Functional Ecology 1999
13, 552–559

Host specificity in parasitic mistletoes (Loranthaceae) in New Zealand

D. A. NORTON* and P. J. DE LANGE†

**Conservation Research Group, School of Forestry, University of Canterbury, Private Bag 4800, Christchurch, New Zealand and †Science & Research Unit, Department of Conservation, Private Bag 68908, Newton, Auckland, New Zealand*

Summary

1. We quantify the degree of host specificity for the five extant New Zealand loranthaceous mistletoes (*Alepis flavida*, *Ileostylus micranthus*, *Peraxilla colensoi*, *Peraxilla tetrapetala* and *Tupeia antarctica*).

2. Host specificity is highest for *A. flavida*, *P. colensoi* and *P. tetrapetala* which primarily parasitize species of *Nothofagus*, and lowest for *T. antarctica* and especially *I. micranthus* which parasitize a wide range of host species.

3. These patterns of host specificity support the suggestion that relative host abundance is a key factor determining the degree of host specialization in mistletoes (resource fragmentation hypothesis). While evolutionary history may be important in the specificity of the mistletoe–host relationship in some situations, our data suggest that for New Zealand mistletoes evolutionary history simply reflects the temporal component of relative host abundance.

4. We conclude that it is the stability of host availability through time and space which is the dominant factor determining host specificity patterns.

Key-words: Loranthaceae, New Zealand flora, parasites

Functional Ecology (1999) **13,** 552–559

Introduction

The degree of specificity of the parasite–host relationship varies both within and between parasite groups (Barlow & Wiens 1977; Bernys & Graham 1988; Rohde 1993; Shaw 1994). We define parasites to include plant parasites, such as mistletoes, viruses, some phytophagous insects, parasitoids, and ecto- and endoparasites of animals, such as lice and liver flukes (Norton & Carpenter 1998). All are distinguished by completing a whole stage of their life associated with a single host individual in a relationship that is beneficial to the parasite but not to the host (Thompson 1994). Few parasites are known to infect a single host species alone, with the usual pattern among specialists being a single common host, and a number of other less frequently used hosts (Shaw 1994; Hawksworth & Wiens 1996). In a similar manner, generalists which use a large number of host species, tend not to be totally unrestricted in their host range and show preference for some host species above others (Bernys & Chapman 1994; Shaw 1994).

Host specificity in parasites may be favoured by the advantages of adapting to interact with a frequently encountered host (Norton & Carpenter 1998). Being a host generalist can also be advantageous, especially in a heterogeneous community, as it allows parasites to grow successfully in or on many of the potential hosts encountered. If host populations are unpredictable and ephemeral, generalists are more likely to occur (Thompson 1994). The relative abundance of host species is therefore a key factor determining the degree of host specificity in a parasite (Norton & Carpenter 1998). Given sufficient abundance of a frequently encountered host, the benefits of specializing on that host outweigh the disadvantages of interacting less well with other potential hosts.

The degree of host specialization may also be influenced by the length of time the parasite and its host have been associated. Manter's second rule states that a long association between a parasite and host will result in greater host specificity (Brooks & McLennan 1993). However, Shaw (1994) suggests that parasites have a narrow host range when they first arise as distinct species and that the host range may then subsequently expand. This view assumes that speciation occurs as a result of specialization to a particular host and would not be true of a species evolving as a generalist on several hosts. Some authors have argued against a general trend towards either host specificity or generalization (Brooks & McLennan 1993; Thompson 1994) saying that evolution can proceed towards either outcome.

While there is increasing information on host specificity patterns for some groups of organisms

(Hawkins, Shaw & Askew 1992; Paterson & Gray 1997; Yeates & Greathead 1997; Newton & Haigh 1998) there is a paucity of information for others. For these latter groups our knowledge of specificity is usually based on anecdotal sources (e.g. host lists included in general taxonomic treatments). While differences in levels of host specificity have been recognized for mistletoes (e.g. Barlow 1984; Hawksworth & Wiens 1996), there have been few studies quantifying these differences and this forms the focus of the present study.

