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Vectors, viscin, and Viscaceae: mistletoes as parasites, mutualists, and resources

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Mistletoes are aerial, hemiparasitic plants found on trees throughout the world. They have unique ecological arrangements with the host plants they parasitize and the birds that disperse their seeds. Similar in many respects to vector-borne macroparasites, mistletoes are often detrimental to their hosts, and can even kill them. Coevolution has led to resistance mechanisms in hosts and specialization by mistletoes. Birds act as "disease vectors" for the mistletoe host in a mutualistic relationship. To disperse their seeds, mistletoes attract and manipulate their avian vectors in ways that are typical of both plants (offering a fruit reward) and parasites (changing vector behavior once they have been ingested). Mistletoes are important elements of the landscape that influence the spatial distribution of ecosystem resources. Their patchy distribution and complex interactions make their biology intriguing and their management and conservation challenging.

Mistletoes have long been a source of fascination to humans, and references to these parasitic plants can be found among the legends and superstitions of people throughout the world. Some cultures believed that mistletoes were endowed with mystical powers because they grow from the branches of other plants and because many species fruit in winter when other temperate zone plants are dormant. The word "mistletoe" itself comes from the Anglo-Saxon words meaning "dung-on-a-twig" (Calder 1983). Although the plant doesn't spring spontaneously from bird droppings, as was once believed, the name highlights an early recognition of the importance of a host tree for establishment and of birds for dispersal. The same qualities that have fascinated people for centuries continue to be a source of scientific interest today.

This review will focus on the interactions between mistletoes and other organisms, including mistletoe–host interactions and coevolution, parasite–vector interactions, and a comparison of mistletoes with other diseases.

It will look specifically at parasite manipulation of vectors, vector preference and its effect on parasite spread, and mutualistic interactions between parasites and vectors. It will then examine the role of mistletoes in communities, landscapes, and ecosystems and the interaction of mistletoes with a variety of organisms, and conclude by suggesting areas for additional research.

■ What are mistletoes?

Mistletoes are a taxonomically diverse group of plant parasites found in five families: Loranthaceae, Viscaceae, Misodendraceae, Eremolepidaceae, and Santalaceae (Restrepo *et al.* 2002). Found worldwide, mistletoes parasitize thousands of vascular plant species (Hawksworth 1983; Kuijt 1969). Although some are endophytic (eg *Viscum minimum* and *Tristerix aphyllus*), living entirely within their hosts except to produce flowers and fruit, most are stem hemiparasites – capable of photosynthesis, but dependent on their host for water (Calder 1983). With a few notable exceptions, such as the explosively dispersed dwarf mistletoes (*Arceuthobium* spp) or the wind-dispersed Misodendraceae, most mistletoe seeds are dispersed by birds, many of which are highly specialized to consume mistletoe berries (Reid *et al.* 1995; Restrepo *et al.* 2002). A sticky viscin (known as "bird glue") coats the mistletoe seeds, allowing them to adhere to branches after being deposited there by defecation, regurgitation, or bill wiping (Reid *et al.* 1995, Figure 1). Once positioned on an appropriate host, the seed germinates and forms a specialized structure, a haustorium, which taps into the host's vascular system to absorb water, minerals, and nutrients (Calder 1983).

One of the most interesting aspects of mistletoe systems is the relationship between the parasites and their hosts and dispersers. Mistletoes are simultaneously mutualists of

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In a nutshell:
* Mistletoes are hemiparasitic plants that provide valuable resources for many organisms
* They can harm their host plants, and hosts have evolved a variety of defenses as a result
* Mistletoes form mutually beneficial relationships with the bird species that disperse their seeds
* The birds' preference for infected trees influences the spread of mistletoes
* A better understanding of mistletoes' interactions with other organisms and ecosystem processes would help develop management and conservation strategies

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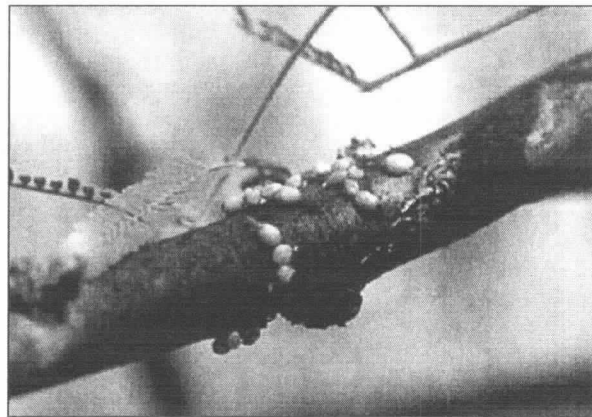
Photos courtesy of Thomas A Carlo

