Evolution is evolving: 13 ways we must rethink the theory of nature

Do species really exist? Are genes destiny? Do only the fittest survive? Can we shape or stop evolution? New insights into nature are providing surprising answers, and a glorious new picture of life's complexity

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Our modern conception of evolution started with Charles Darwin and his idea of natural selection – "survival of the fittest" – to explain why certain individuals thrive while others fail to leave a legacy. Then came genetics to explain the underlying mechanism: changes in organisms caused by random mutations of genes.

Now this powerful picture is changing once more, as discoveries in genetics, epigenetics, developmental biology and other fields lend a new complexity and richness to our greatest theory of nature. Find out more in this special feature.

1 GENES AREN'T DESTINY

The principle of genetic plasticity

IN 1990, an international group of scientists embarked on one of the most ambitious research projects ever undertaken. They would sequence the entire human genome, determining the order of the 3.3 billion base pairs that code for the genes that make the proteins that each of us are built from. There was huge excitement at the prospect of decoding the "blueprint" of humanity. Given the complexity of our species, our genome was expected to contain at least 100,000 genes. What makes us human would finally be laid bare.

It didn't quite work out like that. The Human Genome Project was a resounding success, publishing its results in 2003, two years ahead of target. However, it revealed that humans only have around 22,000 genes, which is about the same number as other mammals. Meanwhile, the blueprint itself turned out to be encrypted in ways we are still trying to crack.

The same thing is true of us that is true of every species: our DNA can be expressed in myriad different ways depending on which combination of sequences is activated. It is this, not the number of genes in the genome, that creates the complexity of life.

The more we learn about genetics, the clearer it becomes that "genetic determinism" – the idea that genes and genes alone fix our destiny – is a myth. A given set of genes has the potential to produce a variety of observable characteristics, known as phenotypes, depending on the environment. An Arctic fox changes its coat colour with the seasons. The presence of predators causes water flea *Daphnia longicephala* to grow a protective helmet and spines.

The power of flexibility

Even a change in social environment can prompt a shift. In the European paper wasp (*Polistes dominula*), for example, when the queen dies, the oldest worker transforms herself into a new queen. But she isn't the only one to respond. Seirian Sumner at University College London and her colleagues found that the death of a colony's queen results in temporary changes in the expression of genes in all workers, as though they are jostling genetically for succession. This flexibility is key to the survival of the colony and the species, says Sumner.

Genetic flexibility allows any paper wasp to become queen
Uwe Grun/Alamy

The power of genetic plasticity can be seen in the humble house finch. In the past 50 years, it has colonised the eastern half of North America, moving into habitats ranging from pine forests near the Canadian border to swampland in the Gulf of Mexico. The finch's underlying developmental plasticity provided the raw material from which novel features evolved, including a range of new colourings and other physical and behavioural traits, says David Pfennig at the University of North Carolina at Chapel Hill. "Stop thinking about this as being like genes or environment, because it's a combination of the two," he says. Carrie Arnold

2 EVOLUTION SHOWS INTELLIGENCE

Natural induction

HOW has life on Earth evolved such a dazzling array of beauty and complexity in the 3.8 billion years since it emerged? The standard answer is that the sheer abundance of life forms means a huge number of random genetic mutations are happening all the time, allowing natural selection to test many prototypes at once (see "The standard model of evolution").

But some researchers suggest a radical twist to that explanation. They argue that evolution can learn.

Their inspiration comes from computer science. Computers can mimic intelligence using algorithms: iterative rules that combine existing knowledge with fresh information to generate novel outputs. A simple algorithm called Bayesian updating, for example, starts with many hypotheses and homes in on the best ones as new information becomes available.

Likewise, natural selection incorporates new information from the environment to favour the best-adapted organisms. Richard Watson at the University of Southampton, UK, decided to look at the mechanisms involved to try to work out what is going on. In evolutionary terms, information about the past is carried in genes inherited by the offspring of fit individuals. But a relatively recent insight is that genes don't code "for" particular traits. They are team players, and their activity is regulated by other genes to create a network of connections. Natural selection favours those connections that work best. This, Watson realised, is just like how a brain learns. Brains consist of networks of neurons whose structure is shaped by learning because the more a connection is used, the stronger it becomes. Sure enough, when Watson and his colleagues built a computer model that took account of the networked nature of genes, they found it could evolve to learn and remember solutions to problems with just a simulacrum of natural selection to reinforce the best attempts.

Brains don't just learn specific solutions to particular problems: they also generalise to solve problems they have never encountered. They do this by recognising similarities between new challenges and past ones, and then combining the building blocks of previous solutions to come up with novel ones. This is called inductive learning. Can gene networks do induction too?