'Mistletoes' are a polyphyletic group of shrubby parasites of aerial stems including species in the Loranthaceae, Viscaceae, Eremolepidaceae, Misodendraceae and Santalaceae (Kuijt 1990; Reid, Stafford Smith & Yan 1995). The Loranthaceae, the largest group of mistletoes (at least 850 species in 65 genera), form the focus of this paper and the word mistletoe is used here to refer to members of this family only. In this paper we quantify the degree of host specificity for the five extant New Zealand loranthaceous mistletoes (*Alepis flavida*, *Ileostylus micranthus*, *Peraxilla colensoi*, *Peraxilla tetrapetala* and *Tupeia antarctica*) and assess the importance of differences in (1) relative abundance of potential host species and (2) evolutionary history in explaining the observed differences in host specificity among these mistletoes. Plant nomenclature follows Allan (1961) and changes suggested in Connor & Edgar (1987) for indigenous species, and Webb, Sykes & Garnock-Jones (1988) for introduced species.

Materials and methods

We examined in excess of 1400 mistletoe herbarium sheets held in the nine main New Zealand herbaria (AK, AKU, CANU, CHR, NZFRI, OTA, WAIK, WELT, WELTU) and in three herbaria outside New Zealand (BM, K, P). For each herbarium sheet we confirmed the identification of the mistletoe and recorded information on the host (either by confirming its identification if it was present or noting if it was mentioned on the label), the collector and date of collection, and the locality from which it was collected. Any sheets that were obvious duplicates of other sheets were excluded. From this, we assembled a database of 1386 herbarium records for the five extant mistletoe species including all records up to the end of 1995.

The herbarium records were sorted by species and hosts parasitized. We distinguished between those herbarium sheets that provided no information on hosts, from those that either had the host present (enabling us to verify its identification) and those that noted what the host was but did not include a specimen for verification. For those sheets that listed several hosts, we recorded the first host only as this was usually the host parasitized by the mistletoe. The most useful information comes from sheets that include a sample of the host species (host verified). However, there were too few of these to enable us to quantify host-specificity patterns and we therefore also included those sheets that listed the host but did not include a sample (host unverified). The verified and unverified records varied in a similar manner between host species ($r^2 = 0{\cdot}613, P < 0{\cdot}001, n = 71$) suggesting that the unverified records provide a reliable indication of host use. This gave us a database of 970 records for which information on hosts was provided (380 verified and 590 unverified).

To compare the degree of host specificity between mistletoe species we used the Shannon–Weiner diversity index H' (Magurran 1988):

$$H' = -\sum p_i \ln p_i,$$

where the quantity p_i is the proportion of records found in the ith host species. Mistletoes with low diversity values are the most host specific, parasitizing a small number of hosts with one host usually dominant, while those with high diversity values are the least host specific, parasitizing many hosts with no one host dominant.

Results

Of the 1386 mistletoe herbarium sheets examined, 970 (70%) included information on the host species. Apart from *I. micranthus* where 82·9% of sheets had host information (Table 1), the proportion of sheets with host information for each species was similar, ranging from 57·9 to 67·7%. However, only 380 of the sheets (27·4%) had the host verified, ranging from 10·8% for *P. colensoi* to 46·1% for *I. micranthus* (Table 1).

The number of hosts recorded on the herbarium sheets was consistently less than the total number of known hosts for all species (43·8–94·1%; Table 1) as the total host list included literature records and personal observation as well as herbarium vouchers (de Lange, Norton & Molloy 1997a). However, much of this difference arose from the generally poorer representation of introduced host species in our data set (47·8% of all introduced host species, range 0–100%), while the representation of indigenous host species was generally greater (79·1% of all indigenous host species, range 64·9–93·3%).

The dominant indigenous host genus for *A. flavida* and the two *Peraxilla* species was *Nothofagus* (84–96·5% of records; Table 2). In contrast the dominant host genera for *I. micranthus* (*Coprosma*) and *T. antarctica* (*Pseudopanax*) accounted for less than half the herbarium records for each mistletoe species. A similar pattern is apparent with the dominant indigenous host species, with *A. flavida* and the two *Peraxilla* species most commonly parasitizing a single *Nothofagus* species (63·4–85·9% of all host records), while the dominant host species for *I. micranthus* and *T. antarctica* account for only 20·8

Table 1. Documented hosts for five extant New Zealand Loranthaceae mistletoes: *Alepis flavida*, *Ileostylus micranthus*, *Peraxilla colensoi*, *Peraxilla tetrapetala* and *Tupeia antarctica*

