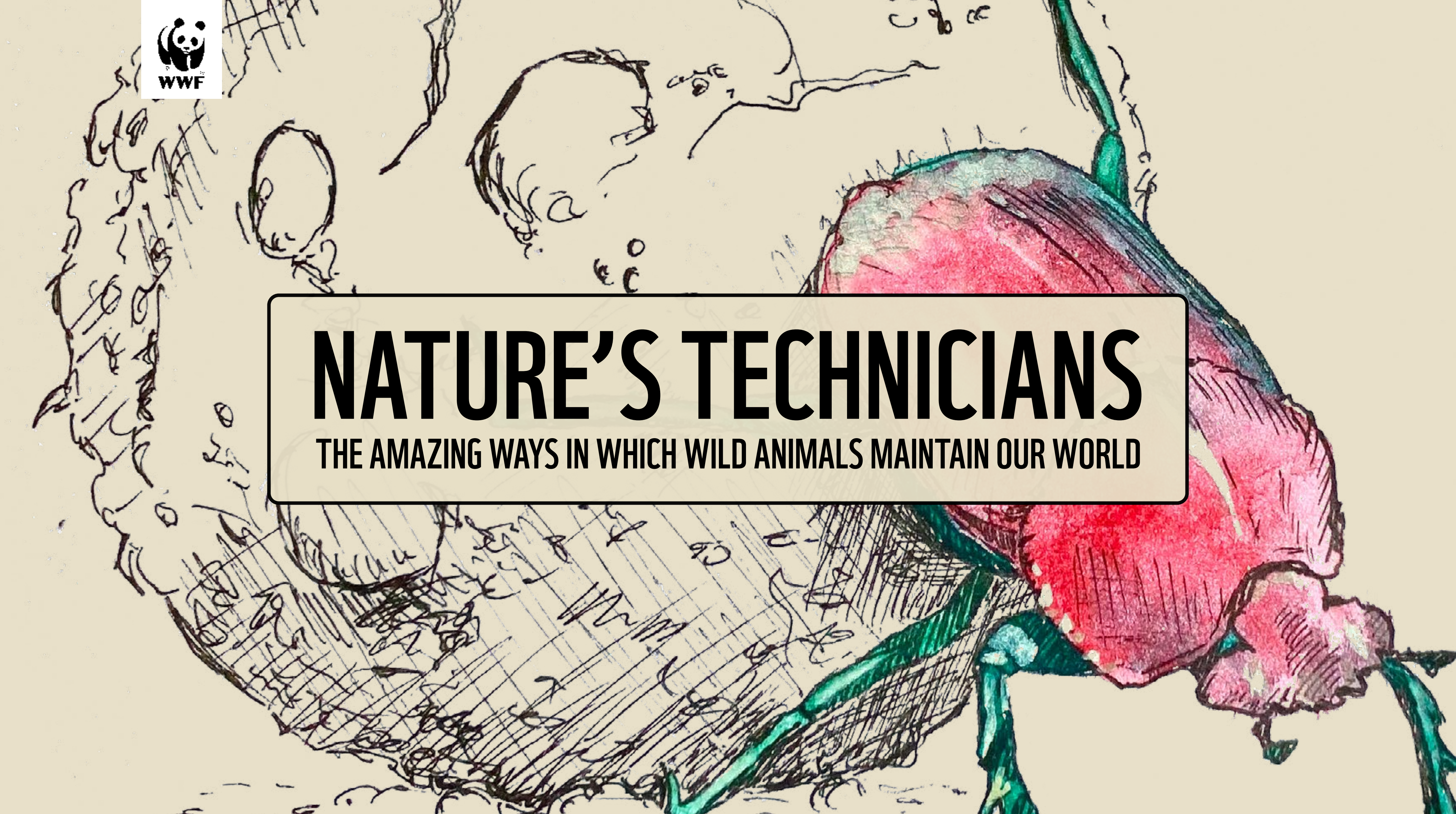

NATURE'S TECHNICIANS

THE AMAZING WAYS IN WHICH WILD ANIMALS MAINTAIN OUR WORLD

Recovering wild animal species should no longer be considered a 'nice to have' but an essential part of securing the future resilience of our planet, and ourselves

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Foreword

I've been blessed in my career with opportunities to study some of the world's most iconic species – on land (tigers and elephants), under water (manatees) and in the trees (primates and birds). While my family and many friends never quite understood my studies, they easily related to the beauty, the power or the quirky behaviours of the animals I studied. And if the creatures of my attention were endangered, my days spent investigating seemed all the more reasonable to them. Many donors had similar reactions – proposals to count tigers and elephants were funded much more readily than those looking into the role of fruit-eating hornbills and gibbons in the dispersal of forest trees. I'm just as mesmerized as anyone by the charm and physical appeal of wild animals, but I'm equally captivated by the myriad roles they play in nature — whether large or small, gorgeous or funny-looking – and the profound impact they have on our lives.

WWF has long embraced charismatic species to advance our biodiversity conservation efforts. These flagships have played – and will continue to play – a crucial role in generating public interest and financial support for conservation. But it's not only the imposing predators or stately herbivores that hold the keys to our ecosystems' health – we need to elevate the less celebrated species that play crucial roles in maintaining the intricate and dynamic balance of nature and provide the ecosystem services on which people depend.

In Nature's Technicians, you will read about the critical contributions of not only charismatic species like elephants, bison and sea otters, but also dragonflies, ants and beetles, as well as the decidedly uncharismatic worms, fungi and oysters in maintaining our forests, grasslands, rivers and oceans.

Our review aims to refocus attention on the vast value that societies, economies and natural habitats obtain from wildlife's contribution to the diversity of nature – something that is commonly overlooked. We provide evidence for the vital roles wild animals play in seed dispersal, pollination, pest control, soil maintenance and nutrient cycling, and show how they are the building blocks of functional ecosystems, emphasizing how these functions are integral to the well-being of human societies. Without healthy wildlife populations, we would have a very different and vastly diminished world.

By showcasing these vital connections, we hope to inspire a deeper appreciation for all wild creatures and the urgent need to protect and conserve their habitats. We also hope the suite of examples helps governments see the value of living up to their commitments to the goals and targets of the Convention on Biological Diversity's Kunming-Montreal Global Biodiversity Framework and the importance of implementing their National Biodiversity Strategies and Action Plans.

As you read the review, I encourage you to consider the broader implications of wildlife conservation. Recognize that every species, no matter how small or seemingly insignificant, contributes to the tapestry of life. Our collective efforts to preserve biodiversity are not just about saving individual species, but about sustaining the natural systems that support us all.

— DR. MARGARET KINNAIRD, GLOBAL WILDLIFE EXPERT

Foreword

We are all touched in our daily lives by wild animals – whether it be the song of a garden bird, or the fish on our plate at dinner time. But rarely do we consider the fundamental roles that the staggering diversity of wild animal species play in our own survival. I'm delighted that this report will help illuminate these often-hidden roles, helping us understand how we are all connected; how wild animals from the mighty whale to the humble dung beetle are all essential pieces of the puzzle that make up life on Earth.

Understanding the importance of wild animal species can be fascinating and inspiring, but can also quickly be followed by a sense of dread, given the alarm bells that have been sounding for decades warning us that wild animals are in peril. It is estimated that over a million species may be facing extinction and that wild vertebrate species have declined on average by over 70%, just in my lifetime. These declines are devastating in their own right, but are particularly so when we realise that this is not only bad for wildlife, but bad for us too.

And yet, hope is not lost. In fact hope is very much alive and kicking. We know that wild animal species can be recovered from the brink of extinction, because this has been done in almost every corner the world. The Iberian lynx, once the most endangered cat species in the world, has experienced a 10-fold population increase since 2002, thanks to decades of dedicated recovery efforts. The snow leopard is also increasing in countries like Bhutan, including through conservation of its high mountain habitat, which is the source of rivers on which over 330 million people directly depend. Similar species recovery stories from tigers, to white and black rhinos, to mountain gorillas, and even our logo species the giant panda, show us that these are not isolated incidents, but real evidence that wild animal recovery is achievable. These successes are not limited to charismatic megafauna; the bettong or kangaroo rat, a mini but mighty marsupial, is making a brave comeback in Australia thanks to dedicated recovery efforts. The bettong's digging plays an important role in the decomposition of leaf litter, reducing fuel loads and fire risk, vital in a country where fires have been so devastating for people and nature.

So how do we take these species conservation and recovery successes to scale? In my view, it's about integrating wild animals into the growing number of powerful frameworks and approaches that could truly be groundbreaking in the global effort to halt and reverse biodiversity loss. The Global Biodiversity Framework, adopted by 196 governments, is one of those. The accelerating drive around Nature Based Solutions is another. However, it is crucial to keep front of mind, in implementation, the incredible importance of wild animal species to the success of these efforts, ensuring that we restore not just the trees but also the wild animal species that truly bring forests to life.

But we won't get there without a massive scale up in the finance needed to bridge the biodiversity funding gap. We won't get there without innovation, to ensure we can achieve impact faster, more efficiently, and with longer lasting impact. And we won't get there without all of us, working together, recognizing we all have a role in saving wild species, to save ourselves.

— WENDY ELLIOTT, PRACTICE LEADER, BIODIVERSITY (INTERIM)

Executive summary

Wild animals of all shapes and sizes play crucial roles in ecosystems and ecosystem services, and therefore in our own survival. Conserving and recovering wild animals (mammals, birds, reptiles, amphibians, fish and myriad invertebrates) is essential for securing the future resilience of our planet, and ourselves. This report assesses the evidence by examining guilds, groups of species that exploit the same kinds of resources in comparable ways. Each guild plays a different role.

As well as focusing on guilds, we include shorter sections looking at:

Services Focusing on roles that animals play in climate regulation, along nutrient arteries like rivers, for water quality, regulation and erosion control, in disaster risk reduction and in disease prevention.

Amazing animals Describing specific animals (Hornbills, Oysters, Lynx, Bees and Salmon) and their roles in providing ecosystem services.

GUILDS Groups of species that exploit the same kinds of resources in comparable ways

PREDATORS manage populations of prey & competitors, with outsized effects on ecosystems & their services.

BROWSERS & GRAZERS maintain plant diversity & biomass through grazing, browsing, trampling, transporting & fertilizing seeds in their dung, migrating and dying.

PLANKTON-EATERS feed phytoplankton & ocean productivity – moving nutrients captured deep underwater & excreting them near the surface.

SEED DISPERSERS 50% of all plants rely on animals to disperse their seeds, ensuring habitat diversity, connectivity, resilience & plant genetic resources, with implications for climate adaptation, disaster reduction & water security.

POLLINATORS Globally nearly 90% of all flowering plant species and 75% of food crops rely to some degree on animals to pollinate them, making pollination one of the most important ecosystem services.

SOIL ENGINEERS move & create soil, cycle nutrients, store water, support food production, & help climate regulation.

BIOMES The benefits of wild animals in particular places, and the implications of their loss

THE AMAZON FOREST

THE ARCTIC OCEAN

THE CORAL TRIANGLE

THE MEKONG RIVER BASIN

THE KAVANGO-ZAMBEZI GRASSLAND

Biomes Drawing together the benefits of wild animals, and implications of their loss, across five examples from around the globe: The Coral Triangle, Mekong river basin, Arctic Ocean, Amazon and Kavango-Zambezi landscape.

Wild animals play irreplaceable roles in providing ecosystem services for humanity. Abundance is almost as important as existence: populations need to be large enough to function properly. Conservation is the priority, usually cheaper and always more effective than recovering wild populations. But species recovery can have fast, positive impacts. All conservation actions need to be planned and managed carefully; even if the impacts are positive, there will often be a minority of people who lose out and trade-offs need to be acknowledged. Stakeholders need to be part of the planning and implementation and compromises worked out.

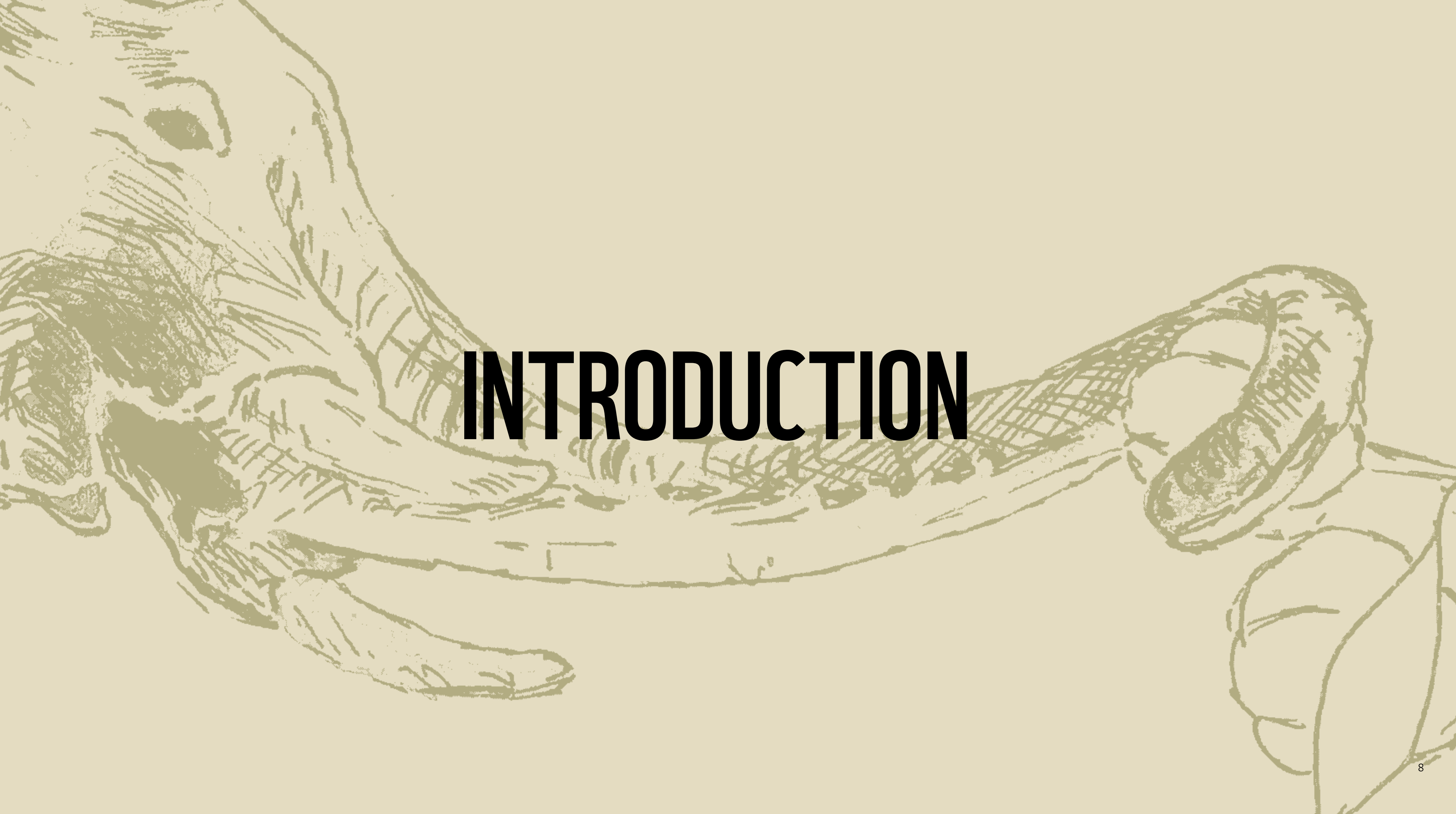
Spotlighting wild animals and the services they provide

SERVICES

- Plant & fungi services
- Disease preventers
- Climate regulation
- Disaster risk reduction
- Nutrient arteries
- Water quality, regulation & erosion control
- Non-material contributions of wildlife to people

AMAZING ANIMALS

- Lynx
- Pacific salmon
- Oysters
- Hornbills
- Bees



INTRODUCTION

Atop a hill in East Africa under the pink rays of an early morning sun, a young bull elephant (*Loxodonta africana*) is destroying an acacia tree, butting it, grabbing the trunk with his own trunk and generally behaving like a vandal. He may be acting logically, accessing nutrients from the roots.[1] Or he may indeed just be a grumpy teenager away from parental control, working off frustrations on the nearest thing at hand.[2] But in the process he is playing an important ecosystem role, opening up the ecosystem for regeneration and increasing plant diversity.[3] This in turn improves ecosystem stability, the variety of genetic material, the rate of carbon sequestration[4] and an array of other values, still often poorly understood.

The impacts of elephants are not straightforward; too many elephants in a confined space can reduce diversity[5] and threaten endemic species.[6] But ecologically balanced elephant populations play a key stabilizing ecosystem role, with many knock-on effects for human communities both positive and negative.[7]

Conservation is all too often presented as a black and white choice between nature and development, implying that any emphasis on the former is seen as

Many large fruits and seeds have co-evolved with elephants, often few other animals are large enough to disperse them.
© Hannah L. Timmins

a luxury compared with the practicalities of feeding a global population or extracting materials for a healthy economy. Over the past three decades, this has been effectively challenged in the case of plants. The emergence of concepts like 'ecosystem services' and 'nature-based solutions' have highlighted the critical role of vegetation, particularly forests, in providing a wide range of goods and services to humans. These include, but are not limited to, contributions to food and water security, Disaster risk reduction, human health, carbon sequestration and adaptation to climate change.[8] International bodies, governments, industry and civil society now broadly accept the crucial role of habitats such as forests, grasslands and wetlands to humans, albeit not always applying the knowledge very effectively in practice.

Yet wild animals are still often seen as less important from a pragmatic point of view, or even worse as simply a problem; human-wildlife conflict understandably generates headlines while the role of animals in the provision of many ecosystem services is not widely understood. This has real world implications: some ecosystems that appear healthy when viewed remotely in satellite images or to the casual visitor have been stripped of most of their large and medium-sized animals,[9] leading to the phenomenon of 'empty forests'. First recognized over 30 years ago,[10] this has still not been effectively addressed in conservation strategies[11] and empty forests are sometimes reported as 'intact' in global studies that focus on habitat extent. Yet empty forests are, as we will show below, not healthy forests, nor are they forests that will retain their ecosystem integrity over time. The same is true for all ecosystem types – from wetlands to grasslands, marine to mountain ecosystems, wild animals are crucial for long-term resilience.

This publication aims to help redress the imbalance, by outlining some of the important roles that wild animals – mammals, birds, reptiles, amphibians, fish and myriad invertebrates – play directly and indirectly in supporting human well-being. This is not to trivialize issues like the intrinsic rights of wildlife to exist or the ethical or cultural aspects of conservation, nor to ignore the fact that 'biodiversity rights' can sometimes bump up uncomfortably against human rights.[12] But unless we also understand the more tangible value of wildlife to humans, it is more difficult to build effective arguments for the investment of time and money and the negotiations and trade-offs needed to achieve effective conservation.

We look at these issues from three main angles: by examining the role of different ecological guilds (such as seed dispersers, browsers & grazers, and plankton-eaters); through the lens of a handful of 'Amazing animals' that illustrate the broad range of benefits provided; and finally, by considering the benefits animals provide – and the potential impacts of their loss – in a series of important biomes. While the report is written for the non-specialist, we draw deeply on peer-reviewed literature and conversations with many people working in the field. We cover a broad portfolio of issues in a short space, so have to be illustrative rather than comprehensive.

First, some general observations about what we stand to gain or lose. Most ecosystem services are deteriorating.[13] Wild mammals have suffered a dramatic loss of range (the geographical area or habitat where the species live), with 40% of species studied having lost over 80% of their range,[14] and many are threatened with extinction.[15] As a result, wild mammals now make up only a tiny 4% of total mammal biomass compared with humans (36%) and livestock (60%).[16] The sixth mass extinction, the fastest in the planet's history, is under way.[17] Many of the benefits we describe below are already disappearing.

