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Associations and Assembly Rules of a Vascular Epiphyte Community in Monteverde, Costa Rica

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ABSTRACT

The existence of "assembly rules" and the importance of deterministic versus stochastic processes in ecological communities have been important subjects of debate in community ecology for over 20 years. To add to the debate, I tested for associations in Zone Three vascular epiphyte communities of *Ficus tuerckheimii* in Monteverde, Costa Rica. Community composition of the 102 recorded species varied widely between trees but tended to be more similar between trees of similar height and location. Also, a negative association was found between epiphytic Araceae and Orchidaceae ($P < 0.016$), which I suggest is due to abiotic factors rather than interaction. The results are inconclusive in deciding the importance of stochastic versus deterministic processes but lay the foundation for future research.

RESUMEN

La existencia de "reglas de asamblea y la importancia de procesos determinísticos y fortuitos en comunidades ecológicas han sido sujetos importantes de debate en ecología comunitaria por los 20 años pasados. Para contribuir al debate, examiné asociaciones en comunidades de epífitas de Zona Tres de *Ficus tuerckheimii* en Monteverde, Costa Rica. Composición comunitaria de los 102 especies recordados varió mucho entre árboles pero había más similar entre árboles de la misma altura y lugar. También una asociación negativa había encontrado entre Araceae y Orchidaceae ($P < 0.016$) que sugiero que es por razones abióticos y no es interacción. Los resultados son inconcluyentes para decidir la importancia de procesos determinísticos y fortuitos pero construyen una fundación para estudios del futuro.

INTRODUCTION

For the relatively young science of community ecology, one of the most interesting topics of debate remains a question of self-identity: what is an ecological community? Since its infancy, the definition of a community has been guided by the dichotomy between deterministic (equilibrium) and stochastic (non-equilibrium) models. Roughgarden (1989) stated that this "central question of community ecology was posed decades ago: Do the populations at a site consist of all those that happened to arrive there, or of only a special subset—those with properties allowing their coexistence?" Though not explicitly so named, a deterministic model of community structure was championed by Elton while Gleason favored stochastic processes (Roughgarden 1989).

In support of deterministic models of community structure Gilpin and Diamond (1984) defended Diamond's (1975) set of "assembly rules" that govern species composition of a community, emphasizing interspecific interactions such as competition. The debate over the validity of assembly rules has generated supportive laboratory and experimental field evidence as well as criticism of their consistency and predictive ability,

and it remains an issue "whether assembly rules can be inferred from nonexperimental data, specifically from combinations of coexisting species, usually on islands" (Gotelli and Graves 1996). Nonetheless, observational data may be useful in testing predicted patterns of association.

Literature is sparse on the subject with regard to existing plant communities, even though epiphyte communities in forest canopies may be good island analogies and would prove interesting subjects in tests of association and assembly rules. Wolf (1995) studied non-vascular epiphytes in the canopy of a Colombian Upper Montane Rain Forest and found associations for four groups of species at different positions from outer to inner canopy. She suggested that competitive interactions were at play because of decreased diversity from outer to inner canopy despite longer possible colonization time in the inner canopy. Catling and Lefkovitch (1989) studied vascular epiphytes in a Guatemalan Cloud Forest and found small, closely related species to be associated with small, young branches and larger, unrelated species associated with larger, older trunks. They conclude that both non-equilibrium and equilibrium processes, respectively, are at play (Catling and Lefkovitch 1989).

In a continuation of this type of study, I conducted an inventory of vascular epiphytes at multiple sites near Monteverde, Costa Rica. Hypothesizing that I would find none beyond what could be explained by chance; I tested for associations at the species and family levels, then analyzed possible causes of observed patterns in light of assembly rules, ultimately to better understand stochastic and deterministic models of community organization.

METHODS

Study Site:

The study site was in a cattle pasture located on the Campbell property in the community of Monteverde, west of the Monteverde Cloud Forest Reserve on the Pacific slope of the Cordillera de Tilarán, Costa Rica. Lying at 1540 m elevation and receiving approximately 2.5 m of rainfall per year, the site is classified as Lower Montane Wet Forest in the Holdridge life zone system (Holdridge 1967). The dry season is buffered by frequent misting from the Atlantic side of the Continental Divide, which maintains an abundant epiphyte load in 30-40 m primary forest canopies (Nadkarni and Wheelwright 2000).