	A. flavida	*I. micranthus*	*P. colensoi*	*P. tetrapetala*	*T. antarctica*
ALL MISTLETOE RECORDS*					
N native hosts	13	114	7	15	37
N introduced hosts	0	92	9	2	11
Total hosts known	13	206†	16	17	48
HERBARIUM MISTLETOE RECORDS					
N vouchers	223	497	130	285	251
% with host	66·4	82·9	67·7	57·9	62·5
% with host verified	24·2	46·1	10·8	14·0	17·1
N native hosts‡	10	74	5	14	33
% all known native hosts	76·9	64·9	71·4	93·3	89·2%
N introduced hosts	0	49	2	2	7
% all known introduced hosts	–	53·3	22·2	100·0	63·6%
Total hosts	10	123	7	16	40
% all known total hosts	76·9	59·7	43·8	94·1	83·3%
VERIFIED MISTLETOE HERBARIUM VOUCHERS					
N native (% of all verified)	148 (100)	331 (80·3)	86 (97·7)	163 (98·8)	132 (84·1)
N introduced (% of all verified)	0 (0)	81 (19·7)	2 (2·3)	2 (1·2)	25 (15·9)

*From de Lange *et al*. (1997b). †Excluding the three hosts from Norfolk Island. ‡These data include hybrids, but exclude host records at generic level when records of species in the same genus have been made.

and 25·4% of host records, respectively (Table 2). The much greater degree of host specificity in *A. flavida*, *P. colensoi* and *P. tetrapetala* species is also evident in their low diversity values ($H' = 0{\cdot}80$, 0·71 and 1·47, respectively) compared with the higher diversity values for *T. antarctica* ($H' = 2{\cdot}27$) and especially *I. micranthus* ($H' = 3{\cdot}37$; Table 2).

Patterns in introduced host species were only analysed for *I. micranthus* and *T. antarctica* because of the small numbers of introduced hosts for the other three mistletoe species (Table 1). The dominant introduced host for *T. antarctica* was *Chamaecytisus palmensis*, accounting for 76% of introduced host records (Table 3). In contrast, the two dominant host genera for *I. micranthus* (*Prunus* and *Salix*) accounted for only 9·9 and 8·6% of host records, respectively (Table 3). Interestingly, *C. palmensis* was the dominant host species for *I. micranthus*, but accounted for only 7·9% of all host records. *Ileostylus micranthus* had a comparable diversity of introduced hosts as it had indigenous hosts ($H' = 3{\cdot}72$ cf. 3·37; Table 3). However, the diversity of introduced hosts for *T. antarctica* was much lower than for indigenous hosts ($H' = 0{\cdot}98$ cf. 2·27; Table 3) reflecting the dominance of *C. palmensis* as its principal introduced host.

There is some evidence for regional variation in indigenous host-species use among individual mistletoe species. For *P. tetrapetala*, *Nothofagus* species are the predominant host (132/141 records) south of *ca.* 38°S (Fig. 1b) but north of this *Quintinia serrata* is the predominant host (16/18 records) although further south this host species is apparently not parasitized. Similar regional patterns also occur for *I. micranthus*. In Northland and Auckland (northern North Island north of *ca.* 35°S) *Podocarpus hallii* and *Podocarpus totara* are the predominant hosts (13/21 records), in the southern North Island (south of *ca.* 40°S) *Coprosma crassifolia* and *Melicope simplex* are the most commonly used hosts (11/37 and 6/37 records), while on the west coast of South Island *Coprosma propinqua* is the predominant host (23/28 records). For *T. antarctica*, *Pseudopanax arboreus* is the dominant host in the Taupo volcanic zone of the central North Island (23/32 records) and the eastern North Island (10/12 records), while *Myrsine australis* (Myrsinaceae) is the dominant host on Banks Peninsula in the eastern South Island (6/11 records), and *Carpodetus serratus* the only indigenous host in the Dunedin region, south-eastern South Island (8/8 records). Comparable analyses were not undertaken for *A. flavida* and *P. colensoi* because of smaller sample sizes and less obvious regional variation.

