

Distribution and dispersal of desert mistletoe is scale-dependent, hierarchically nested

Juliann Eve Aukema

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Spatial patterns are important to many ecological processes, and scale is a critical component of both patterns and processes. I examined the pattern and scale of the spatial distribution of infection of host plants by the desert mistletoe, *Phoradendron californicum*, in a landscape that spans several square kilometers. I also studied the relationship between mistletoe infection and seed dispersal. I found elevated seed rain in areas with a high prevalence of mistletoes and I found that a greater proportion of trees receive seeds than are infected, suggesting that mistletoes will be aggregated in space. Using nested analysis of variance and variograms, I found that mistletoe infections were distributed in hierarchical patches. Mistletoes were aggregated within trees and mistletoe prevalence was correlated at scales of <1500 m, and at scales >4000 m. Patterns at the largest scales were correlated with elevation: sites at higher elevations showed reduced mistletoe infection compared to those at lower elevations. I propose that at small scales, mistletoe distributions are primarily the result of aggregation of seed-dispersing birds, and that the elevational effect could reflect the recent colonization of higher elevations by the mistletoes' mesquite hosts or the limits of the mistletoes' physiological tolerance to freezing-induced cavitation.

J. E. Aukema (jeaukema@ncsu.edu), Dept of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, AZ 85721-0033, USA (present address: International Institute of Tropical Forestry, Jardín Botánico Sur, 1201 Calle Ceiba, Rio Piedres, PR 00926-1119 Puerto Rico).

A recognition of spatial patterns and processes is important to understanding the factors that shape distribution, dynamics, and interactions of organisms (Kareiva 1994). The description of spatial distribution patterns and of their variation in time depend on identifying the scales at which patterns occur (Turner 1989, Levin 1992). Because patches at different scales often form nested hierarchies (Kotliar and Wiens 1990), studies conducted at several scales provide better resolution of patterns and the interrelationships of scales (Wiens 1989). Disease systems display heterogeneity in exposure and transmission processes across multiple spatial scales, making a hierarchical approach very useful (Bolker 1995). Models of disease dynamics suggest that patterns of disease spread depend on

many factors including vector preference, prevalence of disease, and spatial structure of host and disease (Real et al. 1992, McElhany et al. 1995). Although hierarchical patchy distributions of organisms are predicted to be common, there are few examples in plant populations (O'Neill et al. 1986, Kotliar 1996, van Coller et al. 2000).

Mistletoes are plant parasites that are usually dispersed by birds, in often highly specialized relationships (Kuijt 1969, Godschalk 1983, Reid 1989). They are examples of both a seed dispersal mutualism and a vector transmitted disease in which an appreciation of their distribution and dispersal in space can facilitate our understanding of species interactions and transmission processes (Aukema 2003). *Phoradendron californicum* (Viscaceae) is a parasite of legume trees in the North

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American arid southwest. Its seeds are dispersed primarily by *Phainopepla nitens* (phainopeplas), although the berries are consumed by many other birds as well (Larson 1996). During their winter breeding season, coinciding with the fruiting of mistletoes, both male and female phainopeplas defend all-purpose nesting and feeding territories (Walsberg 1977). Phainopepla breeding failures have been linked to the absence of mistletoe berries due to drought (Chu 1999) and freezing (Larson 1991). Phainopeplas consume mistletoe berries and defecate the seeds onto host branches. The seeds germinate, penetrate the branch and tap into the host's xylem to absorb water, minerals and nutrients (Calder 1983). Phainopeplas respond to the distribution of mistletoes in their foraging, and by distributing mistletoe seeds differentially among hosts, they create mistletoe patches in the landscape (Herrera 1985, Aukema 2001). Phainopeplas both respond to, and contribute to shaping the spatial distribution of the mistletoes whose fruits they feed on and whose seeds they disperse. These birds are disease vectors responsible for the spread of the parasites. Examining patterns of seed deposition is a way of indirectly assessing the behavior of the disperser-vectors and the process generating mistletoe distributions.

