7 Mistletoes as Parasites and Seed-dispersing Birds as Disease Vectors: Current Understanding, Challenges and Opportunities

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Introduction

Most mistletoes are vector-borne parasites whose vectors are their avian seed-dispersers (Martínez del Rio *et al.*, 1996). In most vector-borne parasites and diseases, the vector maintains a parasitic or, at best, a commensal relationship with the parasite (Price, 1980). Mistletoes are unique among vector-borne parasites because they maintain a mutualistic interaction with their vectors (Martínez del Rio *et al.*, 1996; Fig. 7.1). Birds obtain nutrients, energy and, in the desert, water from mistletoes (Walsberg, 1975; Reid, 1991). In turn, mistletoes receive directed movement of their propagules into safe germination sites (Reid, 1991).

Because of the apparently specialized nature of the interaction between mistletoes and birds, the dispersal of mistletoes has received considerable attention (Cowles, 1936; Reid, 1991; Overton, 1994; Martínez del Rio *et al.*, 1995; Sargent, 1995; Larson, 1996). Here we attempt to place the interaction between birds, mistletoes and host plants in a broad context. We argue that mistletoes present unique opportunities to integrate seed-dispersal ecology with several other, seemingly disparate, areas of biology, such as plant physiology, parasitology and metapopulation ecology. We also contend that the biology of mistletoes makes them well suited for developing and testing models of how seed dispersal shapes the spatial and temporal dynamics of plant populations. To emphasize the connection between seed dispersal and parasitism, we use parasitology terminology, such as 'prevalence' and 'intensity' of infection to refer to mistletoe infection frequency and the number of mistletoes per host, respectively (Price, 1980). The ideas presented here were shaped by our research on two desert mistletoes: *Tristerix aphyllus* (*Loranthaceae*) and *Phoradendron californicum* (*Viscaceae*). The natural history of these two species is described in detail in Martínez del Rio *et al.* (1995) and Larson (1996). Briefly, *T. aphyllus* infects several species of columnar cacti in semiarid regions of Chile. Its seeds are dispersed primarily by the Chilean mockingbird (*Mimus thenca*).
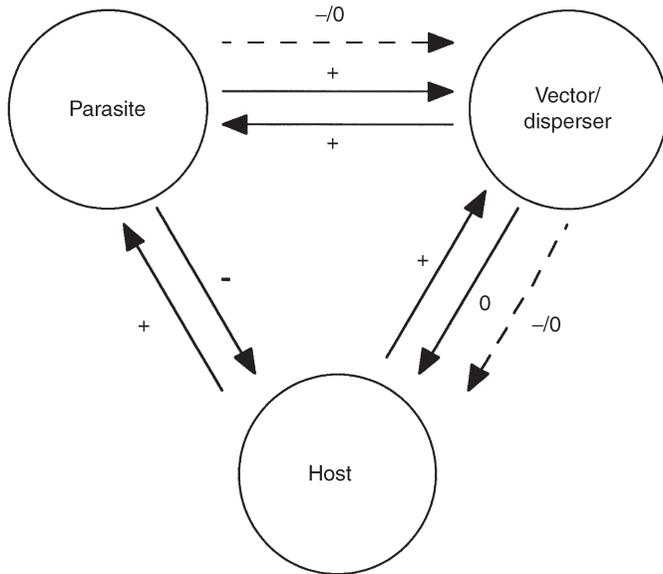
Fig. 7.1. Relationships between mistletoes (parasites), their hosts and the birds (vectors) that disperse mistletoe seeds. Solid arrows indicate the direction of interaction between two participants of the mistletoe system, and the signs above the arrows indicate whether the interaction is beneficial (+), detrimental (–) or has no effect (0) on the participant at the arrow's head. The mistletoe is both a parasite of its host plant and a mutualist of the birds that feed on its berries and disperse its seeds. These birds act both as seed-dispersers and as disease vectors. Dashed arrows indicate interactions in which most other parasites differ from mistletoes. In many parasitic systems, the parasite has a negative or neutral (–/0) effect on its vector. Also, the mistletoe dispersers do not have a direct negative effect on the host, as do many vectors that are themselves parasites, such as mosquitoes or ticks.

Phoradendron californicum infects leguminous trees and shrubs in arid environments from the south-western USA to central Mexico. Its seeds are dispersed primarily by phainopeplas (*Phainopepla nitens*).

