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BIRD DISPERSAL OF LORANTHACEOUS MISTLETOES TO REMOTE PACIFIC ISLANDS: SYMBIOSIS IN DEFAULT

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ABSTRACT

Mistletoes of the family Loranthaceae have characteristically low dispersibility. Whereas the family is represented by c. 400 species on the continental masses and intervening archipelagos on the western Pacific rim, and by a similar number in South America, only a few species have reached remote South Pacific islands. Recent bird dispersal of *Ileostylus micranthus* from New Zealand to Norfolk I (c. 700 km) is comparable in distance with island-to-island bird dispersal in the most widespread species, *Decasynina forsteriana*, from New Guinea to the Marquesas in Quaternary time. Once established in island communities, even species of generally low dispersibility may have an increased probability of further waif dispersal. For mistletoes a shift in avian vectors is the likely cause, from berrypeckers (Dicacidae) in Malesia-Australia to probably campephagids (Campephagidae), glossy starlings (Sturnidae) and fruit doves and imperial pigeons (Columbidae) in the Pacific islands. This shift has disrupted the association which exists between mistletoes and their specialized co-adapted bird dispersal agents in their continental source area on the western Pacific rim. When the mistletoe fruits become exclusively available to more generalist feeders, dispersal may be less efficient but extend over longer distances.

INTRODUCTION

This paper presents a simple case study of range extension in several related flowering plants to remote Pacific islands. It suggests that once distance dispersal by birds to remote oceanic islands has occurred, the plant species may be freed from constraints imposed by co-adapted avian dispersal agents in its continental area. The likelihood of further range extension may then be increased.

That is, there may be a self-generated distance dispersal syndrome for the Pacific which has arisen by default.

The principal plant in this study is the mistletoe, *Decasynina forsteriana*, of the family Loranthaceae. Loranthaceae comprise about 60 genera and 1000 species, with centres of species richness in the tropics of all continents.

MISTLETOE DISPERSIBILITY

Loranthaceous mistletoes usually have very low dispersibility. Their fruit is a small drupe, containing a single seed surrounded by a copious viscous layer rich in sugars. Its dispersal agents on the western Pacific rim are fruit-eating birds, principally berrypeckers of the genus *Dicaeum*, which show remarkable co-adaptation with their food plants (Mayr & Arnadon, 1947). After ingestion, the skinned seed passes through the bird rapidly, sometimes in as little as 8-10 minutes (Docters, 1954). Whilst the sugars are presumably digested, the seed is voided with its viscous layer otherwise intact. If the seed is deposited on the branch where the bird perched, the drying viscous layer cements it in place and germination follows spontaneously.

Dispersibility by *Dicaeum* is limited by the short time the seed spends inside the bird, and by the birds' erratic local flight patterns. Dispersal distances are commonly of metres rather than kilometres (Keast, 1958), even though berrypeckers may wander widely within range-constraining land masses, e.g. *Di. hirundinaceum* throughout mainland Australia. The elaborate symbiotic interaction with these bird dispersal agents is therefore a major constraint on wider distribution of the Loranthaceae.

It is not surprising, therefore, that the mistletoe family has an essentially continental distribution that, on the western Pacific rim, is almost coincident with the range of the berrypecker family Dicaeidae. Beyond the western Pacific rim, the berrypeckers are replaced by other avian vectors in continental Eurasia, Africa/Madagascar and Central/South America, and these generate similarly small dispersal ranges for their food plants. In America, for example, the phainopepla (*Phainopepla nitens*) and euphonias (*Euphonia* spp.) feed on mistletoes and appear to have adaptations analogous to those of *Dicaeum* (Walsberg, 1975).