The spatial variation in abundance of *P. californicum* depends on the distribution of its host trees, on the behavior of seed dispersers, and on its own physiological tolerance to abiotic factors. Previous studies have shown that mistletoes have a clumped distribution within trees (Overton 1994, Aukema and Martínez del Rio 2002a, b) and that parasitized trees are preferred by phainopeplas and receive more seeds than unparasitized trees (Aukema and Martínez del Rio 2002a, b). Overton (1994) found that mistletoes were not spatially autocorrelated at small scales, but I found spatial correlation of *P. californicum* infections to more than 145 m and of seed deposition to approximately 70 m (Aukema 2001). In a previous report, I documented a positive correlation between prevalence of mistletoes in a neighborhood and seed deposition into unparasitized trees (Aukema and Martínez del Rio 2002a). In addition, temporal correlation of seed deposition into pairs of infected trees suggests that phainopeplas respond to neighborhood characteristics (Aukema and Martínez del Rio 2002b). These results suggest that mistletoes will be spatially aggregated, but the scale at which they are aggregated in the landscape is unclear.

Spatial variation in nature can take place over a wide range of spatial scales (Oliver and Webster 1986). For example, at the scale of a few meters, *P. californicum* is aggregated within host trees (Overton 1994, Aukema and Martínez del Rio 2002a, b); and at the scale of many kilometers, host trees in one mountain range may be heavily infected whereas those in another range may be uninfected (unpubl.). Scales of landscape pattern vary

depending on the organisms and ecological processes being investigated (Kotliar and Wiens 1990). Because organisms differ in their response to the environment, and because their ecological neighborhoods differ in size, appropriate scaling is particularly important in studies of interactions between and among species (Wiens 1989).

In this study, I describe spatial variation in the distribution and seed dispersal of *Phoradendron californicum* (desert mistletoe) and the scales at which this variation occurs. My purposes are to describe mistletoe distributions and seed dispersal patterns at the scale of several kilometers, to generate hypotheses about the processes that lead to these patterns, and to identify the scales at which future studies should focus to better understand processes affecting mistletoe distribution and dispersal. I used a combination of techniques to examine the spatial distribution of desert mistletoes. First, I conducted an exploratory analysis to detect patterns that could suggest hypotheses about the spatial distribution of mistletoes and mistletoe seeds. Next, I used spatially explicit statistical methods to conduct a formal spatial analysis.

Methods

This study was conducted at the Santa Rita Experimental Range (SRER, 31°53'N, 110°54'W), south of Tucson, Arizona, USA. The Santa Rita Experimental Range consists of 53 159 acres of semidesert grassland scrub habitat (Burgess 1995) at the base of the Santa Rita Mountains. Over the last 100 yr, velvet mesquite *Prosopis velutina* has become dominant on as much as 30 000 acres that were previously dominated by grassland (Martin and Turner 1977). SRER ranges in elevation from <900 m in the northwestern corner to about 1300 m in the southeast. Average annual rainfall increases with elevation, ranging from 250 to nearly 500 mm (Martin and Turner 1977). The main hosts of *P. californicum* at SRER are *Prosopis velutina* (velvet mesquite) as well as *Acacia greggii* (cat-claw acacia) and *Cercidium microphyllum* (yellow palo verde), although the latter two hosts are much less abundant.

