CLOCKWISE FROM ABOVE: Aldabra giant tortoises have been used on Mauritius as surrogate seed dispersers, replacing the island's extinct giant tortoises; on Madagascar, some fruits are only eaten by lemurs; gorillas' habit of defecating in open areas, where seedlings face less competition, makes them important seed dispersers; fruit bats can disperse seeds over hundreds of kilometres; estimates suggest that 70–100 plant species depend on the cassowary for seed dispersal; cassowary plums and quandongs are among the fruits whose seeds are dispersed by cassowaries; when elephants disappear from an area, some tree species suffer; **OPPOSITE:** soursop seeds are dispersed by large fish in the Amazon

Seeds of doom

Around the world, many plant species rely on specific animals to disperse their seeds away from the parent plant. But many of those animals are now facing extinction, raising fears of a cascade of further extinctions, with wide-ranging impacts on the health of the world's forests. **Kara Moses** reports on the impending 'dispersal crisis'

Global food production is at the mercy of insects. Without the work carried out by millions of bees and other pollinators, agriculture would simply grind to a halt. So, when bee colonies in Europe and the USA began to mysteriously collapse, and details emerged of the declining fortunes of populations of bumblebees and other insects, concerns were raised about an imminent 'pollination crisis'.

But pollination isn't the only part of a plant's life cycle that requires outside help. Many plants also depend on other organisms to spread their seeds, sometimes forming partnerships whereby the plant provides some sort of payment – often in the form of a tasty, nutritious fruit – for the animal's help in moving its seeds to new, more suitable territory. In some cases, these partnerships have become exclusive, with particular tree species only able to reproduce if their seeds are eaten, digested and then deposited in pastures new by particular animal species.

Enter humanity. The wave of extinctions that we've initiated is breaking up those partnerships by taking out the active partner, and the consequences could be disastrous. Scientists warn that a decline in seed dispersal could trigger a cascade of extinctions, altering ecosystems so dramatically that they eventually collapse. The scale could be global, affecting the carbon-storage capacity of forests and, ultimately, global climate change. However, the issue is virtually unknown outside of academic circles.

ABOVE: woolly monkeys can disperse hundreds of seeds per day; **OPPOSITE:** the fruits of the African breadfruit can weigh up to ten kilograms. Bonobos have been observed carrying them long distances before sharing and eating them

According to Professor Richard Corlett of the National University of Singapore, declining seed dispersal isn't just more worrying than the decline of pollinators, but more immediate. 'The seed dispersal crisis is upon us,' he says.

DISPERSE OR DIE

Seed dispersal is a vital ecological process that underpins almost all terrestrial ecosystems. 'It's the only chance that plants get to move – for offspring to get away from their parents and siblings, to colonise new areas, or to migrate in response to climate change,' Corlett explains.

For most plants, it's essential that seeds are spread to new sprouting grounds rather than simply falling beneath their parents, where competition is greater and the risks of inbreeding, and of being eaten or infected with disease, are higher. Research in Panama, for example, has shown that 99.96 per cent of wild nutmeg seeds dropped beneath the parent tree die within 12 weeks, but those moved 45 metres away are 44 times more likely to survive. For many seeds, it's quite simply a case of disperse or die.

This life or death scenario extends to the population and species level. 'Seed dispersal promotes gene exchange between different populations, helping species to maintain genetic diversity,' says Dr Wolfgang Stuppy, a seed morphologist at the Royal Botanic Gardens, Kew. 'A species with a highly diverse gene pool is more likely to successfully adapt to adverse or changing environmental conditions – the shrinking of populations usually goes hand in hand with the loss of genetic diversity.'

Plants have evolved numerous strategies for spreading their seeds: in temperate regions, they're often carried on the wind or by flowing water, or scattered by exploding seed pods. But in tropical ecosystems, more than 95 per cent of seeds are dispersed by animals. Here, the relatively constant heat and humidity lend themselves to year-round fruit production, and numerous animal species have evolved to exploit this bountiful food supply. In return, they provide plants with a reliable seed-dispersal service.

