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Insect biodiversity in *Ficus tuerckheimii* Moraceae: Which model fits best?

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ABSTRACT

Understanding how biodiversity is maintained is important both for ecology and conservation biology. Models of biodiversity fall into two broad categories: resource-based models and deterministic models. Local communities of insects on *Ficus tuerckheimii* (Moraceae) in the Bullpen, Monteverde, Costa Rica were sampled in order to determine whether the predictions from a resource-based model or Hubbell's stochastic model better fit real data. Results could not conclusively support or disprove either model. Positive trends existed between diversity and resources as well as richness and resources; however these were not statistically significant. Species richness and evenness were not correlated, which does not support Hubbell's model. However, when comparing individual trees to the metacommunity, the incidence of common species in local communities was more similar to their incidence in the metacommunity than the incidence of rare species in local communities was to their incidence in the metacommunity. This is consistent with Hubbell's model.

RESUMEN

Entender el mantenimiento de biodiversidad es importante para ecología y conservación. Los modelos de biodiversidad caen en dos categorías anchas: los modelos recurso-basal y modelos estocástico. Las comunidades locales de insectos en el *Ficus tuerckheimii* (Moraceae) en el Bullpen, Monteverde, Costa Rica, fueron muestreados para determinar si las predicciones de un modelo recurso-basal o el modelo estocástico de Hubbell serian mejores para predecir los datos reales. Los resultados no podrían apoyar o refutar en forma concluyente cualquiera de los dos modelos. Las tendencias positivas existieron entre H' o riqueza de especies y recursos, sin embargo estos no fueron estadísticamente significativos. La riqueza y la uniformidad de especies no fueron correlacionados, lo cual no sostiene el modelo de Hubbell. Sin embargo, la incidencia de las especies más comunes en comunidades locales comparado con la incidencia en la metacomunidad fue más semejante que la incidencia de las especies raras en comunidades locales comparado con la incidencia en la metacomunidad, lo cual es consistente con el modelo de Hubbell.

INTRODUCTION

Understanding how biodiversity is maintained is important both for ecology and conservation biology. Biodiversity is thought to serve as "ecosystem insurance" by building functional redundancy into a community (Stone 1995). Models of biodiversity are also used when planning and managing biological preserves. In order to make informed conservation decisions, it is important to know how biodiversity arises and is maintained.

Models of biodiversity fall into two broad categories: resource-based models and stochastic models. Resource-based models propose that community composition is determined by the interaction of species with specific biotic factors (e.g. competition with other species) and abiotic factors (e.g. availability of food or nutrients). These models propose that niche

partitioning occurs such that each species uses a particular segment of the resource base. They predict that the size of resource base and species richness should be positively correlated.

On the other end of the spectrum are the stochastic models. These theories of biodiversity propose that community composition is assembled randomly. Rather than resources being important for biodiversity, factors such as dispersal, birth rate, and death rate, combined with community drift, determine biodiversity in a community. Though the number of species may be predictable, the specific species present constantly change.

The most well-known stochastic model of biodiversity is MacArthur and Wilson's (1967) island biogeography theory. However Hubbell's (2001) unified neutral theory of biodiversity and biogeography is an improved model that provides more testable predictions about community structure than island biogeography theory. Hubbell's (2001) model states that there are *local communities* composed of "trophically similar species that actually or potentially compete in a local area for the same or similar resources." Local communities that are connected by dispersal compose a regional *metacommunity*.

Hubbell's model assumes that all individuals within a metacommunity are competitively equivalent. Each individual that dies will be replaced by the offspring of another individual in the local community, by an immigrant, or on a longer time scale, by a newly evolved species (Hubbell 1995, 2001). Because each species is competitively equivalent, the likelihood of the new individual being species A, for example, is directly proportional to the relative abundance of that species in the metacommunity. This process of death and replacement Hubbell calls a "zero-sum game," because the total number of individuals in the community does not change. In the absence of immigration and speciation, a zero-sum game results in community drift toward a monodominant community. Therefore, on an ecological timescale, immigration between local communities is important for maintaining local biodiversity.

This model of community dynamics results in several testable predictions. First, as species richness increases, each individual species will decrease in relative abundance, and species evenness should increase. Therefore, within a trophic group, species richness and evenness should be positively correlated. Second, because the likelihood of replacement by a species is dependent on the relative abundance of that species in the metacommunity, local communities of common species should be more similar to the metacommunity than local communities of rare species. A third prediction of the Hubbell model states that species richness increases with an increase in the number individuals present (J). Because a larger area can support a larger number of individuals, species richness is positively correlated with the physical size of the local community.