Figure 1. Mistletoe vectors consume mistletoe (Phoradendron californicum) berries (left) and deposit the sticky viscin-covered seeds (right) on the host branches where they germinate. The seeds' haustoria penetrate the host bark and tap into the xylem (and in some cases the phloem) of the host. Because mistletoe seeds deposited on hosts are easily visible, it is possible to measure the relative exposure to the parasite of different host types.
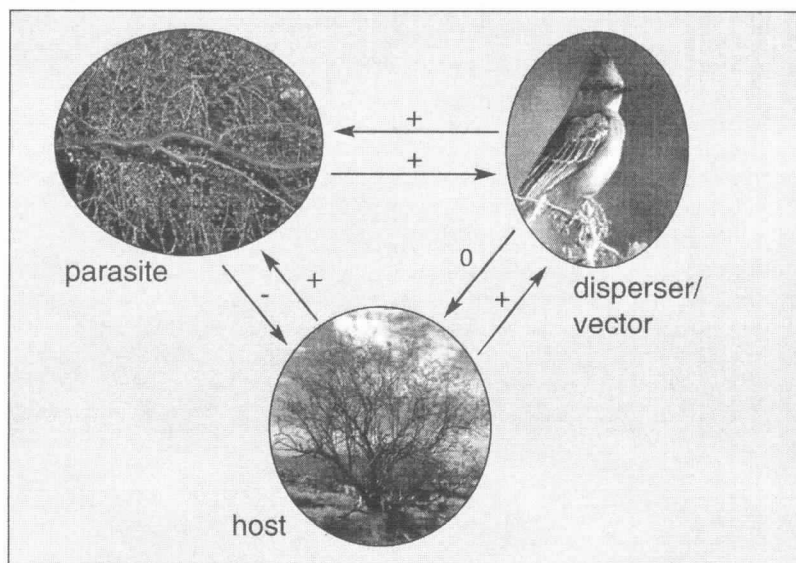
their animal dispersers and parasites of their host plants. The birds that consume their berries and disperse their seeds are both seed dispersers and disease vectors (Figure 2). Because parasites (mistletoes), infective propagules (seeds), and vectors/dispersers (birds) are visible and relatively easy to track, and because the sessile hosts/safe sites (trees or shrubs) are easy to mark and follow over time (Figures 1 and 2), mistletoe–host–vector systems offer a unique opportunity to examine parasitic and mutualistic interactions in space and time. Furthermore, the dual roles of mistletoes and seed dispersers make them especially interesting subjects when looking at the broad-scale consequences of coevolutionary relationships. Examining mistletoes in the light of both parasitology and seed dispersal ecology can help illuminate the role of these plants in the ecosystems they inhabit.

■ Parasite–host relationships

Mistletoes have many similarities to other parasitic organisms: they are often detrimental to their hosts, reducing growth and fecundity, killing branches, and in the case of heavy infestation, even killing hosts (Hawksworth 1983). These negative effects are largely the result of mistletoes diverting important resources from their hosts. Most mistletoes only tap into the xylem of their host plant, but some parasitize the phloem as well (Lamont 1983; Marshall and Ehleringer 1990). Mistletoes obtain water from their hosts, and often accumulate host-derived nitrogen and other minerals in greater proportions

than are found in host branches (Lamont 1983; Pate *et al.* 1991). Phloem-tapping mistletoes obtain a large proportion of their carbon from host plants, but even some xylem-tapping parasites can obtain as much as 60% of their carbon from host photosynthate (Hull and Leonard 1965; Marshal and Ehleringer 1990).