Watson and his colleagues argue that they can. The key, they say, is that energy is required to connect genes, because proteins must be produced to achieve this. So, for efficiency, evolution favours networks with fewer connections, which are loosely linked with other subnetworks. These building blocks can be recombined in different ways to generate novel solutions to the problems that challenge life. Thus, evolution's simple processes form an inductive-learning machine that draws lessons from past successes to improve future performance.

This conception of evolution has far-reaching implications. For a start, it can explain how entire ecosystems evolve to be well-adapted despite natural selection favouring fit individuals, not fit communities. Think of the connections between organisms within an ecosystem as a network, and they too can learn by induction, as Watson and his Southampton colleague Daniel Power have demonstrated using computer modelling. "An ecosystem can't be adapted by natural selection, but it can be adapted by natural induction," says Watson.

This raises an intriguing question. If natural induction isn't about survival of the fittest, what is it about? "Maybe, evolution is less about outcompeting others and more to do with co-creating knowledge," says Watson. That really is a radical idea. Kate Douglas

3 MOVE OVER, SELFISH GENE

Cultural group selection

Kenya's Samburu people show how cooperation evolves
Ton Koene/VWPics/Science Photo Labs

EVOLUTION traditionally has a problem with Good Samaritans. If only the fittest individuals survive, then those who are nice to others at their own expense will surely be weeded out. Yet cooperation is widespread in nature, from plants that alert each other to danger and colonial insects that work as one to dolphins cooperating to round up fish.

A decades-old idea called kin selection can explain some of this: if organisms have enough DNA in common, then they can further their own selfish genes by helping one another. Bees, ants and wasps have a system of reproduction called haplodiploidy, which leaves colony members so closely related that they act almost as a single superorganism. And among any sexually reproducing species, parental care helps individuals propagate their genes.

But kin selection cannot explain why humans are so nice to strangers. One idea is that we have evolved to be super-cooperative because, over time, more cooperative groups have outcompeted less cooperative ones. But there generally isn't enough genetic variation between groups to allow natural selection to favour more cooperative ones.

Some researchers think the solution lies in an idea called cultural group selection. Forget shared genes, they argue: selection can favour cooperative groups if the people within them share enough culture. The idea is controversial because to work it requires that groups remain culturally distinct. As critics point out, people tend to migrate between groups, which should homogenise ideas and customs. Those who back the concept counter that groups have ways to retain their distinct culture, including a process called norm enforcement. Put simply, if someone migrates into a new cultural group, they are pressured into following the local rules because failing to do so leads to punishment.

Earlier this year, Sarah Mathew and Carla Handley at Arizona State University published a pioneering field study testing the idea. They sampled 759 people from four pastoral ethnic groups in Kenya – the Turkana, Samburu, Rendille and Borana – who compete intensively for land, water and livestock. The pair estimate that genetic differences between individuals from different groups was generally less than 1 per cent. Cultural practices and beliefs varied much more, by 10 to 20 per cent. People cooperated most with members of their own group, as cultural group selection predicts, and to a lesser extent with members of other groups whose norms most closely matched their own. That makes sense if culture rather than genetics is what matters. "I think this is one of the most explicit tests of cultural group selection theory so far," says Mathew.

Not everyone is persuaded. Max Krasnow at Harvard University sees no theoretical flaw with the idea, but says that some of his research undermines it. He has found that people don't just enforce the rules within their group, but also punish people from other groups who fail to follow their own group's norms. Mathew counters that it is reasonable to enforce the norms of outsiders as a step towards incorporating them into your cultural group. "This is often how empires expand," she says. Colin Barras

4 THERE IS MORE TO INHERITANCE THAN JUST GENES

Epigenetic marks

Plants can vary their fruit size because of epigenetic marks
blickwinkel/Alamy

IF GENES form the words in the book of life, then epigenetic marks are the punctuation. These chemical tags affect which genes are turned on and off in an organism. They are created in response to changes in conditions within cells or the external environment, such as temperature, stress or diet. Since their discovery in the 1950s, scientists had thought that all epigenetic marks were erased before genes are passed from parents to offspring. A dark episode in human history provided an early hint that this might not be so

In late 1944, as retaliation for a Dutch rebellion against German occupiers, the Nazis cut off food and fuel supplies to the Netherlands. By the time the country was liberated, adults were subsisting on an average of 580 calories per day. Children born to women who were pregnant during this time were small and had low birth weights. Surprisingly, though, later in life they had unusually high levels of obesity, diabetes and schizophrenia. So, too, did their children.