Low dispersibility in mistletoes is reflected in geographic distribution patterns. Firstly, even narrow water barriers may restrict range. For example, mistletoes have not recolonized Tasmania since its last isolation from mainland Australia

some 15,000 years ago. Whilst mistletoes are now absent from Tasmania, pollen records attributed to Loranthaceae have been found there, spanning a time interval from late Early Eocene to 120,000 years ago (M.K. Macphail, pers. comm.). Even across Torres Strait between Australia and New Guinea, the full potential of mistletoe dispersal to comparable habitats on either side has not been realized. The single Australian berrypecker, *Dicaeum hirundinaceum*, does not occur in Tasmania and does not reach mainland New Guinea across Torres Strait; nor do any New Guinean berrypeckers reach Australia.

Secondly, Recent land connections resulting from changes in sea level appear to have strongly influenced dispersal in continental archipelagos. In Malesia, for example, the loranth species which are widely distributed over major islands on the Sunda or Sahul shelves are common to lowland habitats (Barlow, 1991). These islands also share many of the species of *Dicaeum*, most of which are limited to altitudes below 1200 m. Conversely, the mistletoe species which occur in highlands are often narrow endemics.

PACIFIC MISTLETOE GEOGRAPHY

Around the western Pacific rim there are c. 400 loranth species with essentially continental distributions. The few species which do not fit this pattern are therefore very striking, occurring as they do mostly outside the range of the Malesian-Australian dicaeid vectors.

The most spectacular of these is *Decaisnina forsteriana*. The other 24 species of its genus have characteristically continental distributions in eastern Malesia and northern Australia (fig. 1). *Decaisnina forsteriana*, however, ranges from the Louisiade Archipelago off the eastern tip of New Guinea eastwards to the Solomons, Fiji, Tonga, Samoa, the Cook and Society Islands and the Marquesas (fig. 2). It ranges therefore in a narrow east-west band across the tropical southern Pacific, with distances between recorded occurrences sometimes exceeding 1000 km and reaching a maximum of 2000 km. The affinities of the spe-

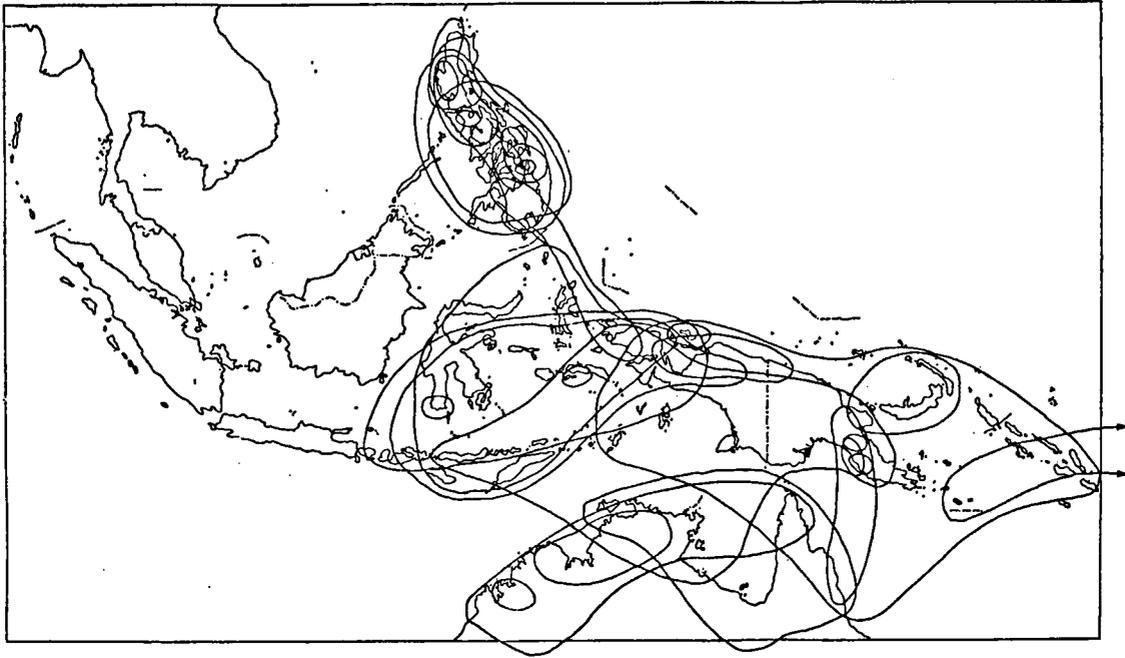


Fig. 1. Species distributions in the genus *Decaisnina*.