I used a balanced hierarchical sampling scheme in a nested survey (Oliver and Webster 1986) of mistletoe infection, seed deposition, and host attributes. Samples were gathered throughout SRER in a nested design with four levels. I selected four widely spaced primary sample areas. Within each of these areas, I sampled at 16 points, nested as follows. Within each primary area, I chose pairs of points 2000 m apart (level 1); from each of these points, I chose a second point 1000 m distant (level 2); from each of these points, I chose pairs 500 m apart (level 3) and from each of these, I chose points 250 m apart (level 4). I did this by obtaining a sample at an arbitrary point at least 50 m from a road. I then chose a

random direction with the second hand of a watch and a compass and walked 250 m, measured with a pedometer, for another sample. I then walked in a semi-random direction (constrained to 180° so that I would not return to my original point) 500 m for a sample. Next, I walked 250 m for a sample. Then I sampled at 1000 m, 250 m, 500 m and 250 m. I then returned to my starting point and drove 2 km to repeat the sampling scheme. All samples were taken in upland areas, if the random point took me to a point near an arroyo (dry stream), I selected the closest upland point for the sample. Likewise, roads were avoided to keep the vegetation as physiognomically homogeneous as possible (Norton and Smith 1999). At each sample point I recorded the location in UTM coordinates using a Garmin II Plus handheld GPS receiver (± 100 m).

Samples at each point consisted of all of the *P. velutina*, *C. microphyllum*, and *Acacia* spp. trees within a 20 m radius circle, determined with a laser range finder. For each tree, I recorded tree species, height, number of mistletoes, and number of deposited mistletoe seeds. I measured height with a measuring pole and counted mistletoes and seeds by thoroughly inspecting each of the trees. For each sample point, I calculated mistletoe infection prevalence and intensity, seed infection prevalence and intensity, mean host height, host tree density, and host species composition. Because >80% of the total trees observed and all but three of the parasitized trees were *P. velutina*, all analyses reported here are for *P. velutina* hosts only. I use the parasitological term prevalence to imply the fraction of hosts with a given attribute (in this case, infected with one or more mistletoes or receiving one or more seeds). Similarly, I use intensity to denote the mean number of parasites or seeds present per tree in my samples.

Analysis

I began with an exploratory analysis of patterns and correlations in the data. Then I used nested analysis of variance and geostatistics to examine spatial correlation of mistletoe infections and mistletoe seed deposition (Isaaks and Srivastava 1989, Webster and Oliver 1990, Rossi et al. 1992). The hierarchical sampling protocol was designed to facilitate both of these methods (Webster and Oliver 1990). Combining both methods provided corroboration of the results and extended the range of distances that I could examine.

I analyzed logit transformed infection prevalence and seed prevalence with nested analysis of variance in which distances were nested random effects (Model II, Marquardt 1949, PROC NESTED, Anon. 1989). From this analysis, the components of variance contributed by each distance can be estimated and relative contributions to the total variance can be calculated as a percentage

(Webster and Boag 1992). High variance components indicate levels with greater spatial dependence (Webster and Oliver 1990).

For the geostatistical analysis, I used all of the points from the hierarchical sampling survey plus an additional two points (selected in the same way as the original points, 2000 m apart) for a total of 66 points. I constructed variograms using all pairwise comparisons of points and fitted models using Geocis (Englund and Sparks 1991) and Variowin (Pannatier 1996) software packages. I compared model fits using indicative goodness of fit and cross-validation.

Results

Patterns of distribution

In the area of the study, elevation ranged from 880–1190 m. Mesquite host tree density ranged from 48 to 756 trees ha⁻¹, while average height ranged from 1.4 to 3.7 m. Mistletoe infection prevalence (proportion of trees infected) ranged from 0 to 75%, intensity (mean number of mistletoes per tree) ranged from 0 to 10.5 and mistletoes were aggregated within trees (variance: mean ratio = 18.8). Seed deposition prevalence ranged from 0 to 88% of trees receiving one or more seeds, mean seed deposition intensity ranged from 0 to 92 seeds per tree, and seed deposition was aggregated within trees (variance: mean ratio = 578.9).