Logistics:

I chose to study a group of *Ficus tuerckheimii* (Moraceae) for its abundance, ease of canopy access, favorable climbing and epiphyte-supporting architecture, and to minimize variation between tree species that could complicate tests of association among epiphytes. I accessed the canopy using single rope techniques as described by Nadkarni (1984), or by free climbing when possible. Only Zone Three was inventoried, which is defined here as the area within a 2.5 m radius circle centered upon the bole of the tree at its first major branching and generally spanned one third to one fifth the diameter of the crown (Fig. 1; Johansson 1975). Presence of all vascular epiphyte species located in Zone Three of each tree was noted and samples were taken for later identification. Unidentifiable species were classified as specifically as possible and given a unique morpho-species label. I also recorded diameter at breast height (DBH) and estimated height to the beginning of Zone Three (HZ3) for each tree.

Analysis:

Richness values of vascular epiphytes were calculated at family level (with Division Pteridophyta lumped as one), and species level for each and all trees combined. To test for associations between different taxa, I compiled the data into a presence-absence matrix for

all taxa on all trees and performed Q-mode and R-mode analyses (Gotelli and Graves 1996). In Q-mode analysis, compositional similarity of epiphyte communities was measured by calculating Jaccard similarity index (scale 0 to 1, dissimilar to similar, respectively; Gotelli and Graves 1996) within taxonomic levels for all tree pairs ($n = 28$ comparisons for eight trees). Jaccard index values were compared for a variety of dichotomous groupings of trees such as upper pasture location versus lower, near forest edge versus far, large crown versus small, shady versus sunny, and tall (accessed by ropes, HZ3 = 5.0 to 12.5 m) versus short (free climbed, HZ3 = 2.1 to 4.4 m). Jaccard indices for comparisons within the same group (e.g. tall-tall) were tested for variation from comparisons between groups (e.g. tall-short) by Mann-Whitney U test. Opposing within-group comparisons (e.g. tall-tall versus short-short) were also tested for variation by Mann-Whitney U test. Additionally, Jaccard indices for each tree pair were regressed versus the difference in height to Zone Three between trees. In R-mode analysis, the richness values of the five most species rich families plus Division Pteridophyta were compared together across all trees in a 6x8 contingency table and pairwise across all trees in 2x8 contingency tables, using Chi-square values to test significance of associations.

RESULTS

Two hundred forty one vascular epiphytes comprising 102 species from 20 angiosperm families and the Division Pteridophyta were documented in Zone Three of eight *F. tuerckheimii* individuals (Fig. 2). Distribution of species richness among the most species rich families (except Bromeliaceae, for which identification to species was mostly unsuccessful) closely followed previously described trends for the Monteverde area (Ingram et al. 1996) and for worldwide vascular epiphyte diversity (Fig. 3; Kress 1986).

Similarity between vascular epiphyte communities increased at higher taxonomic levels with Jaccard indices between trees ranging from 0.09 to 0.42 for species comparisons, and 0.29 to 0.75 for families, though the significance of variation between species and family levels was not tested. At the species level there was a marginal negative correlation between compositional similarity and the difference in height to Zone Three between tree pairs (Fig. 4; $R^2 = 0.131$, $P < 0.059$). Species composition was more different for tall-short tree comparisons than for tall-tall and short-short tree comparisons (Mann-Whitney U = 26; $P < 0.002$; $n = 28$), while similarity for tall-tall and short-short comparisons ($n = 12$) was not significantly different. Also, species composition compared between upper-lower pasture was more different than when compared for upper-upper and lower-lower pasture (Mann-Whitney U = 31.5; $P < 0.003$; $n = 28$), but similarity did not vary significantly between upper-upper and lower-lower comparisons ($n = 13$). Jaccard indices for species in other dichotomous groupings and all family groupings did not vary significantly.

No associations were found among the most common epiphyte families when richness values for all families were compared for all trees in a 6x8 contingency table (Chi-square = 34.93; $df = 35$; $P > 0.471$). However, pairwise comparisons of family richness across all trees in 2x8 contingency tables revealed a negative association between Araceae and Orchidaceae (Fig. 5; Chi-square = 17.27; $df = 7$; $P < 0.016$).

DISCUSSION

The results of this study show that community composition among vascular epiphytes varies widely by location, even for a single host tree species at small spatial scales. Jaccard indices at the family level show relatively high similarity, with approximately 30 to 75% of families shared between trees. However, familial similarity does not necessarily translate to species similarity.

