

Mistletoes as parasites: host specificity and speciation

David A. Norton and Margaret A. Carpenter

It has been estimated that c. 1% of all angiosperm species are parasitic and that about 40% of plant parasites are shoot parasites, parasitizing the above-ground parts of their host plants, while the other 60% are root parasites¹. Although much of the parasite literature focuses on animal parasites, plant parasites are ecologically and economically significant¹⁻³ and share many features in common with animal parasites. Parasites can be defined as organisms that complete 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^{4,5}. This definition includes all plant parasites, viruses, some phytophagous insects, parasitoids, and ecto- and endoparasites of animals such as lice and liver flukes.

Mistletoes (Box 1), the predominant group of angiosperm shoot parasites, are a fascinating and diverse group of plants found in a wide range of ecosystems including boreal forests, tropical rainforests and arid woodlands. While seed of many plant parasites germinates only in response to chemical signals from host plants¹, mistletoe seeds germinate readily in almost all situations. However, the key limiting step in a mistletoe's life cycle is establishment, which is dependent on an appropriate disperser, deposition on a suitable sized branch, and mistletoe-host compatibility^{6,7}. In having such tight establishment requirements, mistletoes have much in common with many animal parasites. Like other plant and animal parasites, mistletoes also live in an intimate association with their hosts and derive nutrition from the host, and, of course, share a life-long association with a single host individual.

Mistletoes, as with other plant parasites⁸ have recently been described as both agricultural pests and as threatened species in different parts of the world⁷. If we are to manage these species appropriately, it is important that we understand such basic aspects of their biology as patterns of host specificity and the ways in which they speciate. These aspects of mistletoe biology are, however, only beginning to be understood. Recent advances in our understanding of host specificity and speciation patterns in a variety of animal parasites provide valuable insights into similar patterns in plant parasites and especially in mistletoes, but also highlight key areas where our knowledge is still limited for these groups.

Patterns of host specificity

Parasites vary in their host specificity. Groups of parasites tend to include a spectrum from highly host-specific through to host generalists^{9,10}. Few are known to infect only

Recent research on parasite evolution has highlighted the importance of host specialization in speciation, either through host-switching or cospeciation. Many parasites show common patterns of host specificity, with higher host specificity where host abundance is high and reliable, phylogenetically conservative host specificity, and formation of races on or in different host species. Recent advances in our understanding of host specificity and speciation patterns in a variety of animal parasites provides valuable insights into the evolutionary biology of mistletoes.

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a single host species, and such instances may reflect a poor knowledge of the parasite's range rather than specialization on one host¹¹. The usual pattern among specialists is a single common host, and a number of other hosts less frequently parasitized. The common host is required to sustain the parasite population, as the sporadic hosts alone are not sufficient for this although they may be important in the maintenance of genetic variation within the parasite population¹². Generalists, which infect 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.

Unlike most angiosperm root parasites, which typically have broad host ranges¹, mistletoes show a variety of patterns of host specificity from generalist to specialist¹³ in a similar manner to many animal parasites. For example, in the New Zealand loranthaceous mistletoe flora, *Alepis flavida*, *Peraxilla colensoi* and *P. tetrapetala* are specialists, primarily parasitizing different species of *Nothofagus* (southern beech), although they have occasionally been recorded as parasites on other plant species¹⁴. In contrast, *Ileostylus micranthus* (Fig. 1b) and *Tupeia antarctica* are generalists and have been recorded parasitizing a large number of host species¹⁴. Similar variation in host specificity can be seen in other mistletoe flora such as in Australia¹⁵.

An emerging trend in host specificity in several unrelated parasite groups follows the latitudinal climate gradient from temperate to tropical regions. Data from different types of parasite (e.g. digenean trematodes⁹ and parasitoid Ichneumenidae¹⁶) indicate greater host specificity in temperate regions. This pattern is also clearly evident in loranthaceous mistletoes, which show low host specificity in