Mistletoes typically have high rates of transpiration, and can alter the water balance of infected hosts (Ehleringer *et al.* 1986; Marshall *et al.* 1994). Dwarf mistletoes can affect the water relations and biomass allocations of whole trees,

Photos courtesy of Thomas A Carlo

Figure 2. Mistletoes play a dual role in ecological systems. They are mutualists of their dispersers (positive arrows run both directions) and parasites of their hosts (negative arrow from mistletoe to host, positive arrow from host to mistletoe). The birds that consume their berries and disperse their seeds are both seed dispersers and disease vectors. In the system from the North American desert southwest illustrated here, the parasites are the desert mistletoe (Phoradendron californicum), the vectors are phainopeplas (Phainopepla nitens) and the hosts are velvet mesquite (Prosopis velutina) and other legume trees.
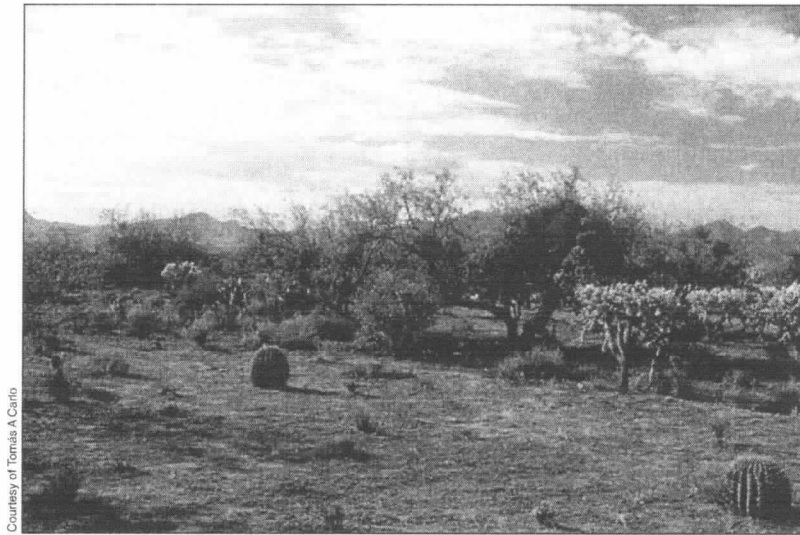
Courtesy of Tomás A Carlo

Figure 3. Phoradendron californicum *parasitizing* Prosopis velutina. *Like many macroparasites, mistletoes are aggregated within hosts. Most hosts have no or very few mistletoes, while a few hosts harbor most of the parasites.*

although the effects vary with parasite and host species and with season (Sala *et al.* 2001). Reduced growth and survival of host trees has been documented for many dwarf mistletoe–host associations, as well as those involving xylem-tapping mistletoe species (Hawksworth 1983; Reid *et al.* 1995). *Tristerix aphyllus* infection was correlated with reduced flower and fruit production of cactus hosts (Silva and Martínez del Rio 1996). It has been hypothesized that the effects of phloem-tapping mistletoes, such as *T aphyllus* and *Arceuthobium* spp, are more severe than those caused by mistletoes that only parasitize xylem (Hawksworth 1983; Silva and Martínez del Rio 1996), but few comparative studies have tested this. The severity of mistletoes' effects on their hosts is also often related to the intensity of infection (the number of mistletoes infecting a single host) (Hawksworth 1983; Reid *et al.* 1995).

Because they have a long generation time and cause persistent infections with continual reinfection of the host, mistletoes can be considered macroparasites (Anderson and May 1979). Like other macroparasites (Pacala and Dobson 1988; Shaw *et al.* 1998), mistletoes are frequently aggregated at the scale of individual hosts – most hosts have no parasites, or just a few, whereas a small number of hosts harbor most of the population (Figure 3). In addition, mistletoes tend to be more prevalent on larger individuals within a host population (Norton *et al.* 1995; Aukema and Martínez del Rio 2002a). Many mechanisms have been proposed to explain this aggregation of macroparasites (Pacala and Dobson 1988; Shaw *et al.* 1998). In mistletoes, these hypothesized mechanisms often depend on heterogeneity in the probability of infection among hosts, and in some cases this has been documented. For example, phainopeplas (*Phainopepla nitens*), the primary dispersers of desert mistletoe (*Phoradendron californicum*), perch preferentially in both desert mistle-

toe-parasitized trees and tall trees, paralleling both seed deposition patterns and infection frequency (Aukema and Martínez del Rio 2002a; Figure 2).

Mistletoe hosts have evolved defenses to prevent parasitism. Resistance mechanisms include physical characteristics that deter the deposition of seeds, and biochemical and structural defenses that prevent mistletoes from establishing after seeds have been deposited (Reid *et al.* 1995; Medel 2000). In columnar cacti, for example, spines act as a defense against the mistletoe *T aphyllus* because the mistletoe's dispersers, Chilean mockingbirds (*Mimus thenca*), avoid perching on hosts with extremely long spines (Martínez del Rio *et al.* 1995; Medel 2000). Several species of potential hosts of *Amyema preissii* and *Lysiana exocarpi* can block haustorial penetration of the bark or xylem through mechanical resistance, development of wound periderm, or by means of changes in the host tissue surrounding the haustorium (Yan 1993).