It makes sense if epigenetic marks are being passed down the generations. Marks created when food was scarce became associated with a high incidence of metabolic diseases in times of plenty.

Subsequent studies in plants and animals suggest that epigenetic inheritance is more common than anyone had expected. What's more, compared with genetic inheritance, it has some big advantages. Environments can change rapidly and dramatically, but genetic mutations are random, so often require generations to take hold. Epigenetic marks, by contrast, are created in minutes or hours. And because they result from environmental change, they are often adaptive, boosting the survival of subsequent generations.

Take the pea aphid. It is capable of both sexual and asexual reproduction, and comes in two varieties: winged and wingless. When scientists exposed a group of genetically identical pea aphids to ladybirds, the proportion of winged aphids increased from a quarter to a half. This adaptation, which helped them escape the predatory ladybirds, persisted for 25 generations. The aphid DNA didn’t mutate, the only change was epigenetic.

Epigenetic bequests aren’t always beneficial. Experimenting with nematode worms, Martin Lind at Uppsala University in Sweden and his colleagues have discovered that the key factor is whether environmental conditions remain stable. If they change, then adaptations may be detrimental to subsequent generations – as happened with descendants of the Dutch Hunger Winter.

The extent of epigenetic inheritance is contested. Some sceptics point out that, during mammalian reproduction, the creation of sperm and egg cells involves erasing epigenetic markers. Others argue that epigenetic transmission across generations is extremely widespread and useful. In plants, for example, it can account for differences in fruit size, flowering time and many other survival-boosting traits. Carrie Arnold

5 SPECIES DON’T REALLY EXIST

Taxonomic anarchy

The African elephant is now seen as two species not one
Wim van den Heever /naturepl.co

FOR most of history, we have had little trouble defining species. There was a general assumption that a finite number of distinct forms of life had existed unchanged since creation, each sitting in a clearly defined pigeonhole: human, housefly, hawthorn and so on. Within the past few centuries, and particularly after Darwin, evolutionary theory has emerged as a more satisfactory way to explain how species came into existence. Yet in doing so, it has made species far harder to define.

There are several aspects to the problem. One is that if we accept the idea of species evolving from other species, then we must allow that an ancestral species can gradually morph into one or more descendants. We would still like to place organisms in discrete categories, but doing so is difficult if species blur into one another through time. "As we have come to terms with evolution, it has highlighted a problem with the machinery in our heads we use for classifying," says Frank Zachos at the Natural History Museum of Vienna in Austria.

For Jody Hey at Temple University in Philadelphia, the more important problem is that biologists often have two objectives in mind when they define species: one is the traditional desire to divide nature into easily recognisable packages; the second is to explain, in evolutionary terms, how those species came into existence. "Humans have conflicting motivations towards species," he says.

Some researchers argue that these two objectives can never be achieved simultaneously. Down the decades, biologists have come up with a few dozen clever ways to define species. Some make it easy to classify the organisms we encounter – by their physical appearance, for example – but tell us little about the evolutionary process itself (see "Sadistic cladistics"). Other definitions get to the heart of how species come to exist, but can be difficult to use in the real world.

Hybrid bonanza

In principle, advances in genetic sequencing could have helped by indicating how genetically distinct different groups of organisms are and how long ago lineages diverged. But sequencing has arguably made the problem worse by revealing that interbreeding – more technically, introgression – between closely related "species" is common across the tree of life. "It does seem to be the rule, not the exception," says Michael Arnold at the University of Georgia in Athens. Indeed, evidence of introgression stretches right to our front door: our ancestors interbred with various ancient hominins that might, in the eyes of some, count as distinct species.

Another problem is that looking at genes rather than observable features makes it easier to find new species, leading to what some researchers have called taxonomic anarchy. For instance, a biologist can argue that a previously recognised species should really be split into two or more "new" species, as happened when genetic analysis of the African elephant led to its being separated into savannah and forest-dwelling species.

To help add more rigour to the business of defining new species, earlier this year Zachos and other biologists proposed establishing the first single authoritative list of the world's species. "Species" itself will remain a slippery concept, but at least we could all agree on where to draw the lines. Colin Barras

6 ADAPT FIRST, MUTATE LATER

Neo-Lamarckian adaptation

IN THE 1880s, August Weismann began cutting the tails of mice. He wasn't sadistic, he just wanted to find out whether animals can inherit traits their parents have acquired during their lifetime. In 1807, French biologist Jean-Baptiste Lamarck had argued that this is how novel traits evolve – the giraffe's long neck, for instance, arising as the result of successive generations of animals reaching to higher branches for food. But according to Darwinian evolution, organisms must acquire a genetic mutation before they can adapt to a new environment. To survive on land, for example, fish first had to evolve the ability to get oxygen from the air.