One of the problems of recognizing the impacts of species loss is that they are at first sight quite subtle and often slow-moving, sometimes multi-generational in human terms. It's not usually like a house of cards, where one careless removal leads to the whole edifice (in this case the whole ecosystem) collapsing. This can happen in extreme cases,[18] and there are fears that it will become more common with rapid climate change,[19] but it has not been the rule until now. Instead, as we will see repeatedly in the following pages, the changes are more nuanced, and sometimes only visible to people who know what to look for, but nonetheless carry an extremely high cost.

We describe many of these below. When forests lose key animal species, the carbon-rich large-seeded trees that depend on these species to disperse their seeds may gradually be replaced by quick-growing species that store less carbon, produce fewer edible fruits and are more vulnerable to fire. Mass killing of the great whales has had major negative impacts on marine productivity. Loss of small mammals that dig and burrow in the soil reduces soil health and eventually overall productivity. Who knew? Even as ecologists we have been surprised by some of the linkages that we've uncovered during this study.

A regular pattern emerges. Loss of a key ecosystem component causes a change, often

Decline in wild mammal populations, coupled with nearly exponential growth of human and our domesticated mammals, have led to dramatic losses in their share of total mammal biomass.

harmful, to the ecosystem service provided, which is then replaced with a more expensive artificial alternative. This in turn often has unforeseen side effects, sometimes causing further biodiversity loss, requiring further interventions, with additional risks and costs, requiring yet more interventions, and so on… The impacts are less like the collapse of a house of cards than a gradually crumbling building, held up by an expensive and continuing patchwork of cheaply built structures, with costs rising all the time and the whole structure still inexorably falling apart. There are examples everywhere: a spiral of increasing pesticide use, expensive artificial flood defences, intensive pollination by human hand, 'seeding' oceans with iron supplements, tree diseases racing through monoculture plantations and many more.

It doesn't have to be like this. In the same way that the world is gradually recognizing the positive role of forests, grasslands and wetlands, we need a parallel acknowledgement of the importance of animal species. As the evidence we present suggests, ecosystem services generally need an entire functioning ecosystem to provide benefits over the long term.

Demonstrating a workable alternative is, unfortunately, only the first step. Wider uptake of nature-based solutions will almost inevitably be hampered by the fact that many businesses make their profits from the alternatives and have a vested interest in maintaining the status quo. Civil society has not caught up with the research showing the importance of ecosystem services. Pesticide use continues to increase globally, despite the existence of lower-impact biological controls. Changing the status quo will not be easy. But a proper understanding of the values of what we have been losing is a good place to start.

This publication summarizes complex issues of zoogeochemistry[20] (how animals influence nutrient cycling, including of carbon, nitrogen and phosphorus entering and exiting their ecosystems) for non-specialists. The issues we discuss often involve ongoing, cutting-edge research. Figures may change as we learn more, and there will be debates about some of these issues for years to come. The focus here represents quite a new way of thinking for many people. But our overall message – that wild animals are critical providers of ecosystem services – is hard to dispute.

Plant & fungi services

Ecosystem services from plants are now widely recognized, which is why, in this report, we concentrate on the role of wild animals. Plants play many crucial roles in the functioning of ecosystems and provide multiple benefits including sequestering and storing carbon; stabilizing soils, slopes and coastlines; increasing water capacity of soils; and providing foods, medicines and fuels. These are all fundamental building blocks for human society. Plants are the living framework around which we build our lives.[34]

The importance of fungi, which belong to a separate kingdom from both plants and animals, is less well known, but just as critical. The role of yeast, a fungus that grows as a single cell rather than as a mushroom, in producing bread and beer was discovered long before the development of settled agriculture;[35] the start of a huge role of fermentation in food security[36] with fungi and bacteria becoming major components of the modern food industry.

Fungi are great enablers, working with plants and animals in often mutually supportive partnerships. Over 90% of plant species have symbiotic relationships with mycorrhizal fungi (<u>Soil engineers</u>);[37] the fungi enhance the supply of nutrients that support the growth of plants, such as nitrogen and phosphorus, in exchange for carbon. Mycorrhizae can supply up to 80% of a plant's nitrogen[38](<u>Nutrient arteries</u>)[39]. Fungal hyphae networks (their branching filaments) pass carbon and other nutrients between plants.[40, 41] increasing net productivity and supporting forests' ability to sequester and store more carbon. Mycorrhizal fungi can alter plants' attractiveness to insects such as bees and other pollinators.[42] Some plants rely on fungi to stimulate seed germination.

Despite their ancient uses by humans, there is still much to learn about the range and significance of the ecosystem services that fungi provide.

People have been using fungi medicinally for millenia © Hannah L. Timmins

PREDATORS

Predators play a critical role in controlling and maintaining populations of their prey, their prey's food and their competitors. This control has outsized effects on ecosystems in their entirety and the services they provide. In ecosystems where predators have been eradicated or restored, we can see in real time the importance of the roles they play.

During the 1980s, a lively debate raged in ecology: was the more powerful force influencing ecosystems top-down or bottom-up? Ecologists such as E.O. Wilson drafted papers on 'the little things that run the world', extolling the importance of invertebrates in shaping ecosystem functions.[43] John Terborgh fired back a sequel to Wilson's piece, *The Big Things that Run the World*,[44] trotting out examples of jaguars (*Panthera onca*), pumas (*Puma concolor*) and harpy eagles (*Harpia harpyja*) having outsized effects on their ecosystems. As always in ecology, the truth is far more complicated than we can imagine; millions of interactions and indirect effects ripple out in all directions and in both ways from predator to prey and back again.

The restoration of wolves to Yellowstone is one of the most famous stories in reducing herbivore over-browsing and regrowing forests. © Hannah L. Timmins

A sea otter plucks a herbivorous urchin from the kelp forest floor thereby maintaining the forest and its role in storm protection, carbon storage and fish habitat provision. © Hannah L. Timmins

Limiting prey and other impacts of direct predation

The term 'trophic cascades' originally described the influences cascading down through an ecosystem from the feeding behaviours (hence *trophic*) of 'top' species like apex predators: for example, the control a predator like a lion (*Panthera leo*) has on limiting prey populations like wildebeest (*Connochaetes* spp.) and the impacts that has in reducing the herbivore's trophic limitations on grasses. Simply put, lions keep wildebeest numbers in check which means grasses have time to recover. A disproportionate loss of predators is unbalancing ecosystems around the world; restoring predators' regulating role is a major priority for conservation management.

Perhaps the first example of actively reintroducing an apex predator was along the Pacific north-west coastline of North America where sea otters (*Enhydra lutris*) had been hunted to local extinction for their lucrative fur. Sea otters had once been abundant, from the coast of Japan, stretching up and across the Aleutian Islands and down the Canadian and American coastline all the way to Baja, Mexico.[45] But by the turn of the 20th century there were only a few hundred surviving in isolated pockets, including Amchitka Island on the western edge of the Aleutians. When Amchitka was proposed as a nuclear test site, environmental organizations worked between 1965 and 1972 to relocate and reintroduce 710 otters to their historic range.[46, 47] As otter populations began to recover, local ecologists noticed a shift in their ecosystems. Many of the reintroduction sites had been sea urchin barrens – areas where large populations of herbivorous urchins had cleared the kelp forests. As the otters reestablished, they returned urchin populations to a dynamic but regulating equilibrium. The kelp forests regrew, hundreds of feet tall, and their fin fish and abalone inhabitants came back.[48, 49] The otters' kelp forests not only offer enhanced fish stocks; they also dampen coastal waves and currents, reducing the impacts of sea storms on coastal human communities.[50]

The kelp forests with otter populations also had much higher carbon density, sequestering 92% more carbon.[51] On Vancouver Island, sea otter tourism has been valued at US$31 million per year and all ecosystem services provided by otters have been valued at US$40 million per year.[52]

The impact of the reintroduction of grey wolves (*Canis lupus*) to Yellowstone National Park in the US is now famous worldwide. By the 1990s, half a century since the eradication of wolves, elk (*Cervus canadensis*) populations had skyrocketed to well over the park's carrying capacity, over-browsing the willow and aspen and denuding the mountains' slopes and valleys.[53] The reintroduction of wolves from 1995 onwards brought the elk population under control and within two years remarkable tree growth was being recorded.[54] Returning wolves over a larger area could result in nationally significant carbon gains.[55]

The presence of large carnivores in particular has been correlated with not only biodiversity gains and increasing biomass but also reduction of diseases in ungulate prey populations; this reduces the potential for disease spillover effects into people and our livestock.[56]

Over the last 100 years, reductions in range and population sizes of large carnivores globally may be one of the most pervasive human impacts on nature.[57, 58] Apex predators, particularly carnivores, are often wide-ranging and found at low densities because of their positions at the top of food webs; they are simultaneously some of the most admired and imperilled species on the planet.[59] Removal of this guild has led to diminished species richness and ecosystem functioning through the blocking of trophic cascades.[60, 61] Knock-on effects where predators are extirpated from or repatriated to ecosystems are seen globally.[62] In the UK, the dearth of large predators costs the country over £13.5 million (over US$17 million) every year in damage to forests and agriculture (Amazing animals: Lynx).[63]

Hunting cooperatively, lions are a major top-down force maintaining herbivore numbers in African ecosystems. © Hannah L. Timmins

STORKS

ONCE KNOWN AS THE FARMER'S FRIEND, CAN EAT UP TO

30

CRICKETS PER MINUTE

Predators of pests and invasive species

Predators are also responsible for controlling pest numbers, playing a critical role in maintaining ecological balance, contributing to sustainable agriculture and our health.

In the tropics, insect herbivores have huge potential to consume and limit plant growth. However, flying insectivorous predators like bats and birds limit insect damage to trees. In Papua New Guinea, for example, birds and bats can more than halve herbivorous insect density, reducing leaf damage by over 40%.[64] Flying vertebrate insectivores here have a big impact on plant biomass.

Pest predators offer economic benefits to farmers by reducing crop damage and increasing yields without the need for costly chemical interventions. Insects are often seen as pests, but predatory insects such as ground beetles increase crop yields by keeping weeds and pest species in check.[65] Storks (*Ciconia* spp.), once known as the farmer's friend, can eat up to 30 crickets a minute; a flock could consume 2 million African army worms (*Spodoptera exempta*) per day.[66] Wasps help prevent populations of caterpillars, spiders and crickets from reaching pest levels, providing an estimated US$416 billion in pest control each year.[67] In Australia, adult eastern brown snakes (*Pseudonaja textilis*), often persecuted as pests themselves, can collectively remove thousands of mice per square kilometre of farmland each year, substantially increasing farm productivity.[68]

Wetlands often provide breeding grounds for mosquitos, now an increasing problem in northern latitudes.[69] In these still waters, amphibians play the role of pest control and mosquito-borne disease prevention, making newts, frogs and salamanders an important defence against West Nile virus, yellow fever, dengue fever and malaria (Disease preventors).[70]

By controlling pest numbers, predators help reduce the need for chemical pesticides, which can have harmful effects on the environment, non-target species and human health.[71] Investing in the conservation and restoration of pest predators can lead to more sustainable and resilient agricultural systems.[72]

Landscapes of fear: indirect behavioural impacts

Landscapes of fear is the term coined to describe the impact that predators have on ecosystems through non-lethal effects on herbivores; the ecological impacts of being afraid.[73, 74, 75, 76] One version of this effect is when fear of predators deters herbivores from low-visibility habitats, producing variation in herbivore densities across the landscape, which is then reflected in variation of plant communities, creating a patchwork of scrub, trees and grasses.[77] For example, in Yellowstone, steep valleys present a risk to elk that know wolves may be present and able to ambush them quickly. This means that elk use these areas briefly to access water sources or move through without presenting too high a browsing pressure.[78]

The presence of nursery web spiders causes grasshoppers to stress-eat, reducing woody encroachment and ultimately resulting in 40% more carbon retained in soils. © Hannah L. Timmins

This has led to a denser regeneration of vegetation in the valleys of Yellowstone,[79] reduced stream bank erosion, improved water quality,[80] cooler water temperatures and the return of fish species, and North American beaver (*Castor canadensis*) which now have water-side access to willow.[81]

Landscapes of fear also play out at the micro-level; nursery web spiders (*Pisaurina mira*) are classic ambush predators, waiting and pouncing on grasshopper prey like a puma. In the presence of these spiders, redlegged grasshoppers (*Melanoplus femurrubrum*) stress-eat carbohydrate-rich plants instead of nitrogen-rich plants, changing the chemistry of their bodies. Their bodies and waste offer up less nitrogen to the ecosystem, slowing woody encroachment and conversion of grasslands to forests. In maintaining the grasslands and their grass root systems, the presence of nursery web spiders increases soil carbon retention by 40% (Browsers & grazers).[82]

Timescapes of fear describes the presence of predators making prey more vulnerable during certain periods. For example, American bison (*Bison bison*) in Badlands National Park in the US prefer open plains with better visibility when they have calves, allowing vegetation to recover elsewhere.[83]

Keeping the herds, or pods, moving is equally important in the oceans. Orca (*Orcinus orca*) may be at least partially responsible for driving calving whales from orca-populated, nutrient-rich, high-latitude waters to the nutrient-poor waters of the tropics. The tropics have fewer orcas and mother whales can keep their calves safer in their comparatively shallower coastlines; in doing so, they bring with them tonnes of nutrients (Plankton-eaters), increasing the fish productivity of these areas.[84]

Back on land, once predators are spotted their presence can cause a stampede, the rushing herd smashing the ground's surface, aerating soils and creating millions of hoof-sized niches for seeds, fungi, insects and more (Soil engineers).[85, 86]

Landscapes of fear also apply to mesopredators (medium-sized predators) like foxes (*Vulpes* spp.); when wolves, Lynx (*Lynx* spp.) and bear (*Ursus* spp.) are present, mesopredators hang around less, allowing their prey (e.g., rabbits) some protection. This smaller prey also feeds other predatory species like hawks, which control disease prevalence by keeping pests like rats in check.[87]

But landscapes of fear do not need to apply to humans that share space with predators. Human-wildlife conflict paradigms are slowly shifting towards human-wildlife coexistence through conflict-to-coexistence approaches – these need to be people-centred, taking into account the concerns, livelihoods and lifestyles of communities who live alongside predators.

Scavengers

Predation has a much bigger sphere of influence than just the prey and the prey food source: the carcasses of prey form mini-ecosystems themselves for scavengers,[88] insects, soil biota and microbial communities. These improve soil health and nutrient cycling (Soil engineers; Nutrient

Spotted hyenas have some of the strongest bites in the animal kingdom, allowing them to crunch through bone and fast-track the movement of calcium into surrounding animals and soils. © Hannah L. Timmins

arteries),[89] which again results in better plant growth.[90] Better vegetation health improves carbon storage and reduces erosion; this may be especially true in highly productive tropical regions where declines in plant biomass have been recorded after predator extirpation.[91, 92, 93]

Spotted hyenas (*Crocuta crocuta*) are 'bone-crackers', with some of the most powerful jaws and teeth among the large carnivores.[94] These adaptations, along with their low stomach pH,[95] allows them to break and digest the bones of both their own kills and scavenged carcasses, accessing nutritious marrow and minerals. Bones contain high levels of calcium and phosphorus, important not just to the hyenas but to the broader ecosystem too. Without bone-crackers, skeletons could take hundreds of years to decompose, depending on the environmental conditions.[96] Hyenas defecate in communal latrines; the concentrations of calcium and phosphorus in the soils of these latrines are between 1,000 and 20,000 times greater than surrounding areas, making them islands of enriched vegetation and insect life.[97] Lastly, the hyenas' discarded bone splinters are critical for the health of another important scavenger: in the absence of hyenas 17% of vulture chicks have been found to develop osteodystrophy (abnormal changes in formation of bone) and chick survival rates drop.[98]

Aside from nutrient dispersal, we need scavengers like hyena and vultures for their roles in removing rotting carcasses, reducing the outbreaks of diseases like anthrax and botulism (See Disease preventers).

Services: Disease preventers

COVID-19 taught us that, when it comes to disease, humans are inseparable from the natural world. Viral, bacterial and eukaryote (an organism whose cells contain a nucleus within a membrane) pathogens are part of the biosphere; consequently, disturbance can release such pathogens into the wider world, especially when such disturbance increases or establishes new contacts between humans and wild animals.[99] Just over 60% of emerging infectious diseases are zoonoses – meaning they are transmitted between animals and people.[100]

Extirpating, depleting or moving wild species can lead to pathogens switching hosts.[101, 102] A reduction in macaque (*Macaca* spp.) populations in Borneo prompted mosquitoes to switch hosts from monkeys to humans, resulting in a significant rise in malaria (*Plasmodium knowlesi*) prevalence among the human population.[103] Likewise, human exposure to West Nile virus rises as bird diversity drops;[104] and Lyme,[105] Chagas[106] and hantavirus[107] exposure increases with a decline in mammal diversity.[108]

Predators are particularly important for controlling disease vectors. Dragonflies suppress mosquitos by consuming hundreds in a single day and protecting us from malaria, dengue and zika virus.[109] Birds of prey play a central role in reducing rats and their bacterial infections.[110] Scavengers, decomposers (like bacteria and fungi breaking down organic matter into inorganic substances through external chemical and biological processes) and detritivores (like earthworms, millipedes and termites ingesting and digesting dead matter internally) complete the clean-up by consuming carrion and the pathogens it contains. African vultures consume 70% of all dead ungulates; their stomachs have the pH of battery acid, allowing them to sterilize the carcass and site of pathogens that cause botulism and anthrax.[111] Where vultures have been lost, carcasses can take up to four times as long to decompose, increasing the opportunity for disease transmission.[112] Such areas have seen an increase in carrion prevalence, feeding a growth in feral dog populations and heightened risk of transmitting rabies to humans. In India, the loss of vultures increases human mortality by over 4%[113] and cost the country INR1,046 billion (approximately US$23.4bn at the end of 2006)[114] between 1992-2006 in rabies control.[115]

But these species do not work alone: they are emblematic of the wider global web of clean-up crews. These include larger carnivores, mesopredators, carrion-feeding insects,[116] fungi and soil biota, not to mention the impacts of having more diverse and abundant wildlife on reducing prevalence of diseases like malaria and Chagas (Biome: The Amazon forest). As we remove these key biodiversity components for reducing disease prevalence, we simultaneously bring ourselves into closer contact with disease vectors through habitat degradation and wild meat consumption: creating the conditions for zoonotic diseases to spill over into human populations.[117]

Through their carrion clean-up, vultures are capable of protecting us from rabies, anthrax, botulism and more. © Hannah L. Timmins

Amazing animals: Lynx

While much has been written about wolf trophic cascades, relatively little has been observed of the wolf's more cryptic co-predator, the Eurasian lynx (*Lynx lynx*). Aspersions have been cast that this medium-sized cat may not have much of an ecosystem impact. However, evidence to the contrary is mounting, revealing the special role that lynx play.