Box 1. Mistletoes – a polyphyletic group of shrubby aerial stem parasites

The Loranthaceae (Figs 1a,b) are the largest family within the mistletoes with c. 950 species, while the Viscaceae (Fig. 1c) contains c. 365 species⁶. The Loranthaceae are predominantly southern or tropical in their distribution, suggesting a Gondwanan ancestry, while the Viscaceae are more common in northern latitudes⁴⁰. The two groups have probably been derived independently from non-mistletoe ancestors. All mistletoes derive water and nutrients by tapping the host xylem but differ in their dependence on the host for carbon. Dwarf mistletoes (*Arceuthobium* and *Korthalsella*, Viscaceae) are considered to be primarily heterotrophic, tapping the host phloem for carbon compounds²⁷. Other mistletoes are usually regarded as autotrophic, depending on their host for water and inorganic nutrients only, although even in these mistletoes there is evidence for carbon uptake from the host⁶. While dwarf mistletoes have explosively dispersed seeds, most mistletoes are reliant on birds for dispersal and have developed close associations with particular bird groups for dispersal⁶.

heterogeneous tropical rainforests (e.g. in New Guinea) and high host specificity in relatively species poor temperate forests (e.g. in eastern Australia and New Zealand¹³). An interesting exception to the latitudinal pattern of host specificity is also an exception to the latitudinal pattern of species richness: tropical mangrove forests contain few host species which mistletoes can parasitize, and in these areas mistletoes show higher host specificity¹⁷.

This latitudinal pattern can be explained in terms of host abundance. As species richness in many groups is greater in the tropics, most tropical areas do not have a high relative abundance of any one potential host species, making it difficult for a parasitic species to use one host exclusively¹⁶. In contrast, many temperate ecosystems contain plant and animal communities in which usually only a few species dominate, whose abundance makes specialization a more viable option. Host specificity of phytophagous insects also appears to be related to abundance and reliability of host plants¹⁸. The relationship between abundance and specificity has also been illustrated in a recent community study involving five trophic levels (plant, phytophage, parasite, parasitoid and hyperparasite) in which specialization was greater at the lower trophic levels correlating with a greater relative abundance of host species¹⁹.

It has been suggested that as host species become increasingly scarce, they are unable to support specialized parasites (resource fragmentation hypothesis¹⁶). For each parasite species there must be a threshold of absolute host abundance required to support the parasite population. This host population will be made up of a few species if their density is sufficient, otherwise a wider range of hosts will be used to make up the required host numbers. Of course, a parasite can only specialize on a host it is able to use in the first place, so host specificity is in fact related to the abundance of suitable potential hosts, as determined by biochemical and physiological constraints.

Host specialization is thought to be favoured by the advantages of adapting to interact more profitably with a frequently encountered host. Given sufficient abundance of such a host, the benefits of specializing on that host outweigh the disadvantages of interacting less well with other potential hosts^{18,20}. Probably the most significant aspects of host specialization are those that increase the parasite's efficiency in capturing resources from the host^{20,21}. Also important is the ability to overcome host defenses⁹. Parasites may also specialize on a host where they are less susceptible to predation, providing the impetus for evolution of cryptic mimicry of the host^{13,22}. For some parasites, host specialization may facilitate the location of potential mates or the potential for pollination and dispersal by making them easier to find^{9,20}. Being a host generalist can also be advantageous, especially in a heterogeneous community, as it allows a parasite to grow successfully in or on many of the potential hosts encountered. If host populations are unpredictable and ephemeral, generalist parasites are also more likely to occur⁴.

The degree of host specificity can be seen as an equilibrium of two opposing drives: (1) to use a maximum number of the hosts encountered, and (2) to make best use of the most frequently encountered hosts. However, as the number of hosts increases, the probability that a specialist parasite can locate a suitable host decreases, reducing the advantages gained through specialization. Thus, relative host abundance is the key to host specificity. As relative host abundance is variable, host specificity must be seen as dynamic, variable in both space and time, and dependent on

the opportunities available in any one time or place^{4,23}. Not only does the level of specificity change but also the identity of the host species used. The changeable nature of host specificity has been demonstrated repeatedly by parasites which become pests on introduced species, especially crops grown in extensive monocultures^{2,4}. Even among mistletoes, some species have been able to widen their host range with the arrival of new potential host species into a country. For example, the New Zealand mistletoes *Ileostylus micranthus* and *Tupeia antarctica* parasitize a large number of host trees that have been introduced into New Zealand since European settlement 150 years ago¹⁴. In the case of *Tupeia*, the introduced tree *Chamaecytisus palmensis* is now the main host in several parts of New Zealand as habitat loss has removed much of the indigenous vegetation.

