6 The Role of Vertebrates in the Diversification of New World Mistletoes

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> Birds feeding on berries of *Loranthaceae* become quite a nuisance in gardens and citrus plantations, by spreading these pests on to trees.
>
> (Haverschmidt, 1968)

Introduction

Mistletoes are unique among woody plants in that all species are parasites (Kuijt, 1969; Calder and Bernhardt, 1983). Even though being a parasite may seem to constrain possibilities for diversification, mistletoes have successfully radiated into a wide array of species, genera and families with different lifestyles (Barlow, 1964; Polhill and Wiens, 1998). Some mistletoes, for example, are terrestrial and others are aerial root parasites (Hoehne, 1931; Kuijt, 1963; Fineran and Hocking, 1983). Most species, however, are aerial stem parasites that vary in their preferences for hosts (Barlow and Wiens, 1977; Hawksworth and Wiens, 1996), substrates within compatible hosts (Sargent, 1995) and degree of dependence on the host for the acquisition of resources (Fisher, 1983; Lamont, 1983; Ehleringer and Marshall, 1995). This has led to the hypothesis that host–mistletoe interactions may have driven the diversification of mistletoes (Fig. 6.1; Norton and Carpenter, 1998), as postulated for other host–parasite systems (Price, 1980; Brooks, 1988). In fact, variation in parasite virulence and host resistance have been shown to influence host switching and host specificity, two phenomena that can explain diversification among parasites mediated through host–parasite interactions (Page, 1994; Hoberg *et al.*, 1997).

An alternative, but not mutually exclusive, hypothesis is that diversification among mistletoes has been driven by vertebrate–mistletoe interactions and their outcome, seed dispersal (Fig. 6.1). Indeed, most mistletoes are dispersed by vertebrates and patterns of mistletoe distribution within and among hosts are strongly influenced by the behaviour of these dispersers (Restrepo, 1987; Sargent, 1994; Martínez del Río *et al.*, 1996). This has led to the suggestion that mistletoes may be more dependent on their vectors than non-parasitic plants for the delivery of seeds to suitable sites

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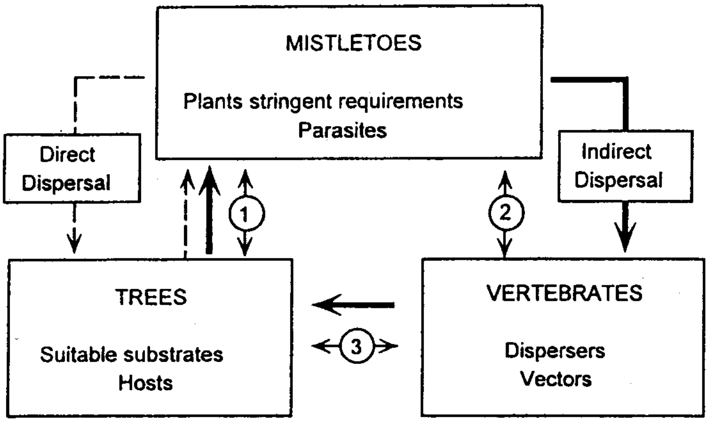

Fig. 6.1. Three hypotheses, alone or in combination, may explain the diversification of mistletoes mediated through interactions under the apparent constraints imposed by a parasitic life: (1) host–parasite, (2) vector–parasites and (3) host–vector interactions.

(Reid, 1991). Mistletoes, however, exhibit a variety of dispersal modes, which range from direct to indirect or vector-mediated dispersal (Fig. 6.1; Orfila, 1978; Reid, 1991; Hawksworth and Wiens, 1996). We hypothesize that variation in dispersal mode, coupled with specialized requirements for germination and establishment (Frochot and Sallé, 1980; Sallé, 1983; Hoffman *et al.*, 1986; Sargent, 1995), may have influenced the diversification of mistletoes through vector–parasite interactions.

In other parasitic organisms there is strong evidence that vector-mediated dispersal has strongly influenced the diversification of parasites. First, traits that influence dispersal of parasites, such as parasite virulence and compatibility and vector competence and resistance, are under strong selection (Collins *et al.*, 1986; Yan *et al.*, 1997; Failloux *et al.*, 1999). Secondly, vectors contribute to the movement of parasite propagules to 'safe sites' and facilitate the exploration of 'host space' (Kim, 1985; Collins and Besansky, 1994; Azad and Beard, 1998). Thirdly, vector, rather than host, phylogenies explain parasite diversification either through associations by descent–vector specificity or associations by colonization–vector switching (Chiykowski, 1981; Davis, 1992; Carreno *et al.*, 1997; Luke *et al.*, 1997), as postulated for host–parasite systems (Brooks, 1988; Brooks and McLennan, 1993). The signatures for associations by descent and colonization are congruent and incongruent phylogenies, respectively (Hoberg *et al.*, 1997). Alternatively, associations between vectors and parasites that seem to be the result of vector switching may actually be the result of sorting events, such as parasite extinction, parasite absence from the vector founder population at a speciation event or sampling error (Paterson and Gray, 1997).

To evaluate the hypothesis that vector–parasite interactions have played a role in the diversification of mistletoes, we tested three predictions. First, mistletoe taxa that are most diverse are predominantly vertebrate-dispersed. Secondly, vectors associated with mistletoes represent a narrow subset of local vertebrate assemblages. If true, we expect to find little variation among mistletoe species in terms of their vectors. Thirdly, vector–mistletoe associations found within local assemblages are likely to reflect a long-term history of association. If true, we expect to find a high degree of congruence between bird and mistletoe phylogenies. To test these predictions, we focused on New World mistletoes and their dispersers, because both are relatively well known.