Deer control

Unlike wolves, lynx are specialist ambush predators, typically preferring large woodlands with plenty of roe deer (*Capreolus capreolus*).[118,119] Roe deer overpopulation is a significant issue in parts of western Europe,[120] where they cause traffic accidents[121] and crop damage and suppress growth of forest vegetation.[122,123] Overpopulation can also reduce the health of the deer themselves.[124]

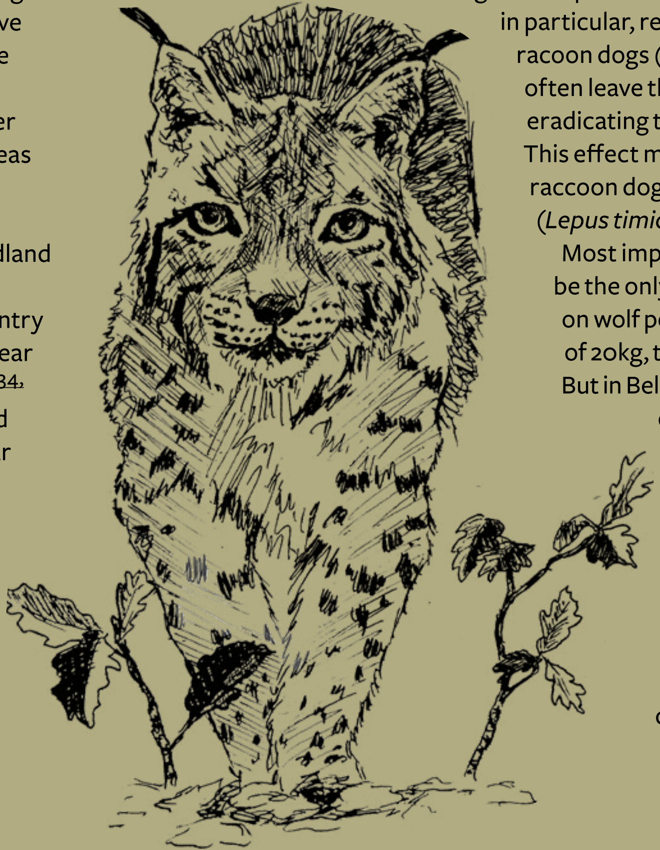
Roe deer constitute up to 80% of the lynx's diet,[125] and an individual lynx takes between 46 and 75 roe per year.[126] Lynx can cause around 44% of deer deaths[127] and, like wolves and nursery spiders (<u>Predators</u>), the presence of lynx can change behaviour in their prey – deer become more vigilant, leaving less time to graze.[128] We once thought lynx were fairly solitary animals, but ecologists are now uncovering more about how this cryptic predator behaves.[129,130, 131] There is growing evidence of lynx teaming up to hunt, particularly when bringing prey back for their kittens,[132] potentially amplifying their significance as a deer control agent.

In the UK, where all large terrestrial predators have been lost and non-native deer species have been introduced, deer number around 2 million with areas of significant overpopulation.[133] This an severely hinder woodland regeneration and crop growth, costing the country over US$17 million per year (adjusted for inflation).[134, 135] The population would expand by 30% each year without expensive culling efforts. Lynx could help to stabilize deer populations, create landscapes of fear and reverse these negative impacts.[136, 137, 138, 139]

Predator control

Lynx, particularly in combination with wolves, can exert a significant pressure on mesopredators in a landscape – in particular, red fox (*Vulpes vulpes*) and invasive racoon dogs (*Nyctereutes procyonoides*).[140, 141] Lynx often leave these carcasses uneaten, possibly just eradicating them to prevent attacks on lynx kittens. This effect may reduce the pressures of foxes and raccoon dogs on smaller prey like mountain hares (*Lepus timidus*)[142, 143] and ground-nesting birds.[144]

Most impressively, it is possible that lynx may be the only animal capable of exerting pressure on wolf populations. Weighing in at an average of 20kg, they are about half the size of the wolf. But in Belarus, where lynx and wolves overlap over large landscapes and live at higher densities, there is a growing body of anecdotal evidence documenting lynxes stalking wolf pups[145] and visiting dens, fearful wolves investigating lynx marking spots,[146] and lynx killing wolf pups, pregnant females and occasionally even adult males.[147] This risk might alter wolf behaviour with cascading effects on wolf prey.[148, 149]



A lynx pads through the oak saplings that her presence protects from deer over-grazing. © Hannah L. Timmins

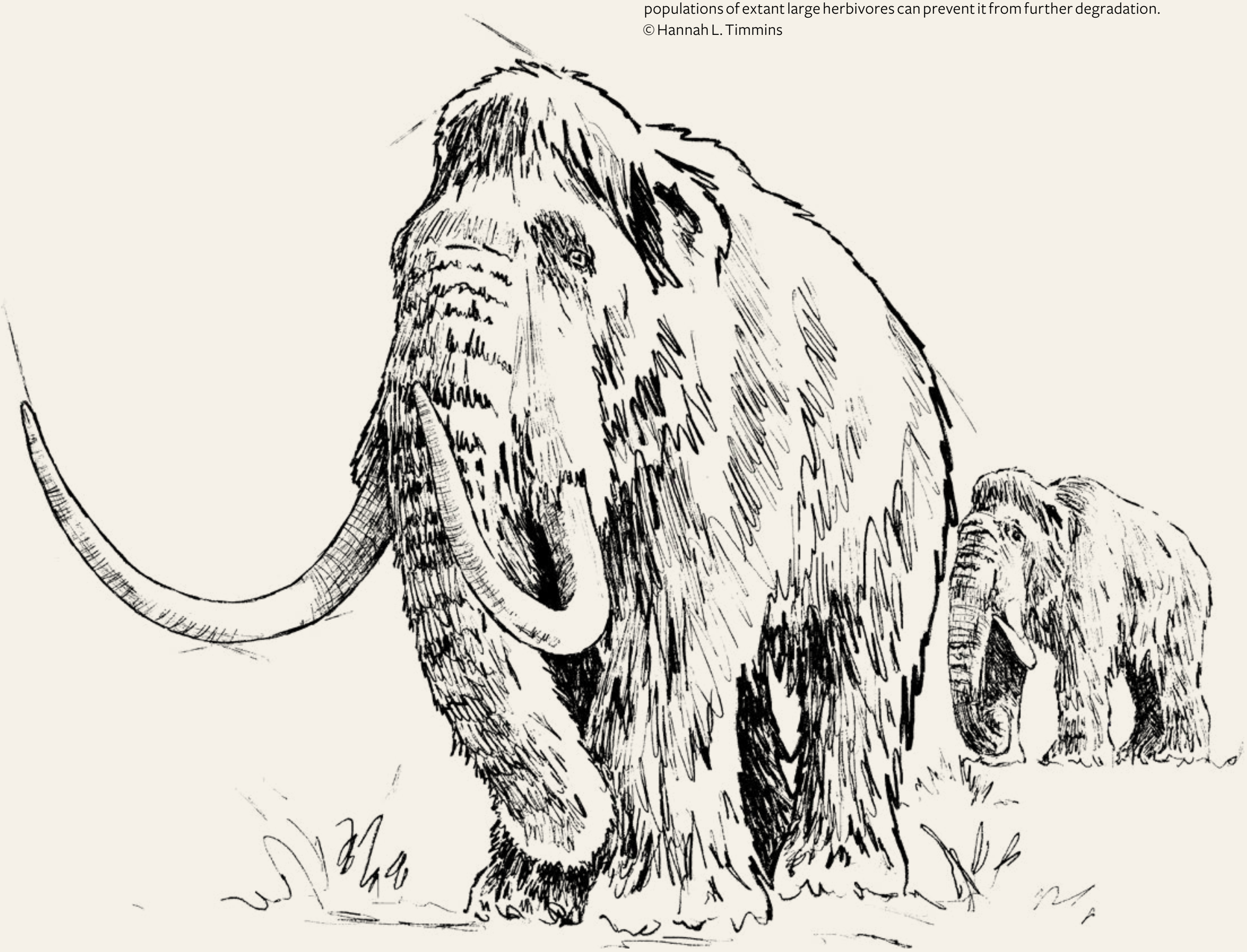
BROWSERS & GRAZERS

Herbivores are key players in maintaining their habitats through grazing, browsing, trampling, smashing, wallowing, transporting and fertilizing seeds in their dung, migrating and dying. They are a force altering plant community richness and biomass. As wild populations of herbivores dwindle, we are learning more and more about how much we rely on them.

Large terrestrial herbivores play a proportionally large role in ecosystem maintenance but are disproportionately impacted by human activities. The loss of these large wild herbivores is pervasive and has consistently resulted in ecosystem simplification and ecological shifts globally. Their replacement with range-restricted domesticated species like cattle, sheep and goats (often with different feeding patterns and diets) does little to restore balance.[150, 151]

Grazers, ecosystem diversity and carbon

Many grass species have coevolved with herbivores; when herbivores decline or are lost, plant diversity within grassland ecosystems declines.[152] Migratory megafaunal grazers like American bison and



Although the mammoth have been lost, the mammoth steppe remains and restoring populations of extant large herbivores can prevent it from further degradation.
© Hannah L. Timmins

Recovering populations of wildebeest have shifted the Serengetti ecosystem from a carbon source into a carbon sink. © Hannah L. Timmins

wildebeest modify grasslands through their intense, irregular and ever-shifting herbivory; their impacts cause grasslands to green up faster, more vividly and for longer seasons.[153] A synthesis of 297 studies and 5,990 individual observations across six continents demonstrated how herbivorous megafauna significantly alter soil nutrient availability, promote open vegetation structure and increase the diversity of smaller animals at large scales.[154]

Unlike trees, which grow from the top, grasses grow from the bottom and regular grazing helps stimulate their growth. Bison and wildebeest grazing keeps grasses green, young and digestible for other species.[155] Their dung provides nutrients, and helps decomposers convert biomass into soil organic carbon.[156] Because of this, the restoration of bison to the American plains could significantly increase the uptake of CO2 (Climate regulation).[157]

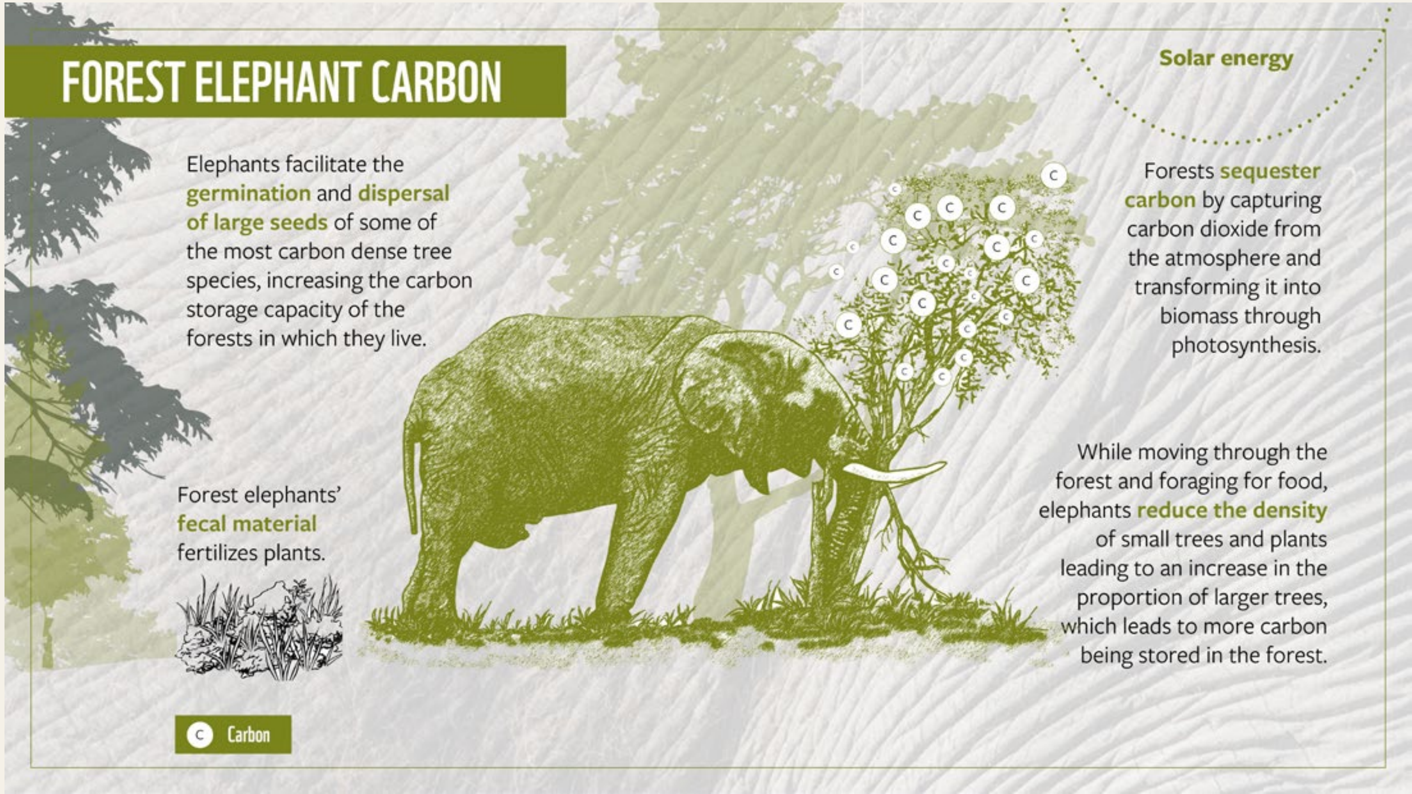
Removing dry grass reduces fuel load and fire prevalence,[158] as grasses store most of their carbon in below-ground root systems; in arid climates prone to wildfires, this is usually a safer location than above-ground forest carbon.[159] In Africa, due to exposure to the livestock pathogen, rinderpest, and unregulated poaching, 75% of the Serengeti wildebeest population disappeared before the 1960s. Dry grass grew out of control, increasing the frequency and intensity of wildfires; 80% of the ecosystem would burn each year, turning the Serengeti into a source of carbon emissions.[160] But when the disease was eradicated, populations bounced back. In restoring the wildebeest population and their biannual migration, fewer wildfires have been recorded – switching the Serengeti ecosystem back to a carbon sink that absorbs several million tonnes of CO2 annually.[161]

The role of grazers in maintaining these grasslands and converting above-ground grass carbon into dung and soil organic carbon has led scientists to propose reintroducing horses and bison as restorers of the long-lost Arctic mammoth steppe. Bison would open up woody vegetation and horses would maintain grasslands, enhancing the protection of carbon-rich permafrost, increasing carbon captured in soils and reducing emissions from permafrost thaw.[162] Increasing the population density of existing large herbivores in this region could protect 80% of permafrost soils until 2100, even under strong global warming pathways.[163]

Large herbivores have faced dramatic population declines and range contractions and approximately 60% of large herbivores are faced with extinction.[164] This has caused worldwide destabilization of grassland nitrogen and soil carbon stocks,[165] an increase in the numbers of invasive plant species and fire frequency,[166] and a reduction in grass and shrub richness and diversity.[167] Across much of the world, full ecological recovery of grasslands will require the restoration of large herds moving over extensive and diverse landscapes.

African elephants and forest carbon

The most well-known of these ecosystem engineers are the elephants – weeding out small trees, trampling vegetation, and dispersing and fertilizing seeds of hardwood trees which sequester more carbon than their wind-dispersed relatives (Seed dispersers). African forest elephants (*Loxodonta cyclotis*) have big appetites — they dramatically reduce the density of smaller understorey trees, freeing up space and reducing



competition for water, nutrition and light. Trees left unbroken have an advantage and can grow tall and large (Climate regulation).[168]

In the Congo Basin, elephant disturbances increase above-ground biomass by 26–60 tonnes per hectare; it is projected that the extinction of forest elephants from central African rainforests would result in a 7% decrease in above-ground biomass.[169] However, as Africa becomes more densely populated by humans and elephants are forced into increasing contact with humans due to habitat fragmentation and lack of food, human-elephant conflict is a major issue across the region that needs to be addressed with greater urgency.

Herbivores as nutrient arteries

Grassland ecosystems are often phosphorus and nitrogen limited and migratory grazing herds also play a huge role in delivering – or subsidizing – these nutrients (Nutrient arteries).[170] Their excrement helps to fertilize the grasses and their long migratory patterns bring nutrient subsidies from areas of high concentrations to areas of low concentrations,[171] keeping the grasslands healthy and less vulnerable to climate instability. In the case of American bison, this effect is what many biologists are now referring to as the 'green wave', a phenomenon many Native American groups have been aware of for thousands of years.

In the tropical forests of the Amazon, the few remaining large herbivores (tapirs *Tapirus* spp., peccaries, *Tayassu* spp., howler monkeys *Alouatta* spp. etc.) may move around US$900 million worth of phosphorus each year from nutrient-rich riparian areas deep into the nutrient-poor forests.[172]

Herbivore carcasses also fertilize habitats, sometimes en masse. In East Africa, migratory herds are regularly subject to mass drownings when making dangerous river crossings. Their bones release phosphorus into the water and soils, often over many months.[173, 174] In the North American Great Plains, it is estimated that bison, once numbering in their millions, would have lost

LARGE HERBIVORES IN THE AMAZON MAY MOVE AROUND US$900M WORTH OF PHOSPHORUS EACH YEAR FROM RIPARIAN AREAS DEEP INTO THE FOREST

Parrot fish simultaneously graze choking algae from corals and excrete important algae back onto corals © Hannah L. Timmins

200,000 in similar annual mass drownings, donating 90,000 tonnes of phosphorus each year.[175]

Gardeners of coral reefs and seagrass meadows

In the oceans, coral reefs protect our coastlines from storms, tsunamis, floods and erosion, and provide nurseries for our commercial fish (Disaster risk reduction).[176] This essential habitat is maintained by algae- and coral-eating animals like the 80 species of parrotfish (*Scaridae*) found in coral reefs all over the world. The famous 'beak' of a parrotfish is made up of a thousand teeth cemented together which they use to bite chunks of coral and grind up with another set of 'teeth' in their throats, called a pharyngeal mill, all to get at seaweeds, algae and microbes growing on the coral (Biome: The Coral Triangle).[177] Scraping off and removing these algae and seaweed ensures that such plant growth does not smother the corals and block out light.

A single parrotfish takes about three bites of coral per minute, then excretes it as sand, producing up to 450kg of sand each year (the weight of a baby grand piano!).[178] With the sand, they excrete nutrients and a dense load of live algae into the coral scars they leave behind. In doing so, they disperse symbiotic, single-celled organisms – called zooxanthellae – to new corals (like the seed dispersers), kick-starting their growth[179, 180] Coral reefs in marine reserves that prohibit parrot fishing are six times more resilient to coral bleaching and other disturbances.[181]

In tropical seagrass meadows, manatees (*Trichechus* spp.) occupy this important position, clearing the grasses of algae and – in much the same way as bison and wildebeest – helping to keep the grasses short and healthy.[182] In the Caribbean, these meadows are estimated to provide US$255 billion in ecosystem services including storm protection, fish habitat and carbon storage.[183]

Manatees maintain the health of seagrass meadows providing storm protection, | fish habitat and carbon storage. © Hannah L. Timmins

Services: Climate regulation

Healthy wild animal populations are naturally adapted to their environment and help combat climate change, primarily by driving ecological processes that maintain and/or increase carbon sequestration in plants and store it in woody biomass and in peat and soil.