In determining the host range of a parasite, dispersal is an important influence on the potential hosts which the parasite contacts and therefore has the opportunity to use as hosts. Mistletoes, with the exception of the explosively dispersed dwarf mistletoes, are almost totally dependent on avian dispersers⁶ and can only establish and grow on the host plants where their avian dispersers deposit seeds. Mistletoes are therefore only likely to develop specificity to hosts on which they are frequently deposited¹². Monteiro *et al.*²⁴ demonstrated the importance of an avian disperser for the loranthaceous mistletoe *Psittacanthus robustus* which occurred on a secondary host only when present under the crown of the primary host. Aspects of the dispersers' behaviour, such as the way they use different potential host plants and the length of time between ingestion and egestion of a mistletoe seed, influence the probability of dispersal to the same or a different host^{25,26}.

There is a tendency among parasites that infect more than one host species to infect closely related hosts – that is, species within the same genus or family. For example, many species of the dwarf mistletoe *Arceuthobium* parasitize only one of the two subgenera of *Pinus*²⁷. Closely related parasites also tend to infect closely related host species. For example, six of the eight species of *Lysiana*, an endemic Australian loranthaceous genus, parasitize *Acacia* species¹⁵. Similarly, closely related Australian species within the large loranthaceous genus *Amyema* parasitize hosts in the same genus¹⁷.

Many parasites described as host generalists have, on closer inspection, been shown to actually be specialists at a local level; that is, over the whole of the parasite species range they might use a large number of host species, but are specific to only a few hosts in any one area. This has been shown for North American mistletoes in *Arceuthobium*²⁷ and *Phoradendron*²⁸, and recently for the Australian mistletoe *Amyema miquelii*²⁹. The occurrence of local host specificity suggests that differences in host utilization may be genetically based as differential success of individuals of one mistletoe population when grown on a different host species has been shown. For example, Clay *et al.*²⁸ showed significant differences in haustorial disk formation when *Phoradendron tomentosum* individuals were swapped between host species, with greatest success when they were grown on the source host species. These differences lead to the formation of different races of the parasite that may appear morphologically similar but are distinct in their host utilization.

Mechanisms of parasite speciation

Recent reviews of parasite evolution have discussed the role of host specificity in parasite speciation^{4,10,11}. Both the formation of distinct parasite races and the tendency for



Fig. 1. (a) *Peraxilla tetrapetala* (Loranthaceae), a large, leafy host-specialist mistletoe with fleshy bird-dispersed fruit. This mistletoe most commonly parasitizes tall *Nothofagus solandri* trees in cool temperate New Zealand rainforests, although it has been recorded from 16 other host taxa¹⁴. (b) *Ileostylus micranthus* (Loranthaceae), a leafy host-generalist mistletoe parasitizing a wide range of shrub and tree genera throughout New Zealand, and also on Norfolk Island, photographed here parasitizing *Coprosma propinqua*. This species has been recorded from 209 different host taxa¹⁴, although it primarily parasitizes trees and shrubs in the genera *Coprosma*, *Podocarpus* and *Pittosporum*. (c) *Korthalsella clavata* (Viscaceae), a primarily heterotrophic mistletoe that parasitizes a range of shrub genera in New Zealand, photographed here parasitizing *Coprosma propinqua*. The dwarf mistletoes differ from most other mistletoes in that their seeds are released from the pericarp either explosively (*Arceuthobium*) or spontaneously (*Korthalsella*), and birds are only involved in subsequent seed dispersal.

closely related parasites to infect closely related hosts appear to be important in speciation by specialization on different hosts.

The formation of parasite races involves genetic changes which are part of adaptation to improved growth on a particular host. Parasite races are likely to form when the gene flow between parasite populations is diminished by factors such as distance, limited range of dispersal, and patchy host populations. This limited gene flow over a substantial period is likely to lead to allopatric speciation. However, speciation through parasite race formation is really only part of another process, that of host-switching.

A host-switch is a two-step process. First, the parasite must include a new host in its range. This requires preadaptation to that host, either through phylogenetic similarity to its existing host or through a chemical or ecological similarity which fortuitously allows the parasite to use the new host. Second, the parasite has to adapt to the new host in a way that restricts itself from previous hosts (parasite race formation). Thus, host-switching involves both an initial decrease in host specificity and a subsequent increase in host specificity as specialization to the new host occurs. Without both these steps, the change is not a host-switch but rather a contraction or expansion of the existing host range. As host-switching involves both expansion and contraction of the host range, it can occur without producing any general trend towards either high or low host specificity.