Methods

Mistletoe diversity and dispersal mode

Mistletoes are in the *Santalales* and represent the largest assemblage of parasitic woody angiosperms (Kuijt, 1968). In the New World, they are represented by four families (*Eremolepidaceae, Loranthaceae, Misodendraceae* and *Viscaceae*), 24 genera and approximately 700 species (Table 6.1; J. Kuijt, personal communication). *Loranthaceae* and *Misodendraceae* represent basal clades, whereas *Eremolepidaceae* and *Viscaceae* are derived clades (Nickrent, in press).

Most mistletoes produce fleshy fruits with a single seed associated with viscin, a highly sticky tissue (Kuijt, 1969). Unlike seeds of other angiosperms, those of mistletoes lack a seedcoat; thus, the unit of dispersal consists of an embryo and endosperm, often photosynthetic, and various tissues, including viscin (Bhandari and Vohra, 1983; Bhatnagar and Johri, 1983). Viscin functions in the attachment of seeds to the host (for other functions, see Gedalovich and Kuijt, 1987). The achenes of *Misodendraceae* with their feather-like structures represent the only exception to this pattern (Kuijt, 1969).

Mistletoe species were classified according to dispersal mode and family to test the prediction that dispersal mode has influenced mistletoe diversity. At least three dispersal modes have been reported among New World mistletoe species: anemochory – wind dispersal (Orfila, 1978) – autochory – ballistic dispersal (Hawksworth and Wiens, 1996) – and endozoochory – animal dispersal via fruit ingestion (Walsberg, 1975; Davidar, 1987; Restrepo, 1987; Sargent, 1994). The autochorous genus *Arceuthobium* produces explosive fleshy fruits, capable of short-distance seed dispersal; however, long-distance dispersal may occur when the sticky seeds get attached to vertebrate feathers and fur (Hawksworth and Wiens, 1996). We term this type of dispersal facultative epizoochory. In addition, species in the predominantly endozoochorous genus *Dendrophthora* may have explosive fruits that eject their single seed when manipulated within birds'

Table 6.1. Diversity of New World mistletoes and associated dispersal modes. 'Mixed' mode includes autochory/facultative epizoochory and facultative autochory/endozoochory (see text).

		Dispersal		
		Anemochory	Endozoochory	Mixed
Misodendraceae	*n* (genera)	1	–	–
	n (species)	12	–	–
	Species per genus	12	–	–
Loranthaceae	*n* (genera)	–	17	–
	n (species)	–	278	–
	Species per genus	–	16.3 (18.2)	–
Eremolepidacea	*n* (genera)	–	3	–
	n (species)	–	12	–
	Species per genus	–	4.0 (3.4)	–
Viscaceae	*n* (genera)	–	3	2
	n (species)	–	359	35
	Species per genus	–	120.0 (119.5)	17.0 (22.6)
Total	*n* (genera)	1	23	2
	n (species)	12	650	35
	Species per genus	12	28.3 (53.7)	17.0

Number of species (in parentheses): *Loranthaceae*: *Desmaria* (1), *Gaiadendron* (1), *Notanthera* (1), *Ligaria* (2), *Tripodanthus* (2), *Tristerix* (12), *Maracanthus* (3), *Oryctanthus* (12), *Oryctina* (8), *Panamanthus* (1), *Phthirusa* (35), *Struthanthus* (*c.* 55), *Cladocolea* (30), *Dendropemon* (30), *Ixocactus* (15), *Aetanthus* (15), *Psittacanthus* (*c.* 55). *Eremolepidaceae*: *Lepidoceras* (2), *Eubrachion* (2), *Antidaphne* (8). *Misodendraceae*: *Misodendrum* (12). *Viscaceae*: *Dendrophthora* (120), *Phoradendron* (240), *Arceuthobium* (34).

bills (Sargent, 1994). We term this type of dispersal facultative autochory. Anemochory and autochory represent direct modes of dispersal, whereas endozoochory and epizoochory represent indirect or vector-mediated modes (Fig. 6.1).

Mistletoe diversity and vector-mediated dispersal

Local-scale assemblages

We conducted observations at two sites rich in mistletoe species, one in Colombia and one in Costa Rica (Table 6.2). These sites are heavily covered by forest and second-growth vegetation and are classified as lower montane wet forest (Restrepo, 1987; Haber, 2000). At the Colombian site, we recorded bird activity at clumps of five mistletoe species (Table 6.2); we spent an average of 25 h month^{-1} observing each species (February 1983–March 1984). A feeding visit was defined as a bird landing on a mistletoe clump to feed and departing afterwards (Restrepo, 1987). At the Costa Rican site, we recorded bird activity at mistletoe clumps belonging to six species (Table 6.2). These clumps were found along a 3 km loop transect, which was surveyed on a weekly basis (September 1989–July 1990). At both sites, we identified and recorded the number of visits and behaviour of the birds feeding on mistletoe fruits. We used bird visits to mistletoe species as the response variable. Bird visits were classified according to mistletoe and bird species to test the prediction that vectors associated with mistletoe species represented a narrow subset of vertebrates.