Wild animals transfer carbon across the landscape, seascape and riverscape,[184] including to places where it is stored for longer periods (Nutrient arteries) and help mediate carbon exchange between ecosystems and the atmosphere. For example, their role in soil organic matter decomposition[185] can turn ecosystems that are net carbon sources into carbon sinks, or vice versa (Browsers & grazers). Absence of predators can stimulate high herbivore numbers, suppressing vegetation and reducing carbon storage,[186] so conserving predators can help maintain stored carbon (Predators). Tropical fruit trees tend to contain high levels of carbon in their wood and are distributed by fruit-eating mammals and birds; loss of the latter can lead to a gradual decline in net carbon storage of forests, due to declines in fruiting trees (Amazing animals: Hornbills and Seed dispersers).[187]

Elephants tend to reduce the density of tree stems, leading to larger trees storing proportionately more carbon. Forest elephants prefer to browse leaves from trees with low wood density, which generally store less carbon, thus favouring slower-growing, high-density species that store more carbon for longer periods. Further, by eating fruit from the latter they spread seeds through the forest in their dung.[188] In dry, fire-prone areas like savannahs, removal by herbivores of above-ground plant material can actually ensure more carbon is stored underground by reducing the number and severity of fires (Browsers & grazers). Wild animals may play particularly positive roles in areas of intensifying fire incidence and severity, through changes to albedo (the proportion of solar radiation that is reflected) including a shift from closed to open canopy caused by herbivores, and by increasing vegetation and soil carbon stocks in grasslands.[189] Conserving forest wildlife [190] and rewilding to restore these ecological processes are key steps in carbon capture.

Past methods of calculating carbon in ecosystems did not factor in the role of animal populations in mediating carbon uptake, but this is changing with new methodologies available.[191] Researchers at Yale recently calculated the carbon benefits of a herd of 170 European bison (*B. bonasus*), reintroduced with support from WWF into Romania's Tarcu Mountains. They estimate that rewilding bison on 50km² of grassland can increase carbon capture and storage up to 9.8 times.[192]

European bison are capable of amping up grassland carbon storage by almost tenfold.
© Hannah L. Timmins

Services: Disaster risk reduction

The role of natural ecosystems in mitigating disasters caused by weather or earth movements – floods and droughts, storms and tidal surges, wildfires, soil erosion, desertification and landslides – is one of the most important but underrated ecosystem services.[193]

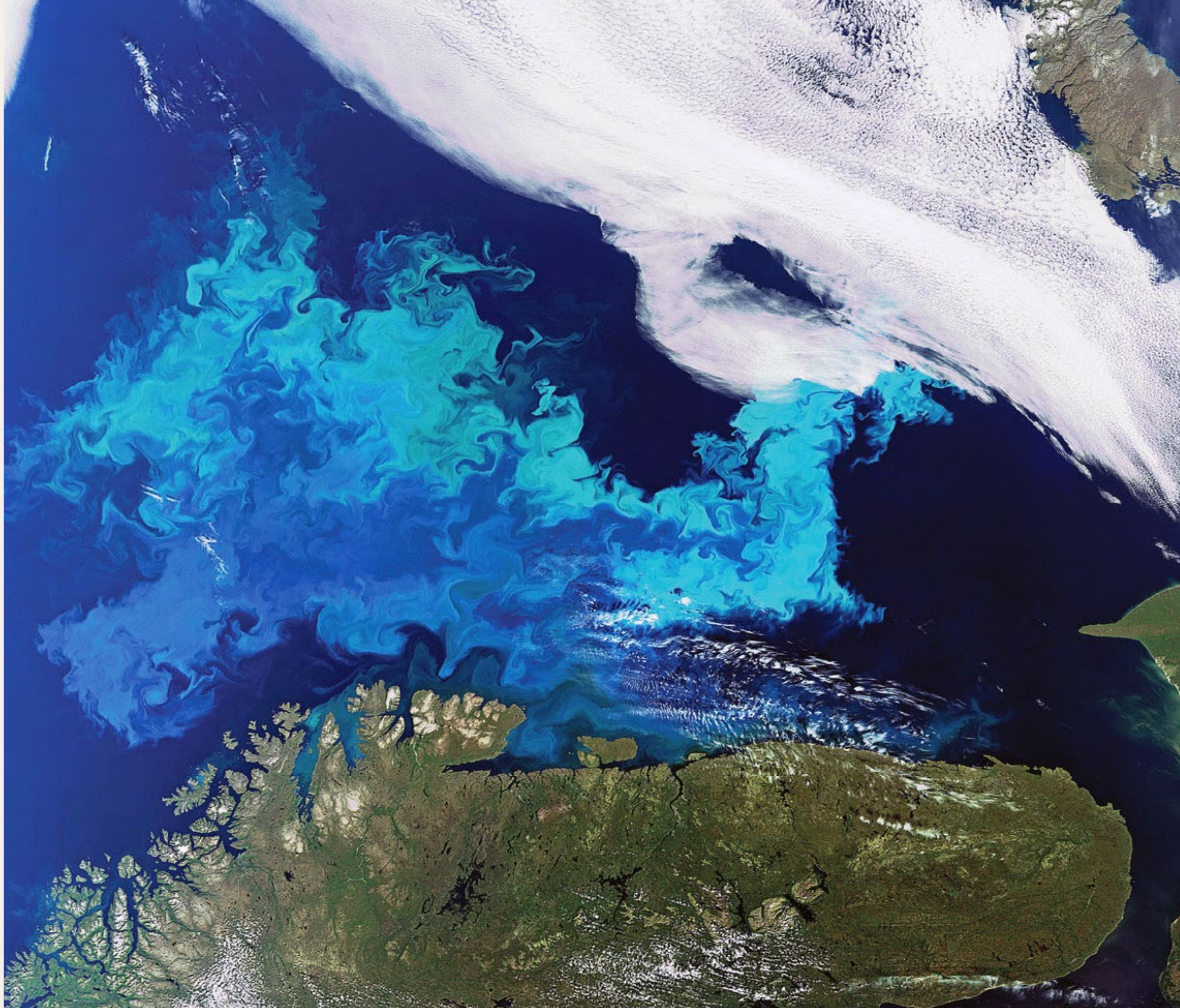
Animals help protect shorelines by building defensive coral reefs,[194] with an annual value in reducing storm damage worldwide of over US$4 billion. [195] Both the coral polyps themselves (Biome: The Coral Triangle) and the species that clean reefs of growth-reducing algae (Browsers & grazers) are important.[196] Sulphide-metabolizing bivalve molluscs support growth of mangroves, another important coastal protection ecosystem (Amazing animals: Oysters), by reducing sulphide stress which can otherwise inhibit growth.[197] Beaver dams alleviate flooding by diverting water onto floodplains, reducing flow rates during periods of high rainfall and contributing toward less flooding downstream (Water quality, regulation and erosion control).[198,199] Conversely, by storing water, beaver dams also help to keep water flowing during drought,[200, 201] with research in Oregon finding dams increase stream flow by up to six weeks in dry summers.[202] Studies of five wildfires in the western United States found beaver-dammed river corridors less affected by fire than undammed corridors.[203] Grazing herbivores maintain structural diversity and therefore biological diversity in grasslands (Browsers & grazers),[204] which in turn reduces the potential for soil erosion; [205] large and small, vertebrate and invertebrate herbivores all play a role.[206] Birds and bats are important seed dispersers on unstable slopes liable to landslides and bird perches have been used to encourage restoration in such areas in Puerto Rico.[207]

PLANKTON-EATERS

The microscopic marine realm consists of an entire ecosystem of life inexorably linked to some of the largest animals on the planet – whales. Plankton-eaters (planktivores) move nutrients vertically and laterally across the oceans, underpinning ocean productivity.

What are phytoplankton and zooplankton?
Phytoplankton are primary producers: like grasses and trees, they convert light energy into biomass and chemical energy, taking in carbon dioxide and releasing oxygen. Zooplankton feed on the phytoplankton: they are the smallest and most abundant grazers on the planet and make up a critical step for transferring energy and nutrients up the trophic ladder. Zooplankton include animals like copepods and tiny aquatic crustaceans like krill.

Phytoplankton are essentially the ocean's gardens, the foundation of all marine and indeed all terrestrial life. These tiny creatures (five of them could fit on the head of a pin)[208] produce 50% of the oxygen in our atmosphere,[209] regulating the climate and the formation of clouds.[210] Diatoms, one of the most abundant groups of phytoplankton, contribute 40% of the total primary productivity of the oceans[211] and fix 10-20 billion tonnes of organic carbon every



A satellite image of a phytoplankton bloom. © Alexis Rosenfeld/ WWF

Humpback whale 'faecal plumes' are millions of times more iron-rich than the surrounding seawater. © Hannah L. Timmins

year (comparable to all global rainforests combined).[212] For comparison, humanity produces 36 billion tonnes of CO_2 (~10 billion tonnes of carbon) per year.[213]

Phytoplankton and zooplankton are also essential sources of food. Plankton-eaters range from the tiny phytoplankton-grazing zooplankton, through to invertebrates like oysters (<ins>Amazing animals: Oysters</ins>); to bony fish like salmon (<ins>Amazing animals: Salmon</ins>), sand eels and sardines; to cartilaginous fish like the megamouth (*Megachasma pelagios*), basking (*Cetorhinus maximus*) and whale (*Rhincodon typus*) sharks; to seabirds like auklets (*Aethia* spp.), storm petrels (*Hydrobatidae* and *Oceanitidae*) and some penguins (*Spheniscidae*); to the largest animals that have ever lived: the blue (*Balaenoptera musculus*), humpback (*Megaptera novaeangliae*), bowhead (*Balaena mysticetus*) and right (*Eubalaena* spp.) whales.

The whale pump – vertical nutrient arteries[214]

To make use of all the sunlight, phytoplankton live in the photic zone at the surface of the ocean. The herbivorous zooplankton hide hundreds of meters deep in the aphotic zone during the day to avoid their predators and migrate to the photic zone at night to feed on phytoplankton. Known as the 'diel vertical migration', this mass movement is the equivalent of a human swimming 80km in an hour.[215] It is the planet's largest migration of biomass – and it happens daily!

This interaction might go on indefinitely, fuelling ocean productivity and feeding our fisheries, except that photic zones are typically limited in phosphorus and nitrogen that the mitochondria and chlorophyll in the phytoplankton need to function.

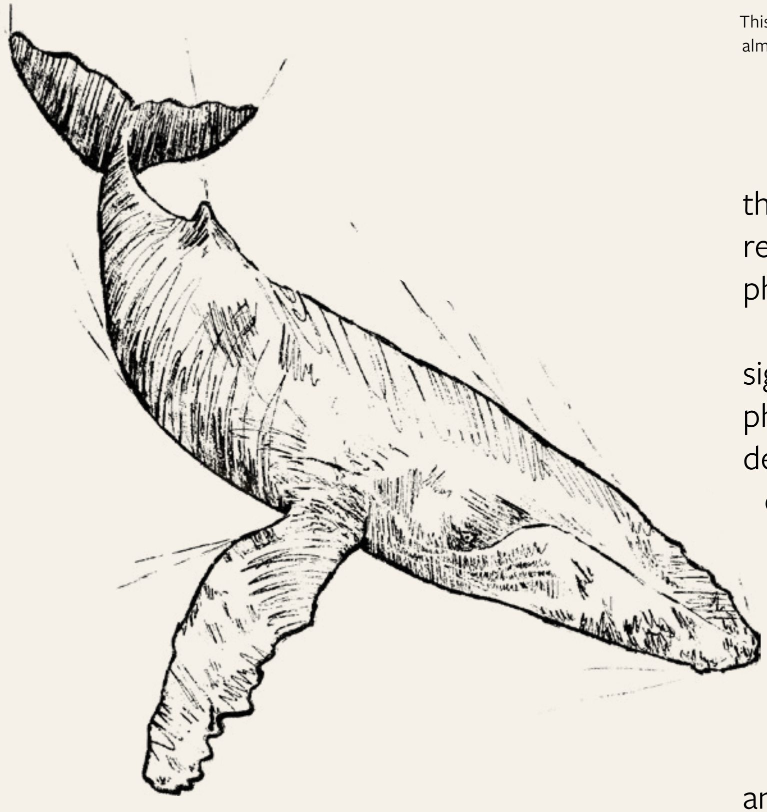
This is where whales come in: all whales dive underwater to feed and return to the surface to breathe. The pressures of the deep ocean shut down many bodily functions, and when whales surface they need to rest, sleep (log), digest, socialise, and, most importantly, excrete buoyant faecal plumes; that are rich in those scarce nutrients. This is known as the 'whale pump': whales pull nutrients from the ocean depths through the thermocline wall – which would otherwise block the flow of nutrients – into the photic zone, fertilizing the phytoplankton.[216, 217, 218] And while phytoplankton, enhanced by whales,[219] underpin our fisheries,[220] the combined effect of phytoplankton and zooplankton excrement sinking to the ocean floor is responsible for 70% of total global carbon export.[221]

Phytoplankton are already stressed in the face of climate change and maintaining this nutrient cycling is critical for what phytoplankton remain. Since 1950, we have lost a staggering 40% of the world's phytoplankton primarily to climate change and sea temperature rise[222] and taking out this primary producer is having massive knock-on effects on our fish stocks.[223]

The whale conveyor belt – lateral nutrient arteries

The 'whale conveyor belt' works in much the same way as the whale pump, turned on its side. It relies on a key aspect of whale behaviour: migrations. Every year, many whales migrate from their summer

50% OF THE OXYGEN IN OUR ATMOSPHERE IS PRODUCED BY PHYTO PLANKTON



This humpback, nicknamed Frodo, is a record-setting long-distance swimmer, having swum almost 7,000 miles in a year. © Hannah L. Timmins

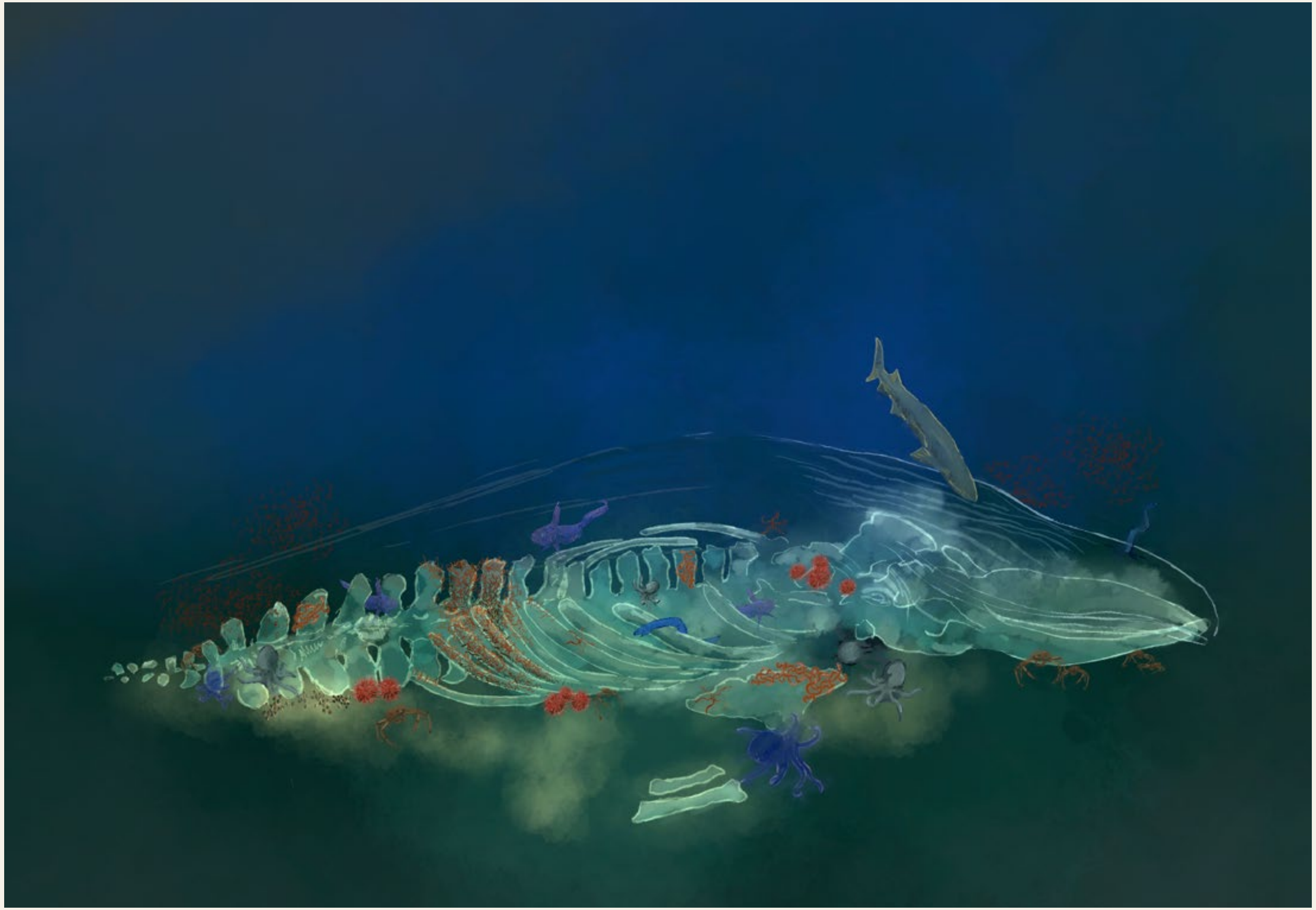
feeding ground in the northern and southern latitudes to their winter breeding grounds in the tropics. The cooler summer feeding grounds are richer in nutrients; the whales spend their summer feeding season there building up fat reserves before going on their annual fast to the nutrient-poor tropics. When they arrive in the tropical waters, they excrete faecal plumes and urea, shed dead skin, release placentas – all nutrient-rich, stimulating phytoplankton growth.[224]

In the Southern Ocean, krill abundance can vary significantly from year to year, seemingly driven by phytoplankton abundance[225] and possibly the iron-deficient nature of the waters – unlike the other oceans, the Southern Ocean doesn't receive the iron-rich dusts of Africa.[226] This ocean also lost 99% of its whales during the 20th century,[227, 228] and whale faecal plumes are 10 million times more iron-rich than the surrounding seawater.[229] Combining the loss of sea ice (due to climate change) and the large quantities of whale faeces, and their ability to fertilize phytoplankton and enrich the waters with iron at scale, krill stocks seem to be on the decline.[230] [231] [232] Models predict negative future impacts of climate change on krill and all whale species here, including concerning declines for Pacific populations of blue, fin and southern right whales, and Atlantic/Indian fin and humpback whales. Antarctic krill are key prey for whales. Whales need to store energy to fuel their long migrations between high latitude foraging areas and low latitude breeding. A drop in these energy sources year to year impacts their health, creating a massive negative feedback loop.

Whale fall and beached carcasses – giant gifts to the land and seafloor[233]

While recovered living whale populations can transfer vast quantities of nutrients, it is in death that whales give their final gift in nutrient transfer. Whether sinking to the seafloor, floating at the water's surface or beached at the coast, whale carcasses gift the recipient ecosystems a pulse of phosphorus, calcium, iron and nitrogen (Nutrient arteries).[234] The deep sea is a particularly energy-poor ecosystem; whale falls present giant islands of nutrients and energy, creating their own ecosystems of bone-eating worms and snails, microbial communities and their grazers. In this way, for 50 million years whales have provided the conditions for prolific evolution,[235] generating over 100 species of whale-fall specialists.[236] Many more of these specialists are likely to have already disappeared, undocumented and unnoticed, and without whale population recovery, many more are headed for extinction.[237]

Whales are cosmopolitan, found in every sea. Without human interference, whales can thrive; they are eponymously large and have an equally large impact on their ecosystem. But the massive Antarctic blue whale, the largest animal that has ever lived, is currently at just 2% of its pre-whaling population.[238] Whaling, by targeting the largest animals, has also reduced the average size of whales by a third.[239] While this shrinking may never reverse, if all populations of blue, bowhead, Bryde's, fin, grey, humpback, minke, right and sei whales (all planktivores) were restored there would be millions more whales in the sea. Every whale is an asset in the fight to preserve ocean health with benefits to nature and people. For the oceans to be well fertilized with iron and nitrogen, we need to restore the millions of whales that once swam in them.[240]



Whale fall carcasses transfer tonnes of nutrients to the desolate ocean floor, providing food and shelter for a huge diversity of wildlife like hagfish, rattail fish, sixgill sharks, bone-eating worms, pom-pom anemones, octopus, giant isopods, grooved tanner crabs, mussels, snails, starfish, shrimp and lobster © Hannah L. Timmins

Services: Nutrient arteries

In terms of nutrients, not all ecosystems are equal. When a new land mass is created through volcanic activity, the earth tends to be nitrogen limited but rich in volcanic phosphorus. As the land ages, its phosphorus is washed away by rains and rivers over millions of years, gravity slowly depleting phosphorus reserves into the oceans. This is the case with older mountain chains like the Appalachians and tropical forests like the Amazon.