A host-switch could also be seen as a change in the most frequently used host, such that a previously minor host becomes the major one. This is likely to happen if the relative abundance of the hosts changes (e.g. as a result of climatic or other environmental changes) or if the parasite expands its range into an area where relative host abundances differ to those normally encountered. In this way, selection for specialization on the most abundant host will have different outcomes, initially producing two parasite races and potentially producing distinct species with time.

Parasite speciation can also occur in response to host speciation. Closely related parasites tend to use closely related hosts, which can lead to the parasites and their hosts having congruent phylogenies³⁰. This tendency (known as Farenholz rule) has received considerable recent attention from parasitologists, through use of parasite phylogenies to help establish host phylogenies, and vice versa¹¹. The rule also has important consequences concerning parasite speciation, as it suggests that parasites and their hosts cospeciate⁴.

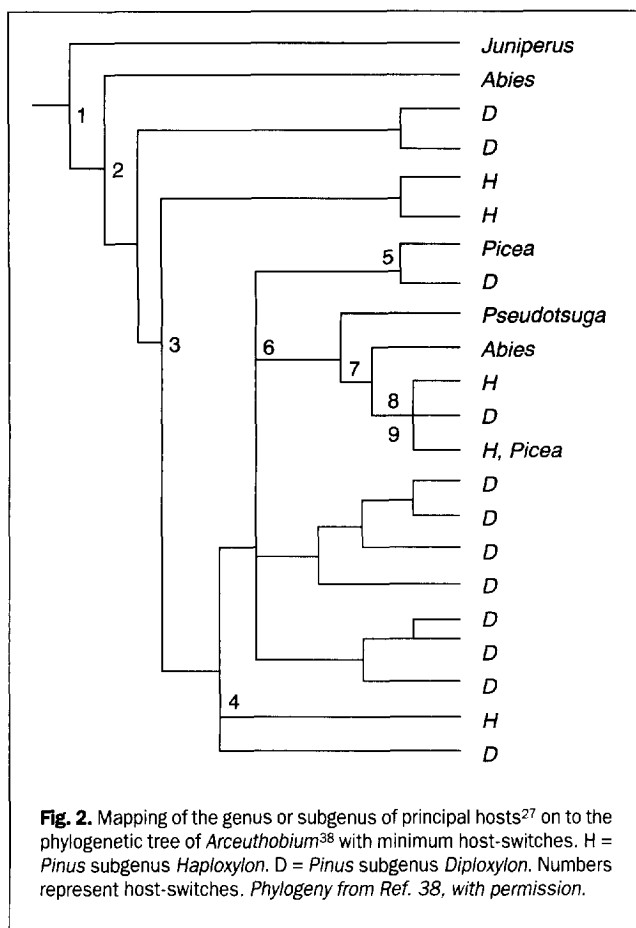
Investigations of the Farenholz rule have revealed that cospeciation does occur^{31,32}, although host-switching events can also be common^{33,34}. Two studies have suggested that both events are approximately equally common among parasite groups^{11,35}. It has been suggested that the frequency of cospeciation tends to be higher if host specificity is also high, because host-specific parasites are frequently phylogenetically conservative in their host choice⁹. Cospeciation seems less likely to occur in a generalist parasite, as speciation of one host would not be a strong influence on a parasite using several other hosts. However, if populations of both the parasite and its hosts became geographically isolated, cospeciation through allopatric speciation might occur, irrespective of levels of host specificity. The prevalence of cospeciation probably varies considerably between different groups of parasites, but may be influenced by aspects of the parasite's ecology such as host specificity and mechanisms of dispersal to new hosts³⁶.

There are a few problems associated with testing the Farenholz rule. One is the difficulty in distinguishing a cospeciation event from a host-switch to a closely related host, especially as this is likely to be the kind of host-switch which would occur most readily due to similarities between closely related hosts. A second difficulty is that the host-parasite association does not always reflect the phylogenetic relationships even in the absence of host-switching. This can occur if some host speciation events are not matched by speciation in the parasite³⁰.

Parasite speciation resulting from changes regarding the host can therefore occur in two ways: parasite cospeciation with their hosts and parasite speciation by changing host specificity. In addition, parasite speciation can also occur without changes in the host. Each of these modes of parasite speciation could occur following the allopatric, peripheral isolates or sympatric models of speciation^{11,37}.