cies are with several New Guinean species, and the apparent sister taxa include *De. longipes* and *De. hollrungii* (Barlow, 1993). Because its nearest relatives are Australo-Papuan, it is likely that its ancestral stock arose in that region and spread eastwards. Compared with other widespread loranth species, it shows a moderate but not exceptional level of polymorphism, consistent with limited genetic differentiation in its disjunct populations. Prior to taxonomic revision by one of us (Barlow, 1974; 1993), the populations on different islands had been treated as several distinct species.

There are a few other loranth in the Pacific, none of which are narrow endemics either. The three species which occur in New Caledonia are all found in New Guinea as well. One of them, *Amyema artensis*, extends from New Guinea and the Louisiades to the Solomons, New Caledonia, Vanuatu, the Caroline Islands and Samoa, again apparently from Papuan sources (Barlow, 1992).

The remaining example of a loranth occurring on a remote southwest Pacific island illustrates chance distance dispersal from a dif-

ferent source and direction. *Ileostylus micranthus* is a seemingly relictual species that is widespread throughout New Zealand (Barlow, 1966). It is also present on Norfolk Island (fig. 3) in a small but conspicuous population near the summit of Mt Pitt, the frequently visited highest point on the island. The low fruit set and paucity of young plants suggest that the population is barely sustaining itself. It is tempting to consider this pattern as relictual, the outcome of postulated land connections along the late Tertiary Norfolk Ridge which spanned the 700 km between New Zealand and Norfolk Island. However Norfolk Island has been subject to several thorough botanical surveys, and in those prior to 1900 *Ileostylus micranthus* was never recorded; in contrast it has always been recorded in subsequent surveys. Given the close morphological similarity between the New Zealand and Norfolk plants, it seems more likely that *Ileostylus* reached Norfolk Island by distance dispersal within the last 100 years. Judged by this example, the other Pacific patterns described above may also be explained by distance dispersal.