In order to determine whether the predictions from a resource-based model or Hubbell's model better fit real data, I sampled local communities of insects in *Ficus tuerckheimii* (Moraceae). I chose *F. tuerckheimii* because there is a known population with relatively isolated crowns in the Bullpen, Monteverde, Costa Rica. These served as definable local communities. I analyzed the insect metacommunity, paying special attention to herbivorous insects because several estimates of resource availability could be made for that trophic group. I aimed to answer (i) are species diversity or species richness positively correlated with tree height, crown volume, or epiphyte diversity, (ii) within each local community, do species diversity correlate with species evenness, and (iii) is the incidence of common species in local communities more similar to the incidence in the metacommunity than incidence of rare species in local communities is to incidence in the metacommunity?

METHODS

Study site

Two pastures owned by the Campbell family near the Monteverde Cloud Forest Preserve, Monteverde, Costa Rica, (elevation = 1500 m) were the sites of this study. The two pastures were separated by a wind break (width < 100 m). The eastern pasture (the Bullpen) was entirely surrounded by lower montane wet forest (Haber et al. 2000), while the western pasture only had lower montane wet forest on its eastern edge. These pastures were cleared approximately 50 years ago, however many large trees were left standing (Dr. Karen Masters, personal communication). There is much contact among the crowns of trees in the Bullpen.

Tree selection and measurement

Six *F. tuerckheimii* trees were included in this study. Only two trees had a completely isolated crown. The other four trees had neighboring trees growing under or next to the crown. These neighboring trees made contact with study trees, but only at the branch tips. Approximately 20% or less of the crown circumference was in contact with another tree in this manner, and this was all localized to one area of the study tree. One tree contained a living host. None of the trees appeared to be fruiting.

Tree measurement

The bottom and top of the crown were estimated by comparing the height of the tree to a one meter standard. Diameter of the crown was measured twice on perpendicular axes. Volume was calculated using the following formula:

$$V = \pi(b^2x - \frac{b^2}{3a^2}x^3) \quad \text{Eq. (1)}$$

where a and x are the average of the two crown diameters divided by two, and b is the distance between the bottom and the top of the crown.

Estimation of epiphyte species richness

Epiphyte species richness in the region of the tree where the first branches arise referred to here as Zone three was used as an estimate of tree canopy plant species richness. Most of this data was collected by Ivan Welander, who generously allowed me to use his data for this study. Zone three was defined as having its center at the point on the trunk from where the first branch extended. The boundary of Zone three was the semi-circle extending 2.5 m up and out from the center. A sample from each plant in Zone three was taken and assigned a morphospecies designation. Epiphyte species richness was calculated as the total number of morphospecies in a particular tree.

Sampling of insects

Sampling took place between the hours of 9 A.M. and 2 P.M. Each tree was sampled on two or three different days to minimize possible effects of variation in weather conditions. Single rope climbing techniques, as described in Nadkarni (1984), were used to gain access to the canopy. Insects were mainly collected using an aspirator on the leaf surfaces. Sixty clusters of leaves were sampled. Clusters were sampled according to what was accessible, and when possible, all areas from Zone 3 to the branch tips were sampled. The number of samples was approximately evenly distributed among all branches sampled. After aspiration, the contents were put in ethanol to both kill the insects and for storage. The three mm diameter of the mouth of the aspirator restricted the size of the insects that could be caught by this method.

Because of the size limitation imposed on the insects by the aspirator, aspiration was supplemented by a modified beating umbrella technique (Borror et al. 1989). This was done by beating the underside of a branch ten times with an insect net (diameter = 38 cm). Beatings were performed five times per tree. Contents from each beating were put in a jar containing acetone in cotton. Due to the larger size of the insects caught by this method, the specimens were then pinned.

Identification of insects

Each insect specimen was assigned to a morphospecies designation. In addition, insects were keyed to order, superfamily, family, or subfamily, in order to identify the trophic group to which the specimen belonged (Borror et al. 1989; Hanson P.E. and Gauld, I.D. 1995). Parasitoids that were known to have an association with the fig system, either as a parasitoid of the fig or the pollinating fig wasp (Agaonidae) were classified as interlopers, separate from other parasitoids (West et al. 1996).