Like many parasites, mistletoes may exhibit local adaptations to their hosts and specialize on a subset of potential host species (Norton and Carpenter 1998). In some cases, mistletoes do not use the host species they are capable of parasitizing in proportion to their abundance, or they use different species in various parts of their range (Martínez del Rio *et al.* 1995; Norton and Carpenter 1998; Aukema and Martínez del Rio 2002b). Distinct genetic races of *Arceuthobium americanum* associated with three different pine species were recently identified in different geographical areas (Jerome and Ford 2002). Snyder *et al.* (1996) found differences in biochemical features of phloem and xylem, both within and between species of trees infected with dwarf mistletoe (*Arceuthobium vaginatum*). They suggest that these differences are related to susceptibility to infection, and could provide a mechanism for both host speciation and host race formation by mistletoes.

■ Parasite–vector relationships

Dispersal is important in the life history of most organisms and often depends on another organism to facilitate it (Harwood 1981; Wenny 2001). Vector-borne pathogens and zoochorous plants (dispersed by animals) are two obvious examples, and mistletoes fall into both of these categories. Because the behavior of vectors is critical for effective dispersal, it is not surprising that both parasites and plants have evolved ways of manipulating vectors (or hosts) that can increase their probability of transmission (Harwood 1981; Sorensen 1986; Dobson 1988). *Leishmania*-infected sand flies, trypanosome-infected tsetse flies, and malaria-infected mosquitoes bite

hosts more frequently than their uninfected counterparts (Dobson 1988; Koella *et al.* 1998). Zoochorous plants manipulate their vectors by offering a reward, such as a fruit or elaiosome (a nutritious appendage on some seeds), or by requiring animals to groom in order to dislodge their seeds, as with burrs (Sorensen 1986). Not only do mistletoes offer a fruit reward to potential dispersers, they also manipulate vector behavior once the fruits have been ingested. Mistletoe seeds are covered with a sticky substance (viscin) that allows them to stick to host branches, but makes them difficult for birds to expel. Several mistletoe dispersers rub their bills or abdomens against a perch to dislodge seeds after regurgitating or defecating them (Reid 1991).

■ Vector preferences and parasite spread

The preferences of disease vectors for particular hosts often reflect the vectors' responses to visual or chemical indicators of host quality. If parasites can manipulate the actual or perceived quality of a host, they may be able to attract vectors to that host and thereby increase their transmission. Parasites can influence the attractiveness of infected hosts by modifying a host's color, odor, body temperature, or behavior (Kingsolver 1987; Eigenbrode *et al.* 2002). The vectors' response to infected or uninfected hosts can have a strong influence on the pathogens' spread, spatial distribution, and persistence in populations (Kingsolver 1987; McElhany *et al.* 1995; Altizer *et al.* 1998). While some vectors may select hosts opportunistically, or may prefer healthy hosts, some vectors, including tsetse fly vectors of trypanosomes, mosquito vectors of malaria, aphid vectors of potato leaf roll virus, and the avian vectors of mistletoes, prefer infected hosts (Kingsolver 1987; Baylis and Mbwabi 1995; Castle *et al.* 1997; Aukema and Martínez del Rio 2002a). In desert mistletoes, this preference causes a positive feedback in which infected hosts continually receive more seeds and become more heavily infected. The tendency of seed-dispersing birds to visit infected hosts more often than non-infected ones is probably the mechanism that causes the aggregation of mistletoes within hosts (Aukema and Martínez del Rio 2002a).