Mistletoe infection prevalence and intensity were strongly positively correlated ($r^2 = 0.965$, $p < 0.0001$, $N = 66$). Thus, in the analyses that follow, I will only consider prevalence. Prevalence of seed rain was positively correlated with infection prevalence ($r^2 = 0.92$, $p < 0.0001$, $N = 66$), but the slope of a regression fitted through the origin (1.19 ± 0.04) was significantly >1 ($t = 4.42$, $p < 0.005$; Fig. 1A), indicating that at any level of prevalence, nearly 20% more trees receive seeds than are infected. By separating infected and uninfected trees, I found that, although seed rain was higher in infected trees than in uninfected trees, prevalence of seed rain increased with overall infection prevalence in the neighborhood for both uninfected (Spearman's $\rho = 0.59$, $p < 0.0001$) and infected (Spearman's $\rho = 0.40$, $p = 0.0077$) trees (Fig. 1B). The seed deposition patterns suggested that mistletoes will be aggregated in space and motivated the following spatial analysis.

Spatial patterns

Nested analysis of variance indicated spatial variation in the prevalence of both mistletoe infections and seed deposition (Table 1). For both infection and seed prevalences, nearly half of the variation occurred at the

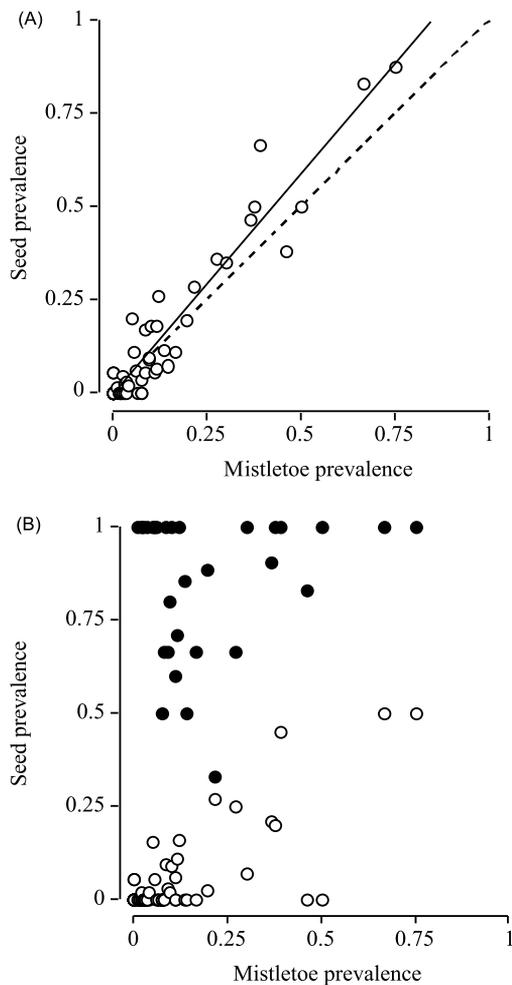


Fig. 1. Relationship between mistletoe infection prevalence and seed rain prevalence. (A) Prevalence of seed rain at sample points increased with mistletoe prevalence, but the slope was 19% greater than that of a one-to-one relationship (dashed line). In (B), each point from (A) has been separated into infected and uninfected trees. Seed rain increased with mistletoe prevalence for both infected (filled circles) and uninfected (open circles) trees, although infected trees had a higher probability of receiving seeds than uninfected trees (logistic regression: $\text{logit}(p(\text{seeds})) = -1.3 + 2.4(\text{infection})$, $\chi^2 = 685$, $p < 0.0001$, $N = 2834$).

largest distance of 2000 m, whereas the components of variance for the three lowest levels account for another 40% of the variation. There was considerable residual variation ($> 10\%$), representing variation occurring over distances of < 250 m, random variation, and variation due to measurement error. Because the largest distance level accounted for the majority of the variation, there is the possibility of additional spatial structure at larger scales.

