linators. Few, if any, of our plants are pollinated only by birds so there is no evidence that any particular bird species and particular flowers are mutually dependent. For example, the flowers of kowhai, a tree which is commonly regarded as being pollinated by honeyeaters, are visited in New Zealand by at least four bird species, as well as bees, butterflies and moths. In Chile, where the kowhai species *Sophora microphylla* also occurs naturally, hummingbirds and large bumble bees spread its pollen.

Seed dispersal

Birds which spread seeds by eating fruit play a vital role in the lives of a great number of plants, including those of some of our largest trees. About 70 percent of the woody plants of the New Zealand mainland have fleshy fruits suited for animals to eat. Some of these species may have evolved primarily for dispersal by lizards (see article by Tony Whitaker, August 1987 issue), but the majority – and especially those with orange, red and black fruits – are undoubtedly dispersed by birds.

Birds and fleshy-fruited plants have evolved together over millions of years and are now strongly dependent on each other. The plants provide nutritious fruit pulp to encase their seeds and encourage birds to swallow them. The birds eat the fruits, digest the pulp and carry seeds away from the parent plant, depositing some of them in suitable sites for germination and subsequent growth. For some plants a seed probably germinates better after the bird's gut has stripped away the fruit pulp and weakened its coat. Virtually all of the seeds left in uneaten fruit on a parent plant or dropped beneath it will eventually be destroyed by insects, rodents or rot, or (if they do germinate) will die from shading. However, among the seeds carried away inside birds, a few will drop in good sites, sometimes away from established forest, and will eventually grow into mature plants.

In this way seed-dispersing birds act as a vital link in the regeneration of forests. Among the plants which use this means of dispersal are several of the species (e.g. wineberry, fuchsia, mahoe) which are important in the process of plant succession, helping the eventual re-establishment of forests in areas which have been cleared and then left to revert. By transporting seeds into such areas birds speed up the process, so that mature vegetation begins to appear earlier than it would without their help.

The results of seed dispersal by birds are all around us whenever we walk through a forest or across a scrubby hillside which is reverting to native cover. A miro seedling growing in the beech forest hundreds of metres from the nearest miro tree can only have been carried there as a seed inside a kereru, and the clump of wineberry seedlings growing under a kanuka tree must also have arrived in the gut of a bird. We still know far too little about which birds are important for the regeneration of which plants, but there is no doubt that seed-dispersing birds are essential to the survival of forests and shrublands throughout New Zealand.

Most New Zealand forest birds eat some fruit. Even insect eaters such as the grey warbler, fantail and pied tit occasionally take small berries. The fleshiness, juiciness and bright colours of many New Zealand fruits make them highly attractive to birds and it seems that most are eaten by several different species. However, not all of these fruit eaters disperse seeds. The parrots – kea, kaka, kakapo, red-crowned parakeet and yellow-crowned parakeet – eat lots of fruit, but they also chew and crack the seeds with their powerful bills. In this way kaka destroy many green and ripe miro and matai seeds. Although some small seeds, such as *Coprosma pseudocuneata* and mingimingi, are swallowed whole and dispersed by keas and kakapo, parrots probably destroy more seeds than they disperse.

Extinct birds

Several of New Zealand's extinct birds were probably important seed dispersers in prehistoric times. These include moa, which ate the fruits or seeds of various plants, including trees such as matai, pokaka and putaputaweta. The extent to which they could have spread seed is uncertain but, like cassowaries in the rainforests of North Queensland, they may have been important for dispersing seeds of understorey shrubs and fallen fruit. Thin-coated seeds like tawa and karaka may have been crushed and ground by the stones in moa gizzards, but the woody seeds of species such as puriri, miro and hinau could have passed intact (although somewhat abraded) through the digestive tract of a moa. Brown kiwi also take woody seeds, including miro, hinau and nikau, and may use these as substitutes for gizzard stones.

The germination rate of woody seeds may improve once abrasion in the gizzard has weakened the seed coat. Some seeds may even have become woodier to resist crushing and grinding in the gizzards of the birds that swallow them. This could lead to the evolution of seeds which are so woody that they cannot germinate without first being weakened by grinding in a gizzard. On the island of Mauritius in the Indian Ocean there is a tree *(Calvaria major)* which has become increasingly rare in the past 300 years, apparently because its large woody seeds do not germinate. It has been suggested that this tree was dependent on the extinct dodo to disperse its seeds and that, without the grinding action of a dodo gizzard, the woody coats of the seeds now prevent them from germinating. In New Zealand there do not seem to be any such extreme examples of plants dependent on extinct dispersers such as moas. Nevertheless, when important seed-dispersing birds declined or disappeared, some native plants must have been affected in more subtle ways.

We know a little about the diet of moa because they have left subfossil gizzard contents behind them, but it is more difficult to guess what fruits were eaten by other extinct birds. For example, all we know about the fruit diet of the huia and piopio (from the writings of early naturalists) is that huia ate fruits of hinau, pigeonwood and *Coprosma* sp., and piopio ate *Fuchsia* fruit. In fact, both species probably ate a wide range of fruits, but their diet was never properly recorded.

Because of the spate of recent extinctions of fruit-eating birds, and the decline of others, New Zealand now has a relatively small number of birds which can disperse seeds. This has particular implications for plants such as tawa, karaka and miro, which have fruits greater than a centimetre in diameter. They now depend almost entirely on kereru for their dispersal. This is a precarious situation, especially where kereru are being threatened by habitat loss, predation or hunting as in some parts of the North Island. Kereru eat the fruits of at least 70 species of plants, move about freely and are found in most parts of the country. They are therefore probably the most important seed-dispersing birds in New Zealand forests. Previously, kokako may also have been important seed dispersers because they eat the fruit of at least 35 different forest plants. Kokako can swallow fruits up to about one centimetre in diameter, including those of plants such as supplejack and pigeonwood, but they do not carry seeds far because they cannot fly well, are confined to forest, and stay within individual territories. Unfortunately kokako are now restricted to only a few North Island forests.

Some introduced birds such as the blackbird and song thrush disperse seeds in native forest, but they cannot swallow large fruits. They are therefore not able to take the place of the larger native fruit eaters which are now declining or extinct.

A reduction in the number of bird species is a feature not only of New Zealand, but also of other island groups in Polynesia, where many birds (including several known or probable fruit eaters) have become extinct since humans arrived. The precise effects of this loss of birds remains unclear. We are sure, nevertheless, that patterns of regeneration are different, and probably slower, now that there are fewer carriers of seed. If the remaining species of seed-carrying birds were to be severely reduced or lost, the effects on forest regeneration would be profound.

Mick Clout and Rod Hay are ecologists with DSIR Ecology Division. Their specialist field of interest is ornithology, especially of New Zealand native birds.