SPATIAL CLUMPING OF *TUPEIA ANTARCTICA* AT WAINUI

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Introduction

The distribution of fleshy-fruited plants is affected by the pattern of movement of their animal dispersers. Nowhere is this more clearly seen than in the native mistletoes (Loranthacae) because these species have an obligate relationship with their bird dispersers (Ladley & Kelly 1996). Because the mistletoes are hemiparasites, they must be moved from one suitable host tree to another, rather than germinating on the ground. Moreover, the seeds cannot germinate unless the fruit skin is removed, and the only way this happens in the field is by passing through an animal's gut. Therefore every mistletoe plant seen growing in the field must derive from a seed which was processed by a bird.

Some plants show marked clumping at various spatial scales. This is very evident in a large population of the endemic white-berried mistletoe *Tupeia antarctica* at Wainui, Banks Peninsula. At the southern end of the beach many tree lucerne (*Chamaecytisus palmensis*) along the roadside carry one or more *Tupeia*. Some hosts have much more mistletoe foliage than tree lucerne foliage, while others have no mistletoes at all. The distribution seemed markedly clumped, on a range of scales from single plants up to landscape scales.

This study was designed to measure the degree of clumping of *Tupeia* at Wainui, and determine to what extent it may represent a pattern imposed by the behaviour of the main dispersing birds (bellbirds, *Anthornis melanura*; New Zealand pigeons, *Hemiphaga novaeseelandiae*; and silvereyes, *Zosterops lateralis*).

Methods

A 750 m linear transect was marked out along the lower edge of the road in the area where *Tupeia* was common. Each tree lucerne closest to the road was sampled so that a series of adjacent trees was measured. For each potential host, measurements were made of its diameter at ground level, the number of discrete *Tupeia* plants, and the total volume of foliage of all *Tupeia* plants on that host. *Tupeia*, unlike other New Zealand Loranthaceae, does not spread with runners so retains a single point of attachment on the host tree, making it possible to distinguish individual plants. Where there were mistletoes higher in the tree lucernes, identifying individuals was harder and some smaller plants may have been lumped together. Hence the number of mistletoes per host is a minimum estimate, but the total volume of foliage should be relatively accurate. (N.B. Some quite detailed statistics follow. Contact the author if there is anything you can't comprehend. *Ed.*)

To analyse for spatial pattern at the single tree level, the number of hosts with various numbers of mistletoe per host was compared to a poisson distribution (see glossary for explanation of terms) calculated from the mean number of mistletoes per host (3.109). A chi-square test was used to compare the poisson distribution with the actual counts. Regressions of host basal area (in cm^2) versus number of mistletoes, and total volume of mistletoes (dm^3) were calculated, using log transformations for basal area and total volume to improve normality. The amount of mistletoe per unit size of host was also investigated (mistletoe number or volume per unit basal area) again with log transformations applied.

To test for spatial pattern at a higher level, spatial autocorrelation was used to see if trees were more likely to have mistletoes if their neighbours had them. The autocorrelation was run out to lag 15 (i.e. comparing trees to neighbours up to 15 trees away).

Results

All three potential dispersing birds (bellbirds, pigeons and silvereyes) were seen feeding in the area, though all seemed to be eating other material (tree lucerne nectar in the case of bellbirds, tree lucerne leaf buds for pigeons, and presumed insects for silvereyes) rather than *Tupeia* fruits which were present on the female plants at the time of sampling.

Altogether 110 tree lucerne hosts were recorded on the 750 m transect, and of these 42 hosted a total of 346 mistletoes. The number per host ranged from zero to 23. This distribution was significantly more clumped than expected from the poisson distribution, which assumes independence of mistletoe establishment (Table 1; chi-square = 950.2, $P < 0.001$). There were many more zeros, and many more hosts with large numbers of mistletoes, than expected.

Table 1. Frequency distribution of *Tupeia* mistletoes on tree lucerne hosts at Wainui.