Regional–scale assemblages

We compiled a database on vertebrates feeding on mistletoe fruits or dispersing their seeds. Each record (542 in total) includes information on mistletoe (family and species) and vertebrate (class, family/subfamily and species) taxonomy, vertebrate fruit- and seed-handling methods, site of the observation (site name, geographical coordinates, elevation) and source. Records were compiled from the literature, an on-line mistletoe database (http://www.rms.nau.edu/mistletoe/mtbib.html), and from unpublished records and theses made available through personal communication with researchers. We used vertebrate species as our response variable. Although simplistic, this was necessary for several reasons. First, few studies report data on the relative importance of vertebrate species to mistletoes. Secondly, most studies report only casual observations of vertebrates feeding on mistletoes. Thirdly, some 'sites' are over-represented in the database, yielding several records for the same species. Fourthly, we could not differentiate between 'legitimate' seed-dispersers and seed predators because the fate of seeds was rarely mentioned. More importantly, however, 'legitimate' dispersers and seed predators are both likely to influence seed-dispersal systems (Herrera, 1984).

Table 6.2. Location and characteristics of study sites in Colombia and Costa Rica. Species that were intensively studied are listed below the table.

Site	Coordinates	Elevation (m)	Families and number of species
Zingara and La Frizia, Colombia	3°20′N, 76°38′W	1950	*Viscaceae* (9) *Loranthaceae* (5) *Eremolepidaceae* (1)
Monteverde, Costa Rica	10°18′N, 84°48′W	1550	*Viscaceae* (5) *Loranthaceae* (6) *Eremolepidaceae* (1)

Colombia: *Phoradendron colombianum, Phoradendron inaequidentatum* and *Phoradendron dipterum, Viscaceae*; *Cladocolea lenticellata, Loranthaceae*; and *Antidaphne viscoidea, Eremolepidaceae.* Costa Rica: *Phoradendron robustissimum, Phoradendron chrysocladon, Phoradendron robaloense, Viscaceae*; *Struthanthus oerstedii* and *Oryctanthus spicatus,* Loranthaceae; and *A. viscoidea, Eremolepidaceae.*

Vertebrate species were classified into taxonomic groups to test the prediction that vector–mistletoe associations found within local assemblages are likely to reflect a long-term history of associations. These groups were: non-passerine (NONP), suboscine passerines (PSOS), oscine passerine birds (POSC) and other (OTHE); the latter includes mammals and fish. We further classified PSOS and POSC species into families and/or subfamilies to explore the occurrence of associations by descent–vector specificity and associations by colonization–vector switching. We made use of recent phylogenies based on molecular data showing that: (i) *Euphonia/Chlorophonia* forms a clade that is sister to the Carduelini (Fringillinae) and not the Emberizinae; (ii) *Tersinia*, *Cyanerpes*, *Dacnis*, *Coereba*, *Diglossa*, *Chlorophanes* and *Saltator* belong to the Thraupini; and (iii) *Spiza*, *Pheuticus*, *Passerina* and *Piranga* represent a clade within the Cardinalini (Sibley and Ahlquist, 1990; Burns, 1997; Klicka *et al.*, 2000).

In all instances we used chi-square tests and included individual taxa when sample sizes were large enough so that > 80% of the expected cell frequencies were > 5; taxa that did not meet this criterion were pooled (Siegel and Castellan, 1988). We partitioned the $r \times k$ contingency tables into a series of 2×2 subtables to identify the cells contributing to significant results; the 2×2 subtables were analysed as if they were independent from each other by using a modified χ^2 test (Siegel and Castellan, 1988). The groups were arranged a priori to reflect meaningful comparisons between mistletoes and vertebrates. We calculated the standardized residuals for the 2×2 subtables for which the chi-square values were significant. We used Matlab to program the routines used to partition the contingency tables and to calculate the chi-square values.

Results

Mistletoe diversity and dispersal mode

Endozoochory is disproportionately common among New World mistletoes, whether analysed with number of genera or number of species (goodness-of-fit test, $\chi^2 = 28.5$, d.f. = 2, $P \leq 0.0001$ and $\chi^2 = 1324.0$, d.f. = 2, $P \leq 0.0001$, respectively (Table 6.1)). Yet, when we discriminate among mistletoe families, we find that there is a significant association between dispersal mode and family. In the *Loranthaceae* more genera than expected are endozoochorous, whereas in the *Misodendraceae* and *Viscaceae* (*Arceuthobium* and *Dendrophthora*) more genera than expected exhibit the anemochorous and 'mixed' dispersal modes, respectively (chi-square test, $\chi^2 = 14.8$, d.f. = 3, $P \leq 0.002$ (Table 6.1)). The same pattern holds at the species level (chi-square test, $\chi^2 = 193.0$, d.f. = 3, $P \leq 0.0001$, anemochorous and 'mixed' dispersal modes pooled (Table 6.1)).

Within endozochorous genera and species, *Loranthaceae* are genera-rich and *Viscaceae* are species-rich (goodness-of-fit test, $\chi^2 = 9.8$, d.f. = 2, $P \leq 0.002$ and $\chi^2 = 10.5$, d.f. = 2, $P \leq 0.001$, respectively (Table 6.1)). Three mutually non-exclusive hypotheses may explain this pattern. First, differences in the biogeographical origin and age of the lineages (Barlow, 1983) may have contributed to the differential accumulation of genera among mistletoe families. Secondly, differences among vectors (i.e. vector competence) may have contributed to the diversification of mistletoes in different ways. Thirdly, mistletoe families may differ in terms of their compatibility with vectors: that is, some mistletoe taxa may be more restrictive in terms of the vectors they attract.