The two most similar communities at the species level shared roughly 40% while the least similar had only 10% shared species, indicating very high turnover for species from host to host.

Despite high turnover, the variation in species composition shows some predictable patterns. When the height or location of compared trees is similar, the epiphyte communities found in them are also relatively similar and when pairs of trees differ more in height or location, they differ more in species composition. The relative importance of each of these factors to the similarity of species found in trees is confused due to the fact that the short trees were all in one location (lower pasture) and three of the four tall trees were in the other location (upper pasture).

Even without knowing whether height or location of trees is more important in shaping species composition, this information may help demonstrate the importance of deterministic versus stochastic processes. For deterministic models, height of the host tree may dictate how epiphyte community composition is affected by biotic factors such as incidence of accidental epiphytes, secondary hemiepiphytes, climbers and vines, as well as ease of access to the canopy-by mammals (all qualitatively observed). For stochastic models, variations in abiotic factors like microclimatic changes, including light, temperature, and exposure to mist and wind, may be caused by differing height or location. Parameters important to colonization such as tree "island" size and distance to epiphyte source populations (MacArthur and Wilson 1967) may also be affected by height and location.

The observed associations may be explained using the previously mentioned combined model proposed by Catling and Lefkovitch (1989). The model suggests that early on in a tree's life its epiphyte load consists mainly of colonizers that arrive as a result of stochastic processes, while deterministic processes become important as the tree ages, epiphytes have a chance to interact, and the community reaches equilibrium with larger dominant species. This could explain differences between tall and short tree communities because of differing age (if a relationship between tree height and age is assumed), and near and far communities because of differing colonizer availability. However, since height and location are related here these effects are indistinguishable.

The study also reveals a negative association at the family level between Araceae and Orchidaceae. The relationship is not the checkerboard pattern observed in some negative associations, but a pattern of inverse proportions of species richness by family at each location. Neither family was observed overtly dominating space or resources, but abundance data were not recorded, which would have been useful in assessing the ability of each family to compete with the other.

It is possible that the negative association is a result of interspecific interactions, as usually asserted by assembly rules. However, a more likely scenario is that abiotic factors, determine whether orchids or aroids are able to establish and survive at a given site. Interestingly, causes of epiphyte community composition often cited in the past, such as bark texture and canopy architecture, are ruled out in this case since the association was found within one tree species. I assert that shade and moisture tolerance along with

dispersal limitation cause the negative association. Superficially, the tree with the most species of aroids and no orchids in Zone Three had a small, shady, closed canopy, and high bryophyte cover, while the three trees in which orchids were most species rich had large, sunny, open canopies, and little bryophyte cover. This trend is consistent with Orchidaceae being high sun and drought resistant while Araceae is shade tolerant and moisture limited. Indeed, Orchidaceae originated from and still contains many "sun-loving" plants (Rundel and Gibson 1996), while Araceae contains many understory and shade-loving plants. Additionally, in the drier sites across rainfall regimes epiphytic aroids are absent while orchids represent one of few groups of epiphytes present (Gentry and Dodson 1987). The observed association is also consistent with the dispersal syndrome of each family in that bird dispersed aroid seeds may reach more crowded inner parts of the canopy and wind dispersed orchid seeds would reach more windy sites, as suspected by Delacroix (2001).

Overall, this study generated some interesting results that further the understanding of how communities are structured. Specifically, community composition of vascular epiphytes can be highly variable, but the variability can be somewhat predicted by similarity of host tree height or location. In addition, the two epiphytic families Araceae and Orchidaceae tend to be more species rich on different individuals of the same host tree species, probably due to interaction with abiotic factors rather than interaction. These results prevent definitive assertions as to the nature of the processes that shape community composition, whether stochastic or deterministic and assembled. However, this study does lay the foundation for a more conclusive one that would include quantitative observations of species abundance and variation in environmental conditions.