First, we outline patterns of variation in mistletoe infection. This section identifies the contrasting scales at which these patterns are found and the mechanisms that shape them. In a second section, we propose a unified framework for the study of mistletoe populations. This framework emphasizes the role of mistletoes as plant parasites, recognizes that they have a patchy metapopulation-like structure and accentuates the fact that their seeds are dispersed by mutualistic birds. The two final sections identify areas that we believe can increase our understanding of mistletoe–host–vector systems, and summarize our primary conclusions.

Mistletoes at Different Scales: Patterns and Mechanisms

Like many other parasites, the distribution of mistletoes among individual hosts is often heavily clumped (Overton, 1996). Why are some individual hosts more intensely parasitized than others? If the site contains several potential host species, the frequency of parasitism may differ among host species (Lamont, 1982; J. Aukema and C. Martínez del Rio, unpublished data). Why does the prevalence of mistletoes differ among host species?

At a larger spatial scale, the overall prevalence and intensity of infection may vary among sites (Overton, 1996). Why are mistletoes more abundant in some sites than in others? Providing mechanistic answers to these questions requires consideration of all the steps in the life history of mistletoes: seed

rain, seed establishment, mistletoe persistence and mistletoe reproductive success.

Seed rain, seedling establishment, mistletoe persistence and reproductive success

The actions of seed-dispersers can lead to differential deposition of seeds among hosts or sites. Birds may choose to perch on individual hosts and may move preferentially among sites with predictable characteristics. Seedling establishment is the next step that can lead to variation in mistletoe prevalence and intensity among hosts and sites. Once a seed is deposited on to a host and germinates, the probability that the seedling will become established is dependent on the match between the characteristics of the host and those of the mistletoe. After germination, successful mistletoe seeds establish an intimate haustorial connection with their hosts (Yan, 1993, and references therein). The growth, survival and reproductive output of mistletoes depend, to a large extent, on their success at using this connection to tap their host's resources.

Mistletoes, parasitism and metapopulations

The natural history of mistletoes reveals potential mechanisms that can lead to differences in mistletoe prevalence and intensity among hosts and sites. Here we attempt to incorporate these mechanisms into an integrative, potentially predictive framework that emerges directly from recognizing that mistletoes are parasites with a metapopulation structure. This section poses several predictions that spring from this view and uses data on *P. californicum* and *T. aphyllus* to evaluate these predictions.

What are the consequences of the mutualism between mistletoes and birds for the population biology of mistletoes? Like other consumers, mistletoe-feeding birds tend to concentrate their activity at sites with relatively high resource densities (Martin, 1985; Sargent, 1990). The response of birds to mistletoes is likely to take place at two scales: birds should perch in fruit-bearing parasitized trees more frequently than in non-parasitized trees (Martínez del Rio *et al.*, 1995), and birds should be more abundant and spend more time at sites with higher mistletoe prevalences (Martínez del Rio *et al.*, 1996). Furthermore, prevalence and intensity of infection are often correlated in host–parasite systems (Fig. 7.2, for example). Fruit abundance at a site is a multiplicative function of the number of fruits per parasite, infection intensity and prevalence. Thus, fruit abundance should increase in an accelerating fashion with prevalence.

The mutualism between birds and mistletoes leads to two simple predictions:

1. Because birds should preferentially visit hosts that are infected by mistletoes, already parasitized hosts should receive seeds more frequently than non-parasitized hosts.
2. Because birds should show higher densities and/or spend more time at sites with higher mistletoe infection frequencies, seed deposition by birds should increase with mistletoe prevalence.

Several studies have provided support for the first prediction (see Figs 7.3 and 7.4). In general, seed rain is higher on parasitized than on non-parasitized hosts (Martínez del Rio *et al.*, 1996) and experimental removal of mistletoes from hosts leads to reduced seed deposition (J. Aukema, unpublished data). Unless infection by mistletoes induces host resistance (Hoffmann *et al.*, 1986), increased seed deposition on to already infected hosts should lead to reinfection and increased parasite loads. The extremely clumped distribution of mistletoes among host individuals exhibited by many mistletoe populations is probably a result of the disproportionate number of seeds deposited by birds on to already parasitized hosts (Overton, 1996). Preferential seed dispersal on to already parasitized hosts is a special case of 'conspecific attraction' (i.e. preferential dispersal to occupied patches over suitable empty ones (Smith and Peacock, 1990)), a phenomenon that can lead to a lower frequency of occupied patches and hence to lower mistletoe prevalences (Ray *et al.*, 1991; see also below, Overton's model).