Data analysis

Linear regressions were performed using Statview (Altera Software Inc. 1994) to test whether insect diversity was dependent on tree height, crown volume, or epiphyte diversity in zone three. Mean values of for the Shannon-Weiner diversity index (H') were calculated for trees five trees using the software Estimates S 6b1 (Colwell 1997). H' for the sixth tree was calculated by hand due to the low number of individuals present ($n = 3$). Species richness and evenness were also calculated (Magurran 1988). A Spearman rank correlation was performed to test whether species richness correlated with species evenness.

Common and rare species were defined based on their relative abundance in the metacommunity, the metacommunity being the composition and relative abundance of all species across all six trees sampled. Species having a relative abundance of 1% or higher were defined as common. This resulted in 28% of species being designated common and 72% being designated rare. Estimate S 6b1 was also used to determine Jaccard similarity values (Magurran 1988.) between the insect communities of pairs of trees and also between individual trees and the metacommunity. A Wilcoxon sign-rank test was performed to determine if Jaccard values for the common community were statistically different than those for the rare community.

RESULTS

Species diversity and richness

The metacommunity of insects caught on all trees sampled was composed of insects from a variety of trophic groups (Fig. 1). Thirty-nine percent of insects found were herbivorous, while an additional 32% were parasitoids and 10% were known fig interlopers, a special class of wasp thought to either parasitize the fig tree or the fig wasps (West et al. 1996). More specific data on morphospecies found is in Appendix 1. Sampling effort did not result in species area curves asymptoting for any of the six trees (Fig. 2).

Analysis of diversity and richness focused on the entire metacommunity as well as the class of herbivorous insects. Unless stated otherwise, analyses gave the same result for both groups. Species richness and species diversity were calculated for all six local communities and the metacommunities (Table 1). Tree B had high diversity ($H' = 2.67$) and richness ($S = 37$) (values for all trophic groups combined). The relatively high diversity of Tree F ($H' = 1.09$) was due to high evenness ($E = .992$) despite low richness ($S = 3$) (values for all trophic groups combined).

Resource dependency

Linear regressions were performed to determine if H' was dependent on various estimates of resource availability. These estimates were tree height, crown volume, and epiphyte species richness in zone three. While regressions showed slight trends (e.g. Fig. 4), none were statistically significant (Table 2).

Stochastic model data

Hubbell's model predicts that species richness and evenness should be positively correlated. However, for both the herbivores and all trophic groups combined, there was no correlation between species richness and evenness (Fig 3). A Wilcoxon sign-rank test was used to determine whether Jaccard values comparing local communities to the metacommunity were statistically different between common species and rare species. There was a significant difference between common and rare species for both the herbivores alone and all trophic group combined ($p = 0.0277$ for both).

DISCUSSION

Despite the increasing need to better understand how biodiversity arises and is maintained, the factors that are essential for maintaining regional and local biodiversity remain elusive. This study set out to determine whether plant resources were important for insect biodiversity or whether stochastic processes could account for the patterns of biodiversity observed.

Implications for a resource based model

H' and species richness both showed positive trends with respect to various estimates of resource availability (i.e. tree height, canopy volume, and Zone three epiphyte richness; Fig.

4). No regressions were significant, however with a small sample size ($n = 6$), this result is not surprising. Therefore, these positive trends may be indicative of a relationship between resource availability and insect diversity. Panzer (1998) found that after removing the effects of area, plant species richness remained positively correlated to insect richness for insects in temperate prairie reserves. This finding lends support for a resource-based model of biodiversity, but whether this pattern holds true for tropical forest ecosystems has not been determined. Thus, results are inconclusive as to whether resource availability is important for maintaining biodiversity.

Implications for Hubbell's stochastic model

If the positive trends between H' and tree height or canopy volume reflect a real relationship, this could also be support for Hubbell's neutral model. This is because Hubbell's model states that a community with larger area can support more individuals, i.e. have a higher J . A higher J is correlated with higher species richness. Other support for the Hubbell model can be found in the patterns of commonness and rareness in the metacommunity. As predicted, common species in this metacommunity (defined as having a relative abundance of 1% or higher) were found to have a higher similarity of occurrence to the metacommunity than the rare species.