Vector preference is predicted to have a strong influence on the spread of disease, but may depend on local host spatial structure, the frequency of infection, and the persistence of

the pathogen in vectors (McElhany *et al.* 1995). The preference of the avian vectors of the desert mistletoe for infected hosts occurs not only at the level of individual hosts, but also at the level of neighborhoods. In neighborhoods with a high prevalence of mistletoes, both infected and uninfected hosts have a higher incidence of exposure to infective propagules (seed rain) than those in neighborhoods with a low prevalence of mistletoe infection (Aukema 2001; Aukema and Martínez del Rio 2002c). This creates a second positive feedback, in which heavily infected neighborhoods become even more heavily infected. This mechanism probably generates and maintains the patchy distribution of mistletoe-infected trees found on the landscape. Because of the strong preference of phainopeplas for both infected individuals and areas of high infection prevalence, colonization of isolated trees or uninfected neighborhoods by desert mistletoes is probably rare. Furthermore, in areas of low infection prevalence, mistletoe infection is likely to spread slowly until a threshold density of parasites is reached (Aukema 2001). Some mistletoes, including the desert mistletoe, are dioecious (having separate male and female plants) and require pollination to produce seeds (Figure 4). In an area with one or very few mistletoe infections, limited pollination may restrict seed production, if pollinators have difficulty locating isolated mistletoes. A similar situation exists with schistosomes (parasitic blood flukes). When mean schistosome burdens are low, the parasites cannot be maintained in the host population because they remain unmated (May and Anderson 1979).

Courtesy of Tomás A Carlo

Figure 4. *Mistletoes are a resource for insects such as this fly. Many mistletoes are dioecious; some plants, like this* P californicum, *are male, while others are female. Only female plants will produce fruits and then only if a pollinator first visits a male plant, and seed disperser activity is low in areas with low mistletoe densities. Therefore, it is probably difficult for a new focus of mistletoe infection to become established.*

Courtesy of Tomás A Carlo

Figure 5. *Mistletoes appear to be coevolved with their seed-dispersing vectors, and this relationship seems to have contributed to the diversification of mistletoes. This Euphonia musica is discarding the peel of one of the mistletoe (Phoradendron trinervium) fruits that compose the bulk of its diet. It will swallow the berry, and later defecate and rub the seed off on the branch of a host. If successful, the seed will germinate, parasitize the tree, and eventually produce berries to be consumed by another Euphonia.*

■ Mutualism between vectors and parasites

The preference of disease vectors for infected hosts is often associated with a mutualistic parasite–vector interaction. For example, mosquitoes feeding on hosts infected with *Plasmodium chabaudi* malaria or Rift Valley fever located blood vessels more rapidly than those feeding on uninfected hosts. The parasites inhibit platelet aggregation in their hosts, and this is believed to facilitate feeding by the vector (Rossignol *et al.* 1985). On the other hand, at some stages in the parasite life cycle, *Plasmodium* spp parasites can have a detrimental effect on their vectors' survival or fecundity (Ferguson and Read 2002). Thus, without an examination of the costs and benefits of the relationship over the lifetime of the mosquito, malaria–mosquito relationships cannot yet be considered mutualistic. Aphids and thrips, on the other hand, do appear to be mutualists of some of the viruses they transmit, at least in the laboratory. The aphid *Myzus persicae* and the thrip *Frankliniella occidentalis* not only prefer to feed on virus-infected hosts, but also have higher fecundity when they do so (Bautista *et al.* 1995; Castle *et al.* 1997; Eigenbrode *et al.* 2002). Seed-dispersing frugivores are a classic example of mutualism. There are clear benefits to both parties that translate directly into increased fitness – nutrients for the animals and dispersal for the plants (Reid 1991; Wenny 2001). In addition, seed dispersing animals are sowing future resources for themselves or their descendants.