Mistletoes per host	Observed number	Expected (from poisson)
0	68	4.91
1	7	15.27
2	1	23.73
3	2	24.60
4	4	19.19
5	3	11.89
6	3	6.16
7+	22	4.32

However the poisson assumes that all hosts have an equal chance of carrying mistletoes, whereas larger hosts may be more likely to catch a mistletoe seed. To see if the clumped distribution was partly a reflection of host size, the fraction of hosts with mistletoes was tabulated in various size ranges (Table 2). Large hosts were significantly more likely to carry mistletoes (chi-square = 33.52, df = 3, $P < 0.001$).

Table 2. Tree lucerne hosts carrying *Tupeia* mistletoes by host trunk diameter.

Host DBH (cm)	Number with *Tupeia*	Number without *Tupeia*
0-4.0	1	24
4.1-8.0	6	23
8.1-16.0	18	16
16.1-36	17	5

Therefore regressions were carried out to see if larger hosts had more mistletoes solely because they were larger, or if some positive feedback to do with bird behaviour meant they had disproportionately more. The amount of mistletoe (number and volume) per unit basal area of host was calculated, and regressed against host basal area. Mistletoe number per unit area was not related to host basal area ($F = 0.69$, $n = 110$, $P = 0.408$), showing that the number of mistletoes on larger hosts was about the same as expected given their larger size (which means more branches to carry mistletoes). However the total volume of mistletoe foliage per unit host basal area was significantly higher on large hosts ($F = 16.2$, $n = 110$, $P < 0.001$, $\log(y) = -0.117 + 0.194 (\log x)$, $R^2 = 0.130$; see Figure 1).

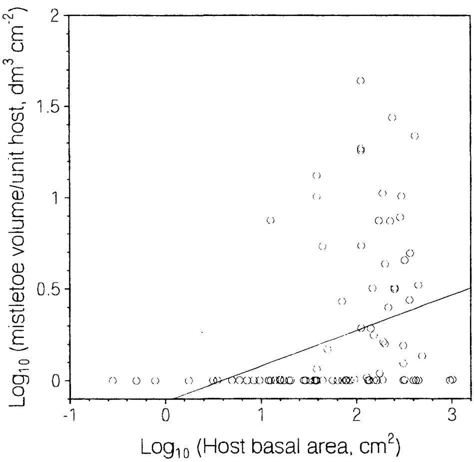

Figure 1. Amount of *Tupeia* mistletoes per unit area of host (dm^3/cm^2 basal area) versus host size (basal area in cm^2). Larger hosts carry significantly more mistletoe than expected.

The spatial autocorrelation was significant only at lag 1 ($R = 0.329$). All other autocorrelations out to lag 15 were non-significant.

Discussion

At the smallest scale (individual plants), *Tupeia* is highly clumped, with some hosts having many more mistletoes than expected and many others having none at all. The frequency distribution was highly contagious, and departed significantly from the poisson distribution. This would suggest that mistletoes are more likely to establish on a host tree if it already has one or more mistletoes in it.

However, some of this clumping was shown to be due to host size. Larger hosts are more likely to carry mistletoes, and carry greater volumes and numbers of them. This could be because they are larger and hence have more surface area to catch and support mistletoes, or it could be because they are older and have had longer for seeds to land on them.

The regression analysis corrected for host size by using mistletoe abundance per unit basal area of host (which is usually closely related to total host biomass). Mistletoe number was directly proportional to host basal area. There was no tendency for larger hosts to have more mistletoes than expected given their size. However, larger hosts did have disproportionately more mistletoe volume than smaller hosts. Because identifying separate mistletoes is more prone to error than recording the total volume of a patch of *Tupeia*, the volume analysis may be more reliable. This does therefore support the idea that there are positive feedback loops involved in establishment of mistletoes.

At a medium scale, the autocorrelation showed that there was a small degree of clumping between plants, so that hosts were more likely to have mistletoes if their immediate neighbours did. This was relatively minor, being only significant out to lag 1.

At the largest scale, there is considerable clumping. The *Tupeia* patch at Wainui is restricted to the southern end of the beach. There is abundant tree lucerne at the northern end which has no *Tupeia* present. Similarly the road from Wainui to Barrys Bay has much suitable host with no *Tupeia* present. However there is another large population of mixed *Tupeia* and *Ileostylus micranthus* on the opposite side of Akaroa harbour, part way up Long Bay road.