Discussion

While providing much information, at least three limitations are associated with using herbarium sheets in assessing host specificity patterns. (1) The lack of information on host species meant that we were unable to use 416 sheets, while a further 590 sheets provided host information that could not be verified and was therefore of lower reliability. However, we chose to use the unverified host records primarily because the correlation between unverified and verified records was significant and as most collections were by botanists who could be expected to have correctly identified the host species based on our experience with other collections they have made. (2) There is bias in the collections towards mistletoes present on unusual hosts (see also de Lange *et al*. 1997a) as numerically there are far fewer collections of the most common hosts (e.g. *Nothofagus solandri*) than would

Table 2. Main indigenous hosts for New Zealand Loranthaceae. Genus abbreviations (and families) are: Not., *Nothofagus* (Fagaceae); Cop., *Coprosma* (Rubiaceae); Pod., *Podocarpus* (Podocarpaceae); Lep., *Leptospermum* (Myrtaceae); Mel., *Melicope* (Rutaceae); Pit., *Pittosporum* (Pittosporaceae); Qui., *Quintinia* (Escalloniaceae); Car., *Carpodetus* (Escalloniaceae); Pla., *Plagianthus* (Malvaceae); Hoh., *Hoheria* (Malvaceae); Ole., *Olearia* (Asteraceae); Ile., *Ileostylus*. Pse., *Pseudopanax* (Araliaceae)

	A. flavida	%	*I. micranthus*	%	*P. colensoi*	%	*P. tetrapetala*	%	*T. antarctica*	%
Genus*	*n* = 148		*n* = 331		*n* = 86		*n* = 163		*n* = 132	
	Nothofagus	95·9	*Coprosma*	40·2	*Nothofagus*	96·5	*Nothofagus*	84·0	*Pseudopanax*	31·1
			Podocarpus	13·3					*Pittosporum*	12·1
Species†	*n* = 127		*n* = 307		*n* = 71		*n* = 145		*n* = 122	
	Not. solandri	76·4	*Cop. propinqua*	20·8	*Not. menziesii*	85·9	*Not. solandri*	63·4	*Pse. arboreus*	25·4
	Not. fusca	7·1	*Pod. totara*	11·4	*Not. fusca*	7·0	*Not. menziesii*	11·7	*Car. serratus*	14·8
	N. solandri × *fusca*	7·1	*Cop. crassifolia*	4·6	*Not. solandri*	4·2	*Qui. serrata*	10·3	*Pla. regius*	9·0
	Not. menziesii	3·1	*Lep. scoparium*	2·9			*Not. fusca*	5·5	*Pit. eugenioides*	7·3
			Mel. simplex	2·9					*Hoh. lyallii*	4·9
			Pit. tenuifolium	2·9					*Ole. paniculata*	4·9
									Pit. tenuifolium	4·1
									Ile. micranthus	3·3
Host diversity (H')†	0·80		3·37		0·71		1·47		2·27	

*Calculated for all indigenous hosts identified to genus and species level. †Calculated only for those indigenous hosts identified to species level, or to genus level where no species identification has been made

be expected if mistletoe sampling had been random with respect to hosts. (3) The geographical coverage of herbarium sheets is also uneven, with more collections from areas with easy access, for example along major roads and around urban centres (Fig. 1, and distribution maps in de Lange *et al.* 1997b). The main effect of this has been to increase the number of introduced host species and uncommon indigenous host species recorded (de Lange *et al*. 1997a). While these limitations do affect our estimates of the degree of host specificity, they are common to all five mistletoe species and should therefore not affect the comparative analyses undertaken.

Our results quantify the patterns in host specificity among the extant New Zealand mistletoes, with *A. flavida* (H' = 0·80), *P. colensoi* (H' = 0·71) and *P. tetrapetala* (H' = 1·47) all showing high host specificity, primarily parasitizing species of *Nothofagus*, while *T. antarctica* (H' = 2·27) and especially *I. micranthus* (H' = 3·37) exhibit considerably lower levels of specificity and parasitize a wide range of host species. As a framework for assessing the factors that might explain these differences in host specificity, we evaluate the importance of relative host abundance and evolutionary history as possible causes based on our results.

RELATIVE HOST ABUNDANCE

Alepis flavida and the two *Peraxilla* species occur most commonly in *Nothofagus* forests (Fig. 1), except in the far north of New Zealand where *P. tetrapetala* locally parasitize *Q. serrata* in mixed-species angiosperm forests. *Nothofagus* forests are usually characterized by the dominance of one or more canopy *Nothofagus* species, with other tree species being of minor importance (Ogden, Stewart & Allen 1996). *Nothofagus* species are relatively long-lived (typically 250–450 years) and, although a variety of disturbances regularly affect these forests, *Nothofagus* species quickly reestablish after such disturbances. This environment provides considerable spatial and temporal stability with respect to host availability, with the predominant hosts of *Alepis* and *Peraxilla* usually being the most abundant species in the forests (Norton, Ladley & Owen 1997). When the relative abundance of different *Nothofagus* species changes, differences in host use occur. For example, in South Island, *P. tetrapetala* primarily parasitizes *N. solandri* when it is the predominant species present, but when *N. solandri* becomes a minor component of the forest (e.g. in higher rainfall regions), other *Nothofagus* species become the predominant host (e.g. *Nothofagus fusca* and *Nothofagus truncata*; D. A. Norton unpublished data).