Because the greatest distance between points was 12 635 m and because the number of pairwise comparisons was high, I could reasonably construct variograms to approximately 6300 m. The variogram for both infection prevalence and seed prevalence (Fig. 2) rose to a plateau between 1000 and 4000 m, then, starting at about 4000 m, the variogram again began to rise sharply, indicating that even at these large scales, points closer together (4000 m apart) were more similar than points

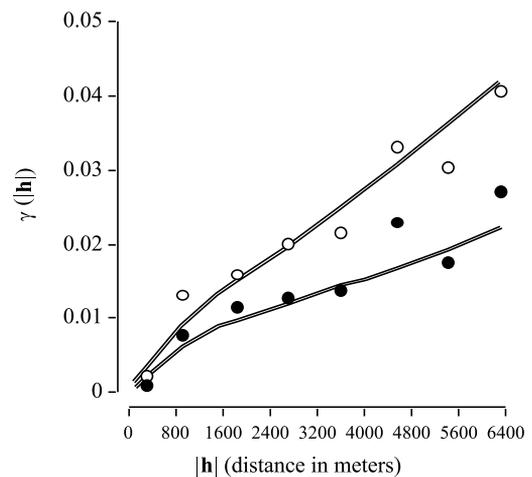


Fig. 2. Variogram of mistletoe infection prevalence (filled circles) and seed prevalence (open circles). Both variograms were best fit by a nested spherical (sill at approximately 1500 m) and power model [infection prevalence (solid line): $\gamma(h) = 0.0003 + 0.0057 \times \{1.5(h/1534) - 0.5(h/1534)^3\}$ if $h \leq 1534$; 1 otherwise] + $0.0000007h^{1.15}$; seed prevalence (dashed line): $\gamma(h) = 0.0004 + 0.0059 \times \{1.5(h/1503) - 0.5(h/1503)^3\}$ if $h \leq 1503$; 1 otherwise] + $0.00000152h^{1.15}$].

Table 1. Nested analysis of variance results. Logit transformed mistletoe prevalence and seed prevalence were dependent variables and sources of variation were distances, which were nested random effects. The greatest component of variation was at the 2000 m scale.

Source	DF	Variance component		Percent of total	
		mistletoes	seeds	mistletoes	seeds
2000 m	3	1.314727	1.618807	49.9574	45.7671
1000 m	4	0.251261	0.281546	9.5475	7.9599
500 m	8	0.423055	0.737210	16.0754	20.8425
250 m	16	0.372093	0.416814	14.1389	11.7842
20 m (error)	32	0.270558	0.482679	10.2808	13.6463
Total	63	2.631693	3.537056	100	100

farther apart (6000 m apart). The variograms were best fit by nested spherical and power models (Fig. 2).

I suspected that the large-scale (>4000 m) effects were due to elevation, because SRER is at the base of the Santa Rita Mountains and elevation increases in a southeasterly direction. In fact, infection prevalence was significantly negatively correlated with elevation (Spearman's $\rho = -0.73$, $p < 0.0001$; Fig. 3A) and with host tree density (Spearman's $\rho = -0.42$, $p = 0.0005$; Fig. 3B). Because host tree density increased linearly with elevation ($r^2 = 0.69$, $p < 0.0001$; Fig. 3C), it was difficult to disentangle the relative effect of each factor on infection prevalence. To separate the contributions of density and elevation, I examined the correlation between the residuals of the relationships between prevalence and elevation and that between density and elevation. However, I found no correlation between them ($r^2 = 0.02$; $p = 0.32$). Hence, it is impossible to separate these two effects.

I repeated the spatial analyses on the residuals of prevalence and elevation and the residuals of prevalence

and density. The results were qualitatively identical, so only the residuals of elevation are presented here. Using these residuals, the variograms of infection prevalence and seed prevalence reached a sill at approximately 1500 m (Fig. 4). Performing the analysis on the residuals effectively removed the effect of elevation. Therefore, this analysis reflects the spatial effect of prevalence independent of elevation.

Because the spatial analysis of mistletoe seed prevalence so closely matched that of mistletoe infection prevalence (Table 1, Figs 2, 4), I suspected that seed prevalence was reflecting infection prevalence. Therefore, I examined the residuals of seed prevalence vs infection prevalence and found a pure nugget variogram (Fig. 5). A pure nugget variogram is a horizontal line and indicates no spatial correlation for the values. In this case the best fit nugget model was equivalent to the overall covariance, indicating no signal in seed prevalence that is independent of that in infection prevalence.