Mistletoe diversity and vector-mediated dispersal

Local-scale assemblages

We recorded 33 bird species belonging to eight taxa (Columbidae, Tyrannidae, Pipridae, Vireonidae, Muscicapidae, Fringillinae, Thraupini and Cardinalini) feeding on mistletoe fruits in Colombia and Costa Rica (21 and 12 species, respectively (Fig. 6.2)). Even though mistletoes belonging to different species could be found parasitizing the same or neighbouring trees, they attracted distinctly different subsets of birds. In both sites, the proportion of visits contributed by each bird species differed significantly among mistletoe

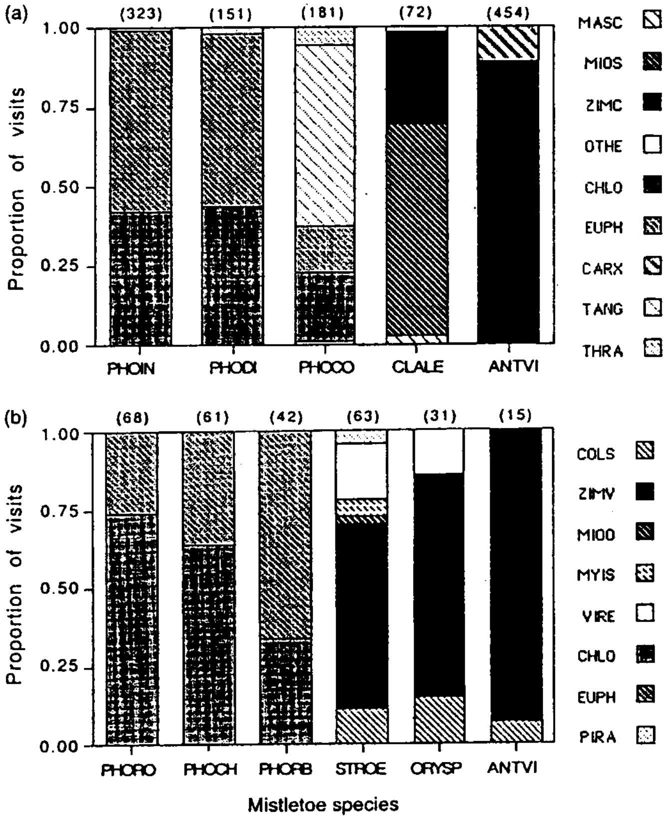

Fig. 6.2. Local assemblages of mistletoes and their avian dispersers. (a) Colombia. EUPH: *Euphonia* spp. (*E. xanthogaster*, *E. laniirostris* and *E. musica*); CHLO: *Chlorophonia* spp. (*C. pyrrophrys* and *C. cyanea*); TANG: *Tangara* spp. (*T. labradorides*, *T. nigroviridis*, *T. ruficervix*, *T. xanthocephala*, *T. arthus*, *T. heinei*, *T. cyanicollis* and *T. vitriolina*); THRA: Thraupini–other (*Chlorochryssa nitidissima* and *Anisognathus flavinucha*); MIOS: *Mionectes striaticollis*; ZIMC: *Zimmerius chrysops*; MASC: *Masius chrysopterus*; CARX: *Carduelis xanthogastra*; OTHE: *Entamodestes coracinnus and Cyclarhis nigrirostris*; PHOIN: *Phoradendron inaequidentatum*; PHODI: *Phoradendron dipterum*; PHOCO: *Phoradendron colombianum*; CLALE: *Cladocolea lenticellata*; ANTVI: *Antidaphne viscoidea*. (b) Costa Rica. CHLO: *Chlorophonia callophrys*; EUPH: *Euphonia* spp. (*E. luteicapilla*, *E. hirundinaceae* and *E. musica*); ZIMV: *Zimmerius villisimus*; COLS: *Columba subvinaceae*; VIRE: *Vireo* spp. (*V. flavifrons*, *V. leucophrys* and *V. philadelphicus*); PIRA: *Piranga flava*; MIOO: *Mionectes olivaceus*; MYIS: *Myiozetetes similis*; PHORO: *Phoradendron robustissimum*; PHOCH: *Phoradendron chrysocladon*; PHORB: *Phoradendron robaloense*; STROE: *Struthanthus oerstedii*; ORYSP: *Oryctanthus spicatus*. Number of species in parentheses.

taxa (chi-square test, $\chi^2 = 2551$, d.f. = 24, $P \leq 0.0001$ and chi-square test, $\chi^2 = 339$, d.f. = 25, $P \leq 0.0001$, for Colombia and Costa Rica, respectively (Fig. 6.2)). Partitioning the contingency table revealed large differences within and among mistletoe species in terms of the birds feeding on their fruits (Tables 6.3 and 6.4). First, species in the genus *Phoradendron* (*Viscaceae*) differed in the proportion of visits made by *Euphonia* and *Chlorophonia*. Secondly, species in the genus *Phoradendron* differed in the proportion of visits made by the *Euphonia*/*Chlorophonia* group and *Tangara* spp.; this difference became more noticeable

Table 6.3. Birds feeding on mistletoe fruits in Colombia. The 2 × 2 subtables were used to establish the contribution of bird and mistletoe taxa to the overall significant results. The modified χ^2 for each subtable is in italics; $^*P \leq 0.05$. Abbreviations as in Fig. 6.2. 'Other' includes *Chlorochryssa nitidissima*, *Anisognathus flavinucha* and *Masius chrysopoterus*. Rows and columns represent mistletoe and bird species, respectively. + indicates pooling of species during the generation of the 2 × 2 subtables.