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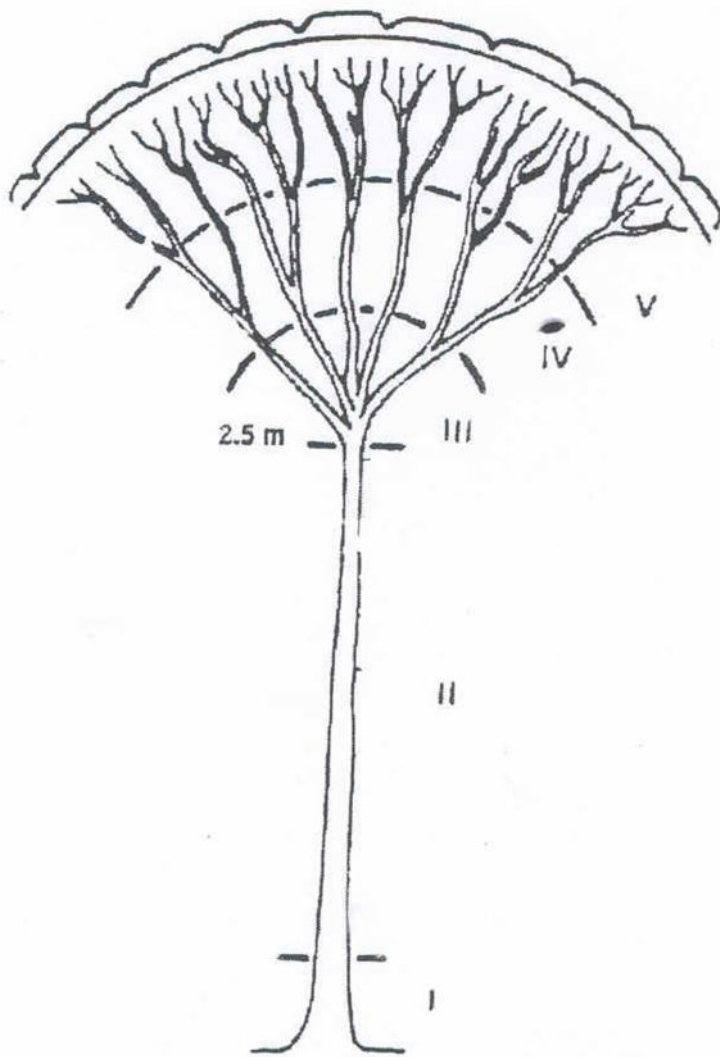


Figure 1. A tree divided into zones by number. Zone Three is defined here as the area within a 2.5m radius circle centered upon the hole at its first major branching. Modified from Johansson (1975).

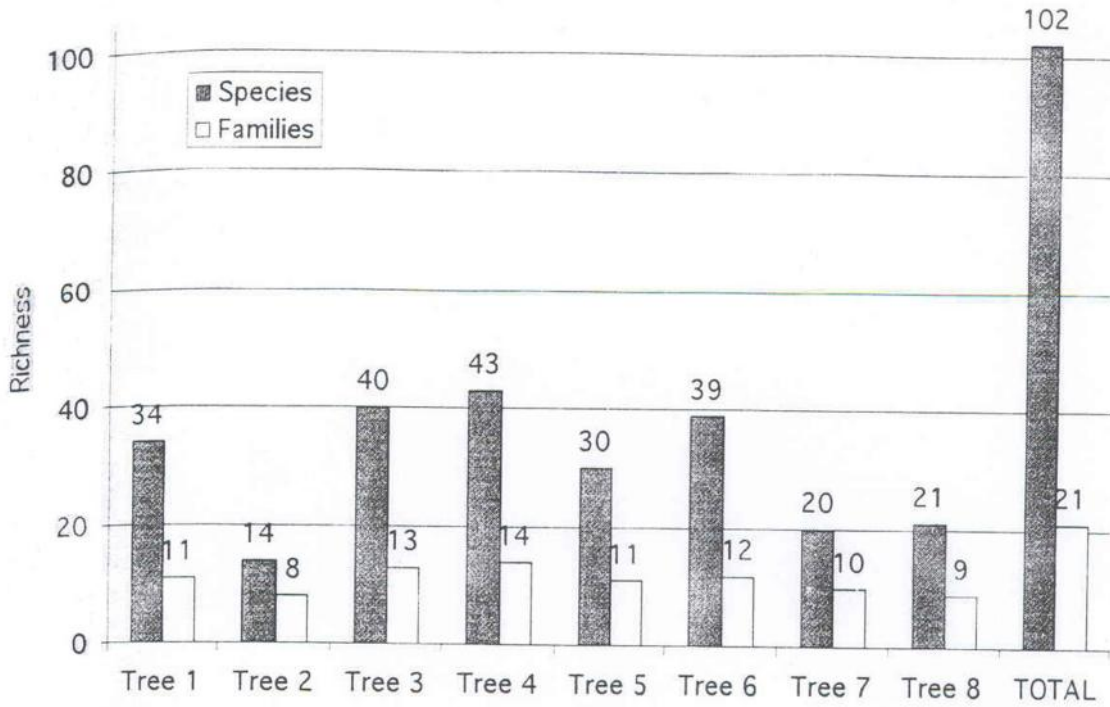


Figure 2. Species and family richness of vascular epiphytes by location.