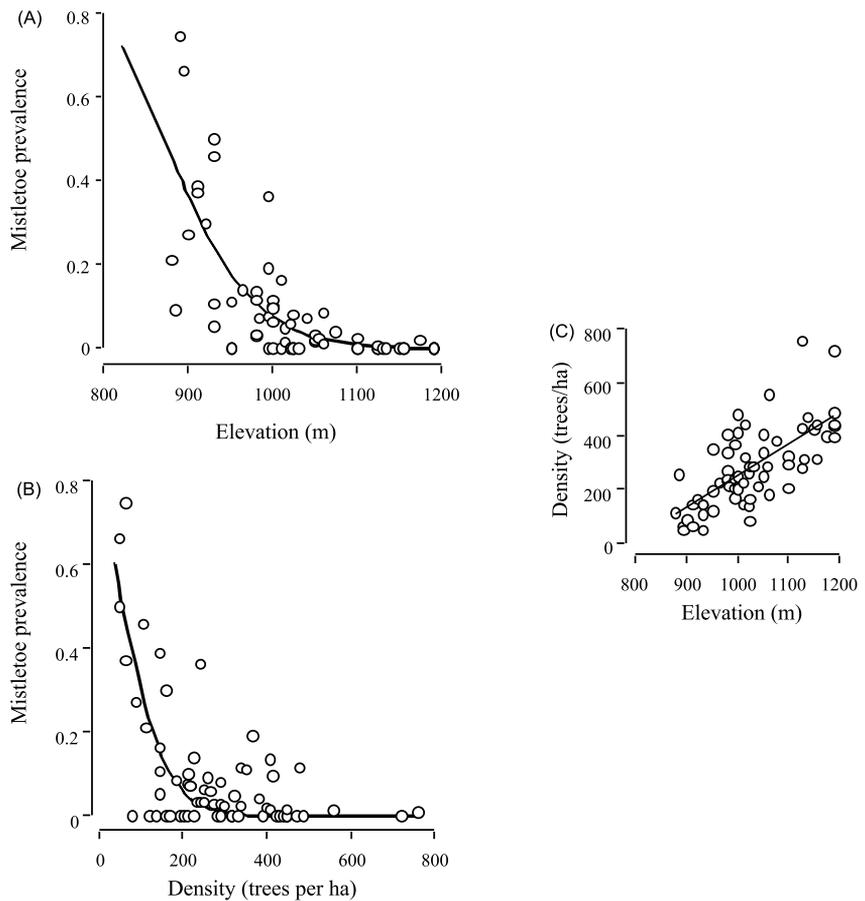


Fig. 3. Relationship between mistletoe prevalence, elevation and host tree density. Mistletoe prevalence decreased with (A) elevation (infection prevalence = $(\text{Exp}(-0.0194 \times (\text{elevation} - 880)))/(1.216 + (\text{Exp}(-0.0194 \times (\text{elevation} - 880))))$, $r^2 = 0.54$) and with (B) density (infection prevalence = $(\text{Exp}(-0.0194 \times (\text{density} - 47.8)))/(0.925 + (\text{Exp}(-0.0194 \times (\text{density} - 47.8))))$, $r^2 = 0.55$), whereas (C) density and elevation were positively correlated (density = $-945 + 1.19 \times \text{elevation}$, $r^2 = 0.49$).