In contrast, *I. micranthus* and *T. antarctica* typically occur in shrubland and low forest communities which tend to be characterized by a greater diversity of potential host species (Wardle 1991). These vegetation types

are often seral, representing a stage in the development of forest after disturbance. When these mistletoes do occur in tall forest, they are often present on host trees that typically regenerate after disturbance (e.g. *P. totara* and *P. hallii*). The predominance of *Ileostylus* and *Tupeia* on host trees and shrubs typical of seral vegetation suggests that host specialization is likely to be less reliable than host generalization. However, locally and especially when the vegetation is dominated by only one or a few species, some specialization does occur (e.g. on *C. propinqua* in saltmarsh shrublands in western South Island). *Ileostylus* and *Tupeia* are also very common in the central and northern North Island in areas that have been regularly modified by volcanic activity (Froggatt & Lowe 1990), again creating disturbed sites dominated by diverse shrubland and low-forest communities. The root parasite *Dactylanthus taylorii* (Balanophoraceae) which parasitizes a wide range of angiosperm shrubs and trees in New Zealand also occurs in seral vegetation, often on the margin of tall forest (Ecroyd 1996). The generalist nature of *Ileostylus* and *Tupeia* is also highlighted by their abundance on introduced host species, especially in areas that have been highly modified by human activities. These introductions represent a form of disturbance to which these two mistletoes have been able to successfully respond.

Table 3. Main exotic hosts for *I. micranthus* and *T. antarctica*. Genus abbreviations (and families) are: Cha., *Chamaecytisus* (Fabaceae); Pyr., *Pyrus* (Rosaceae); Sal., *Salix* (Saliaceae). *Prunus* (Rosaceae), *Cytisus* (Fabaceae)

	I. micranthus	%	*T. antarctica*	%
Genus*	*n* = 81		*N* = 25	
	Prunus	9·9	*Chamaecytisus*	76·0
	Salix	8·6	*Cytisus*	8·0
Species†	*N* = 76		*N* = 25	
	Cha. palmensis	7·9	*Cha. palmensis*	76·0
	Pyr. communis	6·6		
	Sal. cinera	6·6		
Host diversity (*H*′)†		3·72		0·98

*Calculated for all indigenous hosts identified to genus and species level.
†Calculated only for those indigenous hosts identified to species level, or to genus level where no species identification has been made.

EVOLUTIONARY HISTORY

Host specificity in these mistletoes also appears to be related to the history of the individual taxa in New Zealand. At least 12 different mistletoe taxa referable to the Loranthaceae, including the five extant species, have been recorded from New Zealand fossil deposits (D. C. Mildenhall, personal communication, 1993). While the taxonomic relationships of some of these taxa are unclear (Muller 1981) the first record of a loranthaceous pollen type is from the late Cretaceous (*Cranwellia* type; Mildenhall 1980). Pollen that is virtually identical to the modern taxa *A. flavida*, *P. colensoi* and *P. tetrapetala* (D. C. Mildenhall, personal communication, 1993) first appears in the late Eocene (43–37 million years B.P.) while pollen of *T. antarctica* and *I. micranthus* is not present until the Pliocene (5–2 million years B.P.; Mildenhall 1980) although *Ileostylus* may have been present in the Miocene (D. C. Mildenhall, personal communication, 1998). The evolutionary relationships between the extant species and fossil loranthaceous pollen types are unclear