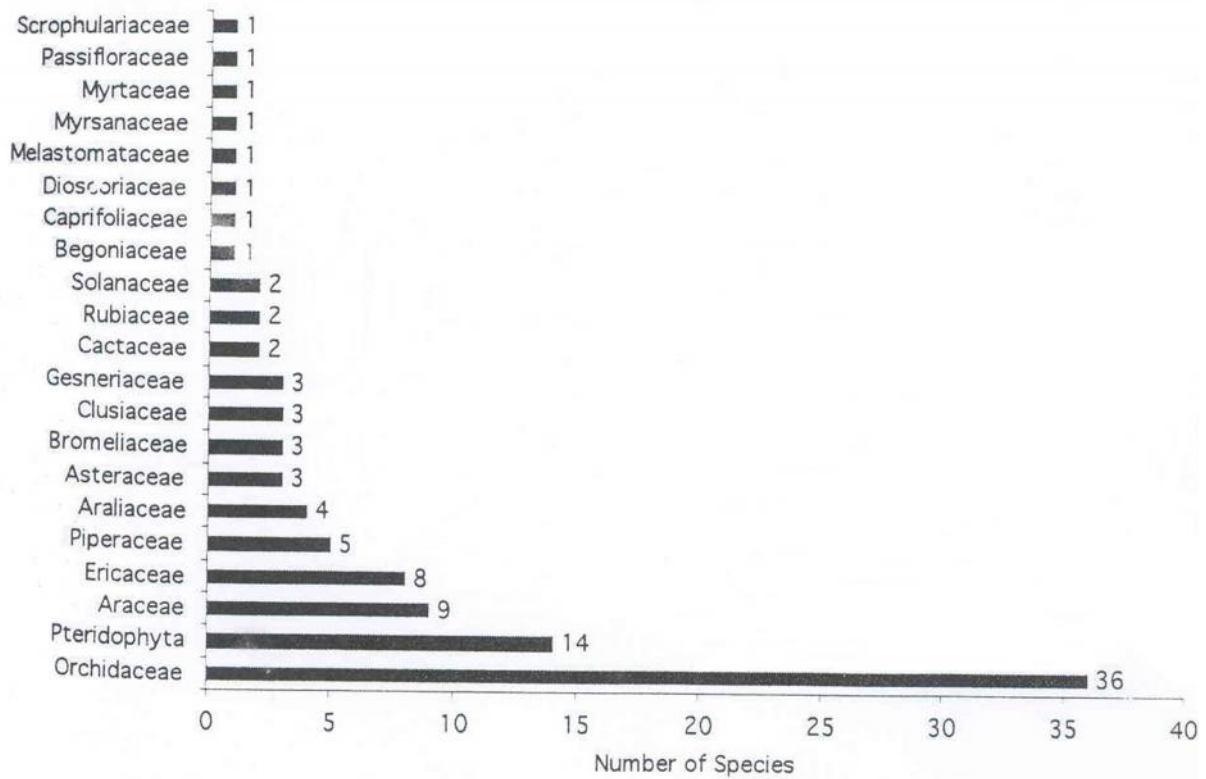


Figure 3. Species richness of vascular epiphytes by family.