The lack of a positive correlation between species richness and evenness does not support the Hubbell model. However, because this could be an effect of small sample size, this result does not provide evidence against the model. The evenness for local communities was approximately the same for most trees, despite their differences in species richness (Fig. 3). Thus, although some results provide limited support for the Hubbell model, it cannot be concluded that stochastic processes are dominant in determining community biodiversity.

Concluding remarks

Based on these results, it is impossible to determine whether resources or stochastic processes play a more important role in maintaining biodiversity. A lack of conclusive results is most likely due to two factors: the small number local communities sampled and non-exhaustive sampling effort.

An interesting observation from this study concerns the trophic composition of the metacommunity. Thirty-nine percent of insects found were herbivorous, while an additional 32% were parasitoids and 10% were known fig interlopers, a special class of wasp thought to either parasitize the fig tree or the fig wasps (West et al. 1996). This result is surprising because species richness usually declines as one moves up trophic levels, but in this community, parasitoid richness is approximately equal to that of the primary consumers, i.e. the herbivores. This could be due to different wasps exploiting different resources, (e.g. flowers, leaves, fig wasps, and other insect hosts), therefore actually being composed of two trophic groups. That this trend is an effect of sampling, however, cannot be ruled out. Janzen (1973) found no difference in species richness of bugs and beetles when sampling during both day and night in secondary growth forest in the Osa Peninsula of Costa Rica. However, other studies have shown that the majority of herbivores feed between dusk and midnight, which may mean that a large number of herbivores in the Monteverde insect community were missed (Janzen 1983).

Future studies could expand on this study by increasing the number of local communities sampled and increasing sampling effort per tree. As part of increasing sampling

effort, it would be worthwhile to sample at different times of day. It might also be worthwhile to investigate other measures of resource availability while keeping the parameter of size constant. For example, it would be interesting to study a group of trees with approximately the same size canopy and determine if they varied in the water content of the leaves (which may differ depending on wind exposure), nutrient content of the leaves (which may differ depending on soils), or number of new leaves. If insect species richness correlated with one of these estimates of resource availability while the physical size of the community was held constant, this would be differentiate effects of resources from effects of J. Clearly there is much more work to be done to determine what factors are important for the maintenance of biodiversity in natural systems before this knowledge can be applied to conservation efforts.

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LITERATURE CITED

- Altura Software Inc. 1994. Statview ®.
- Borror, D.J., Triplehorn, C.A., Johnson, N.F. 1989. *An introduction to the study of insects*. Saunders College Publishing, Philadelphia, PA, USA.
- Colwell, R. K. 1997. Estimate S 6bl: Statistical estimation of species richness and shared species from samples. Version 5. User's Guide and application published at: <http://viceroy.eeb.uconn.edu/estimates>.
- Haber, W.A., Zuchowski, W., and Bello, E. 2000. *An introduction to cloud forest trees: Monteverde, Costa Rica, 2nd edition*. Mountain Gem Publications, Monteverde de Puntarenas, Costa Rica.
- Hanson P.E. and Gauld, I.D. 1995. *The Hymenoptera of Costa Rica*. Oxford University Press, New York, NY, USA.
- Hubbell, S.P. 1995. Towards a theory of biodiversity and biogeography on continuous landscapes. Pages 171-199 in G.R. Carmichael, G.E. Folk, and J.L. Schnoor, editors. *Preparing for Global Change: A Midwestern Perspective*. SPB Academic Publishing, Amsterdam, the Netherlands.
- Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ, USA.
- Janzen, D.H. 1973. Sweep samples of tropical foliage insects: Effects of seasons, vegetation Types, elevation, time of day, and insularity. *Ecology* **54**: 687-708.
- Janzen, D.H. 1983. Food webs: Who eats what, why, how, and with what effects in a tropical forest? Pages 167-182 in F.B. Golley editor. *Tropical rainforest ecosystems: Structure and function. Ecosystems of the world 14A*. Elsevier Scientific Publishing Co., Amsterdam, the Netherlands.
- MacArthur, R.H. and Wilson, E.O. 1967. *The theory of island biogeography*. Princeton

University Press, Princeton, NJ, USA.

Magurran, A.E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, NJ, USA.

Nadkarni, N.M. 1984. Epiphyte biomass and nutrient capital of a neotropical elfin forest. *Biotropica* **16**: 249-256.