Nitrogen and phosphorus are two critical elements for life, forming the main ingredients of DNA as well as being key elements in all proteins. Without them, vegetation growth rates become stunted, soils erode further, rivers are blocked – in short, ecosystems collapse. New phosphorus can be released by natural weathering of rocks, minerals released by water, ice and wind very slowly, or by the eruption of a new volcano, a rare occurrence. Outside of these two processes, animals are the most efficient and reliable vehicles for 'nutrient subsidies'.[241] And nutrient movement is directly proportional to animal abundance.[242]

Nutrient subsidies are the transfer of nutrients, like phosphorus or nitrogen, across ecosystem boundaries from one highly productive, nutrient-rich 'donor ecosystem' to another nutrient-poor 'recipient ecosystem' (Plankton-eaters). Animals crossing these boundaries – seabirds eating in the ocean and excreting on a volcanic island,[243, 244] turtles feeding in the ocean and laying eggs on a beach,[245] the carcasses of bison fed on upland grasses (Browsers & grazers) – all form nutrient resource pulses to recipient ecosystems. Without wildlife faeces, urine, carcasses, afterbirth, eggshells and so on, recipient ecosystems start to falter. The Amazon is a prime example of these mechanisms, and of what happens when they fail (Biome: The Amazon forest).

In this way, wild animals are the world's circulatory system. Their loss can lead to the atrophying of a limb, or an ecosystem, which, apart from a potential cascading loss of biodiversity and ecosystem services, makes the area more vulnerable to climate change.

Seabird excretions transfer important nutrients from the ocean directly onto land. © Hannah L. Timmins

Amazing animals: Pacific salmon

The six species of Pacific salmon in the genus *Oncorhynchus* are all *anadromous*: characterized by their life cycle of living in oceans and migrating to fresh waters to breed and spawn. They are also all *semelparous*, meaning they have a singular burst of breeding once in their lifetime before dying upstream. These two factors make Pacific salmon, and the huge annual pulse of nutrients they bring with them from the oceans into forest-lined rivers, critical for the health of the world's largest temperate forest, running from California to Alaska.[246]

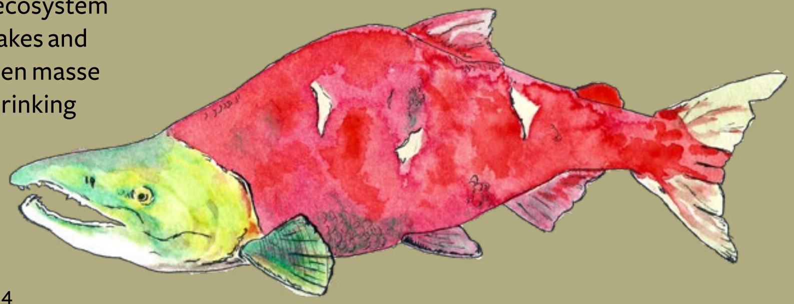
Phosphorus, carbon and nitrogen, key elements in the production of food and trees, are carried downhill, downwind and downstream to the oceans, where they can be locked away for millennia as phosphate and ammonia in the ocean depths. [247] Animals are one of the main forces pushing against gravity to bring these elements back inland (Nutrient arteries). One of the largest movements of animal bodies from the oceans, upstream and eventually inland is the mass migration of salmon, which accumulate 95% of their weight at sea eating shrimp and krill. [248]

Salmon represent millions of packets of nutrients in the form of their carcasses, excrement and gametes. These nutrients either leach directly into riparian soil from the waterbody, are carried onto floodplains by overflowing streams or are dispersed into soils via direct consumption by predators, scavengers and insects, which then leave partially digested carcasses or excrement in the surrounding areas. Bears can move these nutrients a kilometre or so inland from streams, scavengers like ravens (*Corvus corax*) and turkey vultures (*Cathartes aura*) can travel much further. Bacteria decompose excrement and remains and nutrients are taken up by vegetation.[249] In this way, anadromous fish, including salmon, currently move 5.6 million kilos of phosphorus up rivers from the sea globally every year,[250] and it has been estimated that salmon carcasses alone deliver over 80kg of nitrogen per hectare. [251]

Ecosystems with dense salmon populations show elevated marine-derived nitrogen, and corresponding increased productivity or vegetation growth; from space this can be seen as a more intense greenness following a large salmon pulse.[252] Healthier riparian vegetation results in less erosion and cleaner water with reduced sedimentation. Salmon are also physical ecosystem engineers: the fish excavate nests in the gravel of lakes and streambeds for their eggs. The act of nest digging en masse may also lead to decreased silt levels and cleaner drinking water for people (Water quality, regulation and erosion control).[253] In fuelling vegetation growth, salmon facilitate erosion control, water purification and regulation, and carbon sequestration, as well as providing recreation, salmon meat and many more services to people.[254]

Worryingly, Pacific salmon have lost 40% of their historical range due to river blockages like dams, and this, combined with overfishing and threats from industrial hatcheries, has reduced wild salmon to just a fraction of their former numbers. For example, the Columbia river now has just 300,000 wild salmon where once there were 10-16 million.[255]

Salmon are just one family of anadromous fish, many of which are threatened, including sturgeon which have declined globally by an average of 81% since 1970.[256, 257] Historically, anadromous fish may have moved 140 million kg of phosphorus from sea to land each year; this has collapsed by 96%. [258] These collapses are likely already having a strong effect on ecosystem services – the world's riverine nutrient arteries slowing and clogging.



A sockeye salmon (*Oncorhynchus nerka*) body decomposing at the very end of its breeding journey. © Hannah L. Timmins

Amazing animals: Oysters

Many people associate oysters with a romantic night out thanks to their supposedly aphrodisiac qualities, or perhaps the shucking (opening) skills which are subject to international competition. But oysters are also keystone species primarily thanks to their ecosystem engineering services. Found worldwide, oysters form extensive colonies known as beds or reefs that provide habitat, shelter and protection from predators for hundreds of species, including commercially valuable fish such as anchovies, herrings and striped bass (*Morone saxatilis*).[259] Oyster beds also help to stabilize sediment on the ocean floor which can protect shorelines from erosion and storms.[260] Oysters are filter feeders, which means that they filter large amounts of water (in some cases a single oyster can filter over 200 litres of water per day)[261] to extract plankton and other particles for food (Plankton-eaters). In doing so, oysters help to improve water quality by removing excess nutrients and pollutants. These filtration services are particularly important in areas that are polluted or susceptible to eutrophication (excessive plant and algal growth as a result of water pollution (see also: Water quality, regulation and erosion control)). Oysters also help the exchange of nutrients between benthic (ocean floor) and pelagic (open water) habitats (Nutrient arteries).[262]

Oysters' value as a food source is well known, but their value as ecosystem engineers has been assessed at anything between US$5,500 and US$99,000 per hectare per year depending on the area.[263] Oyster populations are however at historic lows. Erosion from development, wetland loss and excessive nutrient pollution have proved devastating. Overfishing and outdated harvest methods have destroyed or damaged reef structures and reduced oyster populations.[264]

Oysters create dense beds and deliver numerous services © Hannah L. Timmins

SEED DISPERSERS

Animal seed dispersers play a crucial role in ecosystem health by ensuring habitat diversity, connectivity and resilience. Their services are important for plant genetic resources and climate change mitigation and adaptation.

How do plants move?

Plants have evolved multiple strategies for dispersing their seeds,[265] with half of all plant species relying on animals for this service.[266] Animals (e.g., elephants,[267, 268] primates,[269, 270] deer,[271, 272] flying foxes,[273, 274] and many birds) are important seed dispersers for tree species,[275] dispersing the majority (70-94%) of large-seeded tree species in tropical forests[276] and up to 62% of seeds in temperate forests.[277] Many other plants rely on birds and insects to disperse their seeds (see below).

Animals eat fruit and seeds, or in some cases just the seed coatings, and as they move seeds are regurgitated or pass through their digestive system (which can help with germination)[278] and are excreted usually at some distance away from the source.[279] Animals also collect, bury (Soil engineers) and store seeds and nuts, creating food larders. Some seeds attach themselves to animals using hooks, spines or sticky surfaces, catching a

Green turtles are key for dispersing the seeds on seagrass meadows with a healthy dose of fertiliser. © Hannah L. Timmins

ride to new locations in which to germinate.[280] In seagrass meadows, researchers have found dugongs (*Dugong dugon*) and green sea turtles (*Chelonia mydas*) are vital seed dispersers, increasing the likelihood of germination up to fourfold.[281] Dispersal by animals has several advantages over other methods such as wind and water, as animals often move seeds to sites suitable for germination due to their specific habitat needs.[282] And of course, heavier seeds are unlikely to be blown far and moving by water depends on weather conditions and proximity to water bodies.

The distance a seed moves from the parent plant is known as the seed shadow.[283] This shadow, which varies greatly depending on the animal involved, is vitally important as it helps plants colonize new areas,[284] adapt to climate change,[285] move away from diseased plants and connect fragmented habitats across landscapes.[286] All this results in more complex and resilient ecosystems – a delicate balance broken when seed dispersing species disappear. One estimate suggests past global species losses caused an almost 60% reduction in plants' ability o adapt to climate change through seed dispersal, and the likely future loss of threatened seed-dispersing species from their current ranges could add a further 15% to this reduction.[287]

Elephants and seeds

Large animals play an irreplaceable role in influencing the structure of many forests. Generally, large, wide-ranging species with slow digestive systems disperse seeds farther than small-bodied species with fast digestion.[288, 289] Forest elephants – now critically endangered – are keystone seed dispersers in African tropical forests; they consume seeds from more species than any other large animal and are the sole disperser of many plants with tough and hard-to-penetrate seeds. These elephants are often referred to as the mega-gardeners of the forest, but as seed dispersers some elephants are likely to be better gardeners than others. A study in Gabon found that on average elephants disperse seeds 5.3km from source. Male elephants disperse seeds farther than females, and more exploratory elephants disperse seeds roughly 1.1km farther than less active elephants. The maximum simulated seed dispersal was just over 100km.[290]

A study in the Belum-Temengor forest complex in northern Malaysia found almost half (48%) of the species dispersed rely on large mammals, with Asian elephants (*Elephas maximus*) being the only effective seed dispersers for barking deer's mango (*Irvingia malayana*). In total, Asian elephants disperse seeds from at least 62 families and over 200 plant species, and new elephant-plant associations are still being found. Many are of economic significance for timber and agriculture or are potentially important genetic resources for crop improvement.[291]

What happens when we lose our seed dispersers?

Plant and animal species associations are being lost.[292, 293] In particular, large seed dispersers are disproportionately affected by habitat loss and fragmentation.[294] The Javan and Sumatran rhinos

(*Rhinoceros sondaicus* and *Dicerorhinus sumatrensis*) are extinct across much of their range, leaving the endangered Asian elephant[295] as the only surviving disperser of the largest seeds, with long-term implications for some tree species.[296, 297, 298] The largest forest seed dispersers in the South American Atlantic forest are the muriqui monkeys (*Brachyteles* spp.) which are no longer found across 88% of their former habitat.[299]

Many plants that have relationships with seed dispersersing wild animals are important food sources for humans. These include fruits, nuts and wild relatives of crops which are the vital building blocks of agriculture.[300] For example, avocado and cocoa fruits coevolved with the now extinct South American elephants and giant ground sloths (*Megatherium americanum*). After their loss, no species existed that was big enough to disperse the large seeds, except humans, who value the fruits and ensure widespread production.[301]

Where humans do not step in, the impacts may be less noticeable but can have serious consequences. A study in the lowland rainforests of the Democratic Republic of the Congo found the loss of forest elephants severely impacted the regeneration of 18 plant species.[302] In general, the reduction of large seed dispersers results in the lack of regeneration of big trees – though the change in forest structure that this leads to is slow, as large plants can live for decades or even centuries.[303] The impacts are more obvious in degraded forests and deforested areas, where seed dispersal is essential for regeneration.[304] For tree species dependent on animal dispersal, without seed dispersers, tree recruitment drops[305, 306] and carbon storage is diminished.[307] Some 59% of the world's above-ground carbon is stored in tropical forests, with larger seeds generally producing larger plants which store more carbon. Simulations in the Neotropics, South Asia[308] and Africa suggest that forests experiencing losses in large animal seed dispersers may have up to 6% less above-ground biomass compared to forests retaining animals, whereas in Southeast Asian and

70-94% OF LARGE SEEDED TREE SPECIES ARE DISPERSED BY ANIMALS

Many plants have evolved seeds with lipid-rich elaiosomes to attract ant dispersers.

Australian forests where carbon-dense trees are dispersed by wind and water there are little to no carbon losses.[309] Plant diversity is also affected. Research in China found that the critically endangered[310] black crested gibbon (*Nomascus concolor*) dispersed more seeds of rare species than common species and shortened the duration of seed germination for 58% of the dispersed species due to gut passage effects.[311]

With a few exceptions, the loss of seed dispersers is hard to quantify economically. The island of Guam in the Western Pacific Mariana Islands has lost nearly all of its native forest birds due to an invasive snake (*Boiga irregularis*), whereas nearby islands have relatively intact bird populations. Research has confirmed that birds were the primary seed dispersers of the socially and economically important naturalized donne' sali chilli (*Capsicum frutescens*). On neighbouring islands local producers can earn between US$500 and US$2,000 each per month for chilli products, indicating the potential economic losses on Guam.[312] Research into the loss of just three seed-dispersing species (two monkeys and a bird) in Carlos Botelho State Park in Brazil suggested a reduction in carbon sequestration of 3.5%.[313]

Where regeneration is feasible, native seed dispersers are low-cost, ecologically effective and efficient restorers,[314, 315, 316] in particular for larger seeds which are buried by birds and animals, unlike smaller wind-blown seeds that can germinate easily on disturbed ground.[317]

Ants: the insect dispersers

Ants are the main insect seed dispersers. They are attracted to lipid-rich bodies called elaiosomes on the seeds of a guild of plants called myrmecochores, which includes some trilliums, ginger, lilies and violets. The elaiosome attracts foraging ants and induces them to carry seeds back to their colony, where the ants consume the lipids but not the seed. This relationship has evolved in over 11,000 plant species worldwide, primarily in the arid nutrient-poor soils of Australia and South Africa. This is no casual or random association, and not all ants disperse seeds; researchers have found around 100 keystone ant species which have a few important traits in common making them highly effective dispersers. They are often large scavenging or omnivorous ants, living in small colonies, are often highly mobile, frequently relocating their nests, have predictable foraging schedules and are very careful foragers, helping ensure the seed remains in a favourable condition for germination and survival.[318]

Amazing animals: Hornbills

Forest hornbills – found throughout tropical and subtropical Asia, Africa and Melanesia in the *Bucerotidae* family – are critical agents of rainforest regeneration through their role in seed dispersal and germination (Seed dispersers). In Asia and New Guinea, 80% of hornbill species have been documented as important for seed dispersal.[319]

Hornbills exhibit all the characteristics of excellent bird seed dispersers: they eat large amounts and have a diverse diet of ripe, and generally large, fruits. Their iconic large beaks help them to manipulate, consume and disperse seeds that would likely be far too large for other birds.[320] They rarely drop fruit accidentally, instead storing it in a throat pouch; they then fly far from the mother tree, gently removing the flesh with their tweezer-like bills and spitting out the seeds after the pulp is eaten, thus ensuring the spread of forest species.[321] Hornbills also consume many fruits and their seeds whole (from figs with many tiny seeds to drupes and berries with single, large seeds); almost all of these remain completely undamaged after passing through the hornbill gut and are expelled in *tree crotches* (from which figs germinate) or on the forest floor with a healthy dose of fertilizer, which enhances germination.[322, 323]

This service can be especially important for rare tree species like the wild nutmeg (*Myristica insipida* or *M. attenuata*), which times its fruiting to coincide with the breeding season of three local hornbill species (great hornbill *Buceros bicornis,* wreathed hornbill *Rhyticeros undulatus* and oriental pied hornbill *Anthracoceros albirostris*). Wild nutmeg is used by people in Arunachal Pradesh for food and chewed as a betel nut substitute.[324]

As forests are fragmenting, leading to a rapid decline of terrestrial seed dispersers in Central Africa, the black-casqued (*Ceratogymna atrata*) and white-thighed (*Bycanistes albotibialis*) hornbills are key for the distribution of certain tree species. Here, these hornbill species are lauded by ecologists as primary vectors for maintaining forests and reversing loss. The white-thighed hornbill in particular has an average range of over 20,200 hectares and prefers more disturbed habitat, making this species critical for forest rehabilitation.[325]

The list of services goes on as these birds also provide pest management (Predators). In India's Western Ghats, coffee farmers look to the Malabar grey hornbill (*Ocyceros griseus*) for control of grasshoppers, crickets, spiders and scorpions, reducing the farmers' costs for pesticides and allowing them to go organic, fetching better prices on the market.[326]

Unfortunately, many hornbill species are seriously threatened and climate change is expected to impact their future ranges, pushing them to cooler altitudes and latitudes where preferred foods and trees large enough for nesting may be unavailable.[327, 328]

The Sulawesi red-knobbed hornbill delivers a seed to his nesting female with an expert tweezer-like beak. © Hannah L. Timmins

POLLINATORS

Globally nearly 90% of all flowering plant species[329] and 75% of all crops rely to some degree on animals to pollinate them.[330] Around one-third of global food production by volume,[331] or one of every three bites of food we eat, relies on animal pollinators.[332] Pollinators also help secure the production of biofuels, fibres, medicines and building materials, and play a role in carbon storage.