Mistletoes have a particularly close mutualistic relationship with their seed dispersers/vectors, and parasite–vector coevolution appears to have been important in the diversification of mistletoes (Reid 1991; Restrepo *et al.* 2002). Mistletoe fruits constitute the majority of the diet of euphonias in the Neotropics (Figure 5), mistletoe birds in Australia, and phainopeplas in North America, for at least part of the year (Kuijt 1969; Reid 1991). Some avian dispersers, such as some Dicaeids, phainopeplas, and euphonias, have specialized digestive systems for handling mistletoe fruits, and many mistletoe dispersers exhibit directed dispersal, in which they deposit mistletoe seeds disproportionately in suitable sites (with appropriate host species and branch size). The high degree of mutualism found in mistletoe–vector relationships is unusual for both parasite systems and seed dispersal systems (Kuijt 1969; Reid 1991; Wenny 2001). The most striking difference between mistletoes and other parasite systems is that mistletoe vectors feed directly on the parasite and consume the parasite's dispersal units. In most disease systems, in contrast, parasite transmission is a side effect of feeding on the host by vectors that are either parasites (aphids, mosquitoes, etc) or mutualists (pollinator vectors). The mistletoe *Phoradendron juniperinum* exemplifies the unusual nature of the disease vector as seed disperser; it may have an indirect mutualistic interaction with its host, *Juniper monosperma*, when it attracts the shared, limiting avian seed dispersers (van Ommerren and Witham 2002). Townsend's solitaires (*Myadestes townsendi*) eat both the juniper berries and the mistletoe fruits.
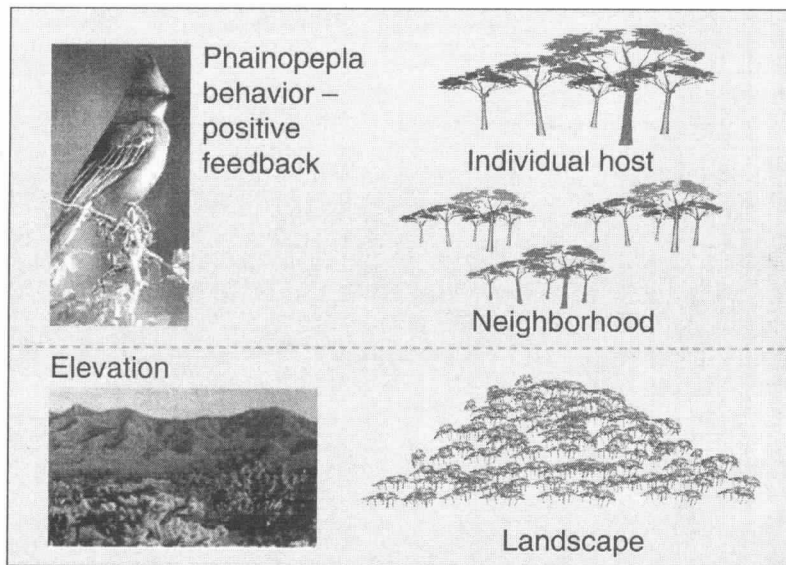
Mistletoes also have mutualistic relationships with their pollinators. Among the Viscaceae, most of the pollinators are insects (Figure 4), whereas the majority of Loranthaceae are pollinated by birds (Kuijt 1969). Several species of Loranthaceous mistletoes in the Paleotropics and New Zealand depend on pollinators to open their flower buds. This explosive flowering sprinkles pollen onto the pollinator and guarantees it an untapped nectar resource. Some birds, such as bellbirds, tui, and flowerpeckers (*Dicaeum* spp), both pollinate and disperse the seeds of mistletoes (Kuijt 1969; Robertson *et al.* 1999).

■ Communities, landscapes, and conservation

It has been suggested that mistletoes are keystone resources in many communities (Watson 2001). Many generalist bird species consume mistletoe berries and nest in the plants themselves or in the "brooms" (dense aggregations of host branches) they can cause in infected trees (Bennets *et al.* 1996; Carlo *et al.* 2002). Herbivorous insects and mammals consume mistletoe foliage, and fungi

and insects take advantage of weakened host trees (Hawksworth 1983; Watson 2001). Bennets *et al.* (1996) found that the abundance and diversity of birds in forest stands were positively correlated with the intensity of infection by the dwarf mistletoe *A vaginatum*, which does not produce bird-dispersed fruit. These mistletoes add complexity to forest structure even when they are not a major part of the diets of the birds (Bennets *et al.* 1996). On the other hand, mistletoes could negatively impact the soil water resources available to plants. Sala *et al.* (2001) suggested that, by increasing water use in infected trees, heavy mistletoe infection could cause these trees to deplete soil water resources, and thus increase water stress in both infected and uninfected plants. We know very little about the ecosystem level effects of mistletoes. Because these plants provide a plethora of resources and can be abundant, the effects are probably considerable. The

Figure 6. Phoradendron californicum *is spatially autocorrelated at three hierarchically nested levels. Desert mistletoes are aggregated within hosts and within neighborhoods of hosts, probably due to the behavior of phainopeplas creating positive feedbacks in seed deposition. They are also aggregated at a larger scale on the landscape, corresponding to elevation. Red represents infected trees.*

birds that disperse mistletoes represent a tiny fraction of an ecosystem's biomass, but by shaping the distribution of mistletoes, they alter the spatial and temporal abundance of important resources. For this reason, I suggest that these birds may play a key role in some communities. As a result of the behavior of seed-dispersing birds, the effects of mistletoes are probably not only large but also spatially heterogeneous.