The response of birds to mistletoe-infected hosts can lead to increased seed rain into
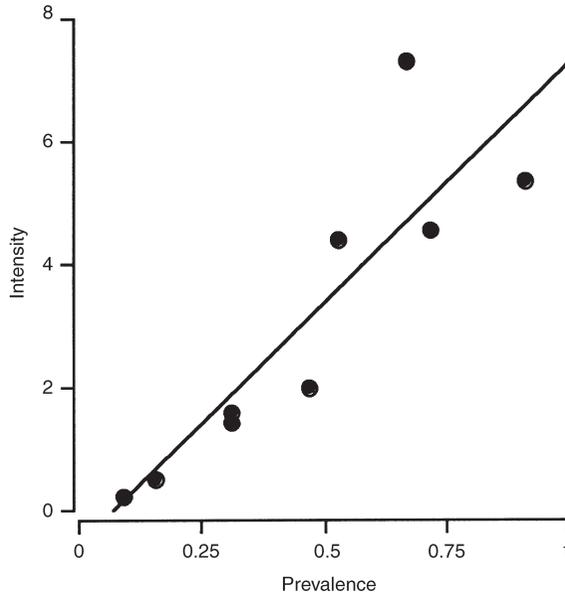
Fig. 7.2. At ten sites in the Santa Rita Experimental Range (Arizona, USA), mean infection intensity (mistletoes per host) of *P. velutina* increased significantly with the prevalence of infection (frequency of infected hosts) by *P. californicum* at each site ($r^2 = 0.77$, $P = 0.0018$; intensity $= -0.584 + 7.93$ (prevalence)).

already infected patches. Can the response of birds to mistletoes be extended to a larger spatial scale? Do sites with higher prevalences also show higher seed rain? Both *T. aphyllus* and *P. californicum* show a positive, accelerating relationship between seed deposition on to non-infected hosts and prevalence (Fig. 7.4; Martínez del Rio *et al.*, 1996). This relationship could lead to a positive correlation between the rate at which new hosts are infected at a site and prevalence. Thus, the response of birds would lead to a positive feedback in infection that could lead to spatial aggregation of parasitism in a landscape and to a positive autocorrelation in prevalence across it (Martínez del Rio *et al.*, 1996). The spatial scale at which this aggregation can be detected, however, depends on the scale at which individual birds and bird populations respond to the density of mistletoes and generate spatial patterns of seed deposition.

Mistletoes and metapopulations

Overton (1994) treated mistletoes as metapopulations, although it may be more appropriate to call them spatially structured patchy populations. Hosts can be identified as 'patches', infection and loss of infection can be characterized as patch occupancy and patch extinction, respectively, and seed dispersal and establishment can be equated with patch colonization. Mistletoe hosts can be viewed as living patches (hosts) inhabited by mistletoe subpopulations. Strictly, a subpopulation is a set of individuals that interact with each other with high probability (Hanski and Simberloff, 1997). Many mistletoes have animal pollinators that can travel and hence can move pollen and genes among patches, one consequence of which is to homogenize the spatial structure of mistletoe subpopulations (Reid *et al.*, 1995).