Unsurprisingly, Weismann's experiment failed: the offspring of his mutilated mice all had normal tails. But perhaps he was just ahead of his time. Today, there is evidence of Lamarckian evolution – of a sort. Take the Mexican spadefoot toad (*Spea multiplicata*). It breeds in ponds that appear after summer monsoons and the newly hatched tadpoles typically survive on a diet of algae and bacteria. However, should tadpoles find themselves in a pond where fairy shrimps are available, they adapt to take advantage of the more nutritious fare, developing larger jaws and shorter guts. To Nicholas Levis at the University of North Carolina at Chapel Hill, spadefoot toads provide a perfect example of plasticity-led evolution. "It reorients how we think about the adaptive process," he says.

The tadpoles of spadefoot toads can switch body type
Rolf Nussbaumer/naturepl.com

Such plastic changes occur because an environmental trigger affects an organism's development in some way. Levis has found that in the spadefoot toads this happens via 14 genes that underpin their ability to switch between the two different body types. Other organisms may achieve a similar result via epigenetic tags that turn genes on and off. Research by Morgan Kelly at Louisiana State University suggests that eastern oysters in the Gulf of Mexico have populations that can survive in low salinity waters because of epigenetic tags.

If the environment remains unchanged – abundant shrimps in the case of the tadpoles and low salinity for the oysters – then subsequent generations will continue to exhibit the traits that help them survive. But these traits are induced anew each time by the environment, not directly inherited from a parent, so how can they affect evolution?

"You can't evolve if you're dead," says Kelly. Plasticity may buy organisms valuable time to adapt genetically. Here's how it might work. In an environment where survival depends on a particular response, only mutations that reinforce that response, or at least don't undermine it, will spread so that eventually a plastic change becomes "fixed".

We don't know how prevalent this sort of evolution is. However, one study found that if you put fish on land they learn to "walk". Admittedly, the fish in question were bichir fish, which can breathe air and haul themselves along out of water if necessary. Nevertheless, simply being on land improved their walking abilities, hinting that plasticity-led evolution might underpin some key transitions in the development of life on Earth, such as the evolution of terrestrial animals. Carrie Arnold

7 WE CAN SHAPE OUR OWN EVOLUTION

Niche construction

EVOLUTION may be a game of chance, but some species load the dice. They modify their environment and so may improve their chances of survival. In doing so, they can change the course of their own evolution. This process is called niche construction.

Birds build nests, termites make mounds, beavers create dams and countless other organisms engineer their environments. Traditionally, biologists thought of niche construction purely as a consequence of natural selection. However, that argument doesn't always work. "It's not the case that genes for building concrete have spread through human populations and that's what led us to build our urban environments," says Kevin Laland at the University of St Andrews, UK. While niche construction isn't always an outcome of evolution, it is often a cause.

A beaver's dam is both a product and cause of evolution
John Webster/Getty Images/Aurora

Our own species provides a classic example. By inventing farming, humans not only modified the landscape dramatically, they also changed their diets. As time passed, human genetics began to change in response. "There was selection on our digestive enzymes that allowed us to process carbohydrates and milk protein," says Laland.

Niche construction isn't a niche activity, says Laland. It happens across the tree of life – in animals, plants and even bacteria – and can have big impacts. With niche construction, organisms can ensure that the selective pressures acting on them are more consistent through time and space. By creating the conditions of their existence, they are active players in their own evolution.

Some believe this is overstating it. "Niche construction plays little, if any, role in most kinds of adaptation," says Gregory Wray at Duke University in North Carolina. But there could be a way to settle the debate. If niche construction is widespread and many species manipulate the selective pressures they experience, then evolution should lead to broadly predictable changes. "A traditional biologist will say you won't be able to predict general patterns in evolution – some of us think we might be able to," says Laland. They plan to test the idea. "We'll find out who's right," he says. Colin Barras

8 CHANGE CAN BE QUICK

Contemporary evolution

MANY people think evolution is something that takes millions of years, making it imperceptible on human timescales. They have it upside down, says Michael Kinnison at the University of Maine. He and others have shown that organisms can evolve extremely rapidly in response to changes in their environment. However, evolution often reverses direction, making it appear slow over long stretches of time.