A diverse array of creatures is responsible for carrying seeds, from birds and insects to elephants, gorillas and even fish. Birds and bats are the marathon dispersers, transporting seeds over long distances – hundreds of kilometres in some cases. Primates are also critical seed carriers; studies have demonstrated that, at a population density of 30 individuals per square kilometre, woolly monkeys in the Colombian Amazon can disseminate an estimated 25,000 seeds per square kilometre each day.

Animal dispersers also provide another vital service: as fruit is passed through their digestive system, the fleshy pulp is removed – essential for the germination of many seeds. 'Seeds and fruits not freed from their soft pulp will inevitably be attacked by bacteria and fungi, which will then not only consume the pulp but also the seed within,' says Stuppy.

DANGEROUS STRATEGY

Relying on animals for seed dispersal may be an effective strategy, but it's also a dangerous one: the vulnerabilities of the disperser are inevitably shared by the plant. In the tropics, the threats from human activities are severe, and some of the most important dispersers are now also the most threatened; for example, according to a study published in the *Proceedings of the National Academy of Sciences* in 2004, more than a quarter of fruit-eating birds are threatened with extinction.

While few pollinating species suffer significant direct exploitation, nearly all of the biggest dispersers do, as they're usually the easiest to hunt. 'They are also the most vulnerable due to their need for large areas to sustain healthy populations,' says Stuppy. Given that the tree species with the largest seeds depend entirely on the larger-bodied dispersers capable of swallowing those seeds, the net result is an extremely delicate web of interactions. Lose the big dispersers and these trees have no means by which to regenerate.

Stuppy points to elephants as a case in point. 'Studies in Africa have shown that populations of trees whose fruits are adapted to elephant dispersal decline significantly over several decades in areas where elephants have disappeared,' he says. 'The same happens to other animal-dispersed species that lose their co-adapted dispersers.'

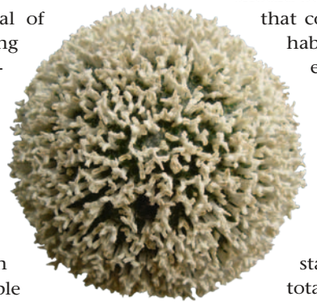
Habitat loss, degradation and fragmentation are also severe threats both to animal dispersers and the plants they disperse. If these animals – and therefore seeds – are unable to cross the gaps between fragmented islands of habitat, then populations become isolated and genetically doomed to local extinction.

DRAMATIC DECLINES

Widespread and intensive hunting and habitat loss in the tropics have forced many disperser populations into dramatic decline. However, the losses of dispersers are unlikely to be isolated events. As mutualisms are severed, ever-widening circles of co-extinctions of interdependent species could ripple through ecosystems, ultimately leading to their collapse. 'A decline in faunistic diversity will inevitably be accompanied by a decline in floristic diversity,' explains Stuppy. 'A decline in species diversity weakens the resilience of ecosystems against adverse changes in the environment, such as droughts and temperature fluctuations, and further reduces species diversity when stress increases. Under unfavourable conditions, the loss of biodiversity can trigger a downward spiral.'

Tree species that have lost their dispersers can then become the 'living dead', faced with inevitable extinction. 'Many national parks are the sites of poaching,' says Dr Pierre-Michel Forget of the Muséum National d'Histoire Naturelle in Paris. 'The parks are thus home to dead-standing plants unable to regenerate without their dispersers.'

Mauritius is a classic example. The arrival of Europeans on the Indian Ocean island during the 16th century eventually led to the extinction of parrots, pigeons (including, famously, the dodo), fruit bats and giant tortoises and lizards. Today, seed dispersal on Mauritius, particularly of large-seeded species, is at a virtual standstill, and the island's few remaining forests face an uncertain future.