Mistletoes form discrete groups that inhabit distinct patches separated by unsuitable habitat. Populations in these patches can become extinct, either when all mistletoes in a patch die or when the host dies. Patches/hosts can be colonized only when propagules from other patches immigrate into them. Mistletoe subpopulations rarely inhabit all patches/hosts available, and hosts show turnover, both because mistletoe populations become extinct and because hosts die. Patch turnover is a
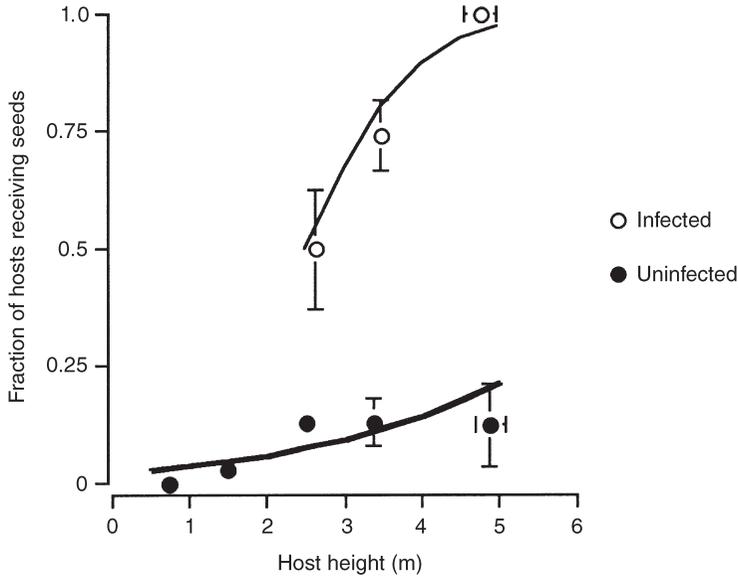
Fig. 7.3. The probability that a *P. velutina* tree host received seeds of the parasite *P. californicum* increased significantly with both height and previous infection (logistic regression *P* < 0.001; open circles are infected hosts and closed circles are uninfected hosts). Points are average values for size classes (bars are standard errors). Data were divided into size classes for visual clarity. Curves were fitted using a logistic regression procedure (logit (π) = −2.56 + 0.66 (height) + 1.46 (infection status)).
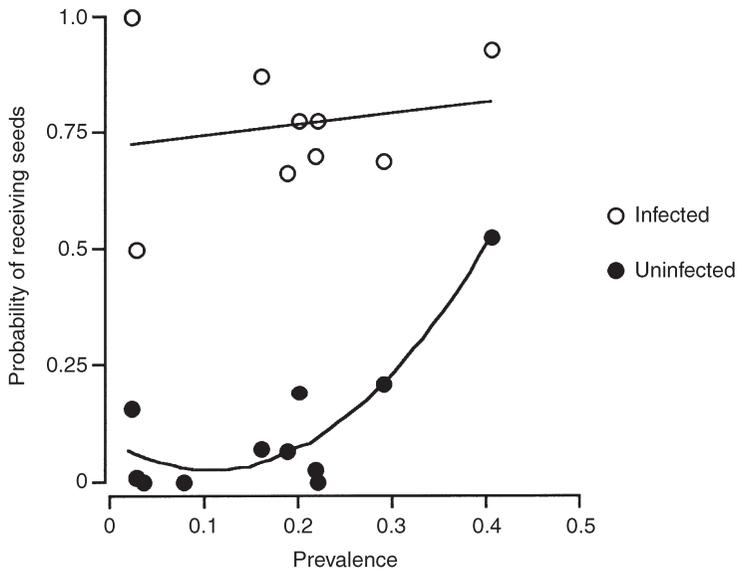

Fig. 7.4. At ten sites in the Santa Rita Experimental Range (Arizona, USA), the probability of receiving *P. californicum* seeds increased with infection prevalence in uninfected *P. velutina* hosts (closed circles). The relationship between the fraction of infected hosts receiving seeds and prevalence, however, was non-linear. For descriptive purposes, we fitted a second-degree polynomial to the data. The quadratic coefficient for this polynomial was significantly positive (*P* < 0.03 indicating an accelerating relationship, $y = 0.05 - 0.91x + 5.10x^2$, $r^2 = 0.81$, *P* < 0.007). For already infected hosts (open circles), there was no significant relationship between the fraction of hosts receiving seeds and prevalence at the site (*r* = 0.06, *P* = 0.62).

key element of the colonization–extinction dynamics that characterize metapopulations (Hanski and Simberloff, 1997).

Overton's model

A variety of host traits can influence the fraction of each host/patch that is occupied and the number of mistletoes inhabiting a host/patch. Overton (1996) modified Levins' (1969, 1970) classical metapopulation model to explore the role of host age on host occupancy. Patch turnover confers an age structure to the patch population, and thus Overton's (1996) model can be used to predict the relationship between host/patch occupancy and age. Overton's model depicts an array of hosts/patches that are either occupied or unoccupied at any point in time. Empty patches are equally likely to receive seeds and occupied hosts are equally likely to produce them. Overton (1996) modified Levins's (1970) model to explore the relationship between host age and probability of infection occupancy by assuming that population occupancy was at equilibrium. Overton's model

yields two predictions: (i) occupancy should increase as a function of host age; and (ii) occupancy should increase with host age at an increasing rate at sites with higher among-host/patch dispersal rates.