The famous finches of the Galapagos islands, which inspired Charles Darwin's thinking about evolution, provide a prime example of this. A single founder species reached the islands around 2 million years ago and gave rise to at least 14 different species, some with large beaks for feeding on big seeds, and some with much smaller beaks for other foods. That was considered fast for evolution, but newer findings suggest that these finches have been evolving far more rapidly than Darwin suspected.

In 1977, a drought on one of the islands, Daphne Major, wiped out ground finches. Only relatively large seeds were available to eat, so birds with larger beaks did better, and within a few generations, beak size had increased by around 4 per cent. Then the wet year of 1983 saw small seeds become abundant again and, over a few years, beak size shrunk back. The finches had evolved quickly but ended where they started.

Likewise, new species of finches may have come and gone. In the 1980s, a male cactus finch arrived on Daphne Major from an island 100 kilometres away and bred with two female ground finches. The offspring were fertile and bred only with each other in subsequent generations. Such genetic isolation, which is the key to creating new species, was once believed to occur over hundreds of generations, but here it happened in just three. Species formation can go rapidly backwards too. On the nearby island of Santa Cruz, finches had split into large and small-beaked birds. But the distinction between these species is starting to erode. Now, most have medium-sized beaks, probably because people feed them rice so they don't need a specialised beak.

Thousands of examples of rapid evolution have been documented. For instance, in just half a century, killifish in the US evolved to cope with pollution many times higher than the usual lethal dose. In fact, Kinnison avoids the term rapid evolution because he thinks this is the norm. Instead, he talks of "contemporary" evolution. Michael Le Page

9 SURVIVAL OF THE... LUCKIEST

Genetic drift

THE Great Ziggurat of Ur – a massive step pyramid – is one of the finest examples of 21st-century urban architecture. The 21st century BC, that is. Large cities were still quite a recent invention when it was built. Urban landscapes are very new in the context of life on Earth. Yet many species now call them home – and their evolution may have had more to do with luck than adaptation.

Natural selection favours certain genes – those that make an organism best adapted to a particular environment. But evolution can also occur through a non-adaptive process called genetic drift, whereby a gene may become dominant in a population purely by chance. Genetic drift is often explained in terms of a bag of tokens with equal numbers of two colours – 20 green and 20 yellow, say. A person draws a token, notes its colour and returns it to the bag, before repeating the process a further 39 times. These picks give a second "generation" of tokens – and chances are it contains more of one colour than the other: 17 green and 23 yellow, for instance. Repeating the process with this new population as a starting point will give a third "generation", which may be even more skewed in favour of yellow tokens. Eventually, the experimenter might randomly pick a generation containing all yellow tokens.

This monochromatic outcome is more likely in smaller populations: it would take countless generations for 1000 green and 1000 yellow tokens to "drift" into a population of 2000 green tokens, for example, but perhaps just a few generations for 10 green and 10 yellow tokens to become a population of 20 green tokens. Such outcomes can and do occur in nature, which shows how a population can lose genetic variability simply through chance.

Biologists have known about genetic drift for a century, but in recent years they realised that it could be especially common in urban settings where roads and buildings tend to isolate organisms into small populations. A 2016 study of the white-footed mouse, *Peromyscus leucopus*, in New York supported the idea. Jason Munshi-South at Fordham University, New York, and his colleagues discovered that urban populations have lost as much as half of their genetic diversity compared with rural populations.

Last year, Lindsay Miles at the University of Toronto Mississauga, Canada, and her colleagues published a review of evidence from about 160 studies of evolution in urban environments, in organisms ranging from mammals and birds to insects and plants. Almost two-thirds of the studies reported reduced genetic diversity compared with rural counterparts, leading the researchers to conclude that genetic drift must have played a role. "Genetic drift can definitely be a significant driver of evolution," says Miles.

These findings have big implications, because populations lose their ability to adapt and thrive if they lack genetic diversity for natural selection to work on. Of course, genetic drift isn't confined to urban settings, but given how much urbanisation is expected to grow, the extra threat it poses to wildlife is concerning. It highlights the need to create green corridors so that animals and plants don't become isolated into ever-smaller populations. Colin Barras

10 GENES DON'T JUST COME FROM PARENTS

Horizontal gene transfer

Gibbons' long arms are a sign of how evolvable apes are
Heather Angel/naturepl.com

CHRIS HITTINGER studies budding yeasts, the group that includes *Saccharomyces cerevisiae*, the yeast beloved of beer brewers and bread makers. It is one of the most diverse groups of organisms with a nucleus (aka eukaryotes), so Hittinger is used to seeing bizarre things in his lab. A few years ago, however, he saw something that really surprised him. "There were a bunch of genes in some of these yeasts that simply should not have been there," says Hittinger at the University of Wisconsin-Madison. The genes were used by bacteria to make iron-grabbing enzymes, and it looked like an ancestor of the yeast had stolen them – as indeed it turned out they had.