	Euph	*Chlo*	*Euph* + *Chlo*	*Tang*	*Euph* + *Chlo* + *Tang*	*Carx*	*Euph* + *Chlo* + *Tang* + *Carx*	*Mios*	*Euph* + *Chlo* + *Tang* + *Carx* + *Mios*	*Zimc*	*Euph* + *Chlo* + *Tang* + *Carx* + *Mios* + *Zimc*	Other
Phco	27	39	66	103	169	0	169	0	169	0	169	12
Phoin	185	136	321	2	323	0	323	0	323	0	323	0
	6.4*		*502.1**		*0.1*		*0.1*		*0.3*		*43.5**	
Phoco +												
Phoin	212	175	387	105	492	0	492	0	492	0	492	12
Phodi	82	67	149	2	151	0	151	0	151	0	151	0
	0.0		*60.5**		*0.0*		*0.01*		*0.0*		*5.6**	
Phoco +												
Phoin +												
Phodi	294	242	536	107	643	0	643	0	643	0	643	12
Clale	0	0	0	1	1	0	1	48	49	21	70	2
	0.0		*0.1*		*8.0*		*803.4**		*24.7**		*0.5*	
Phoco +												
Phoin +												
Phodi +												
Clale	294	242	536	108	644	0	644	48		21	713	14
Antvi	0	0	0	0	0	50	50	0	692	404	454	0
	0.0		*0.0*		*196.1**		*1.0*		50		*0.8**	
									890.7*			

Table 6.4. Birds feeding on mistletoe fruits in Costa Rica. The 2 × 2 subtables were used to establish the contribution of bird and mistletoe taxa to the overall significant results. The modified χ^2 for each subtable is in italics; $^*P \leq 0.05$. Abbreviations as in Fig. 6.2. Rows and columns represent mistletoe and bird species, respectively. + indicates pooling of species during the generation of the 2 × 2 subtables.

	Chlo	Euph	Chlo + Euph	Cols	Chlo + Euph + Cols	Vire	Euph + Chlo + Cols + Vire	Pira + Mioo + Myis +	Euph + Chlo + Cols + Vire + Pira, Mioo, Myis	Zimv
Phoro	50	18	68	0	68	0	68	0	68	0
Phoch	39	22	61	0	61	0	61	0	61	0
	_2.0_		_0.0_		_0.0_		_0.0_		_0.0_	
Phoro + Phoch	89	40	129	0	129	0	129	0	129	0
Phorb	14	28	42	0	42	0	42	0	42	0
	_27.5_*		_0.0_		_0.0_		_0.0_		_0.0_	
Phoro + Phoch + Phorb	103	68	171	0	171	0	171	0	171	0
Stroe	0	0	0	7	7	11	18	8	26	37
	_0.0_		_32.3_*		_48.5_*		_37.6_*		_82.4_*	
Phoro + Phoch + Phorb + Stroe	103	68	171	7	178	11	189	8	197	37
Orysp	0	0	0	5	5	4	9	0	9	22
	_0.0_		_19.1_*		_9.0_*		_0.2_		_43.2_*	
Phoro + Phoch + Phorb + Stroe Orysp	103	68	171	12	183	15	198	8	206	59
Antvi	0	0	0	1	1	0	1	0	1	14
	_0.0_				_0.0_		_0.0_		_37.2_*	

when the 'other' category (*Anisognathus flavinucha*, *Chlorochryssa nitidissima*, *Entamodestes coracinnus* and *Cyclarhis nigrirostris*) was included. These results demonstrate that subsets of species within *Phoradendron* may be associated with different bird taxa. Thirdly, when *Viscaceae* (*Phoradendron* species were pooled) were compared with *Loranthaceae* (*Cladocolea lenticellata*, *Struthanthus oerstedii* and *Oryctanhus spicatus*), it became clear that *Viscaceae* and *Loranthaceae* differed significantly in terms of the bird taxa associated with them. The addition of *Carduelis xanthogastra* (Fringillinae), Tyrannidae (*Mionectes* spp., *Zimmerius* spp., *Myiozetetes similis*), *Columba subvinaceae* (Columbidae) and Vireonidae (*Vireo* spp.) during the generation of the 2 × 2 subtables resulted in significant χ^2 values (Tables 6.3 and 6.4). This shows that there is little overlap between bird taxa visiting *Viscaceae* and *Loranthaceae*. Fourthly, we found that the *Viscaceae* and *Loranthaceae* differed significantly from *Eremolepidaceae* because of the high proportion of visits made by *Zimmerius* spp. to *Antidaphne viscoidea* at both sites. This suggests a high degree of association between *Zimmerius* spp. and *A. viscoidea*.

Regional-scale assemblages

A total of 221 species of vertebrates have been reported feeding on mistletoe fruits or dispersing their seeds: 95.5% are birds, 4.0% are mammals and 0.5% are fish. *Arceuthobium*, the mistletoe genus with the northernmost distribution, is associated with a small assemblage of vertebrates, which includes 28 bird and five mammal species (Appendix 6.1; appendices cited in this chapter are available from the authors upon request). Because of the prevalence of autochory and epizoochory in *Arceuthobium*, we excluded this genus from the analyses that follow.