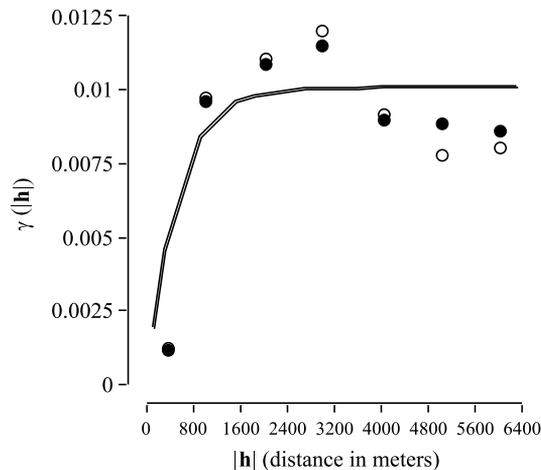


Fig. 4. Variogram of the residuals of mistletoe infection prevalence vs elevation (filled circles) and of seed prevalence vs elevation (open circles). For both infection and seed prevalence, semivariance reached a sill at approximately 1500 m ($\gamma(h) = 0.0002 + 0.00993(1 - \exp(-3h/1511))$; solid line).

Discussion

Hierarchy theory predicts that hierarchical patchiness is prevalent in nature and it has provided a valuable conceptual framework for descriptions of vegetation patterns and studies of heterogeneity, although hierarchical patchy distributions have rarely been demonstrated empirically in plant populations (Kotliar 1996, O'Neill et al. 1986, van Coller et al. 2000). Geostatistics are useful for identifying scales at which variables are spatially dependent; and variograms with nested structures in-

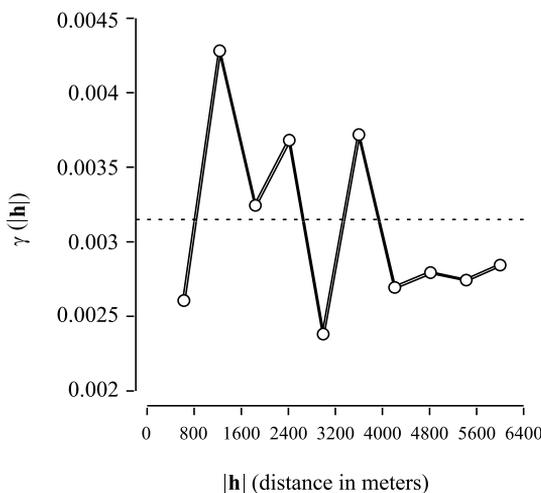


Fig. 5. Variogram of the residuals of mistletoe seed prevalence vs infection prevalence. The variogram was best fit by a pure nugget model equivalent to the overall covariance (dashed line). This indicates that there is no spatial correlation between these variables.

dicating multiple scales of variability (McBratney and Webster 1986). By explicitly addressing the scales at which mistletoe infections vary, I discovered that *P. californicum* distributions are patchy and their patchiness is nested hierarchically across scales.

Mistletoe infection prevalence was highly variable across the landscape, with infection rates ranging from zero to three-quarters of all trees infected within a 1257 m² circle. Patterns of seed deposition changed with infection prevalence. Nearly 20% more trees received seeds than were infected at each sample plot, and uninfected trees in areas of high mistletoe prevalence received more seeds than those in areas of low mistletoe prevalence. This suggested the existence of a positive feedback in which high mistletoe prevalence in an area leads to increased seed deposition in uninfected trees, more new infections, and higher mistletoe prevalences. The positive feedback is also seen at the level of individual trees and is due to phainopeplas preferentially using infected trees and depositing seeds in them and it leads to an aggregated distribution of mistletoes within host trees (Aukema 2001, 2003, Aukema and Martínez del Río 2002b). The neighborhood level positive feedback is probably also due to phainopepla activity: they are probably more abundant and spend more time in areas with high mistletoe prevalence than in areas with low prevalence. In addition, phainopeplas probably exhibit a larger density of breeding territories in more heavily infected areas, and non-breeding floaters are likely to visit these resource-rich areas more frequently. This process should lead to a patchy distribution of mistletoes in the landscape. Indeed, the spatial analysis indicated that the spatial correlation in mistletoe infections was distance dependent.

