Sampling Effects and Host Ranges in Australian Mistletoes

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ABSTRACT

The number of host species utilized by Australian mistletoe species increases with their geographic range sizes. Rather than resulting from deterministic processes, we demonstrate that this pattern results from wider-ranging species being sampled more efficiently, and we discuss how sampling effects might be addressed in future analyses of mistletoe biogeography.

Key words: biogeography; geographic range; macroecology; parasite.

Throughout the evolutionary history of land plants, parasitism has evolved multiple times. Rather than referring to a single taxonomic lineage, the term 'mistletoe' refers to a polyphyletic group of plants that have converged on a similar parasitic lifestyle (see Norton & Carpenter 1998, Press & Phoenix 2005). Most mistletoes belong either to the family Loranthaceae, which evolved in the southern hemisphere, or to the family Viscaceae, which evolved in the northern hemisphere (Shaw et al. 2004, Watson 2004). Both families have since dispersed out of their native hemispheres and many geographic regions, including the continent of Australia, house members of both families.

Unlike free-living plants, mistletoes need to establish on suitable hosts to survive and reproduce. Therefore, an understanding of their spatial distribution requires documentation of their occurrence among potential host species. Herbariums can be a valuable resource in this regard and herbarium collections of mistletoe species often contain specimens that were collected from different host species (Downey 1998, Norton & de Lange 1999). A list of the total number of host species utilized by a parasite species is referred to as its 'host range' (Lymbery 1989), and casual inspection of herbarium records suggests that most mistletoes have large host ranges. Previous work on mistletoe distributions has largely focused on host specificity in local spatial scales (e.g., Reid & Lange 1988, Yan 1990, Dean et al. 1994, García-Franco & Rico-Gray 1996, Arruda et al. 2006, Blick & Burns 2009). While these studies have greatly improved our understanding of mistletoe host use, biogeographic patterns in mistletoe host use remain poorly understood. For example, broad-scale patterns in mistletoe host ranges have never been investigated.

A simple prediction for the size of mistletoe host ranges is that they increase concomitantly with geographic range size. If mistletoes infect common host species in local populations (Norton et al. 1997, Norton & de Lange 1999), host ranges should increase with geographic turnover in host species composition. Positive host range–geographic range relationships have been documented in other host parasite systems, most notably ectoparasitic fleas and their rodent hosts (Krasnov et al. 2005, Shenbrot et al. 2007).

Host range sizes could also be linked to sampling effects. Klompen et al. (1996) showed that the host range of ticks increased with the accumulation of host-specific collection records. Similarly, Poulin (1992) showed that the host ranges of fish parasites were linearly related to the total number of host-specific records (see also Poulin 1997, 2007). Therefore, interspecific variation in recorded mistletoe host ranges could also be driven by sampling intensity.

Here, we investigate biogeographic patterns in host ranges of Australian mistletoes. Using previously published herbarium records, we test two hypotheses: (1) host ranges increase with geographic range sizes; or (2) host ranges increase with sampling effort (i.e., the total number of host-specific collection records). After distinguishing between the two hypotheses, we describe the methodological difficulties associated with investigating biogeographic patterns in mistletoe host use, and discuss analytical techniques that can be employed to overcome problems associated with sampling effects.

Data were gathered from the Flora of Australia and previously published lists of host use compiled from herbarium records. Mistletoe geographic range sizes were obtained from range maps that accompany species descriptions in the Flora of Australia (George 1984). Range maps for all mistletoe species in the families Loranthaceae and Viscaceae were converted into high-resolution digital images using a digital scanner (Palo Alto, CA, U.S.A.). These images were then imported into ImageJ (Abramoff et al. 2004), which is a freely available program that can be used to make measurements on digital images, and the total area (km²) of land occupied by each mistletoe species was calculated following Burns and Neufeld (2009). There is a very steep longitudinal gradient in rainfall extending from coastal to arid-zone Australia, as well as an extensive latitudinal gradient in temperature from north to south. Given that tree diversity and species composition vary across gradients in productivity (water-energy inputs, see Hughes et al. 1996, Storch et al. 2005), we also obtained the maximum latitudinal and longitudinal
range for each mistletoe species to test whether they might account for variation in mistletoe host ranges.

The number of host species utilized by each mistletoe species was obtained from Downey (1998), who conducted an extensive inventory of herbarium records for 88 Australian mistletoe species. For each mistletoe species, the number of recorded host species and the number of herbarium records listing host species information was obtained, which provides an estimate of sampling effort. Species with ranges restricted to offshore islands and those not listed in the flora due to subsequent name changes were omitted, leaving a total sample size of 80 mistletoe species in statistical analyses.