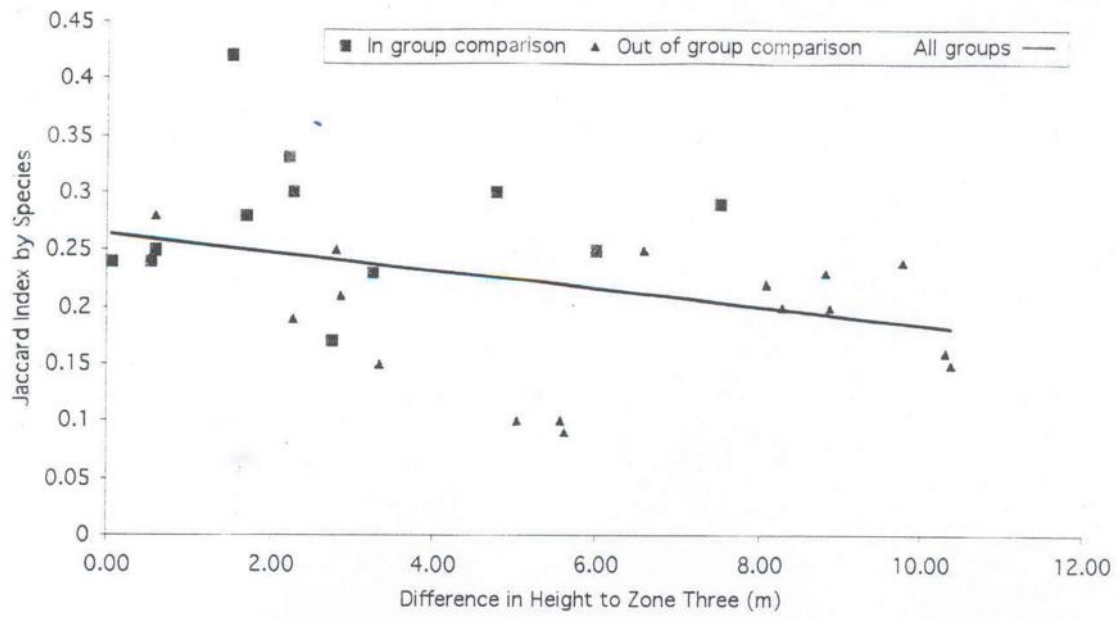


Figure 4. Jaccard index by species versus difference in height to Zone Three ($R^2 = 0.131$, $P < 0.059$). Points labeled “In” were grouped in the same height category (i.e. tall – tall or short-short comparison) and “Out” were from different categories (i.e. tall-short) used in the Mann-Whitney U test ($U = 26$; $P < 0.002$).

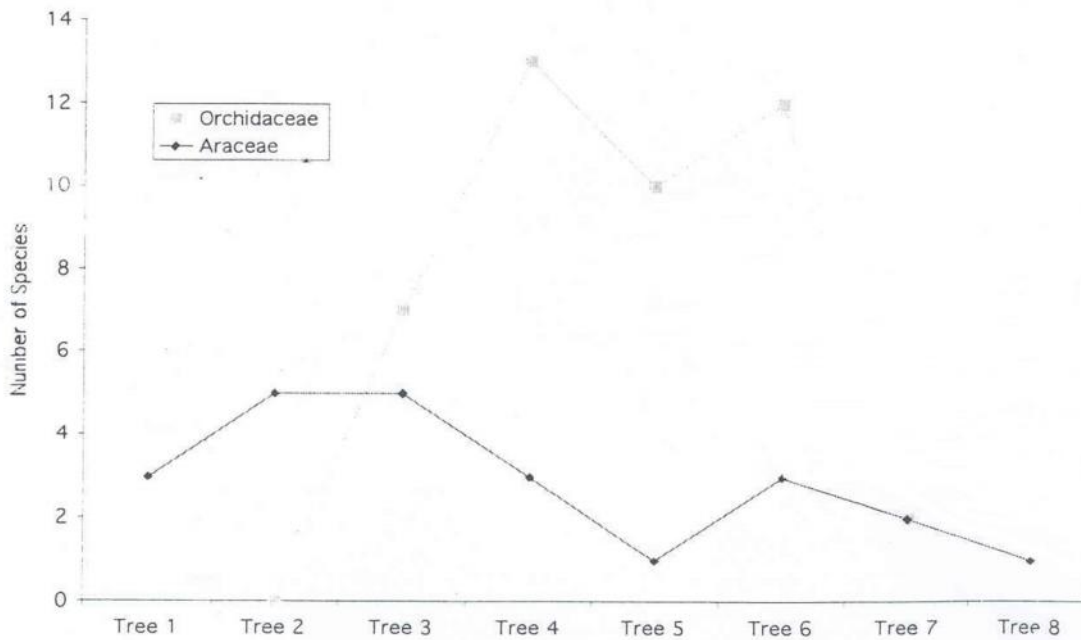


Figure 5. Comparison of species richness for the negatively associated families Orchidaceae and Araceae by tree. Canopy of tree 2 is superficially small and closed, while trees 4, 5, and 6 have large, open canopies.