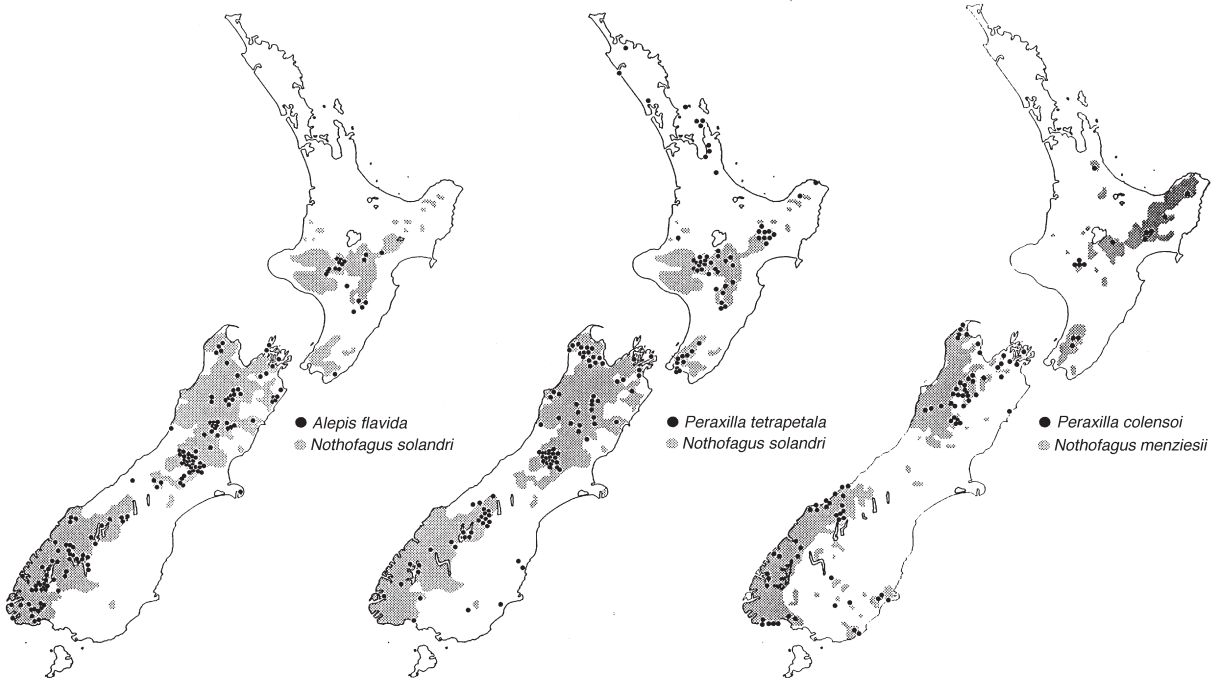

Fig. 1. Distribution of (a) *Alepis flavida*, (b) *Peraxilla tetrapetala* and (c) *Peraxilla colensoi* superimposed on the distribution of their principal host.

(Mildenhall 1980), although Barlow (1983) suggests that all the extant New Zealand species are primitive morphologically and cytologically.

The appearance of *Alepis* and *Peraxilla* pollen in the late Eocene is coincident with an increasing dominance of *Nothofagus* pollen (Mildenhall 1980; Pocknall 1989; McGlone, Mildenhall & Pole 1996), the principal host genus for this group today. Environmental conditions through the middle part of the Tertiary (Eocene to early Miocene) appear to have been relatively stable with New Zealand being characterized by limited relief, infertile leached soils, and temperate climates (Mildenhall 1980; Pocknall 1989; McGlone *et al*. 1996). The forest vegetation was dominated by *Nothofagus* including species related to the modern hosts of *Alepis* and *Peraxilla*. These relatively stable conditions over several millions of years are likely to have favoured specialization by mistletoes on particular host species; the dominance of *Nothofagus* in the vegetation would have been a key factor in this group becoming the preferred host.

Towards the end of the Miocene changing global climate patterns and the onset of the Kaikoura Orogeny resulted in more variable climates and the creation of fresh and more dynamic habitats (McGlone 1985). As a result, the vegetation became more variable spatially and temporally and while *Nothofagus* was still dominant during warmer periods, low forest, shrubland and grassland were extensive during prolonged cooler periods. The origins of *I. micranthus* and *T. antarctica* are unclear, but they first appeared at a time when environmental conditions were far more variable than those encountered earlier in the Tertiary. The major environmental changes that have occurred since they first appear in the New Zealand fossil record are likely to have prevented host specialization happening. The dramatic changes in plant distribution patterns between glacial and interglacial periods (McGlone *et al*. 1996) could have been a major limitation to host specialization. The main indigenous hosts of *Ileostylus* and *Tupeia* today (Table 2) are generally short-lived species that often occur in successional situations (Wardle 1991) and would have been abundant during the oscillating climatic conditions of the Quaternary.