A positive relationship between host size and infection prevalence is commonly found in mistletoe populations (Figs 7.5–7.7; Donohue, 1995; Overton, 1996; Kelly, 1998; Lei, 1999; J. Aukema and C. Martínez del Rio, unpublished data). Thus, prediction (i) appears to hold true, assuming that size is a good proxy for age. However, the positive relationship between infection prevalence and host age that is commonly found in mistletoes can be attributed to two non-exclusive hypotheses: (i) accumulation of mistletoes with age; or (ii) preference of avian seed-dispersers for taller, and probably older, host individuals. Explanations based on larger hosts receiving more seeds should result in a strongly positive size–intensity relationship. Although many mistletoes exhibit a significant and positive host size–infection intensity relationship (Overton, 1996), these relationships are often weak (Fig. 7.5). Two factors may account for the weakness of this relationship: (i) not only
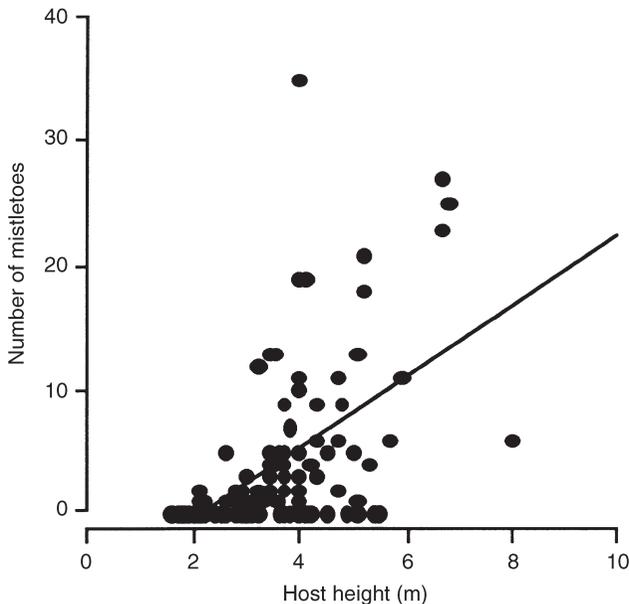

Fig. 7.5. The number of *P. californicum* individuals increased with host (*Prosopis velutina*) height ($r = 0.07$, $P < 0.0001$, $n = 115$), but very little variation was explained by the regression line ($r^2 = 0.269$). Although host height is a good predictor of infection frequency, it is a poor predictor of infection intensity.

are already parasitized hosts more likely to receive seeds and hence become reinfected; but (ii) older/taller trees are also more likely to receive seeds (Fig. 7.3). Age/size-specific differences in seed deposition on to hosts may exacerbate the age–occupancy relationship, but they are not required to generate it (Overton, 1996).