Pollination is the transfer of plant reproductive cells, allowing fertilization and reproduction to occur; pollinators are the animals which help move these cells.[333] Pollinators come in all shapes and sizes, visiting flowering plants for feeding, pollen collection and shelter. While insects are pollinators globally, bird pollinators occur mainly in warm (tropical/subtropical) regions, while bats are important pollinators in tropical forests and deserts; more plants depend on vertebrate pollinators for fruit/seed production in the tropics than at higher latitudes.[334] Bees are critically important pollinators (Amazing animals: Bees), as are other insects like beetles, wasps, butterflies and moths. Among mammals, bats are the principal pollinators, while nearly 1,000 species of birds including hummingbirds, honeyeaters and sunbirds

Hummingbird hovering is not only an efficient adaptation for carefully sipping nectar and pollinating plants, it also requires a lot of energy and sugar, driving the birds to find yet more nectar. © Hannah L. Timmins

Sugary nectar is a high-energy food source for quick-moving geckos, pollen sticks to their skin and is transferred to the next plant. © Hannah L. Timmins

are known to pollinate plants.[335] Flies, ants, midges, monkeys, lemurs, possums, rodents, lizards, mosquitoes, flying foxes, snails, slugs and even a gecko also have a role to play.[336] The vast majority of pollinator species are wild.[337] Overall, the pollinator population of an area is a good indicator of the health of an ecosystem.[338]

From pinhead-sized duckweed (*Wolffia globosa*) to the giant *Rafflesia arnoldii*, plant species have coevolved with their pollinators. A race for resources has taken place over millennia with flowers offering nectar in reward for pollination services, and pollinators finding increasingly efficient and sometimes even devious ways to harvest these rewards.[339, 340] As well as offering food, flowers have made themselves attractive to pollinators through their shape, scent or colour. Some orchids and arums have created trapping mechanisms for their pollinators, allowing escape only when pollen is mature or ensuring exit from a flower is via pollen-rich areas. Others rely on confusion, tricking pollinators into thinking they are a receptive mate. The mirror orchid (*Ophrys speculum*), for example, mimics the female scoliid wasp (*Scoliidae*), and releases its pollen when the male attempts to mate with the flower. Some plants even feign death to ensure pollination; the giant corpse plant (*Amorphophallus titanium*) produces a strong, foul odour that resembles rotting flesh, attracting flies and carrion beetles to its pollen. In return, insects adapted hairs or scales for effective pollen collection and some pollinators have specific behaviours to increase pollen collection. Buzz pollinators vibrate their wings to release pollen; nightshades (*Solanacea*), which include tomatoes, eggplants and potatoes, have specifically adapted to buzz pollination.[341]

Pollinators and the food we eat

Pollination is one of our most important ecosystem services. It is estimated that 75% of all crops profit, to varying degrees, from animal pollination,[342, 343, 344] and between 5-8% of current global crop production is directly attributable to animal pollination.[345] Researchers have put global values on these services ranging from US$195 billion to US$657 billion annually depending on methodology and data sources.[346] Although a massive sum, this figure represents only about 10% of the economic value of crop production globally.[347] These estimates are, however, far from comprehensive, with data lacking from developing countries where the contribution of pollinators to both nutrition[348] and livelihoods is potentially much higher.[349, 350] For example in Southeast Asia, people receive around 50% of vitamin A from plants that rely on pollination.[351]

Significantly, the volume of production of pollinator-dependent crops has increased by 300% over the last 50 years, making livelihoods increasingly dependent on pollination services. The yield per hectare of pollinator-dependent crops has however increased less, and varies more, than for crops that don't depend on pollinators. Research indicates that production declines when pollinators decline.[352] Globally, it has been estimated that 3–5% of fruit, vegetable and nut production is lost annually due to inadequate pollination.[353] The impacts of total pollinator loss could decrease crop production by more than 90% in 12% of primary global crops, and a further 28% of crops would lose between 40-90% of production.[354]

As a result of coevolution, a vast diversity of animal pollinators are needed to ensure crop pollination. Flies play key pollination roles for crops including cocoa, coffee, tea, mangos, coconuts, nutmeg, avocados and many common field crops such as carrots, onions, leeks and parsnips. Moths pollinate yucca, neem, papaya, passionfruit and nutmeg. Wasps are known for pollinating figs[355] but also play roles in pollinating cotton. Beetles pollinate pomegranates and parsnips.[356] More than 90% of leading global crop types are visited by bees (Amazing animals: Bees).[357]

Birds pollinate around 960 cultivated plant species. Plants pollinated by bats, which include economically important species such as agave (from which mezcal comes) and durian (*Durio*

WITHOUT POLLINATORS THERE WOULD BE UP TO

50% FEWER FRUIT & VEG

IN YOUR SUPERMARKETS

Pollinating might not be the first thing that comes to mind when we think of flies but they are responsible for pollinating many plants. © Hannah L. Timmins

zibethinus), show on average an 83% reduction in fruit/seed production when bats are not present.[358] Animal-pollinator-dependent crops supply major proportions of micronutrients, vitamins and minerals in the human diet.[359]

Greater landscape-scale habitat diversity results in more diverse pollinator communities and more effective crop and wild plant pollination.[360] A well-pollinated flower will contain more seeds, with an enhanced capacity to germinate, leading to bigger and better-shaped fruit. Improved pollination can also reduce the time between flowering and fruit set, reducing the risk of exposing fruit to pests, disease, bad weather and agrochemicals and saving on water.[361]

Around 80% of all trees and bushes are pollinated by insects.[362] Tropical forest communities, which play significant roles in carbon sequestration, are dominated by pollinator-dependent species – it is estimated nearly 95% of trees rely on animal pollination.[363]

Bats are the most common mammalian pollinator. © Hannah L. Timmins

Pollinator decline

IUCN's Red List assessments indicate that 16.5% of vertebrate pollinators are threatened with global extinction. Pollinator populations are impacted by land-use change, including habitat loss, fragmentation, conversion, agricultural intensification, abandonment and urbanization, along with pollution, pesticides, pathogens, climate change and competing alien species.[364]

Climate change is a major issue. For fruit from apples to passionfruit, national-scale models project that climate change may disrupt crop pollination because the areas with the best climatic conditions for crops and their pollinators may no longer overlap in the future.[365] In other cases, pollinators may no longer be present when the plants that need them start flowering.[366] In China, farmers are already using pollination sticks to pollinate apple blossoms due to lack of insect pollinators.[367]

For island-based species, it is estimated that over 30% of vertebrate pollinators are threatened, with major consequences for island plant reproduction. For example, functional extinction of bird pollinators has reduced pollination, seed production and plant density in the shrub *Rhabdothamnus solandri* on the North Island of New Zealand but not on three nearby island bird sanctuaries where birds remain abundant.[368]

Without pollinators, the produce sections in supermarkets would look bare, with up to 50% fewer fruits and vegetables, and staples such as apples, carrots, lemons, onions and honey becoming increasingly scarce.[369] To support pollinators we need to allow ample habitat and resources, reduce their exposure to pesticides and other toxins, and protect as many pollinator species as possible to help ensure this essential ecosystem service persists.[370]

Amazing animals: Bees

Bees are the powerhouses of the pollinator world, and they mean big business. So much so that if they were public companies, bees would stack up impressively in the global marketplace: Forbes places a maximum estimated market value on wild native bees at US$4 billion.[371] When combined with the honey and pollinating services of honey bees (US$20 billion), US bees alone would be equal to the world's 817th wealthiest 'company', more valuable than Vodafone, Prada, Panasonic or Suzuki.[372]

Around the world over 100 million beehives produce around 1.77 million tonnes of honey each year, valued at US$9 billion in 2023.[373, 374] But, according to the United States Department of Agriculture, one colony of honey bees is worth 100 times more to the surrounding agricultural community than to the beekeeper — making the actual value of honeybees globally closer to US$909 billion.[375, 376] Yet the Western honey bee (*Apis mellifera*) only accounts for around a third of all pollination services and ironically, too many managed colonies can also threaten wild bee populations, making a balanced approach important.[377]

Worldwide, seven out of ten wild bees are solitary bee species;[378] these are important for cherries,[379] almonds,[380] coffee[381] and rapeseed.[382] Charismatic bumblebees (*Bombus* spp.) are critical for kiwi fruits,[383] apples,[384] sweet peppers,[385] tomatoes[386] and many more. In the tropics and sub-tropics, stingless bees take over pollinating apples in Brazil[387] and cucumbers in Malaysia.[388] Beyond these, there are carpenter bees, long-tongued bees and other types of wild social bees. These wild bees double the pollination rates of domesticated honeybees[389] and it is estimated that they contribute almost US$4,000 per hectare globally (adjusted for inflation) to the production of insect-pollinated crops.[390]

The ancient evolutionary relationship between flowering plants and bees likely began 100 million years ago.[391] They are remarkably in tune with one another. The evening primrose (*Oenothera biennis*) has evolved flowers that perfectly resonate with the buzz of bees. Within three minutes of 'hearing' the bees, the sugar concentration in the plant's nectar increases from 14.5% to 20%. This keeps the bee at the plant for longer, giving it a higher chance of pollination.[392]

However, like many insect pollinators, we are currently at great risk of losing our bees. Colony collapse disorder, first identified in 2006, is impacting honeybee hives globally with annual losses approaching 50% in the USA.[393] Among wild bees, species richness has declined by 25% since the 1980s.[394] Bumblebees are the most well-studied wild species and have exhibited dramatic losses in Europe[395] and North America.[396, 397] This is why people the world over are coming together to create bee-friendly environments[398] and lobby governments to ban bee-killing pesticides.[399]

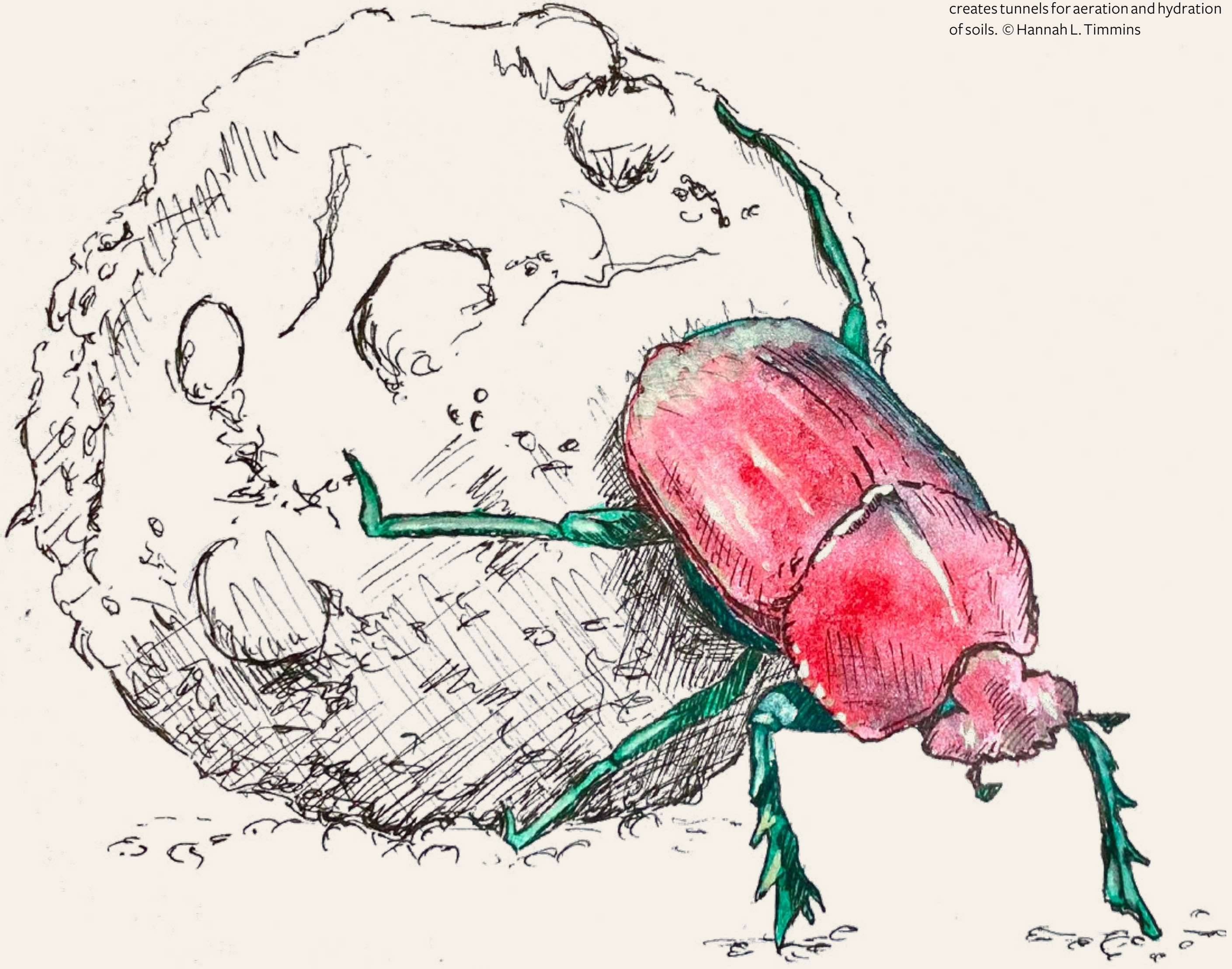
The wild bumble bee is critical for kiwis, apples, tomatoes and many more crops.

SOIL ENGINEERS

Soils are home to more than 25% of the Earth's total biodiversity. Animals move and create soil, contributing to nutrient cycling and retention, water retention, food production, fire and climate regulation and supporting other animals by providing shelter.[400]

Soil, and the animals and plants living in it, make up the 'critical zone', the Earth's living skin, that sustains life and regulates climate.[401] A wide variety of animals rework soils and sediments through foraging, burrowing, burying, wallowing, trampling, ingesting, defecating, resting and nesting. All these actions make animals very effective soil engineers, creating multiple benefits along the way.[402, 403]

Key among these benefits is nutrient cycling, achieved by increasing and protecting organic matter – the carbon-based compounds made up of plants (e.g. leaves and woody materials), animals (e.g. decaying components) and microorganisms (Nutrient arteries).[404] This is also linked to microbiodiversity where animals spread mycorrhizal fungi by creating habitat for fungal growth and through eating soil fungi. Mycorrhizal fungi have a symbiotic association with plantroot systems, thus helping around 80% of all landplants access nutrients.[405] Plant growth is also aided by



The deep burrowing of dung beetles creates tunnels for aeration and hydration of soils. © Hannah L. Timmins

Benefits of animal disturbances to soil

- NUTRIENT CYCLING
- FIRE & CLIMATE REGULATION
- SOIL MOISTURE
- MICROBE DIVERSITY
- PLANT GROWTH
- SOIL PRODUCTION
- HABITAT PROVISION

animals breaking up hard soils, allowing seeds in and thus increasing germination, recruitment and plant growth,[406, 407] and aiding water infiltration, leading to decreased surface run-off and erosion.[408] Animals can also aid soil production, where subsoil or weak bedrock is moved or broken up when animals search for food or shelter.[409] Soil engineers influence fire regulation by impacting moisture and the amount of leaf litter (see below) and undoubtedly have a role in the carbon cycle, although the mechanisms controlling soil organic carbon remain poorly understood.[410, 411, 412] Finally, animals also provide homes for other species through what is known as a burrowing cascade, where burrowing animals move into previously created burrows.[413, 414]

There is growing evidence that these effects are substantial. Depending on the species and where they live, soil engineers can disturb up to 30% of the soil surface annually.[415] A global study found elevated levels of soil nitrogen (by 77%) and phosphorus (by 35%) in soils disturbed by animals, probably due to trapped organic matter and/or nutrient-rich soils being moved up from deeper levels. This resulted in better (by nearly a third in both cases) plant productivity and recruitment (i.e., seed germination and growth) in disturbed areas. The study also highlighted the importance of the burrowing cascade, leading to animal abundance being 12 times greater than in areas without soil engineers.[416] All of these benefits increase biodiversity and resilience and improve ecosystem functioning.[417]

Vertebrate soil engineers

Invertebrates are pervasive in influencing soils worldwide, but in semi-arid and arid regions mammal engineers are common as they escape the heat and find food and shelter underground.[418] Soil engineers are particularly important in grasslands.[419] A mixture of mammal migration and stampedes across some of the planet's vast grasslands affects both soil structure and in turn vegetation growth.[420] In the rangelands of western North America, ground squirrels such as prairie dogs (*Cynomys* spp.) move large amounts of soil in each communal burrow (estimated at 200–225kg of soil per burrow system); this combined with grazing increases nitrogen available to plants, and can improve forage quality for large herbivores.[421]

The impacts of Australia's soil engineer decline

Worldwide, Australia has had the highest mammal extinction rate over the last 200 years. This includes about half of all digging mammal species, with many once described as common now either extinct (such as the rabbit-like marsupial the lesser bilby, *Macrotis leucura*, and the desert rat-kangaroo, *Caloprymnus campestris*) or under threat as their range declines. At the same time, Australian forest and woodland ecosystems have shown marked declines in health and function[422] and plant communities adapted to fire-prone environments are losing their resilience to fire.[423] Although there are many reasons for reduced

ANIMAL ABUNDANCE CAN BE 12 TIMES GREATER IN AREAS WITH SOIL ENGINEERS

The lesser bilby, one of Australia's extinct soil-breakers, spent its life digging and aerating soils in the arid climate. © Hannah L. Timmins

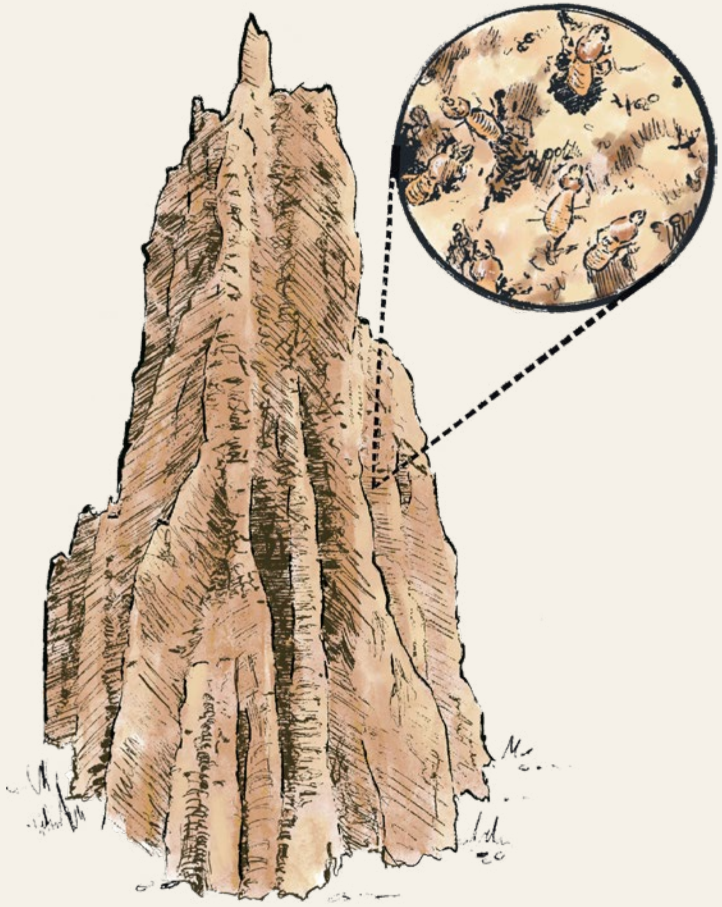
fire resilience, including the impacts of climate change, the loss of medium-sized mammals that once dug organic matter into the soil has left increasing fuel loads. This has led to greater fire intensity, which many trees are unable to withstand.[424] Additionally, the loss of digging mammals has led to decreases in water infiltration, increasing the risk of drought and tree decline.[425] Recovery after fire is also impacted as there is less leaf litter buried by small mammals and secured from flames beneath soil.[426]

The restoration of mammals such as the eastern bettong (*Bettongia gaimardi*), a medium-sized digging marsupial, has allowed for a better understanding of their role in soil movement and coverage, providing evidence of small mammals' potential in soil recovery in former agricultural areas.[427]

The engineers beneath our feet

Invertebrates such as ants, termites, beetles and worms can have significant impacts on soil

Termites generate piles of highly fertile soil while carving out tunnel networks to move nutrients and through which water and air can permeate. © Hannah L. Timmins