In addition to mistletoe aggregation within trees, I found spatial correlation in mistletoe prevalence at small scales of approximately 250 m–1500 m and at much larger scales >4000 m. The scale of spatial correlation can also be thought of as the size of a patch. The relatively small-scale patterns of 250–1500 m are greater than typical inter-nest distances (136 ± 68 m in the Colorado Desert; Chu 1999, but 50–100 m at SRER, Chu pers. comm.). I suspect that this is because phainopeplas aggregate when they establish territories, and such an aggregation of territorial birds could be responsible for small scale patterns of mistletoe distributions. In addition, whereas seed deposition was spatially correlated at the scale of individual territories, 70 m (Aukema 2001), adult mistletoe distributions were spatially correlated to greater distances. This may be because mistletoes are long-lived and year-to-year changes in individual phainopepla territory boundaries could dilute effects of territory size on the spatial distribution of mistletoes. However, at the larger scales examined in this study, seed prevalence did not show spatial correlation independent of infection prevalence,

but was simply a reflection of it (Fig. 5). This result suggests that increased spread of the parasite occurs at relatively small scales.

The relationship of infection prevalence with both elevation and tree density exhibited a threshold or envelope effect (Thomson et al. 1996). Above approximately 1100 m or 500 trees ha⁻¹, prevalence was very low, whereas at lower elevations and tree densities there was greater variance in prevalence. This suggests that a number of factors control mistletoe prevalence at low elevations or host tree densities, while the effects of elevation or tree density have a strong influence on prevalence at high elevations or tree densities.

The spatial analysis of the residuals indicated that elevation or tree density likely was responsible for the larger-scale patterns of infection prevalence. The relatively dense stands of *P. velutina* hosts at high elevations represent fairly recent colonizations. In 1904, mesquites were restricted to the lower elevations of the Santa Rita Experimental Range (Humphrey and Mehrhoff 1958) and they have spread to higher elevations over the last century (Martin and Turner 1977). Thus, it is possible that mistletoes simply have not spread to the mesquite trees at higher elevations yet. My results suggested that mistletoe spread occurs locally, so a larger scale spread of mistletoes could take many years. Also, phainopeplas may prefer less dense stands of mesquites, which could contribute to the slow spread of mistletoes at the higher elevations. Another possibility is that low mistletoe prevalence at high elevations could be due to an inability of the plant to colonize this area. The effect of elevation on infection prevalence may be due to the physiological tolerance of either the mistletoe or its hosts to freezing (Ehleringer and Marshall 1995). *Prosopis velutina* is resistant to drought-induced cavitation (Pockman and Sperry 2000), but is highly susceptible to freezing-induced embolism (Pockman and Sperry 1997).

Because patterns and processes at one scale are constrained by processes at smaller and larger scales (O'Neill et al. 1986, Wu and Louks 1995), recognizing the hierarchical nature of the distribution of mistletoes is important for understanding the processes generating the patterns. Phainopeplas show evidence of hierarchical habitat selection (Aukema 2001, Aukema and Martínez del Rio 2002b) in a positive feedback that creates hierarchical patches of mistletoe infections at two levels. The mutualistic interaction between seed dispersing birds and mistletoes defines many of the processes that mold the spatial infection patterns that we observe. Future studies of the spatial distribution of this plant parasite should focus on scales of approximately 1500 m and on scales of >4000 m. Studies of the spatial distribution of phainopeplas and their response to large-scale mistletoe manipulations, as well as the physiological tolerances of desert mistletoes should help to illuminate the processes and mechanisms under-

lying the patterns I have observed. Adding a temporal component would improve our understanding of the dynamics and interactions of nested patches and the processes of parasite spread. In addition, because mistletoes are important features of landscapes throughout the world and are critical resources in many habitats (Watson 2001, Aukema and Martínez del Rio 2002a, Aukema 2003), multiscale studies of the spatial distribution of mistletoes in a variety of habitats and explicit examination of the processes and mechanisms generating and maintaining observed patterns could give broader insight into the structure and functioning of ecosystems in which they are significant.

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