For nearly a century, microbiologists have known that bacteria can swap genes with each other, acquire viral genes when infected by viruses and even snatch free-floating DNA from the environment. This process is called horizontal gene transfer. As increasing numbers of microbial genomes have been sequenced, scientists have come to realise that it is remarkably common. Microbes aren't passively waiting around to accumulate mutations to adapt to changing environments. Instead, they can pick up genes they encounter, giving natural selection far more variety to work on. "They're all sharing genes with each other, and it's really a massive network of gene transfer events," says Gregory Fournier at the Massachusetts Institute of Technology.

Horizontal gene transfer has been most frequently documented in prokaryotes, single-celled microbes that lack a nucleus and so have few physical barriers to stop DNA from elsewhere being incorporated into their genome. But Hittinger's work shows that even some eukaryotes can borrow from distantly related bacteria. "Yeast and bacteria have fundamentally different ways of turning DNA into protein, and this seemed like a really, really strange phenomenon," he says.

DNA jumble sale

Melanie Blokesch at the Swiss Federal Institute of Technology in Lausanne has shown that physical closeness and the amount of time two organisms spend next to each other is key to their chances of acquiring DNA. Other studies indicate that metabolic and functional genes, such as those that help an organism utilise a novel food source or detoxify a harmful chemical, are the most likely to end up at the ersatz DNA jumble sale. The spread of antibiotic resistance genes in bacteria shows just how important this phenomenon is to the survival of microbes.

What about the wider role of horizontal gene transfer in evolution? "The question is how much [horizontally transferred DNA] persists over long periods of time, and ends up being material that is inherited and passed down to future species," says Fournier. There are hints that it could be quite a lot. Hittinger isn't alone in finding out-of-place clumps of DNA. Others have discovered them in mammals, and analysis of the entire human genome revealed that at least 8 per cent of our DNA derives from viruses. Indeed, by one estimate up to half of all human DNA derives originally from horizontal gene transfer. Carrie Arnold

11 SOME THINGS ARE BETTER AT EVOLVING

Evolvability

MONKEYS didn't stand a chance. When it came to walking on two legs, apes were always going to win out. Our branch of the primate family tree had what it took to evolve long legs, freeing up hands for other functions such as making complex tools – a significant adaptation on the road to becoming human. In this respect, monkeys just aren't as evolvable as apes.

Evolvability is a simple concept. "It's the capacity of a population to evolve adaptively and to generate phenotypic [observable] variation that's heritable," says Tobias Uller at Lund University in Sweden. Some organisms are better at this than others, as the evolution of bipedal locomotion in primates illustrates. Early primates – in common with many animals – had four limbs that were approximately the same length and performed a similar function. All monkeys retain this anatomy. But at some point, apes broke free of this constraint and became more likely to generate front and rear limbs of different lengths. The result is clear to see in the range of ape body shapes today – from long-armed gibbons to long-legged humans.

What isn't so clear is exactly what it means for a group to be evolvable. Biologists have been discussing evolvability for two decades, but there is still no agreement on exactly how to use the term. Rachael Brown at the Australian National University, Canberra, has identified five distinct definitions. She points out that a population might be considered highly evolvable according to one, but not particularly evolvable according to another.

As the climate becomes drier, for instance, some plants grow smaller leaves that lose less water through evaporation. In doing so, they arguably demonstrate a form of evolvability, says Uller. The plants haven't changed genetically, but they have found a way to survive in the short term, buying some time during which they might accumulate genetic mutations and so evolve for a more arid life.

Other biologists argue that this isn't evolvability at all. Rachel Wright at Smith College, Massachusetts, is one of them. She and her colleagues recently published research on the evolvability of reef-building corals in the face of three environmental challenges: rising sea temperature, ocean acidification and increase in infectious diseases. They found that the corals with a tolerance for one of these stressors were also able to cope well with the others. This, they say, shows that these corals have the potential for rapid adaptation under climate change. "If the responses we observed were due to completely non-genetic effects, I would not consider this evolvability," says Wright.