We found a significant association between mistletoe families and the vertebrate taxa feeding on their fruits (chi-square test, $\chi^2 = 17.0$, d.f. = 6, $P \leq 0.008$ (Fig. 6.3 and Table 6.5)). Partitioning of the contingency table showed that this pattern was largely due to differences between *Loranthaceae–Eremolepidaceae* and *Viscaceae*. In fact, more NONP/PSOS species feed on *Loranthaceae–Eremolepidaceae* than expected by chance, whereas an equal proportion of POSC species feed on fruits of *Loranthaceae–Eremolepidaceae* and *Viscaceae* (Table 6.5).

Most records of vertebrates feeding on mistletoes are of passerine birds. Within passerines we found a significant association between mistletoes and high-order passerine

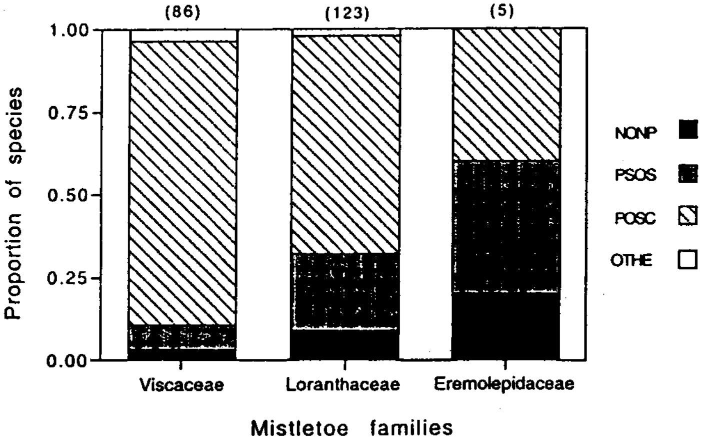

Fig. 6.3. Regional assemblages of mistletoes, *Viscaceae, Loranthaceae and Eremolepidaceae* (excluding *Arceuthobium*), and the vertebrates feeding on their fruits. NONP: non-passerine; PSOS: passerine suboscines; POSC: passerine oscines; OTHE: mammals and fish. Number of species in parentheses.

Table 6.5. Vertebrates feeding on mistletoe fruits in the New World. The 2 × 2 subtables were used to establish the contribution of bird and mistletoe taxa to the overall significant results. The modified χ^2 for each subtable is in italics. *$P \leq 0.05$. Abbreviations as in Fig. 6.3. Rows and columns represent mistletoe and bird species, respectively. + indicates pooling of species during the generation of the 2 × 2 subtables.

	NONP	PSOS	NONP + PSOS	POSC	NONP + PSOS + POSC	OTHE
Loranthaceae	12	28	40	81	121	2
Eremolepidaceae	1	2	3	2	5	0
	0.0		*1.9*		*0.0*	
Loranthaceae + Eremolepidaceae	13	30	43	83	126	2
Viscaceae	3	6	9	74	83	3
	0.0		*14.4**		*0.8*	

Table 6.6. Passerine species feeding on *Loranthaceae* and *Viscaceae* fruits. Numbers indicate number of bird species. Bird taxa with small samples sizes are indicated by – in the χ^2 column. Taxa (subfamilies/tribes) in grey were pooled for analyses. $^{*}P \leq 0.05$, $^{**}P \leq 0.01$.

Suborder	Passerine taxa	*Loranthaceae*	*Viscaceae*	χ^2
Suboscines	Cotingidae	5	0	4.6^{*}
	Pipridae	4	2	–
	Tyrannidae	19	4	9.8^{**}
Oscines	Corvidae	3	1	6.2^{*}
	Vireonidae	8	1	–
	Bombycillidae	5	4	0.1
	Turdinae	6	9	0.6
	Mimini	6	5	0.1
	Certhiidae	2	1	–
	Paridae	1	0	–
	Carduelini	3	1	–
	Euphonia/Chlorophonia	5	16	5.8^{*}
	Emberizini	0	2	6.2^{*}
	Cardinalini	5	1	–
	Icterini	3	0	–
	Parulini	5	0	–
	Thraupini	29	33	0.3

taxa (Table 6.6). First, species in the Cotingidae/Pipridae, Tyrannidae, Corvoidea (Corvidae and Vireonidae) and Emberizini/Cardinalini/Icterini/Parulini feed more often than expected on *Loranthaceae* fruits. Secondly, *Euphonia/ Chlorophonia* species have been recorded more often than expected feeding on *Viscaceae* fruits. Thirdly, species in the Bombycillidae, Turdinae, Minimi and Thraupini feed with equal frequency on fruits of *Viscaceae* and *Loranthaceae*.

Discussion

Results of this study support the hypothesis that vector–parasite interactions have contributed to the diversification of New World mistletoes. First, we found a strong association between mistletoe diversity and dispersal mode. In particular, species-poor mistletoe taxa are anemochorous or autochorous, whereas species-rich taxa are endozoochorous. Secondly, we found that mistletoe families are associated with a narrow subset of vertebrate taxa; the mistletoe families, however, differ in terms of the vertebrates with whom they are associated. Thirdly, these associations have an important phylogenetic component, which may help to establish the origin of these associations either through colonization and vector switching or through descent and vector specificity.

Mistletoe diversity and dispersal mode

Anemochory is found only in *Misodendraceae*, a small family restricted to the Andes of Argentina and Chile (Orfila, 1978). The low diversity of *Misodendraceae* and its restricted distribution may result from dispersal limitation and a high degree of host specificity. In fact, the only reported hosts are species of *Nothofagus* (Orfila, 1978). Recent work indicates that seeds of *Misodendraceae* disperse over short distances (maximum 10 m from the parent (N. Tercero, personal communication)) and that there are strong preferences for hosts within *Nothofagus* stands (Vidal Russell, 2000). Specifically, it has been shown that *Nothofagus* stands that are genetically diverse are heavily parasitized by *Misodendrum* spp. (Vidal Russell, 2000).