According to Overton's (1996) model, occupancy should increase with host age at an
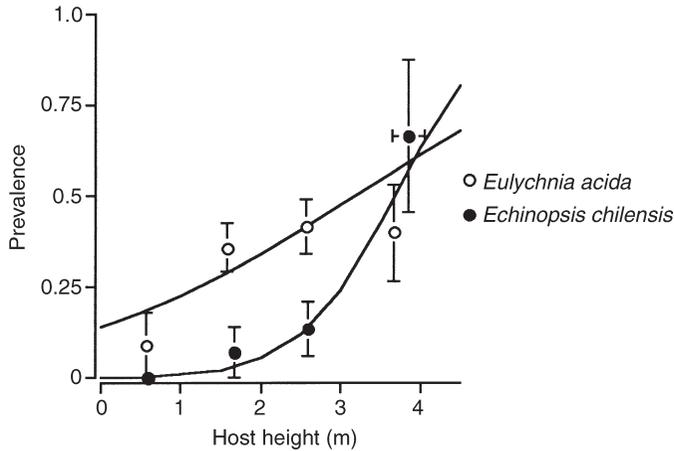
Fig. 7.6. At the Reserva Nacional Las Chinchillas, Chile, the frequency with which hosts were infected by *T. aphyllus* increased with height for both *Echinopsis chilensis* (open circles; logit $(\pi) = -1.779 + 0.5632$ (height), $P < 0.01$, $n = 122$) and *Eulychnia acida* hosts (closed circles, logit $(\pi) = -6.244 + 1.7039$ (height), $P < 0.00063$, $n = 52$). This positive relationship is in accord with that predicted by Overton's (1996) model of mistletoe metapopulations.
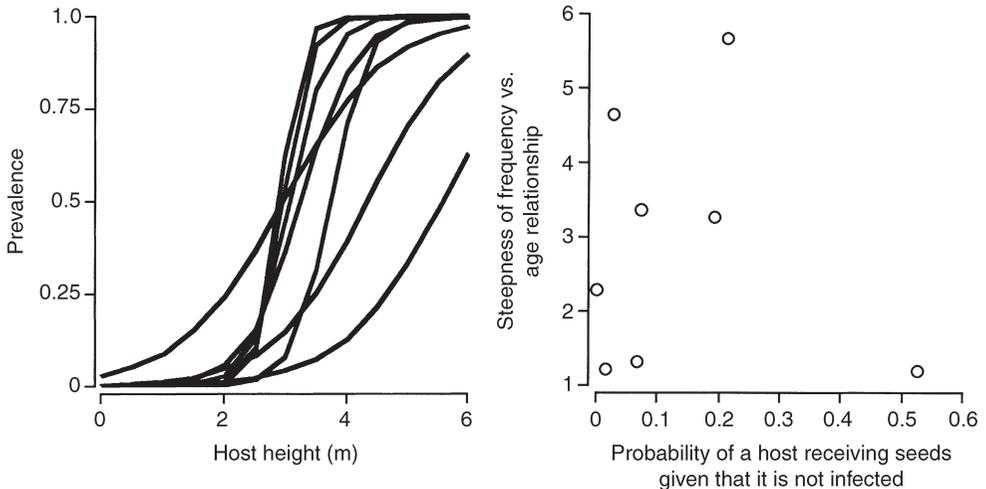
Fig. 7.7. The first prediction of Overton's (1996) model was met by *P. californicum* infecting *P. velutina* at ten sites in the Santa Rita Experimental Range (Arizona, USA). Frequency of infection increased with height at all sites ($P < 0.05$, after logistic regression). Curves in the left panel are relationships between frequency of infection and height at each site constructed using logistic regression. However, the second prediction of Overton's model (1996), namely that the steepness of the relationship between infection frequency and host age/height would increase with the probability of unparasitized trees receiving seeds (dispersal efficiency) was not met ($r = 0.015$, $P = 0.772$, right panel).

increasing rate at sites with higher among host/patch dispersal. For *P. californicum* infecting velvet mesquites (*Prosopis velutina*) at ten sites in Arizona, we found positive relationships between host size and occupancy (Fig. 7.7a), but no relationship between the steepness of these relationships (as measured by the slope of the log odds function (Ramsey and Schafer, 1997)) and seed dispersal into non-parasitized hosts (Fig. 7.7b).

Overton's model assumes that seed dispersal is random. However, most data suggest that dispersal is not random in mistletoes. A disproportionate number of seeds fall on to already infected hosts. Therefore, mistletoes exhibit conspecific attraction (Stamps, 1991). Ray *et al.* (1991) modified Levins's model to incorporate conspecific attraction by assuming that a fraction of all propagules is deposited in already occupied patches. Altering Overton's (1996) model to incorporate conspecific attraction makes mistletoe invasion more difficult, but leaves all other qualitative predictions unchanged. Occupancy still increases as a function of host age, and occupancy increases with host age at an increasing rate at sites with higher among-host/patch dispersal (J. Aukema and C. Martínez del Rio, unpublished data). Conspecific attraction does not explain the lack of a significant positive relationship between the steepness of the occupancy and age curve and dispersal efficiency.

Beyond Overton's model: structured and spatially explicit models

Although conspecific attraction does not change the predictions of Overton's model qualitatively, it is likely to have a significant effect on more realistic, and hence more complex, models. Exploration of the effects of host age and parasite status on infection intensity may be facilitated by construction of structured mistletoe metapopulation models. The goal of these models is to determine how different processes produce a distribution of local population sizes (Gyllenberg *et al.*, 1997, and references therein).