The concept of evolvability is flawed but Brown says biologists need to agree a proper definition if they are to use it effectively. That is important because evolvability goes to the heart of some big evolutionary questions, from the potential effects of global warming to the evolution of bipedalism. Colin Barras

Some corals can rapidly adapt to stressful conditions
Carlos Villoch, magicsea.com/Alamy

12 EVOLUTION FAVOURS CERTAIN OUTCOMES

Developmental bias

AT THE heart of evolution is a random process: mutations to DNA that result in genetic variation. Yet, observe what evolves and you find that some outcomes are more likely than others. Instead of appearing directionless, as you might expect with a truly random process, evolution is full of repeating patterns. Now we know why. "You find some solutions evolving over and over again, not because they're the best, but because the developmental system [of organisms] has the tendency to throw up certain variations," says Tobias Uller at Lund University in Sweden.

This is called developmental bias, and it can be seen clearly in domestic animals. Many of them have floppy ears and curly tails along with shorter snouts and different coat colours compared with their wild ancestors. Yet, these characteristics have no obvious links to the qualities for which these creatures have been bred, such as tameness, milk production and meat yield. The mystery of so-called domestication syndrome was cracked when scientists homed in on a tiny cluster of stem cells in the developing embryo. These "neural crest cells" are involved in the development of a variety of tissues influencing things like face and ear shape and coat colour. They also give rise to the adrenal glands, which play a key role generating the fight-or-flight response that underpins tameness. Increase tameness by breeding for it, and the shorter snout and curly tail are dragged along for the ride.

If certain characteristics can develop more easily than others, than we should expect to see recurring patterns in nature. Developmental bias could be behind a fascinating quirk of evolution called parallel radiation: the phenomenon in which a species in one location diversifies into several distinct forms and, independently, the same diversification occurs in a different location. A famous example is cichlid fishes living in Lake Malawi and Lake Tanganyika in Africa. Each lake contains many different species that show striking similarities in the variety of body shapes to species in the other lake, despite being more closely related to those living in their own lake. These body shapes adapt species to particular niches or diets, so must have evolved by natural selection. But the forms the fish take aren't necessarily the only possible adaptive solutions. This suggests there are features of cichlid development that make some body types more likely to arise.

Despite directing evolution down certain tracks, developmental bias isn't inherently limiting, says Uller, because it can promote variation that is more likely to be beneficial and therefore more likely to survive. It could help explain why cichlids are so diverse and similar bursts of evolution among all sorts of organisms, from the Galapagos finches studied by Charles Darwin to Australian marsupials Carrie Arnold

13 WE CAN STOP EVOLUTION

Anti-evolution

EVOLUTION didn't just happen in the past. It is happening right now, and it is often seriously bad for us. That is why researchers are exploring ways to slow, stop or even reverse unwanted evolution, or out-evolve it.

Perhaps the biggest threat posed to us by evolution is the rise of antibiotic-resistant superbugs, which already kill 35,000 people each year in the US alone. Evolution also enables the growth of cancers that many of us will eventually succumb to. It is also to blame for pesticide-resistant insects that spread diseases such as malaria, "super rats" immune to poison and weeds that shrug off herbicides.

Some solutions are low tech. For instance, companies selling seeds for crops that are genetically modified to produce an insecticide called Bt often mix these seeds with non-Bt versions. If farmers grow only Bt-producing crops then only Bt-resistant pests will survive. Using a mixture allows some Bt-susceptible pests to survive too and mate with others, slowing the evolution of resistant strains.

Winning the arms race

The opposite strategy is to attack organisms on so many fronts that they have no chance of evolving resistance. This has saved the lives of millions of people who are HIV-positive. While the virus rapidly evolves resistance in the bodies of people taking just one antiviral drug, it is overwhelmed by combination therapies. Lee Cronin at the University of Edinburgh, UK, believes combination therapies can tackle antibiotic resistance too. His team is creating a robotic system for generating and testing the new drugs needed to do this. Part of the approach is to predict how superbugs will evolve, to stay ahead in the arms race.

Others are creating “anti-evolution” super-weapons. To reverse antibiotic resistance, they take viruses that attack bacteria and equip them with the CRISPR gene-editing system. The CRISPR system can be programmed to delete genes that confer antibiotic resistance, rendering bacteria vulnerable to antibiotics once more. Groups working on this approach include an Israeli-based company called Trobix Bio. It is developing a pill, codenamed TBX101, intended to target gut bacteria that are resistant to a group of antibiotics called carbapenems. These bacteria can cause deadly hospital-acquired infections.