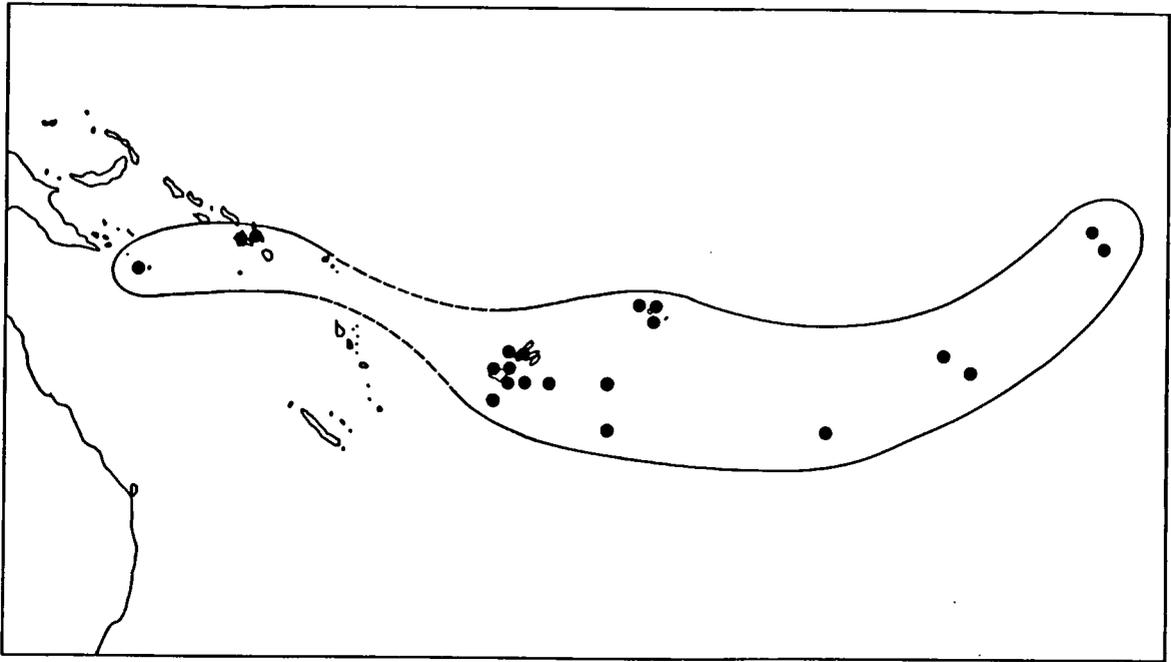


Fig. 2. Distribution of *Decaisnina forsteriana*.

PACIFIC DISPERSAL VECTORS

There are no visible features of the fruits and seeds of the Pacific loranth which are different from the common state uniform throughout the family. Their easterly spread through the Pacific, moreover, runs against prevailing wind and ocean currents. It seems probable, therefore, that a novel guild of avian dispersal agents, rather than any morphological or environmental adaptations in the plants, is responsible for their exceptional distribution.

The most likely of these are the fruit-eating glossy starlings (*Aplonis* spp.) and trillers (*Lalage*, two species with numerous subspecies) which have radiated among the island systems of the tropical South Pacific as far east as the Cook and Society Islands. In *Aplonis*, 16 of its c. 24 species (Sibley & Monroe, 1990) are endemic to island groups east of New Guinea. Taxonomic relationships in this group suggest recent differentiation and probably repeated dispersal between island groups. Glossy starlings are known to feed on mistletoe fruits (G. McCormack, pers. comm.). As with *Lalage*, the source of their radiation lies westwards in Papuasias (Mayr, 1941), co-

incident with the source of *Decaisnina forsteriana*.

Arboreal fruit-eating pigeons of the genera *Ptilinopus* (fruit-doves) and *Ducula* (imperial pigeons) may contribute to dispersal as well. Both of these Papuasian-Malesian genera have also radiated in the southwestern Pacific, the first with 20 species and the second with 10 on island groups east from New Guinea (Cain, 1954; Goodwin, 1960, 1983). Both have reached the Marquesas, the eastern limit of *Decaisnina forsteriana*. Although fruits of laurels, figs and palms form much of their diet, they do eat other fruits including loranth (Frith, 1982; Goodwin, 1983). Unlike the arboreal fruit-eating pigeons (*Treron*) of tropical Afro-Asia, they have a broad, simple gut and void seeds unground and intact (Goodwin, 1983).

In the case of *Ileostylus micranthus*, avian vectors are again probable, perhaps either of the migratory cuckoos *Chrysococcyx lucidus* and *Eudynamis taitensis*, which pass between New Zealand and Norfolk Island each year but which are prevalently insectivorous or carnivorous. An alternative is the silveryeye *Zosterops lateralis*, a fruit-eater which has dispersed naturally from Australia to New Zealand and Norfolk Island, but which has not yet been confirmed moving between the lat-

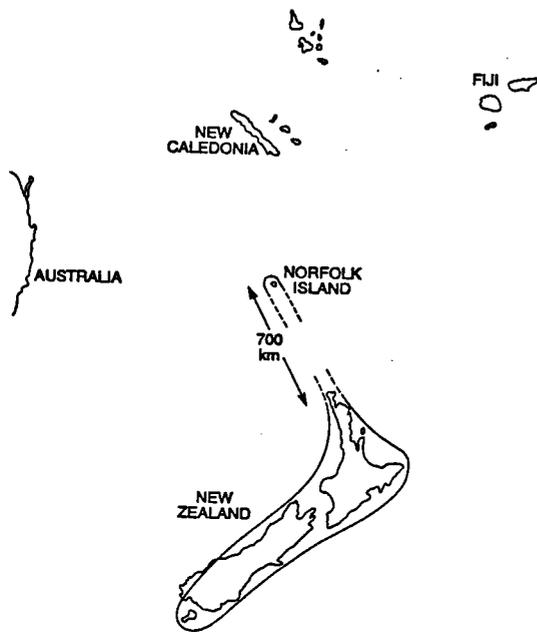


Fig. 3. Distribution of *Ileostylus micranthus*.

not yet been confirmed moving between the latter two island groups.