Stone, R. 1995. Taking a new look at life through a functional lens. *Science*. **269**: 316-317.

West, S.A., Herre, E.A., Windsor, D.M., and Green, P.R.S. 1996. The ecology and evolution of the new world non-pollinating fig wasp communities. *J. Biogeog.* **23**: 447-458.

Tables

Table 1. Shannon-Weiner diversity index (H') and species richness (S) for all trees (A-F) and the metacommunity (MC). Values are reported for all trophic groups combined (subscript T) and the herbivores alone (subscript H').

Tree	H'_T	H'_H	S_T	S_H
A	1.81	1.17	23	10
B	2.67	1.63	37	14
C	1.47	0.61	13	4
D	2.15	1.7	15	10
E	0.45	0.37	5	4
F	1.09	0.69	3	2
MC	1.69	1.86	72	28

Table 2. R^2 values and p-values (in parentheses) for linear regressions of diversity (H') and species richness (S) with respect to three estimates of resource availability. P- values were calculated for both herbivores only and all trophic groups combined. No regressions were statistically significant, although herbivore species richness appears to be weakly linked to tree height ($p = 0.0729$).

	Resource	H'		S	
All trophic groups	Height	0.427	(0.160)	0.220	(0.195)
	Volume	0.128	(0.490)	0.001	(0.962)
	Epiphyte Richness	0.223	(0.344)	0.144	(0.457)
Herbivores	Height	0.526	(0.103)	0.492	(0.073)
	Volume	0.388	(0.186)	0.124	(0.493)
	Epiphyte Richness	0.093	(0.557)	0.091	(0.561)

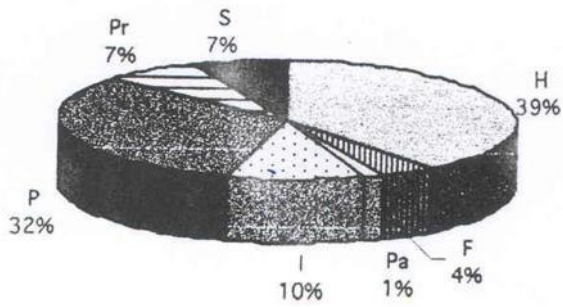


Figure 1. Composition of insect community by trophic group. Insects were categorized as being parasitoids (P), predators (Pr), scavengers (S), herbivores (H), fungivores (F), parasites (Pa), and fig interlopers (I).