Recent work has documented patchiness in mistletoes at a variety of spatial scales. Within a landscape, *P californicum* is aggregated at multiple scales (Aukema 2001; Figure 6); *T aphyllus* is restricted to the discrete north-facing subpopulations defined by its hosts (Martínez del Rio et al. 1996); and the patchy distribution of *Amyema miquellii* is amplified by habitat fragmentation (Norton et al. 1995). Animals respond to this patchiness, and the importance of mistletoes as resources suggests that they will also influence the spatial distribution of other organisms, the patterns of species richness of the animals that use them as resources, and the availability of soil water resources for plants. For example, the abundance of the Chilean mockingbird increased steeply with the prevalence of *T aphyllus* infection in several subpopulations (Martínez del Rio et al. 1996). The naturally patchy distribution and the complex interactions of mistletoes with other organisms in their communities complicate the task of mistletoe conservation and management. In Australia and New Zealand, anthropogenic changes, including habitat fragmentation, land degradation, species introductions, and altered disturbance regimes, are believed to contribute to both mistletoe increases and mistletoe declines and extinctions (Norton et al. 1995; Norton and

Reid 1997; Robertson et al. 1999). Large changes in mistletoe abundance in either direction lead to the deterioration of ecosystem conditions (Norton and Reid 1997). In North America, dwarf mistletoes are slowly beginning to be recognized as an important component of diversity in forests that are managed for multiple values (Bennets et al. 1996; Parks et al. 1999).

■ Conclusions

Combining the perspectives of both parasitology and seed dispersal ecology with the study of mistletoes can help compare mistletoes to other parasite and seed dispersal systems, and suggest avenues of future research. For example, mutually beneficial interactions between parasites and vectors may be particularly common in systems in which vectors prefer infected hosts. Examining apparently mutualistic parasite–vector interactions in natural systems could help us better understand the evolution, spread, and control of some pathogens (Ribeiro et al. 1985; Rossignol et al. 1985; Castle et al. 1997). Also, mistletoes are one of the few clear examples of directed dispersal (Wenny 2001). The narrow requirements of mistletoes, resulting from their parasitic habit and the combination of mistletoe–host and mistletoe–vector coevolution, have probably facilitated the evolution of this directed dispersal. These attributes could be used to suggest other groups, such as epiphytes, in which it would be useful to look for directed dispersal (Reid 1991; Wenny 2001).

Mistletoes represent a patchy resource for a variety of organisms, including mutualistic pollinators and dispersers. Because they are parasites, mistletoes can have

top-down (natural enemy) effects on their hosts. As mutualists, however, they can also have bottom-up (resource-limitation) effects on pollinators and seed dispersers. A better understanding of the spatial distribution of mistletoes and associated organisms at a variety of spatial scales, as well as changes in mistletoe abundance over time, could prove useful in developing conservation and management strategies for threatened and pest mistletoes, as well as for mistletoes that damage economically valuable trees but contribute to high biological diversity. To date, there has been more speculation than research on the role of mistletoes in communities, landscapes, and ecosystems, and there have been few large-scale or long-term studies of their population dynamics, landscape distribution, or spread. Such studies would further our appreciation of these plants and their role in ecosystem productivity and patterns of species diversity, and contribute to our understanding of the spread of disease and our ability to manage the ecosystems in which mistletoes are found.

In the 17th century, Sir Thomas Browne published his *Pseudodoxia epidemica* (1646), which provided evidence to refute a number of "vulgar errors" in popular belief. One of these "commonly presumed truths" was that "Misseltoe is bred upon Trees, from seeds which Birds . . . let fall thereon". Browne did not believe that mistletoes grew from seeds, but rather ascribed to the belief that the plant was an "arboreous excrescence". Today, we can explain biologically some of Browne's evidence. We understand that the "parasitical" nature of mistletoes explains "Why if it ariseth from a seed, if sown it will not grow again". We know that Browne's "Ancients" (Pliny, Aristotle, and Virgil) were correct in their belief that "some Birds do feed upon the berries of this Vegetable . . . the Bird not able to digest the fruit whereon she feedeth; from her inconverted muting ariseth this Plant", and we know that host specificity and differences in host susceptibility can help explain "why it groweth onely upon certain Trees, and not upon many whereon these Birds do light". As for the "Magical vertues in this Plant" – further study is in order.

■ **Acknowledgements**

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