DISCUSSION

In the Loranthaceae on the continental western Pacific rim there are no unequivocal examples of distance dispersal over continuous land areas on a scale comparable with these oceanic examples. Distance dispersal is therefore a Pacific phenomenon in this family, and a shift in the species of avian vectors seems the most likely cause. In continental areas the highly specialized and efficient berrypeckers may monopolize the supply of mistletoe fruit, largely precluding other bird species as effective dispersal agents (see below). Because of the brief time that the seed remains inside them, they appear to have had a constraining effect on mistletoe dispersal. This is reflected in the significant levels of loranth speciation there.

In the Pacific region, however, berrypeckers extend no further east than the Solomon Islands. Beyond there they are replaced by other potential dispersal agents, such as the glossy starlings, trillers and fruit-eating doves and pigeons, which probably eat loranth drupes irregularly as part of

a general frugivorous diet and which may not pass the seed for several hours, particularly if the rind is not removed from the fruit. Unfortunately no data are available on either the specific diet or the intestinal seed transit time for these Pacific birds (Goodwin, 1983; K. Richardson, pers. comm.).

Why such generalist frugivores may not disperse species of Loranthaceae more widely in the continental areas of the western Pacific could depend on several factors. Where berrypeckers are present, generalist vectors may have an insignificant role in founding new populations, especially for mistletoe species which have moderate or high host specificity. In any case, in the richer continental floras generalist vectors may have a preferred diet that largely excludes Loranthaceae. Among 20 birds other than *Dicaeum* that feed on mistletoe in Australia (Blakely, 1922) are some which eat fruits whole, some which only sip the viscous layer, some which grind the seeds, and some which cast seeds in solid masses mixed with insect parts. None of these alternative feeders have the behavioural adaptation of the berrypeckers which attaches the voided seed to the branch on which the bird is perched. However in arid Australia honeyeaters of the genera *Grantiella*, *Acanthagenys* and *Plectorhyncha* are effective dispersers (Reid, 1989), but because they void the seeds rapidly and are territorial they probably do not disperse seeds more widely than do the berrypeckers.

The distribution achieved by mistletoes such as *Decasinnina forsteriana* is therefore probably the consequence of disruption in the association between the mistletoe and its highly specialized co-adapted dispersal agents in the Dicaeidae. When the fruits become exclusively available to more generalist feeders, including perhaps even maritime birds, dispersal and recruitment may be less efficient, but dispersal over longer distances more likely. In the floristically depauperate disharmonic floras on remote Pacific islands, mistletoe fruits may be a relatively more important component of the diet of generalist feeders than in the continental lands to the west.

The initial step of range extension beyond that of co-adapted specialist dispersal agents is there-

fore the critical threshold, opening a window of opportunity for distance dispersal which is not available in the continental homelands. For *Decaisnina forsteriana* this critical step may have provided entry to an eastward-directed corridor in the South Pacific. It appears that Loranthaceae have been afforded only rare use of this corridor. Mistletoe dispersal eastwards across the tropical South Pacific has probably been a sporadic process, at least through Quaternary time, rather than a single event linked with the initial dispersal of particular avian groups to these islands. This is indicated by the common source areas of the birds and the mistletoes, and by their comparable levels of differentiation (even though taxonomic treatment differs). The present day distribution patterns of the few Pacific mistletoes are therefore stages in a dynamic process moderated by infrequent bird dispersal events.

The hypothesis presented here is entirely consistent with our knowledge of the general biology of mistletoes and of their avian dispersal agents. Testing the hypothesis would be difficult, and would depend primarily on critical observations on feeding preferences, behaviour and migration patterns of Pacific birds. The feeding observations of Docters (1954) on *Dicaeum* were made in part on caged birds, but data on generalist feeders obtained in this way may be less robust.

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