers, while plants that activate a pathway that fights fungal disease may reduce their own ability to combat insect attack with a different biochemical strategy. All these and many more multiple interactions (Strauss & Irwin 2004) emphasise that – as in genetics – many of the connections among species within a community are far from simple.

The importance of randomness first came to attention with the 'paradox of the plankton', the discovery that the apparently homogeneous environment of the sea was host to a vast diversity of drifting creatures all apparently in competition for the same resources, in contradiction to the supposedly fundamental principle of exclusion of species with similar demands (Scheffer *et al.* 2003). The plankton have become even more paradoxical with the discovery of vast numbers of new marine bacteria. The same is true of the world beneath the soil, whose organisms differ wildly from place to place, but generate roughly the same mix of nutrients. Perhaps each of those habitats really is filled with a chance assemblage of ecologically equivalent creatures, each arriving more or less by accident.

That radical notion may have a wider validity, for it seems to apply to some very different terrestrial and freshwater habitats. Fish species diversity across eight hundred tributaries in the entire Missouri–Mississippi river system can be explained by the random loss of species of varying dispersal in a pattern that diffuses from a centre of abundance into streams of smaller and smaller size (Muneepeerakul 2008) with no need for any consideration of the nutrient status of streams, of other species, or of climate. The same is true of patterns of diversity in mature forests.

Temporal shifts, too, hint at an underlying lack of order. In a somewhat heroic experiment (Beninca *et al.* 2008) a series of laboratory containers containing samples of plankton from the Black Sea was cultivated for seven years, in – as far as they could be attained – constant conditions. The abundance of the various species varied dramatically with time, and the relative numbers of each type could not be predicted with any confidence over any period longer than a month (which is, incidentally, the longest period for which the British weather forecast is even slightly dependable). The system was driven by something close to chaos – but, even so, most species persisted at high or low frequency within the containers.

Natural ecosystems can also remain stable until a threshold is reached and then collapse. The effect is familiar to fisheries managers, for a trophic

Recent imbalances between sardine and anchovy numbers may have turned on small changes in climate, whilst overfishing can also drastically affect the balance of such ecosystems.

cascade may be set off by overfishing, with unpredictable results. In the Black Sea itself, there was, from the 1970s on, a shift from large (and valuable) fish to anchovies that feed on plankton, and then to gelatinous creatures such as jellyfish and ctenophores, which now teem in huge numbers and have, within a few decades, replaced what seemed a stable ecosystem. A similar shift in the Pacific from sardines to anchovies and back twice in the second half of the twentieth century may also have turned on small changes in climate in a regime poised on the edge of stability that moves unpredictably from one to another. There have been dozens of climate shifts from cool to warm and back again every few hundred or thousand years, in the past hundred thousand years, each of which was no doubt accompanied by sudden upheavals in what might have seemed like stable ecosystems. Even on a much shorter timescale, the numbers of birds and mammals in a particular place when studied for long enough swing wildly for no obvious reason (as in the collapse of the British house-sparrow). Unexpected outbreaks can also destroy whole ecosystems (as in Dutch Elm disease, which appeared from almost nowhere and killed millions of trees). Such fluctuation might maintain a complex community with no external driver, in which case the paradox of the plankton (and, by extension, of land-based ecosystems too) could be explained in terms of random change.

A recent review claims that 'ecological surprises' of this kind have proved to be almost universal (Doak *et al.* 2008). Not only do they reveal our ignorance of the laws behind biodiversity, but they hint that chaos and complexity may be the rule rather than the exception. Darwin himself was well aware of the difficulties of disentangling the patterns of nature. The term 'complexity' appears in *The Origin* almost fifty times, and 'innumerable' and 'endless' almost as often (although 'inextricable web of infinities' makes it just once). The tension between order and disorder remains unresolved and more than a century and a half since that remarkable work we may understand rather less (although we know considerably more) about the patterns of nature than we imagined just a decade ago.

Transportation District, 2007)
Denyan Sudjic *et al.*, *Blade of Light: The Story of London's Millennium Bridge* (London, Penguin Books, 2001)
John van der Zee, *The Gate: The True Story of the Design and Construction of the Golden Gate Bridge* (New York, Simon and Schuster, 1986)
W. Westhofen, 'The Forth Bridge', *Engineering*, 28 February 1890, pp. 213–83.