So far, all the models that we have described for mistletoe populations are spatially implicit. They ignore the spatial location of hosts/patches and hence assume that all subpopulations are equally connected (Hanski and Simberloff, 1997). Although we believe that a large number of questions can be explored with these models, other questions require explicit consideration of space. For example, we have argued that the positive, accelerating relationship between seed deposition into non-infected hosts and prevalence (Fig. 7.4) may lead to spatial aggregation of parasitism in a landscape and to a positive autocorrelation in prevalence across it (Martínez del Rio *et al.*, 1996). Testing the logical merit of this hypothesis requires a spatially explicit model. Overton (1996) and Lavorel *et al.* (1999) offer two elegant examples of spatially structured models for mistletoes. Mechanistic models of seed dispersion patterns can be constructed directly from the characteristics of mistletoes and hosts (density, size and distribution) and from the behaviour of the birds that disperse their seeds (Overton, 1996; Lavorell *et al.*, 1999). Spatial patterns of seed dispersal are the key to understanding plant population dynamics in a spatial context (Nathan and Muller-Landau, 2000). Mistletoes offer an unparalleled opportunity to document the consequences of seed dispersal by animals on the spatial dynamics of plant populations.

Future Directions

In this chapter we have emphasized the consequences of the interaction between seed-dispersers and mistletoes for the metapopulation ecology of these plant parasites. We have placed less emphasis on the fact that the patches occupied by mistletoes are exploited living organisms, and we have ignored the roles they play in their biotic communities. We believe that a more complete understanding of mistletoe population ecology must recognize the intricacies of their interactions with hosts and their roles in biotic communities.

Hosts and mistletoes

The biological characteristics of hosts and the physical environment they occupy can

determine their quality as patches for mistletoe occupancy. In particular, knowledge about the physiology of hosts/patches can allow one to predict which patches are sources that contribute mistletoe colonists to other patches, and which are sinks, where mistletoe subpopulations would go extinct in the absence of immigration (Pulliam, 1988; Hanski and Simberloff, 1997). Because at least some mistletoes can be accurately aged (Dawson *et al.*, 1990), the effect of the host's physiology on the demography of subpopulations can be studied. Mistletoes and their hosts offer a unique opportunity to integrate the physiological details of a plant–plant interaction with their demographic and even metapopulational consequences.

Mistletoes are not only influenced by the physiological status of their hosts, but have important impacts on it. Mistletoes probably degrade the quality of the patches that they occupy and increase their turnover by killing their hosts. Using Burdon's (1991) colourful classification, mistletoes can be castrators, killers or debilitators. Because some mistletoes can infect and damage economically important plants, there is some information on their effects on host growth, reproduction and survival (reviewed by Reid *et al.*, 1995). Little is known, however, about their effects on host populations (Silva and Martínez del Rio, 1996; Medel, 2000). Most models that explore mistletoe population and metapopulation dynamics assume that mistletoe infection has no effect on host survival and reproduction and that host populations are at equilibrium. Addressing how mistletoes affect host populations and how this interaction affects the temporal and spatial dynamics of mistletoes requires that we obtain better empirical data on the effects of mistletoes on hosts and that we incorporate these effects into models of mistletoe–host interactions.

Mistletoes as community members

Mistletoes are intriguing elements of biotic communities because they play the dual role of host scourges and bird mutualist benefactors (Martínez del Rio *et al.*, 1995; Fig. 7.1). In addition to the direct effects that mistletoes can have on the fecundity and viability of their hosts and mutualists, they may indirectly affect the host's competitors, herbivores, pollinators and seed-dispersers. Although community-level effects of plant pathogens have received significant attention (Dobson and Crawley, 1994, and references therein), we know little about the contribution of mistletoes to community composition and function.