Autochory, in combination with epizoochory and endozoochory – our 'mixed' dispersal mode – has probably been important in the diversification of mistletoes. Epizoochory can result in the movement of seeds over long distances; in fact, a small but important proportion of species on oceanic islands produce fleshy fruits with 'sticky' seeds that are carried on the feathers of birds (Carlquist, 1967). All mistletoe genera exhibiting this dispersal mode belong to the *Viscaceae* (*Arceuthobium, Dendrophthora, Korthalsella* and *Notothixos*, the latter two being Old World genera) (Leiva and Bisse, 1983; Liddy, 1983; Kuijt, 1987; Sargent, 1994; Hawksworth and Wiens, 1996). This characteristic, in combination with the observation that the *Viscaceae* are the only mistletoe family consistently found on continental and oceanic islands (Kuijt, 1961; Barlow, 1983), supports the idea that the 'mixed' dispersal mode has contributed to the diversification of mistletoes, possibly through 'founder' effects.

is?

The 'mixed' dispersal mode and its long-distance dispersal component are diverse; seeds may get dispersed when they either attach to the feathers of birds or when fruits discharge seeds (*Arceuthobium*) (Hawksworth and Wiens, 1996) or are dispersed when fruits are manipulated in birds' bills (*Arceuthobium, bicarinatum, Arceuthobium. verticilliflorum, Dendrophthora corynarthron* and *Dendrophthora cupressoides*) (Etheridge, 1971; Leiva and Bisse, 1983; Sargent, 1994; Hawksworth and Wiens, 1996). Fruits of *D. corynarthron*, for example, are routinely taken by *Chlorophonia callophrys* in Costa Rica and their single seed can be ejected up to 1 m when the bird squeezes the fruit in its bill (S. Sargent and S. Mitra, unpublished data).

Mistletoe diversity and vector-mediated dispersal

Most mistletoe species are endozoochorous, and locally are associated with a narrow subset of birds. Furthermore, vector–mistletoe associations found within local assemblages seem to reflect a long-term history of associations, as suggested by the analyses of regional assemblages of vertebrates and mistletoes. We found a significant association between high-order vertebrate and mistletoe taxa, suggesting that vector–mistletoe associations resulted from colonization–vector switching or from descent– vector specificity. The signatures for associations by colonization and descent are incongruent and congruent phylogenies, respectively.

Loranthaceae–*vector associations: a case of vector switching?*

Two observations suggest that vector switching may explain the origin and maintenance of *Loranthaceae*–vector associations and thus the diversification of these mistletoes. First, New World *Loranthaceae* derive from one of two Gondwana lineages that underwent extensive radiation once South America separated from Antarctica, some time in the middle Cretaceous (Barlow, 1983). Secondly, the *Loranthaceae* are consumed and dispersed by both PSOS (in particular, Tyrannidae and Cotingidae) and POSC (in particular, Thraupini and Vireonidae), two groups of birds that do not share a common history in the New World.

The suboscines (PSOS) also have a Gondwana origin and represent the oldest lineage within the passerines (late Cretaceous to middle Tertiary) (Mayr, 1964; Sibley and Ahlquist, 1990; Boles, 1995; Feduccia, 1999; Raikow and Bledsoe, 2000). The largest radiation of PSOS occurred in South America, after which they dispersed into Central America and southern North America and underwent a secondary radiation during the Pliocene (Mayr, 1964; Sibley and Ahlquist, 1990). The oscine passerines (POSC), on the other hand, have a Laurasian origin and appeared in the American continent much later than the PSOS (Oligocene–middle Miocene) (Sibley and Ahlquist, 1990; Burns, 1997; Feduccia, 1999). They entered America through the Bering Strait and the North Atlantic land bridge. Vireonidae represent an exception to this pattern. They arrived in South America via Antarctica, where they radiated and moved north, experiencing a secondary radiation (*Vireo*) in North America during the Pliocene (Sibley and Ahlquist, 1990).

We postulate that associations between *Loranthaceae* and PSOS have a long history, which originated in South America and remained restricted to that continent until connections between South America and the Antilles (Eocene–Oligocene) and North

America (Pliocene) were established (Iturralde-Vinent and MacPhee, 1999). The connection between South America and the Antilles, however, was brief. During the Pliocene, genera within the *Loranthaceae* became associated with POSC birds. Furthermore, we postulate that associations between *Loranthaceae* and PSOS originated through associations by descent and vector specificity and those between *Loranthaceae* and POSC through association by colonization and then vector switching. The combination of these two processes may explain the generic diversity of *Loranthaceae*.