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T. Andersen, J. Carstensen, E. Hernández-García & C.M. Duarte, 'Ecological thresholds and regime shifts: Approaches to identification', *Trends Ecol. Evol. Syst.*, 24 (2009), 49–57
E. Beninca, J. Huisman, R. Heerkloss, K.D. Johnk, P. Branco, E.H. Van Nes, M. Scheffner & S.P. Ellner, 'Chaos in a long-term experiment with a plankton community', *Nature*, 451 (2008), 822–6
J.C. Briggs, 'The marine East Indies: Diversity and speciation', *J. Biogeog.*, 32 (2005), 1517–22
S.J. Clark, 'Beyond neutral science', *Trends Res. Ecol. Evol.*, 24 (2009), 8–15
A. Dance, 'Soil ecology: What lies beneath?', *Nature*, 455 (2008), 724–5
D.F. Doak, J.A. Estes, B.S. Halpern, U. Jacob, D.R. Lindberg, J. Loworn, D.H. Monson, M.T. Tinker, T.M. Williams, J.T. Wotton, I. Carroll, M. Emmerson, F. Micheli & M. Novak, 'Understanding and predicting ecological dynamics: Are major surprises inevitable?', *Ecology*, 89 (2008), 952–61
R. Grenyer, 'Global distribution and conservation of rare and threatened vertebrates', *Nature*, 444 (2006), 93–6
L. Gross, 'Untapped bounty: Sampling the seas to survey microbial biodiversity', *PLoS Biol.*, 5 (2007): e85 doi:10.1371/journal.pbio.0050085
M.J. Heckenberger, C.J. Russell, C. Fausto, J.R. Toney, M.J. Schmidt, E. Pereira, B. Franchetto & A. Kuikuro, 'Pre-Columbian urbanism, anthropogenic landscapes, and the future of the Amazon', *Science*, 341 (2008), 1214–17
M. de Heer, V. Kapos & B.J.E. ten Brink, 'Biodiversity trends in Europe: Development and testing of a species trend indicator for evaluating progress towards the 2010 target', *Phil. Trans. R. Soc.* B. 360 (2005), 297–308
D. Jablonski, 'Extinction: Past and present', *Nature*, 427 (2004), 589 http://www.nature.com/nature/journal/v427/n6975/full/427589a.html
E.G. Leigh, 'Neutral theory: A historical perspective', *J. Theor. Biol.*, 20 (2007), 2075–91
M.W. McKnight, P.S. White, R.I. McDonald, J.F. Lamoreux, W. Sechrest, R.S. Ridgely & S.N. Stuart, 'Putting Beta-Diversity on the Map: Broad-Scale Congruence and Coincidence in the Extremes', *PLoS Biology*, 5(10) (2007): e272; doi:10.1371/journal.pbio.0050272
R. Muneepeerakul, 'Neutral metacommunity

models predict fish diversity patterns in Mississippi–Missouri basin', *Nature*, 453 (2008), 220–23

D. Nogues-Bravo, M.B. Araujo, T. Romdal & C. Rahbek, C., 'Scale effects and human impact on the elevational species richness gradients', *Nature*, 453 (2008), 216–20

W. Renema, D.R. Bellwood, J.C. Braga, K. Bromfield, R. Hall, K.G. Johnson, P. Lunt, C.P. Meyer, L.B. McMonagle, R.J. Morley, A. O'Dea, J.A. Todd, F.P. Wesselingh, M.E.J. Wilson & J.M. Pandolfi, 'Hopping hotspots: Global shifts in marine biodiversity', *Science*, 321 (2008), 654–7

M. Scheffer, S. Rinaldi, J. Huisman & F.J. Weissing, 'Why plankton communities have no equilibrium: Solutions to the paradox', *Hydrobiologia*, 491 (2003), 9–18

J. Schipper *et al.*, 'The status of the world's land and marine mammals: Diversity, threat, and knowledge', *Science*, 322 (2008), 225–30

F. Sergio, T. Caro, D. Brown, B. Clucas, J. Hunter, J. Ketchum, K. McHugh & F. Hiraldo, 'Top predators as conservation tools: Ecological rationale, assumptions, and efficacy', *Ann. Rev. Ecol. Evol. Syst.*, 39 (2008), 1–19

N.S. Sodhi, 'Tropical biodiversity loss and people: A brief review, *Basic and Applied Ecology*, 9 (2008), 93–99

S.Y. Strauss & R.E. Irwin, 'Ecological and evolutionary consequences of multispecies plant-animal interactions', *Ann. Rev. Ecol. Evol. Syst.*, 35 (2004), 435–66

J.E. Vermaat, J.A. Dunne & A.J. Gilbert, 'Major dimensions in food-web structure properties', *Ecology*, 90 (2009,) 278–82

E.O. Wilson & F.M. Peter, *Biodiversity* (Washington DC, National Acad. Press, 1988).

Philip Ball

Agricola, *De Re Metallica*, transl. H.C. Hoover & L.H. Hoover (New York, Dover, 1950)

F. Bacon, *Advancement of Learning and Novum Organum* (New York, Willey Book Co, 1944)

F. Bacon, *New Atlantis* (1627); available at http://www.gutenberg.org/etext/2434

R. Cotterill, *The Cambridge Guide to the Material World* (Cambridge, Cambridge University Press, 1985)

P. Medawar, *Pluto's Republic* (Oxford, Oxford University Press, 1984)

J. Meikle, *American Plastic: A Cultural History* (New Jersey, Rutgers University Press, 1995)

C.P. Snow, *The Two Cultures: And A Second Look* (Cambridge, Cambridge University Press, 1965)

L. Wolpert, *The Unnatural Nature of Science* (London, Faber & Faber, 1992).

Oliver Morton

David Oldroyd, *Earth Cycles: A Historical Perspective* (Westport, Greenwood Press, 2006)

Robert Poole, *Earthrise: How Man First Saw the Earth* (New Haven, Yale University Press, 2008).