Multiple regression was used to evaluate the effect of geographic range size and sampling effort (i.e., the number of herbarium records listing host species information for each mistletoe species) on the mistletoe host ranges (i.e., the number of known host species). Additional analyses were conducted by replacing range size with latitudinal and longitudinal range as alternative independent variables. Multiple regression assumes that independent variables are not strongly related, which would complicate identifying their independent effects on the dependent variable. A variance inflation factor (VIF) was obtained for the two independent variables to check for excessive colinearity. VIF values > 5 indicate the presence of substantial colinearity that would compromise analyses. More generally, Pearson's correlation was used to evaluate the degree of independence between independent variables. All variables were transformed using natural logarithms.

The overall multiple regression model (host range vs. sampling effort and geographic range) accounted for a substantial amount of variation in mistletoe host ranges ($R^2 = 0.846$, $P < 0.001$), although only sampling effort contributed to the model ($t = 11.0$, $P < 0.001$). Geographic range size was unrelated to host use after controlling for sampling effort ($t = 0.320$, $P = 0.750$). Sampling effort and geographic range size were also correlated ($R = 0.681$, $P < 0.001$), indicating that widespread mistletoe species have more host-specific herbarium records. This relationship was not, however, strong enough to violate collinearity assumptions (VIF = 3.18). Qualitatively identical results were found when latitudinal and longitudinal ranges were substituted for geographic range sizes. Therefore, even though mistletoe species with bigger geographic ranges appear to infect greater numbers of host species, this results from a spurious relationship with sampling effort (Fig. 1).

The host range of Australian mistletoes increased with their geographic range size. This result seems to suggest that wider ranging mistletoe species attack a wider range of host species. Similar to many parasitic animals (Poulin 1992, 1997, 2007; Klompen et al. 1996), the number of host-specific sampling records was a strikingly accurate, alternative predictor of mistletoe host ranges. After controlling for sampling effort, the relationship between host ranges and geographic ranges disappeared. Therefore, the host ranges of Australian mistletoes are not associated with their geographic range sizes, nor were they associated with the longitudinal and latitudinal range.

Based on this result, one might be tempted to conclude that the host ranges of Australian mistletoes have not been quantified accurately enough to identify broad-scale spatial patterns in their distribution. Uncertainty in the accuracy of host range information is, however, unavoidable. Although one can demonstrate that a mistletoe species occupies a particular host species via direct observations, establishing that it never infects a particular host species is a difficult, if not impossible task. Very rarely will it be possible to thoroughly inspect every potentially inhabitable tree within the entire geographic range of a mistletoe species, although thoroughly documenting entire host ranges is not the only way of comparing host ranges among mistletoe species.

An alternative way to investigate mistletoe host ranges is to standardize sampling effort among mistletoe species. Instead of trying to fully document entire host ranges, accurate interspecific

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**FIGURE 1.** Relationships between the number of known host species (i.e., host range), geographic range size and the number of host-specific collection records for 80 Australian mistletoe species. Host range is correlated with both geographic range size and the number of collection records. After controlling for the number of collection records (by obtaining the standardized residuals of the host range × geographic range size relationship), the association between host range and geographic range disappears, indicating it is a spurious by-product of sampling effort.
comparisons can be made after standardizing the amount of effort used to sample each mistletoe species. Standardizing sampling effort among replicates is required for many ecological problems, most notably when investigating spatial and temporal patterns in species diversity, and there are a variety of analytical techniques to control for sampling effects. In this study, we standardized sampling effort statistically using standard regression techniques. An alternative method is rarefaction, which generates estimates of species richness on a per-individual basis, by tallying the total number of species in randomly selected subsamples of the total pool of individuals observed (analytical solutions to this procedures also exist, see Gotelli & Colwell 2001). In the case of mistletoes, rarefaction could be used to standardize sampling effort on a per-individual basis, or according to other estimates of sampling effort, such as the number of herbarium records, the number of infected trees or the number of infected host species in standard-area plots. Rarefaction, however, is just one of many ways to standardize sampling effort that can be used to investigate biogeographic patterns in mistletoe host use (Gotelli & Graves 1996, Magurran 2004, Poulin 2007).

The host ranges of Australian mistletoes are not associated with geographic range sizes or longitudinal and latitudinal range. Therefore, identifying the biogeographic determinants of mistletoe host ranges awaits future study. Host ranges are instead strongly associated with sampling effort. This problem is conceptually and analytically similar to sampling problems associated with traditional studies of species diversity, and does not necessarily indicate that broad-scale analyses of mistletoe host ranges are intractable. A variety of well-established techniques can be used to standardize sampling effects on estimates of mistletoe host use, allowing future work to answer a range of interesting and important questions regarding mistletoe biology. For instance, how important is the legacy of evolutionary history on host ranges? Do different lineages of mistletoes wherein parasitism evolved independently show similar host range diversity? Do phylogenetically related mistletoes preferentially attack related host species, or is host taxonomic distinctness unrelated to mistletoe phylogeny? Are mistletoe host ranges determined by latitudinal changes in productivity and host species diversity? Or are they instead determined by ecological drift? After controlling for sampling effects these and other interesting questions concerning mistletoe ecology and evolution can be investigated.

LITERATURE CITED