Mistletoes can have significant effects on bird communities (Turner, 1991; Bennets *et al.*, 1996). Because many mistletoes are pollinated and dispersed by birds, their direct influence on birds is through the abundance of nectar and fruit. For example, *T. aphyllus* and *P. californicum* bloom and produce abundant fruit during the winter, when food resources are scarce. Areas heavily infected by these species are hot spots of activity for nectar- and fruit-eating animals (Martínez del Rio *et al.*, 1995; J. Aukema and C. Martínez del Rio, unpublished data). Mistletoes can also have significant indirect effects on bird communities. For example, prevalence of the dwarf mistletoe *Arceuthobium vaginatum* was positively correlated with bird abundance and species richness (Bennets *et al.*, 1996). Because the fruit of dwarf mistletoes are not extensively used by birds, Bennets *et al.* (1996) concluded that mistletoe infections increase bird abundances by enhancing insects that feed on and pollinate mistletoes or that take advantage of the weakened condition of tree hosts.

Dwarf mistletoes promote bird diversity because they create a mosaic of habitat structures within a forest stand through their effect on tree growth and mortality. They also increase nesting habitat. Several forest bird species use the dense clumps ('witches' brooms') that are formed by branches of the host tree for roosts and nest sites (Bennets, 1991, and references therein). Mistletoes are often considered insidious forest pests that reduce the economic value of timber stands (Wicker, 1984). As such, mistletoe removal is practised in managed forests with the objective of increasing timber production (Hawksworth and Wiens, 1995; Kelly *et al.*, 1997). In areas where management goals are not strictly focused on timber production, the value of

mistletoes for biodiversity may make their control unjustified, impractical or undesirable (Bennets *et al.*, 1996).

Conclusions: a Few Relatively Solid Patterns and Much Work Ahead

The main messages of this chapter can be summarized in the following sentence: 'Mistletoes are *parasitic plants* that exhibit a *metapopulation* structure, and whose seeds are dispersed by *mutualistic* avian seed-dispersers.' The elements emphasized in this sentence are responsible for several patterns that may characterize many, if not most, mistletoe populations. In this final section, we list these patterns and reiterate the mechanisms that probably shape them. Because the patterns listed here have been well documented in just a few mistletoe–host systems, and primarily in desert mistletoes, their generality is uncertain. These patterns should be viewed as testable hypotheses, rather than as general and firmly established results.

Mutualistic avian seed-dispersers seem to respond to the abundance of mistletoes at two scales: individual hosts and sites. The consequence of this response is that seed dispersal is not random among hosts and across landscapes. We hypothesize the following:

1. Seeds fall disproportionately more frequently on already parasitized than on non-parasitized hosts.
2. Seed rain increases with mistletoe prevalence across sites.

Hypotheses 1 and 2 yield two ancillary hypotheses:

1a. Disproportionate seed deposition on to already parasitized hosts leads to super-infection and to a highly aggregated distribution of parasite individuals among hosts.
2a. Disproportionate seed deposition at sites with higher prevalence leads to spatial auto-correlation in parasitism prevalence across a landscape.

Mistletoe populations can be perceived as metapopulations in which hosts are patches. Under fairly general conditions, a simple metapopulation model suggests the following:

3. The frequency of occupied hosts/patches increases with host age.

The logical and empirical validity of hypotheses 1a and 2a and the generality of hypothesis 3 must be tested by the complementary use of structured (1a and 3) and spatially explicit (2a and 3) metapopulation models and, of course, by field research.

Mistletoes provide theoreticians and empiricists with unique opportunities and peculiar challenges. Many of the processes that are difficult to investigate in other species are relatively straightforward to study in mistletoes because they are sessile and hence relatively easy to count. Because in some cases they can be aged (Dawson *et al.*, 1990), their demography can be studied. Their seeds are large and visible and are dispersed by birds whose movements are relatively easy to follow (e.g. relative to vectors such as mosquitoes and tsetse flies (Kitron, 1998)). Wheelwright and Orians (1982) have characterized the task of distinguishing safe germination sites as 'nearly impossible', but this task is relatively straightforward in mistletoes because seeds only establish on suitable hosts (Sargent, 1995). Mistletoes are ideal systems to integrate the ecology of seed dispersal into the larger framework of the temporal and spatial dynamics of plant metapopulations. Because the fine points of the interaction between hosts and mistletoes probably have significant consequences for the population biology of mistletoes, these plants provide a unique opportunity to determine the ecological penetrance of physiological processes. Finally, because data can be generated relatively rapidly in mistletoe systems, they provide an ideal arena for the testing and refinement of plant metapopulation models. We hope that the themes developed here will stimulate empiricists to explore other mistletoe systems and challenge theoreticians to model them.

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