Although vector switching may explain associations between *Loranthaceae* and their vectors, we cannot exclude the possibility of a spurious effect resulting from unresolved relationships among New World *Loranthaceae*. More precisely, two lines of evidence suggest that New World *Loranthaceae* may have derived from, in addition to the South American Gondwana lineage, a second lineage derived from Laurasian stocks. First, three genera in the *Loranthaceae* (*Gaiadendron*, *Aetanthus* and *Psittacanthus*) are significantly associated with POSC: of 47 bird genera, 33 in the POSC feed on these mistletoes, with only eight in the PSOS and five in the NONP (Appendix 6.3). Secondly, fossil pollen of several *Loranthaceae* (*Loranthus* spp. from North American and European Eocene deposits and *Aetanthus* sp. from a Puerto Rican Oligocene deposit) indicate that *Loranthaceae* were present in North America before the connection between South and North America was established (Graham and Jarzen, 1969; Muller, 1981; Taylor, 1990). More recent records of fossil pollen from Caribbean basin upper Miocene and Pliocene deposits include *Aetanthus*, *Oryctanthus*, cf. *Psittacanthus* and cf. *Struthanthus* (Graham and Jarzen, 1969; Graham, 1990, 1991; Graham and Dilcher, 1998), substantially predating the central American land bridge, which formed in the Pliocene.

Viscaceae–*vector associations: a case of vector specificity?*

Two observations suggest that vector specificity may explain the origin and maintenance of *Viscaceae*–vector associations in the New World. First, New World *Viscaceae* derive from a common Laurasian ancestor that reached the North American continent through the Bering strait during the early Tertiary (Barlow, 1983; Kuijt, 1988; Nickrent *et al.*, 1998). Secondly, species in the *Viscaceae* (excluding *Arceuthobium*) are associated with a homogeneous assemblage of vertebrate vectors, the vast majority POSC; these include Thraupini and *Euphonia*/*Chlorophonia*, plus a few records among Bombycillidae, Turdinae and Mimini.

POSC, like the *Viscaceae*, entered the New World from Laurasia sometime in the Oligocene–middle Miocene (Sibley and Ahlquist, 1990; Burns, 1997). The POSC, in particular the nine-primaried oscines, then experienced an explosive radiation (Raikow and Bledsoe, 2000), which mirrors that of the *Viscaceae*. Thus, we postulate that the association between *Viscaceae* and POSC is relatively recent, originating in North America and the Caribbean and reaching its greatest diversity in Central and South America in recent times. The non-monophyly of *Phoradendron* and *Dendrophthora* (Ashworth, 2000), in combination with our data on local mistletoe–bird assemblages, suggests that vector specificity may have contributed to the diversification of *Viscaceae* in terms of species numbers.

Eremolepidaceae–*vector associations*

The associations between *Antidaphne* spp. and their vectors are intriguing and may indicate a case of extreme vector specificity. Our data, although limited to *Antidaphne* (*A. viscoidea*), indicate a high degree of specificity between this family and its vectors. In Colombia and Costa Rica, *A. viscoidea* is mostly associated with *Zimmerius* spp. (*Z. chrysops* and *Z. villisimus*, respectively; PSOS – Tyrannidae). Also, *Antidaphne* is often parasitized by *Ixocactus*, a genus dispersed by *Z. chrysops* (C. Restrepo, unpublished data). The high degree of association between *Zimmerius* spp. and *Antidaphne* may be tied to a South American origin of *Zimmerius* spp. (Ridgely and Tudor, 1994) and *Antidaphne* (Kuijt, 1988). This extreme case of vector specificity may explain why the *Eremolepidaceae* are much less diverse than *Viscaceae* and *Loranthaceae*.

Mistletoe–vertebrate associations: the next step

Our work has generated several hypotheses about vector–parasite-mediated diversification of New World mistletoes. In addition, it has revealed that, at local scales, mistletoe–vertebrate associations appear constrained by the long history of these associations. Two broad questions should be addressed to further explain the diversification of mistletoes through vector–parasite interactions. First, to what degree can vector switching and vector specificity explain the diversification of mistletoes at the generic level? Secondly, what is the potential for evolutionary change among those traits that mediate vector–mistletoe interactions?

To address the first question, we suggest a macro evolutionary approach similar to the one developed here. This will require new data on mistletoe–vertebrate associations and mistletoe fossils, the ordination of mistletoe taxa based on their associated vectors (C. Restrepo and D. Levey, unpublished data), the generation of phylogenetic trees for both mistletoes and vertebrates and information on fruit- and seed-handling methods. Geographical regions for which data on mistletoe–vertebrate associations are badly needed include Mexico, the Antilles, Brazil's *mata Atlantica* and *cerrado* ecosystems and the temperate forests of Chile. For example, are other genera in the *Eremolepidaceae* associated with PSOS? How do vector–mistletoe associations map on to the biogeographical history of the Antilles?

To address the second question, we suggest study of traits that are under selection and that influence the dispersal of parasites. This includes assessing the fitness benefits for both mistletoes and vectors. In vector–parasite systems, the traits include parasite virulence and compatibility and vector competence and resistance (Collins *et al.*, 1986; Yan *et al.*, 1997; Failloux *et al.*, 1999). For example, do mistletoe fruits have compounds, both nutritive and toxic, that affect the behaviour of their vertebrate dispersers? Can mistletoe seeds survive processing in the guts of most vertebrates? Do vector physiology and behaviour affect the chance of mistletoes being dispersed to suitable hosts and suitable substrates within hosts? Do vectors overcome the toxicity of mistletoe fruits? Most of these questions remain relatively unexplored.

Conservation and management implications

Mistletoes are often regarded as pests and, likewise, birds feeding on mistletoe berries are considered a nuisance in anthropogenic ecosystems and landscapes. Yet, in many ecosystems, particularly those in which plants bearing non-fleshy fruits are dominant, mistletoes may not only represent a food resource for vertebrates but may serve as 'hot spots' for the recruitment of other plants bearing fleshy fruits. In this regard, mistletoe–vector associations can contribute significantly to ecosystem diversity and ecosystem function.

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