Meanwhile, Jeffrey Barrick at the University of Texas at Austin is trying to undermine the genetic mutation process itself. He tweaks the proteins that replicate DNA in *E. coli* bacteria so that they make fewer mistakes when copying the genetic code. That means fewer mutations and slower evolution. Ironically, Barrick achieved this using a method for engineering desirable protein variants called directed evolution. Evolution is evolving – and not just through its own devices. Michael Le Page

The standard model of evolution

Twentieth century ideas about evolution rest on three pillars: variation, inheritance and selection. In this "modern synthesis", which combines Darwinian theory with genetics, variation arises in the form of genetic mutations. DNA sequences change at random as the result of external forces, such as radiation, and internal ones, such as damage to DNA or RNA caused by highly reactive molecules called free radicals. Most of these changes are either neutral or detrimental to life, but a few lead to the adaptations on which evolution is built.

Mutations may occur in any cell, but only those in germ cells, such as eggs and sperm, are passed down the generations to produce genetically distinct individuals: this is the basis of inheritance. One of Charles Darwin's greatest insights was the realisation that organisms tend to produce a variety of offspring, not all of which survive to reproduce. Natural selection weeds out those less well suited to their environment, he said, while fitter individuals survive and pass their traits on to their offspring. In this way, variation, inheritance and selection result in evolution, allowing life to adapt and new species to form as conditions change.

Today, evolution remains one of the most powerful ideas in science but, as with all good ideas, it is evolving. Many of the new conceptions arise from a better understanding of the mechanisms involved and a realisation that organisms take active roles in their own evolution. While accepting the underlying biological principles, many people see this model of evolution – the so-called "extended synthesis" – as a ragtag list of special examples. "The movement has identified the problem, but not the synthesis," says Richard Watson at the University of Southampton, UK.

But last year, Watson and his colleague Christoph Thies published a paper in which they argue that the progress of evolution on Earth – from the first single-celled organisms to the complexity of biological organisation we see today – couldn't have happened without the extra mechanisms in the extended synthesis. "In short, the extensions are the 'glue' that make the whole more than the sum of the parts," they conclude. Kate Douglas

Sadistic cladistics

Classifying nature was once so simple. Learned, often bearded, men travelled the world collecting specimens and ordered them on the basis of shared behaviour and traits into their rightful groupings to give a branching hierarchy of kingdom, phylum, class, order, family, genus and species.

All that began to change in the 1950s – and that is in turn changing how we view the products of evolution. Devised by German entomologist Willi Hennig, cladistics is a more systematic way of analysing the relationship between organisms based on traits that aren't just shared, but also genetically derived from one another. As our tools for doing "phylogenetic" analyses have become more powerful, cladistics has run a coach and horses through many familiar and much-loved taxonomic groupings.

In cladistics, the gold standard for a group, or "clade", is to be monophyletic, meaning all species in the clade share one common ancestor. Slightly sniffed at are groupings that turn out to be paraphyletic, meaning that all species in them share a common ancestor, but there are species outside them that also share that common ancestor. Doubleplusungood is for a group to be polyphyletic, with its members having more than one common ancestor.

A prominent casualty of cladistics analysis is the class Reptilia. The common ancestor of all scaly, cold-blooded reptiles – crocodiles, lizards, snakes, tortoises, dinosaurs and the like – also gave rise to the warm-blooded, fur-and-feathered mammals and birds, but at different points. So reptiles are cladistically paraphyletic. To be taxonomically correct, you should refer to birds, mammals and reptiles together as "amniotes". Alternatively, accept that birds are reptiles, since all members of both groups share a common ancestor, and you will be doing just fine. Confusingly, though, both birds (Aves) and mammals (Mammalia) are true, monophyletic clades each with a separate, common ancestor.

Cladistics also causes trouble for the largest group of vertebrates on the planet, the bony fish. Traditionally, they were put in the class Osteichthyes. But given that tetrapods – land vertebrates – evolved from a fish that learned to walk, cladistics would classify all mammals, birds, amphibians and reptiles, including dinosaurs, as fish. (Yes, that makes you a fish, too.) The problem is solved in modern taxonomy by redefining the Osteichthyes as a "superclass" consisting of the tetrapods and lobe-finned fish, which share a common ancestor. Ray-finned fish, which are most of what we consider fish, are hived off into their own satisfyingly monophyletic class, the Actinopterygii.

TANGLED CLADES

But marine taxonomists take note: corals, crustaceans, jellyfish and sponges all officially don't exist either, because they are all paraphyletic. In fact, invertebrates generally aren't a thing, phylogenetically speaking: if they were, they would have to include all vertebrates too. More specifically, you may be pleased to learn that there is also no such thing as a wasp. They are paraphyletic, sharing a common ancestor with ants, of which there are more than 10,000 species. Moths are out too, for the same reason. But butterflies all share a common ancestor, so they can stay. Worms, meanwhile, once misidentified as reptiles, are a complete tangle of long, thin things belonging to a whole host of different clades. Richard Webb

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