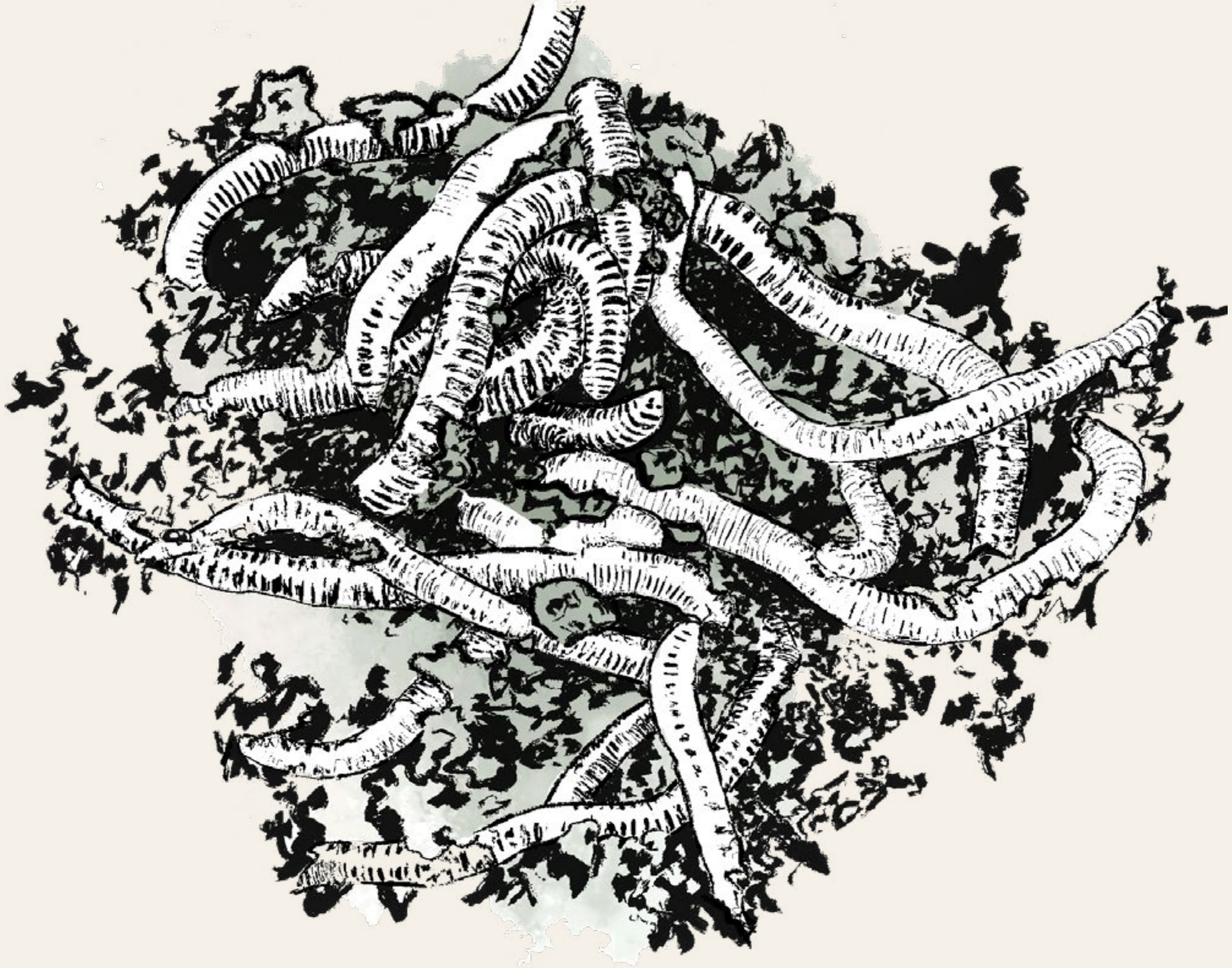
functioning through moving soil and making underground nests, chambers or galleries.[428] Darwin first wrote of the mixing of plant and organic matter in soil by earthworms in the 19th century, but until recently the role of some of the smallest soil engineers has been widely overlooked.[429]

Dung beetles have become one of the better studied soil engineers. A study of seasonally dry tropical forest in southern India found the vertical tunnels of dung beetles significantly decreased soil density and provided a path for water to move through (a 37-fold increase compared with surrounding topsoil).[430] Other burrowing animals such as earthworms provide the same service.[431] In Burkina Faso, increased termite foraging in restored forests increased water infiltration by 2–4 times compared to crop fields and bare ground.[432] But these relationships are complex: earthworm activity can, for example, stabilize soil carbon[433] but also increase greenhouse gas emissions depending on local ecosystem conditions and climate.[434]

The threats to soil engineers

While the evidence of the importance of soil engineers is growing, so is concern over their conservation. A review of IUCN's Red List found 869 non-flying land-dwelling mammals which could be described as soil engineers. Of these, 16% are threatened, 2% are extinct and 8% are data deficient. When divided into three distinct groupings – foragers, semi-burrowers and burrowers – foragers were assessed as the most threatened (35%) with Oceania having the highest percentage of threatened (27%) and extinct (11%) soil engineer species (see above).[435]

The primary threats to soil engineers are activities related to agriculture and aquaculture (29%) and biological resource use, for example the exploitation of soil diggers such as pangolins (22%).[436] Many engineering animals, such as plateau pikas (*Ochotona curzoniae*), zokors (*Eospalax* spp.)[437] and prairie dogs[438] (see above), have been actively exterminated due to the perception that they compete with livestock



Earthworm burrowing creates tunnels for root growth, soil aeration and water runoff. Without them, soil is up to 90 percent less effective at soaking up water.

for forage and that they degrade ecosystems through soil disturbance. It is now well established that it is not the activities of soil engineers but overgrazing by domestic livestock that is the main cause of the degradation, with mounting evidence suggesting that soil engineers facilitate nutrient cycling and grass productivity (see above).[439] Restoration projects need to consider the reintroduction of digging mammals to ensure key ecological processes are secured[440] and coexistence with livestock and native ungulates across broad landscapes needs to be encouraged to ensure stable populations of soil engineers in many areas.[441]

Services: Water quality, regulation and erosion control

Animals of all sizes act as ecosystem engineers in marine and inland waters:[442] hippos (*Hippopotamus amphibius*) keeping water channels open,[443] fish species digging nests,[444] coral reefs protecting coastlines[445] and tiny chironomid worms burrowing into stream beds.[446] Together they improve water quality, reduce flooding, sequester carbon, regulate flow and reduce impacts of pollution.

Filter feeders like bivalve molluscs[447] or net-building trichopteran (caddis fly) larvae[448] repair water quality and accelerate migration of certain chemicals in the water.[449] Animals like crocodiles and antelopes disturb otherwise stagnant pools, preventing development of anoxic (oxygen deficient) conditions.[450] Nest building by salmon is estimated to affect 30% of streambeds in Alaska[451] and has a range of impacts, including sorting sediments into size classes, which is thought to decrease susceptibility to erosion (Amazing animals: Salmon).[452] In coastal areas, oyster and mussel beds both trap sediments and dampen waves (Amazing animals: Oysters).[453]

Beavers are perhaps the best-known freshwater ecosystem engineers, through building lodges and dams, accumulating coarse woody debris and changing sediment dynamics.[454] They play a major role in restoring biodiversity and ecosystem function, including nutrient retention, carbon storage and flood and drought attenuation,[455] the latter by helping regulate water storage and release.[456] A single beaver dam has been calculated as modifying the volume of flowing water by 3,400–628,000m^3 per year, depending on ecosystem and water system characteristics.[457] Beavers also create costs, particularly in terms of timber loss and flooding in places where it is not wanted,[458] although research in Finland suggests global benefits outweigh costs by many hundreds of millions of dollars annually.[459]

As ever, a balanced ecosystem is needed: invasive mussels can on occasion reduce diversity, for instance.[460] Furthermore, many of these ecosystem engineers are under threat; global coverage of living coral has halved since the 1950s and the decline continues.[461] Many salmon populations have also undergone catastrophic declines.[462, 463] Recognition of the role of animals in water management is still largely lacking.

A beaver expertly places a new branch into her carefully constructed dam, plugging a recent leak. © Hannah L. Timmins

INTACT FAUNAL ASSEMBLAGES

Thus far, we have looked at how individual species or families (Salmon, Oysters, Bees and Hornbills) and functional guilds of species (Predators, Grazers, Seed dispersers, Pollinators and so on) deliver ecosystem services. But how are habitats held together by their living assemblages of wild species? Intact assemblages of species create their ecosystems and are ultimately responsible for delivering their ecosystem services; the removal and depletion of species leads to the loss of these services.

Abundance: how the sheer number of individual animals underpins ecosystem services

As mentioned, fauna are undergoing dramatic range losses globally,[464] and wild mammals now make up just 4% of total mammal biomass.[465] We don't have to be ecologists to notice these losses are becoming more tangible. Every spring the buzzing of bees gets quieter, and thinning bee communities struggle to pollinate crops at useful levels. We look up and see fewer vultures and other avian scavengers in the skies; their depleted numbers can only do so much in carcass clean-up

Seeing wildlife in abundance, like these black-tipped reef sharks, is now a rare occurance but was once the natural state with ungulates, insects, fish and many other types of wildlife.

and disease prevention. In our emptying forests, the vanishing populations of elephants, tapirs, monkeys and hornbills are eating, moving and fertilizing fewer and fewer seeds. The full impacts of this on water regulation, carbon storage and sequestration and other ecosystem services may not be seen for tens if not hundreds of years.

Abundant and widespread wildlife are also fundamental in combating risks posed by natural and anthropogenic events like droughts, fires, floods, diseases, pollution and so on. If there are enough individuals, there are more likely to be survivors. The greater the population, the greater the likelihood of adaptations, genetic or cultural, that can deal with new challenges and environmental conditions. This supports a more rapid population recovery and recovery of the services that species or ecosystems provide. In this way, abundance is resilience. And while relatively low levels of abundance might be adequate to provide current ecosystem functions, higher levels might be needed under environmental change.

Other wildlife attributes that contribute to ecosystem services

In addition to abundance, there are a few other attributes that are listed most frequently as being important for delivering ecosystem services: species richness (the number of different species present), body size or weight, and the geographic extent of the community.[466]

In terms of species richness, a diverse set of pollinators can service a diverse variety of plants, including our crops; different pests require a multitude of pest-regulator species; and our water is purified and regulated best hen numerous species are present.[467]

Greater geographical extent of the community is important for water provision, purification and flow regulation, along with their ability to respond to climate change.[468] For example, beavers confined to a small part of one tributary stream can do only so much for downstream flood prevention, and the water soaked into heir immediate surrounding soils will do little

FIVE BIODIVERSITY ATTRIBUTES of importance for ecosystem services

- SPECIES ABUNDANCE
- SPECIES RICHNESS
- LARGE BODY SIZE OR WEIGHT
- GEOGRAPHIC EXTENT OF THE COMMUNITY
- NUMBER OF SPECIES PLAYING A KEYSTONE ROLE

to stop droughts or wild fires in neighbouring water catchments.

Size and weight of individuals is important for many ecosystem services. Larger freshwater fish are good for fishers' catches and larger seeds from larger trees require larger seed dispersers like elephants and hornbills. Larger predators will impact more and larger species of prey. In turn, larger browsers and grazers like bison and wildebeest will have more of an impact on grassland and forest structure. Shifting any of these body-size dials can have big effects on vegetation and subsequent water and nutrient regulation.

Keystones, engineers and ecospace

Keystone species have outsized effects on their ecosystems relative to their abundance. They play critical roles in maintaining ecosystems, determining the makeup and abundance of other species and in turn the functioning of habitats. Like the keystone in an archway (the uppermost wedge-shaped stone), their removal would trigger collapse. Many scientists now prefer the term 'functional species' because the keystone metaphor suggests one central, apex species locking an ecosystem together, but we now know ecosystems are supported by whole networks of organisms.[469] Building on this concept, *ecosystem engineers* are species that create, modify or maintain habitat.[470]

These terms have been coined to elevate species with disproportionate impacts on their environment and the functions or services their environment provides. We have reviewed several of these prominent species (Amazing animals) in this report.

Keystones and engineers might have big impacts but all species create what many are now calling *ecospaces*. When they interact with abiotic aspects of their environment (soil, water etc.), fauna create dung, carcasses and wallows, they plant seeds, pollinate flowers and mow grass. This expands niches for other species.[471]

An ecosystem engineer like a beaver might build a dam to flood the front door of its lodge, subsequently flooding a riparian forest. The roots rot over time, softening the trunks of the trees. Woodpeckers take advantage of the softer wood to find food and excavate a nest. After the chicks fledge, a new colony of bees questing for a home finds the hole vacant and relocates. The idea of ecospace shows how each species creates the potential for the next – they are all intricately connected.

Ecosystems are a spiderweb – cutting even one strand is risky!

If we imagine an ecosystem as a spider's web, we see that cutting any individual strand is fraught with risks, perhaps some more than others, but it is hard to know which strands are most important to the structure. What is well known is the more strands that are cut, the weaker the system is.[472] Some species perform similar functions; some flowers are pollinated by more than one species. The loss of one of the pollinator species may not immediately result in the loss of that plant, but the resilience of the system has weakened. If there

Honey bees build a home in an abandoned woodpecker nest drilled in the soft wood of a tree.

is another change to the ecosystem, an extreme weather event, disease or habitat loss, and another pollinator species is lost, the future of that plant species is at even greater risk. In this way, ecology has in-built redundancy mechanisms; if there is an adverse impact on one species, another species might pick up the slack. This is a bit like a plane having two engines – it only needs one to fly but we have two to reduce the risks from one failing. The depletion of species richness ultimately creates a weak system that cannot adapt to future changes.[473,474,475,476]

Resilience

Nature is not static; it shifts and changes over time. That is why scientists are now using the lens of resilience to understand and communicate about biodiversity and climate change. Resilience describes the capacity of an ecosystem to continually shift and adapt, to absorb disturbance and reorganize, whilst remaining within critical thresholds to retain the same structure, feedbacks, functions and services.[477] Wild animals, living in substantial populations in functioning ecosystems, are key to maintaining this resilience.

BIOMES

THE BENEFITS OF WILD ANIMALS IN PARTICULAR PLACES, AND THE IMPLICATIONS OF THEIR LOSS

The Coral Triangle

Coral reefs are the biggest animal-made structures on Earth.[478] They are built by tiny animals, called polyps, that produce calcium carbonate, which gives corals their hard skeleton. Colonies of polyps grow on top of the remains of former colonies, eventually forming massive reefs. They are home to numerous other animals including sponges, fish and larger marine mammals. Approximately 25% of all marine life depends on coral reefs at some point during its life cycle.[479]

The Coral Triangle has the highest coral diversity in the world.[480] Found in the western Pacific Ocean it includes the waters of Indonesia, Malaysia, the Philippines, Papua New Guinea, Timor Leste and Solomon Islands. With over 100,000km² of reefs, the Coral Triangle makes up 30% of the world's coral reefs, supports 600 reef-building coral species (75% of all species known to science), over 2,000 species of fish[481] (37% of the planet's reef fish species),[482] the most diverse sponge assemblages worldwide (and probably a high number of yet undescribed sponges)[483] and the greatest extent of mangrove forest.[484, 485] The reefs are vital for:

Food security

The reefs benefit 600 million people, providing food, income and protection from storms. Reefs provide flood control worth more than US$400 million each year[486] (Disaster risk reduction) and directly contributes to the livelihoods of 130 million[487] people, providing daily sustenance and income. Commercial fisheries provide over US$3 billion per year to the countries in the Triangle, although not all of this is sustainable.[488]

Tourism

There is a large and growing nature-based reef tourism industry in the region, valued at over US$12 billion annually.[489] The reef fish provide a spectacular show for snorkellers and divers, and are the caretakers of coral reefs. Fish provide nutrients for coral growth and keep reefs healthy and reef pests in check.[490] Corals rely on algae living inside them to supply them with food; it is thanks to these algae that corals appear so colourful – and why corals go white when algae die due to warming seas. Fish ensure the reefs receive enough light by grazing seaweed that otherwise becomes dominant (Browsers & grazers), maintaining the balance between reef-building corals and fleshy algae; fish also predate corallivores (coral eaters) such as the coral-eating starfish (*Acanthaster planci*).[491, 492, 493, 494]

Nutrient transfer

Marine animal life cycles pass between habitats such as seagrass meadows, mangroves and coral reefs, impacting nutrient and energy exchange and ecosystem health (Nutrient arteries).[495] In addition, the nutrient 'sponge loop' is particularly important. Reef sponges (another vital animal of the reefs) filter water by taking up dissolved organic matter and generating particulate organic matter, which provides food for other animals in the reef.[496] Sponges also harbour microbial symbionts that can contribute to reef productivity.[497]

WITHOUT NATURE'S TECHNICIANS

40% of the reefs and mangroves of the Coral Triangle have already been lost over the last 40 years, and unless climate change and other destructive elements are halted, the area will continue to see the progressive loss of most mangroves and coral reefs over the coming half-century. The whole cycle of nutrient arteries and browsers & grazers that form the diversity of reef life will collapse. As a result, coastal fisheries would be severely degraded, with the ability of reef systems to provide food for coastal people decreasing by 50% by 2050 and 80% by 2100.[498] And as the reefs die so does the protection they provide. Without the reefs, the flooding of coastal communities could nearly double and countries like Malaysia, Indonesia and the Philippines could see the costs related to flooding events triple.[499]

The Arctic Ocean

The Arctic Ocean is Earth's northernmost body of water. Much of it is covered by ice throughout the year – although this is retreating each year with global warming. The Arctic is a highly productive ocean. Phytoplankton form the basis of the marine food chain [500, 501] (Plankton-eaters), feeding animals living above and below the sea ice:[502] from anemones living on the ocean floor, to benthic marine predators like the Greenland shark (*Somniosus microcephalus*), seabirds and mammals like walruses (*Odobenus rosmarus*) and bowhead whales.[503, 504, 505]

Along the northwest edges of the European land mass, giant cold-water coral reefs stretch out into the Arctic Ocean, submerged up to a kilometre deep.[506] In these darkened waters, the corals cannot rely on light-dependent symbiotic algae; instead they depend on particulate organic matter and zooplankton for their food. This system is a biodiversity hotspot, home to sponges, polychaete worms, molluscs, echinoderms like brittle stars and urchins, mussels and crustaceans, and provides safe nurseries for commercial fish species. Other Arctic Ocean ecosystems include giant kelp forests, eelgrass meadows and bivalve beds, all supported by a diverse array of wildlife. The Arctic Ocean's wildlife plays a key role in:

Food security

Around 4 million people live in the Arctic, and about 10% are Indigenous peoples.[507] Subsistence economies and livelihoods of Arctic Indigenous peoples are based on access to natural resources and the products that come from them. Many coastal Indigenous peoples rely on whaling, sealing, hunting of seabirds and eggs and fishing for food, clothing, income and other products. [508]

Nutrient transfer
Walrus disrupt the ocean floor sediments, increasing nutrients in the water column by about two orders of magnitude over thousands of square kilometres, supporting plankton and fish stocks (Soil engineers).[509] Seabirds move nutrients via fish protein from the nutrient-rich Arctic Ocean to nutrient-poor lands.[510] The little auk (*Alle alle*) transports vast amounts of nutrients from sea to land, creating conditions that sustain muskox (*Ovibos moschatus*) at 10 times the density within 1km of little auk fertilized vegetation hotspots.[511]

Water filtration and regulation
Filter feeders on the Arctic sea floor, such as bivalves like oysters, remove organic pollutants and toxic or hazardous substances from the water column. They store relatively large amounts of toxins in their bodies without being adversely affected, and remove toxins from the fish food chain that may otherwise be consumed by people. They can also inhibit harmful blooms that reduce the amount of light to plants, algae or corals that live at the bottom and provide habitat for commercial fish species.[512]

Carbon storage and storm protection
Cold-water coral reefs, mostly made of symbionts between coral animals and their internal algae, sponges and the like, contribute significantly to carbon turnover.[513] Arctic kelp forests have been relatively poorly studied compared to their temperate counterparts. Yet they represent a substantial portion of global distribution, cycle a significant amount of carbon, have, along with sea ice, important important storm and coastal erosion protection qualities and are maintained by large predatory groundfish, which control grazing urchin populations (Predators).[514, 515, 516, 517]

WITHOUT NATURE'S TECHNICIANS

Without predator groundfish, grazers like urchins could decimate Arctic kelp forests or eelgrass meadows.[531, 532] The loss of seabirds, walrus, fish, whales and other nutrient arteries could seriously reduce the primary productivity in the sea and on land and even kickstart a negative feedback loop like the iron deficiencies in the Southern Ocean (Plankton-eaters). In the span of the last forty years, Arctic temperatures have surged almost four times faster than the global average;[533] a major challenge with this is the shrinking of suitable habitats for cold-adapted, sea-ice-dependent and associated species, which are unable to shift further north as they are already at the top of the world. This could be particularly problematic for many species – including commercial Arctic fish.[534]

Health
Bioprospecting (the search for nature-derived medical compounds) is just beginning in the Arctic, but scientists believe the harsh environment, reaching a minimum of -50°C in winter, may have resulted in important adaptations in species inhabiting the ocean, including potential antibiotic compounds.[518]

Economy and industrial fishing
Some of the world's largest commercial fisheries are drawn from this ocean.[519] Commercially important fish species such as crab, shrimp and other shellfish, halibut, plaice and cod are provided habitat by cold water corals, kelp forests, eelgrass meadows and communities of other organisms from the Arctic sea floor.[520, 521, 522, 523] In 2018, Iceland alone harvested just under 1.2 million tonnes of fish valued at over US$1.2 billion.[524]

Tourism and other cultural services
Charismatic marine mammals like walruses, bowhead whales and polar bears (*U. maritimus*) play an important role in Arctic tourism[525, 526, 527] (although tourism can disturb Arctic ecosystems).[528] These and other species are also an important resource and hold special cultural significance for many Arctic Indigenous peoples.[529] In the Barents Sea region, harvesting of marine resources is central for social cohesion and a sense of local identity.[530]

Kavango-Zambezi grassland and savannah

Savannah relationships are a delicate balance between grazing, predation and fire. The 520,000km² Kavango-Zambezi Transfrontier Conservation Area (KAZA) spans parts of Angola, Botswana, Namibia, Zambia and Zimbabwe: a vast area (nearly twice as large as the United Kingdom) of arid savannah, woodland and marshland including the Okavango Delta, and the Chobe, Cuando and Zambezi Rivers. KAZA is home to a vast array of animals, many of which are threatened, including the world's largest elephant population[535] and healthy populations of lions.[536] Increasing connectivity, to reduce ecological isolation and genetic weakening, is a key conservation aim.[537, 538] The area provides many animal-related ecosystem functions and services.