Speciation patterns in mistletoes

Speciation in mistletoes is likely to follow the same patterns as in other parasites – cospeciation with hosts and speciation by host-switching. Comparison of mistletoe and host phylogenies has the potential to describe the histories of host associations for particular mistletoe groups and tell us about the speciation patterns in mistletoes, particularly regarding the relative importance of cospeciation and host-switching. There are, however, only limited data available on mistletoe and host phylogenies to do this. The dwarf



mistletoes of the genus *Arceuthobium* are probably the best-known group, and a molecular phylogeny has been recently produced including some members of this genus³⁸. Most of the hosts used by *Arceuthobium* are in the genus *Pinus*, although a few other genera are also used²⁷.

A phylogeny of the hard pines (*Pinus* subgenus *Diploxyton*), the subgenus which includes the majority of *Arceuthobium* hosts, has recently been published by Krupkin *et al.*³⁹ Using the principal host associations described by Hawksworth and Wiens²⁷, the *Arceuthobium* and hard pine phylogenies can be compared; this comparison shows little evidence for cospeciation, suggesting that host-switching is the more common of the two processes among *Arceuthobium*. Mapping of the genus or subgenus of the principal host (as stated by Hawksworth and Wiens²⁷) onto the phylogeny of *Arceuthobium*³⁸ allows estimation of the evolution of host associations of *Arceuthobium* (Fig. 2). *Arceuthobium* has probably evolved primarily as a parasite of *Pinus*, particularly of the subgenus *Diploxyton*. The most parsimonious arrangement involves nine switches between host genus or subgenus.

Conclusions

Patterns of host specificity and the ways in which mistletoes speciate certainly warrant further research. The role of relative host abundance in determining host specificity could be evaluated by examining the abundance of host species in regions where different races of mistletoes occur, to see if host preference is related to host species abundance. This might also allow estimation of the threshold of absolute host abundance required to sustain a mistletoe population. Analysis of the genetic variation within and between mistletoe races, compared to that occurring between mistletoe species, might give us indications of incipient speciation

and allow estimation of how far two populations have diverged along the road to speciation. A biogeographic analysis would determine whether genetic similarity was related to geographic proximity or host species. Phylogenetic comparison of mistletoes and their hosts would reveal the relative importance of cospeciation and host-switching events in mistletoe speciation.

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Phylogenetic supertrees: assembling the trees of life

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Despite the recent explosive growth in phylogenetics, the number of species included in phylogenies to date is still an insignificant fraction of biodiversity. Moreover, most individual studies sample only a few taxa (usually under 50), so that our current understanding of the tree of life is fragmentary. More inclusive phylogenetic hypotheses are highly desirable: systematists wish to be as comprehensive as possible in making statements about phylogenetic relationships, and comparative biologists often study sets of taxa that do not correspond neatly to sets found on available phylogenies, so are forced to cobble together disparate phylogenies^{1–3} into a single tree. Any such tree containing all the taxa from a collection of trees is a ‘supertree’ in the broad sense (Box 1). An ideal supertree, which we term a ‘strict supertree’, is one that agrees with all the trees from which it was derived.

The obvious approach for combining analyses is simply to combine the original data matrices into a single larger matrix, inserting question

Systematists and comparative biologists commonly want to make statements about relationships among taxa that have never been collectively included in any single phylogenetic analysis. Construction of phylogenetic ‘supertrees’ provides one solution. Supertrees are estimates of phylogeny assembled from sets of smaller estimates (source trees) sharing some but not necessarily all their taxa in common. If certain conditions are met, supertrees can retain all or most of the information from the source trees and also make novel statements about relationships of taxa that do not co-occur on any one source tree. Supertrees have commonly been constructed using subjective and informal approaches, but several explicit approaches have recently been proposed.

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marks in cells where taxa from one analysis have not been scored in another⁴ (Fig. 1). This ‘supermatrix’ approach has the advantage that the information retained in individual characters can help sort out relative strengths and weaknesses within and between the different data sets⁵, which is philosophically in keeping with the so-called ‘total evidence’ approach to combining phylogenetic information⁶.

However, as a long-term strategy for assembling ever larger phylogenies, reliance on the construction of a character supermatrix is untenable. If only a few taxa are common between data sets, most of the newly combined data matrix will be scored as question marks. Gathering the new data needed to fill in the gaps would require exorbitant investments of resources. Other drawbacks of the supermatrix approach are that some data sets (e.g. from DNA–DNA hybridization) cannot be included, and that construction of initial hypotheses of homology and/or alignment becomes ever more difficult as the matrix grows.