The processes producing these scales of clumping probably vary. At the within-plant scale, they could be due to bird preferences (a tendency to perch in larger trees, or to move to trees in favourable spots). Another possible factor could be host variability in susceptibility to mistletoe infection; if some hosts are more susceptible this could produce the kind of departure from poisson expectation seen at Wainui. Mistletoe attributes could also play a part, because once a female *Tupeia* becomes established in a host tree, birds may be attracted to it, and excrete seeds in the same tree giving rise to a clump of mistletoes in one host. At least one of these factors seems to be operating since larger hosts had disproportionately more mistletoe; several or all three could be operating in tandem.

At the between-plant scale, the relatively weak clumping probably is due to how readily birds can fly 10 or 20 m. Once a bird takes wing, it can fly to a tree 20 m away almost as easily and quickly as move to the next tree along (and if it has been disturbed, it may be more likely to go some distance away than to land in the adjacent tree). This means that there is not very marked clumping at the meso scale. I would predict that if the disperser was non-flying (e.g. possums) that the effect of adjacent trees would be much stronger.

Finally at the largest scale, there is strong patchiness with dense mistletoe populations at Wainui and Long Bay road but not between. There is a third patch within Akaroa, east of the old lighthouse. The abundant tree lucernes between seem to be perfectly suitable hosts so the most likely explanation for this is that chance and history have so far prevented establishment over these longer distances (of 1 -5 km). Birds less often fly this far within the time that seeds are contained in their guts (20-90 minutes depending on size of the bird). This hypothesis could be established experimentally by planting *Tupeia* at these other locations and verifying that it is able to grow there.

Acknowledgments

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References

Ladley, J.J., Kelly, D. 1996. Dispersal, germination and survival of New Zealand mistletoes (Loranthaceae): dependence on birds. *New Zealand Journal of Ecology*, 20, 69-79.

Glossary

Chi-square test: a statistical test which can compare the number of observed counts (e.g. trees with 0 mistletoes) with some expected number of occurrences (e.g. predicted trees with 0 mistletoes).

Contagious: tending to be associated together, for example cases of tuberculosis (where one person with the disease can infect people near them).

Frequency distribution: a tally of the number of observed number of cases in each category of another variable (e.g. number of trees with 0, 1, 2, etc mistletoes per host).

Lag: see spatial autocorrelation.

Log transformation: an operation where the data are converted to logarithms of the raw values before performing statistical tests. Usually done to make the data more closely approximate the underlying statistical assumptions of the tests (i.e. that frequencies are distributed normally around the mean).

Normality: a data set which is evenly and symmetrically arranged around the mean value in the same way as the normal distribution. Normality of data is assumed when performing certain statistical tests.

Poisson distribution: the distribution that gives the expected number of hosts with 0, 1, 2, 3, etc. mistletoes per host, assuming that each mistletoe is no more or less likely to occur on a host that already has a mistletoe on it (i.e. assuming all mistletoes are placed on hosts independently).

Positive feedback loops: a vicious circle, where a process reinforces itself and operates more and more strongly over time. For example, the rich get richer; or mistletoes may be more likely to establish in trees where mistletoes already present are producing fruits.

Regression: statistical test which calculates the straight line which best describes the effect of one variable (e.g. host size) on another (e.g. mistletoe volume per host).

Spatial autocorrelation: a way of testing for spatial clumping by comparing the value of a variable (e.g. mistletoes in a host tree) with the value of the same variable some fixed distance away (e.g. on adjacent trees, or the 2nd tree away, or the 3rd tree away, etc.). The fixed distance away in a particular comparison is called the lag.

Abbreviations

df	degrees of freedom for statistical analysis (usually number of samples minus one).
F	variance-ratio distribution, used to test for significance in regressions and analysis of variance.
Log_{10}	logarithm to the base 10.
n	number of observations, or samples.
P	probability at the given degree of significance, that there is no difference in the measured variables.
R	the correlation coefficient (+ 1.0 when variables are perfectly associated; -1.0 when they are inversely associated, i.e. one decreases when the other increases; and zero if there is no association).