Carbon sequestration

High biodiversity ecosystems tend to have high carbon value in their vegetation and/or soil.[539] Carbon in grasslands and savannahs is generally lower than in forests, but is globally important due to the huge areas involved.[540] Grassland may also be a more stable carbon store in areas of high fire risk (Climate regulation),[541] with carbon secured below ground in roots and soil.[542] Research is increasingly demonstrating that healthy animal populations can maintain or enhance carbon stocks in ecosystems.[543] Herbivores' nutrient-rich dung[544] and trampling increases soil organic carbon (Browsers & grazers).[545] A study in KAZA found that soil carbon gains mediated by elephants almost offset the woody carbon losses from elephant damage.[546]

Tourism
Wildlife watching supports 80% of annual tourism revenue in Africa,[547] and large predators and herbivores such as elephants are a big draw[548, 549] with overseas visitors.[550, 551, 552] Richness of wildlife is positively related to ecotourism income in Namibia,[553] with a key economic role through hunting and wildlife viewing.[554, 555] Many KAZA countries see trophy hunting as a key income source.[556, 557, 558]

Resilience against climate change
There is growing consensus that ecosystems with high biodiversity are more resilient to climate change (Climate regulation).[559, 560] The Zambezi is likely to face more extreme climate change impacts than many other major African river basins.[561] Rivers that retain their natural flow and species are more likely to maintain their resulting benefits to people, such as fisheries, flood protection and tourism[562] – so conservation is a key part of climate adaptation and risk management.

Protection against degradation and fire
Herbivores suppress tree growth,[563, 564] which decreases above-ground carbon vulnerable to wildfires, shifting more carbon into safer below-ground stores, averting even greater carbon loss over the long term (Browsers & grazers). Elephant paths can also act as fire breaks.[565]

WITHOUT NATURE'S TECHNICIANS

If browsers and grazers decline, forest would soon overwhelm grassland, changing the ecology, while without predators, herbivore populations themselves boom and overgrazing causes degradation. An imbalance between the two can result in carbon stores being lost to fire or erosion, respectively. At the same time, soil organic carbon drops without soil engineers like earthworms to maintain soil health. Without browsers to help keep river channels open, the Okavango Delta would gradually lose connectivity. If pollinators decline, plants suffer too. Furthermore, herbivores like elephants are also important seed dispersers, so that plant groups (like fruit trees) gradually decline if they disappear.

Maintaining river systems
Complex interactions, including with wild animals, maintain stable flows through the multiple river systems. Hippopotami play a major role in channel and lagoon dynamics in the Okavango Delta and extensive Cuando wetlands by trampling open new river channels leading into floodplain lagoons, enhancing water flow in the system, increasing connectivity and facilitating water flow into floodplains (See Water quality, regulation and erosion control).[566]

The Mekong river basin

The Mekong is one of the world's most productive and biodiverse[567] river systems, flowing from the Tibetan plateau through China, Myanmar, Cambodia, Laos, Thailand and Viet Nam. It has 13 unique, connected aquatic ecosystems, which along with highly variable seasonal flows creates exceptional productivity. The area unusually contains five separate freshwater ecoregions,[568] nine biogeographical regions for fish[569] and exceptional biodiversity of freshwater molluscs.[570] Sediments and nutrients sustain landforms, agriculture and fisheries downstream and into the Mekong Delta. Iconic aquatic wildlife includes the world's largest freshwater stingray – the giant freshwater whipray (*Urogymnus polylepis*), Mekong giant catfish (*Pangasianodon gigas*) and Irrawaddy river dolphin (*Orcaella brevirostris*), while in the broader basin the Asian elephant (*E. maximus*) and tiger (*P. tigris*) still roam, albeit in greatly depleted numbers. Despite intensive human use, connectivity remains between many of the ecosystems.[571] However, this connectivity is seriously threatened by dam building,[572, 573] which also negatively impacts the entire ecosystem by altering the quantity and timing of flow, limiting essential nutrients and sediments downstream, and threatening water quality. In addition, some ecosystems are being degraded by pollution,[574] climate change,[575] unsustainable sand and gravel extraction, invasive species and overfishing. The Mekong wildlife plays a key role in:

Food security

The Mekong is the world's most productive inland fishery, producing over 2 million tonnes a year [576] worth US$11 billion,[577] at least 35% from migratory species.[578] Fish like the endangered Tra catfish (*Pangasius hypophthalmus*) are critical for local diets, mainly fished in Cambodia and Laos but often farmed in Viet Nam. Freshwater fish contribute over half of the total animal protein eaten by the human population in the Lower Mekong, averaging 33.4kg per person per year across the region in 2015.[579]

Nutrient transfer

Fish migration plays a significant role in nutrient enrichment (Nutrient arteries), with fish transferring sediment from nutrient-rich downstream floodplains towards more nutrient-poor upstream tributaries,[580] thus maintaining the high productivity in the uplands.

Water purification

Bivalve molluscs filter water, maintaining purity.[581] Herbivorous fish control algae, reducing eutrophication and the consequent oxygen depletion in water.[582] Bottom-dwelling species also create microhabitats for other species while helping to stabilize sediments (Water quality, regulation and erosion control).[583,584]

Health

Predatory fish species help to control mosquitoes and other pests, although the magnitude of this contribution has not been quantified (Disease preventers). However, they are anecdotally important enough that fish are being investigated for use in community-run efforts to prevent dengue fever, in the face of increasing pesticide resistance among mosquitos.[585]

WITHOUT NATURE'S TECHNICIANS

If fish browsers and grazers were lost, the ecosystem could quickly become eutrophic as algae died and rotted. Without soil engineers the river bottom could destabilize, increasing erosion, flooding risk and nutrient loss. Decline of predatory fish could lead to an increase in disease-carrying mosquitoes, devastate fisheries and – because many predators are also migratory – also reduce upstream transfer of nutrients, leading to progressive loss of productivity in the higher reaches. Local economies and food security could collapse, disasters would become more frequent and human health would suffer. Large aspects of human culture would die along with the river.

Cultural values

Fish and other animals play a central role in the cultural and spiritual life of many people in the Mekong Basin. Mekong giant catfish are depicted in rock art in Pha Taem National Park, cooking and eating fish is celebrated in many folk songs [586], and fish feature in regional festivals. [587] The Mekong is sacred to both mainstream and local faith groups.[588,589] The Irrawaddy dolphin is also regarded as a sacred animal by both Khmer and Lao people.[590]

Tourism

The Mekong offers multiple opportunities for fishing, birdwatching [591] and ecotourism. In 2022, the Mekong Delta in Viet Nam alone was estimated to have welcomed over 44 million tourists, with a revenue value of nearly US$1.33 billion.[592]

The Amazon forest

Often dubbed 'the lungs of the planet', the Amazon forest stretches over 6.7 million kilometres across eight countries and one overseas territory.[593] It accounts for about 10% of the world's terrestrial biodiversity and stores an equivalent of 15–20 years of global CO_2 emissions in its vegetation.[594] The Amazon absorbs 2.2 billion tonnes of CO_2 each year and its rivers produce 20% of the world's freshwater discharge.[595] In Brazil alone, the Amazon contributes up to US$8.2 billion each year to the economy.[596] These forests are also home to 25% of the world's terrestrial biodiversity,[597] and it is this biodiversity that underpins the health of the forest. The Amazon's wildlife plays a key role in:

Nutrient transfer

Phosphorus runs from the nutrient-rich Andes into the rivers of the Amazon and is taken up by monkeys, tapirs, jaguars, toucans, leafcutter ants and other wildlife that feed on riparian vegetation, fish or crustaceans. They then walk inland and excrete their waste onto the nutrient-poor soils of the forest floor, preventing vegetation collapse (Nutrient arteries).[598] These species move only a fraction of the phosphorous once deposited by South America's now-extinct megafauna, but its estimated value is still around US$900 million each year.[599]

Carbon storage and sequestration

Vegetation is supported not only by animal-derived nutrients, but also by seed dispersers such as toucans, large monkeys and tapirs, which move and fertilize the seeds of large woody trees. Overhunting of these species is contributing to a long-term

decline in high-biomass tree species and their carbon stocks, even in structurally intact forests (Climate regulation).[600]

Health

In areas of the Amazon with a greater diversity and abundance of wildlife, exposure and prevalence of diseases like Chagas and malaria are reduced in human populations (Disease preventers).[601, 602, 603] This phenomenon is known as the dilution effect: a greater diversity of disease hosts can dilute the pool of hosts that amplify transmission, resulting in decreased exposure to vector-borne disease.[604] Wildlife in the Amazon also presents a wealth of potential medicines: for example, venom from the fer-de-lance viper (*Bothrops asper*) led scientists to identify an enzyme now helping millions of people to control hypertension.[605]

Food security

Amazonian wildlife sustains food security in many ways. Species like agoutis (*Dasyprocta* spp.) disperse the seeds of important food trees like the Brazil nut tree (Seed dispersers)[606] and wild fish and game also provide protein to people living in this region, an especially critical source of nutrition for the poorest.[607]

Economy, agriculture and water regulation

The Amazon's nutrient movers and seed dispersers maintain a forest big enough and healthy enough to generate its own weather system; the trees release around 20 billion tonnes of water into the atmosphere daily and these 'flying rivers' deliver rainfall as far south as Argentina, irrigating the continent's agricultural systems.[608]

WITHOUT NATURE'S TECHNICIANS

By the end of the Pleistocene (approximately 11,700 BCE – the blink of an eye in evolutionary terms), South America had lost 70% of faunal species weighing over 9kg.[609, 610, 611, 612] Before this, species like the giant ground sloths and glyptodonts once played a critical role in transporting phosphorus, a key nutrient for tree growth. Without these giants, the average distance between eating and excreting dropped from almost 9km to just 1.6km.[613] Now only 2% of historical phosphorus levels are transported inland.[614, 615] The eradication of these seed dispersers also reduced tree recruitment and carbon storage.[616, 617, 618] The remaining fauna keep these mechanisms just barely functioning. Between 1970 and 2014 forest vertebrate populations more than halved,[619] pushing the ecological boundaries further. Where predators have been lost, out of control herbivory has created ecological meltdown and the decimation of vegetation.[620] Combining the loss of nutrient arteries, large seed dispersers, pollinators and predators may spell disaster for trees and the water cycles they maintain. The 2005, 2010 and 2016 droughts may be the first signs that species loss, combined with forest clearance and fragmentation, is bringing the Amazon closer to its tipping point.[621]

Services: Non-material contributions of wildlife to people

In addition to the roles wild animals play in delivering tangible ecosystem services, they also make many *non-material* – intangible, though no less important – contributions to people's well-being.

One way wildlife contributes non-materially to people is through physical and psychological experiences, including recreation, tourism and observation. These experiences, in addition to the knowledge that certain species of wildlife exist, have many positive and powerful impacts on physical and mental health, including improvements in cognitive performance.[21] In addition to the well-documented material (including economic) benefits of hunting, fishing, and wildlife viewing,[22] these activities form the basis of many cultural traditions and identities.

Non-material contributions can take the form of learning and inspiration (which elicit positive emotions such as awe and wonder), and support cultural identities and other manifestations of human-wildlife relationships. Direct interactions with wildlife such as 'eye to eye epiphanies' (that is, making eye contact with other species) are a profound spiritual or inspirational experience for many people. [23, 24] In Western contexts, animals support early childhood learning and development.[25]

Birds have been intertwined with human lives for millennia; their melodious songs and tantalizing ability to 'defy gravity' have always captivated humans. Archaeological records of Aztec, Mayan and Incan civilizations indicate that birds were significant in many ceremonial, religious and traditional practices.[26] Birds continue to occupy central roles in oral stories of many Indigenous groups across the world, in addition to Western culture – think of Rachel Carson, who conveyed the deleterious impacts of pesticides by naming her landmark book *Silent Spring*, daring people to imagine springtime without birdsong.[27]

Birds have inspired countless creative endeavours from The Beatles' 'Blackbird' to Shakespeare's depiction of ravens in *Macbeth*. Bird songs have been associated with reduced anxiety and depression,[28] and are used in acoustic therapy. In the United States, over 42 million people (almost 13% of the population) engage in birdwatching.[29] Birds have always contributed to people's well-being and remain a central part of the human experience around the world. This love of birds also generates tangible economic benefits through tourism.[30] In Colombia, a country with more bird biodiversity than any other, birdwatching yields an estimated US$9 million in profits and provides over 7,500 new jobs annually.[31]

Many people share space with mammals that are significant in their culture. Tigers for example are central to many mythologies and spiritual beliefs.[32] Tigers' range spans countries that are religiously, spiritually and culturally rich and varied, with a great diversity of perspectives and beliefs around the tiger in each country. Among Hindus in India the tiger is associated with the goddess Durga whose vehicle is a tiger, in Karen communities in Myanmar the tiger is seen as an ancestral spirit, and there is a fatwa for Muslims in Indonesia that decrees harming tigers is forbidden and protecting them is part of the worship of God.[33] The beliefs and values of these societies shape the way they perceive and value the tiger, which in turn can affect tolerance for coexistence. Similar strong relationships exist between people and animals from jaguars across Latin America to bison across North America, wolves in Europe, elephants in Africa and whales in the Arctic. Most, if not all, human societies have created deep bonds with particular species that are core to who they are as people.

The quetzal was a sacred species for Aztec people. © Hannah L. Timmins

CONCLUSIONS

Our first message is that wild animals play irreplaceable roles in providing ecosystem services for humanity. Their conservation is an essential part of sustainable development. But our second big message, often missed, is that it is not simply a matter of the continued existence of wild animals – they need to be in large enough populations to do their job properly. Abundance is key. Which means that in many cases protecting what remains is no longer enough: recovering wild animal populations is also required.

Wildlife abundance is in decline almost everywhere;[622] a decline that shows no signs of slowing down. Losses affect nearly all groups of species, from huge mammals, freshwater fish and amphibians to the world's insects.[623, 624, 625] These losses have implications for everything from food security to the transfer of nutrients between ecosystems. Although it is often still too early to judge what all these impacts will be, an increasing number can be predicted with confidence[626] – though there is a need for far more research into the role of wild animals as ecosystem service providers as a whole.[627] We need to rebuild populations, focusing particularly on species whose decline is having the most dramatic and damaging impacts on ecosystem services, which will not always be the most famous or charismatic.

Conservation of what remains is the number one priority. This is almost always cheaper and always more effective than recovering wild animal populations. But we are already beyond that stage in many places. The good news is that we have ample evidence that animal-based ecosystem services can be and have been restored. Species recovery can have dramatic positive impacts, far faster than might be supposed. Recovery of sea otters in Alaska and Canada turned unproductive

Squirrels collect, bury and store seeds and nuts creating food larders © Hannah L. Timmins sea-urchin barrens into deep kelp forests in a couple of decades, supporting larger fish populations, sequestering carbon and creating a booming tourism trade in sea otter watching (Predators). Recovered wildebeest populations in the Serengeti and Mara of Tanzania and Kenya flipped the ecosystem from a carbon emitter to a carbon sink, helping slow the rate of climate change, as well as rebuilding one of the world's most iconic wildlife migrations (Browsers & grazers). Recovering beaver populations reduced both flooding and drought problems in parts of the United States (Water quality, regulation and erosion control).[628] Other examples are scattered throughout the preceding pages. We have many convincing lessons to draw from.

However, another important lesson is that for any decision there are almost always trade-offs. For each successful species recovery, even if the impacts are overwhelmingly positive, there will be people who lose out, or who feel they are losing out. Sea otters eat economically valuable bivalves and some fishing communities reliant on these are less enthusiastic about their return. So controlled hunting is now allowed, with otter pelts marketed from Native American companies.[629] Similar tensions are linked with wolves, elephants and virtually every other wild animal recovery initiative.

Indeed, alongside their benefits, animals bring problems to humans, such as crop raiding, livestock killing and direct threats to humans. Rhinos play useful hydrological roles, but too many rhinos can pollute water with their faeces. People facing direct threats to their life and significant economic losses from human–wildlife conflict may not be impressed by the role of these species in long-term mitigation of climate change. Here we have focused on the positive roles, to redress a long-standing imbalance in attitudes toward the role of wild animals. But that does not mean being unaware of the costs.

There are undoubtedly challenges, but these are seldom unsurmountable. They make it important to plan wild animal recovery efforts carefully, to consider all the consequences. A wide range of stakeholders need to be brought into the discussion, including those likely to be opposed, and compromises worked out. It will be impossible to predict everything, so the willingness to practise adaptive management is important. As in every human endeavour, negotiation is essential.

Overall, however, the evidence is clear. Wild animals play crucial roles in ecosystems, and in our own survival. **Recovering wild animal species should no longer be considered a 'nice to have' but an essential part of securing the future resilience of our planet, and ourselves.**

References are hyperlinked from this report and accessible at naturestechnicians.org/references