HOST SPECIFICITY IN NEW ZEALAND MISTLETOES

Both relative host abundance and evolutionary history appear to have had an important influence on the degree of host specificity in the extant New Zealand mistletoes. The *Nothofagus* parasitizing mistletoes, *A. flavida*, *P. colensoi* and *P. tetrapetala*, have a long history in New Zealand, much of which occurred when *Nothofagus*-dominated forests existed for very long time periods providing ideal conditions for mistletoe specialization on this group. In contrast, *T. antarctica* and *I. micranthus* are relative newcomers to New Zealand and the spatial and temporal variability in host availability since their arrival (e.g. the massive reductions in forest cover during glacial periods) appears to have favoured host generalization.

Host-switching and co-speciation have both been suggested as important modes of evolution for a variety of parasites (Brooks & McLennan 1993; Paterson, Gray & Wallis 1993; Shaw 1994; Thompson 1994; Hoberg, Brooks & Siegel-Causey 1997; Paterson & Gray 1997). Host-switching occurs when a parasite establishes on a new host and diverges from the original form as selection favours adaptations to the new host. Co-speciation occurs when the parasite undergoes speciation in response to host speciation; for example, as a result of changing climatic conditions. The main hosts of the two *Peraxilla* species occur in different sections of the genus *Nothofagus* [*P. colensoi* on *N. menziesii* (subgenus *Lophozonia), P. tetrapetala* on *N. solandri* (subgenus *Fuscospora)*; Hill & Dettmann 1996] suggesting that they are unlikely to have evolved through co-speciation. This is especially so as the origin of these two sections appears to be considerably older than the first appearance of *Peraxilla* in the fossil record. However, these two mistletoe–host pairs could represent a good example of host-switching. There is also evidence for ongoing speciation within this group through host-switching: *P. tetrapetala* occurring on *Q. serrata* hosts in northern North Island have a greater incidence of apricot-coloured flowers than *P. tetrapetala* occurring on *Nothofagus* hosts elsewhere in New Zealand where bright red is the predominant flower colour (D. A. Norton & P. J. de Lange unpublished data). Co-speciation is again unlikely as *Nothofagus* and *Quintinia* are not related. Both *I. micranthus* and *T. antarctica* also show some evidence of host-switching through strong local patterns of host specificity even when hosts used elsewhere are present. All these examples suggest that if host-switching is an important mechanism of speciation in New Zealand mistletoes, this process is itself dependent on relative host abundance. The importance of host-switching has been highlighted in a comparison of parasite and host phylogenies for *Arceuthobium*, a plant parasite from the related family Viscaceae (Norton & Carpenter 1998).

The patterns of host specificity in New Zealand mistletoes documented here strongly support the suggestion that relative host abundance is a key factor determining the degree of host specialization in parasites (Norton & Carpenter 1998). The importance of host abundance for parasite specificity has been documented in several parasite groups as well as other host dependent organisms. For example, the reduction in host specificity in tropical compared to temperate areas is considered a consequence of the lower relative abundance of individual host species (Janzen 1981; Hawkins *et al*. 1992; Rohde 1993). Host specificity in phytophagous insects has also been related to the abundance and reliability of host plants (Bernys & Chapman 1994) and similar patterns can be seen in a

plant–phytophage–parasite–parasitoid system (Dawah, Hawkins & Claridge 1995). These patterns in host specialization can be explained in terms of the resource fragmentation hypothesis (Janzen 1981) which suggests that specialized parasites are unable to persist on scarce hosts, thus host generalists dominate in systems with low relative host abundance (high host species diversity). Evolutionary history may be important in the specificity of the parasite–host relationship in some situations (cf. Manter's second rule; Brooks & McLennan 1993). However, our data suggest that for New Zealand mistletoes at least, evolutionary history may simply reflect the temporal component of relative host abundance and that it is the stability of host availability through time, as well as space, which is the key factor in host specificity patterns.

Acknowledgements

We are particularly appreciative of the information on fossil mistletoe pollen provided by Dallas Mildenhall, who together with Brian Molloy, John Ogden and Nick Reid provided helpful comments on a draft manuscript. We also thank the keepers of the various herbaria we utilized for their assistance in collecting the herbarium data for this paper. Thanks to Chris Edkins for preparing Fig. 1. This research was partially funded from the Public Good Science Fund (UOC510).

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Received 6 October 1998; revised 21 December 1998; accepted 26 January 1999