With extinctions biased towards species that produce the largest seeds, the composition and structure of ecosystems are vulnerable to dramatic change, says conservationist Amy Hinsley of Fauna and Flora International. The largest seeds produce the biggest, longest-lived trees, she explains, so the loss of large dispersers can reduce the number of large trees and increase the number of wind-dispersed plants, such as lianas, which gain a competitive advantage. The result is forests of small, short-lived tree species, choked with lianas. Recent research has shown that this scenario is playing out already; studies of forests in Panama, Thailand and Cameroon, for example, have shown that bushmeat hunting has a direct impact on forest composition in this way.

This crisis is more insidious – the effects will creep up on us slowly and unseen, until it's too late and entire ecosystems begin to collapse

Such changes in composition can, themselves, have far-reaching implications. 'Fewer large trees and more lianas results in decreased carbon-storage potential of a forest, which, on a global scale, contributes to climate change,' says Hinsley. Small, short-lived trees sequester much less carbon over their lifetimes than large, dense, long-lived ones. Reductions in carbon storage of up to 60 per cent have been reported following selective logging of large, old trees, a scenario that foreshadows that facing dispersal-impoverished forests.

IMPENDING CRISIS

Such far-reaching and potentially serious implications raise the question of what we're doing to head off the impending crisis. 'Virtually nothing,' according to Corlett, 'except where species are being protected for other reasons.'

Perhaps, then, it's more pertinent to ask what we should be doing. Stuppy sees potential in incorporating greater biodiversity protection into schemes such as the UN-backed REDD+ (Reducing Emissions from Deforestation and Degradation). 'Any approach that takes a holistic view of biodiversity conservation without primarily focusing on human economic interests (so-called "useful" species) would automatically help to preserve dispersal services,' he says.

Corlett believes that properly enforced legal protection for key dispersal agents is one of the best solutions, but is unconvinced that this could be achieved through REDD schemes. 'It would be good for other things, and conservation overall, but it doesn't make any particular sense for dispersal,' he says. 'Legislation is the simplest and probably best way forward.'

The key, he says, is landscape connectivity; more emphasis should be placed on creating seed-dispersal corridors that connect fragmented habitats. 'In particular, habitats need to be protected across steep environmental gradients, such as on mountains, where the distances plants need to move to track climate change are relatively feasible,' he says.

An alternative approach is to reinstate lost mutualisms by reintroducing disperser species where they've been lost. Surrogate dispersers can even be used as stand-ins where dispersers have become totally extinct. The use of such ecological analogues has shown some success in experiments with Mauritian dispersers, in particular the use of Aldabra giant tortoises to replace extinct Mauritian species. But reintroductions are notoriously difficult, fraught with the usual challenges of inadequate habitat, continued exploitation and problems with sourcing animals.

Forget suggests that the answer may lie in putting an economic value on ecosystem services such as dispersal, or on key dispersers themselves. Over the past year, his research has focused on the rodent-dispersed Neotropical tree genus *Carapa*, an important source of natural oil. 'Without seed dispersal by rodents,' he says, 'the tree would die. It's an example for many other species used by humans, such as the Brazil nut in the Amazon.'

Corlett questions how such services for species with no commercial benefit would be valued, and who would pay, but Stuppy sees the potential of such an approach to raise awareness of the importance of seed dispersal in particular and biodiversity in general. 'Examples of flagship species, such as elephants in Africa, and a demonstration of the negative economic consequences of their disappearance in certain areas, could help illustrate the problem to a wider audience,' he says. 'But a price tag won't help us understand the complex and intricate interdependencies that have evolved over millions of years, and of which we humans are still a part.'

Unlike the 'pollination crisis', the steady loss of dispersers won't directly bring food shortages and starvation. This crisis is more insidious – the effects will creep up on us slowly and unseen, until it's too late and entire ecosystems begin to collapse. G

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