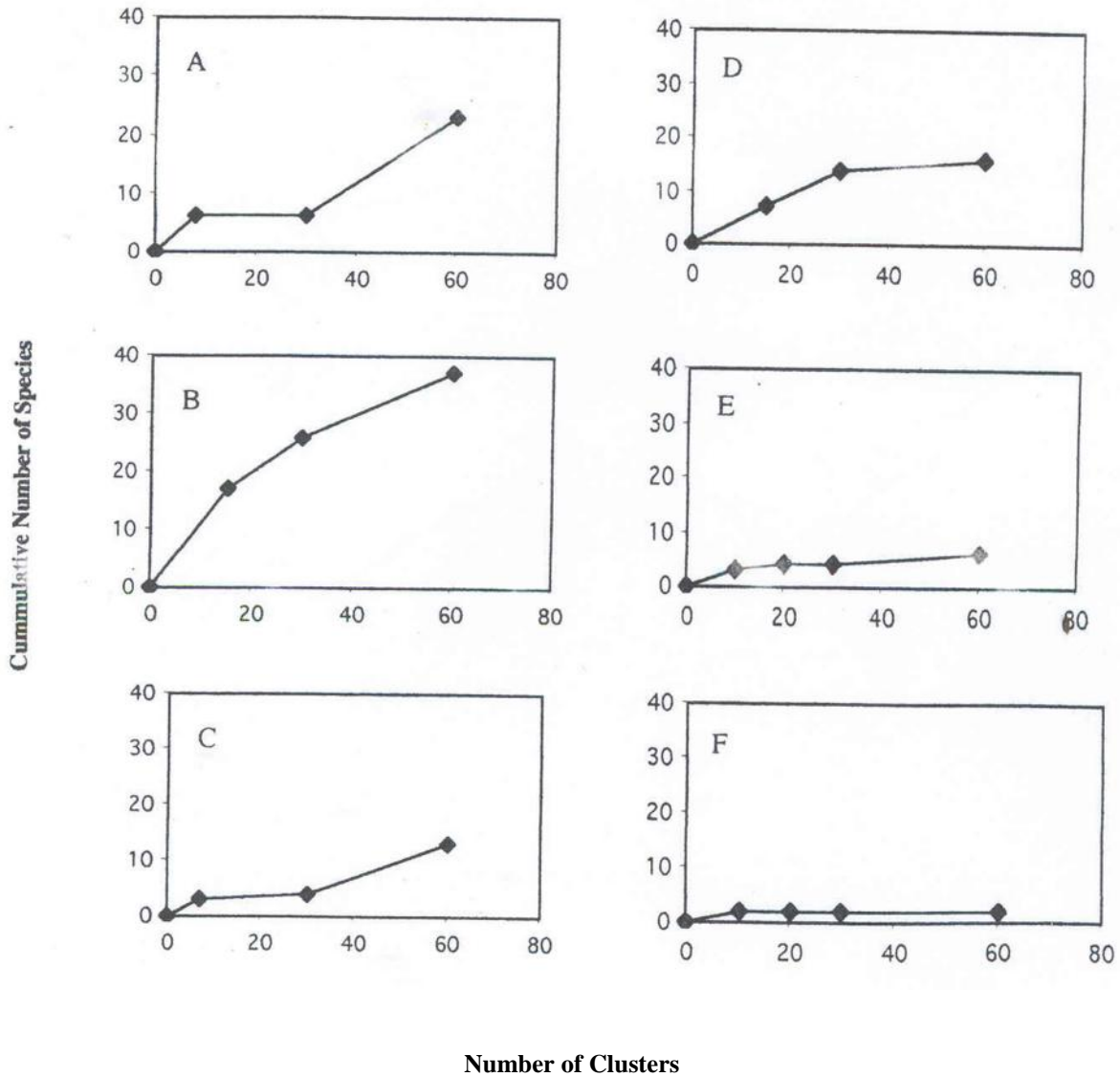


Figure 2. The cumulative number of species found in all trophic groups versus the number of clumps sampled for each tree (A-F) as an estimate of sampling effort.

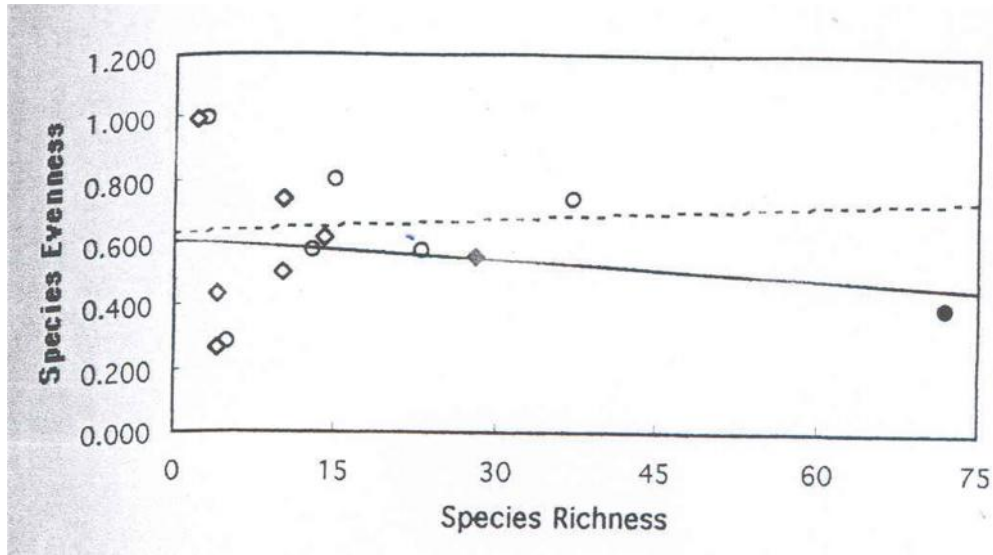


Figure 3. Evenness and richness are not correlated for the six local communities and the metacommunity. The herbivore community is shown in diamonds while all trophic groups together are shown in circles. Local communities are shown as open points and metacommunities are shown as filled points. Trendlines are shown (herbivores solid, all trophic groups together dashed), however these are not statistically significant (Spearman rank correlation, $r_s = 0.0286$ and $r_s = -0.0286$ respectively, degrees of freedom = 5).

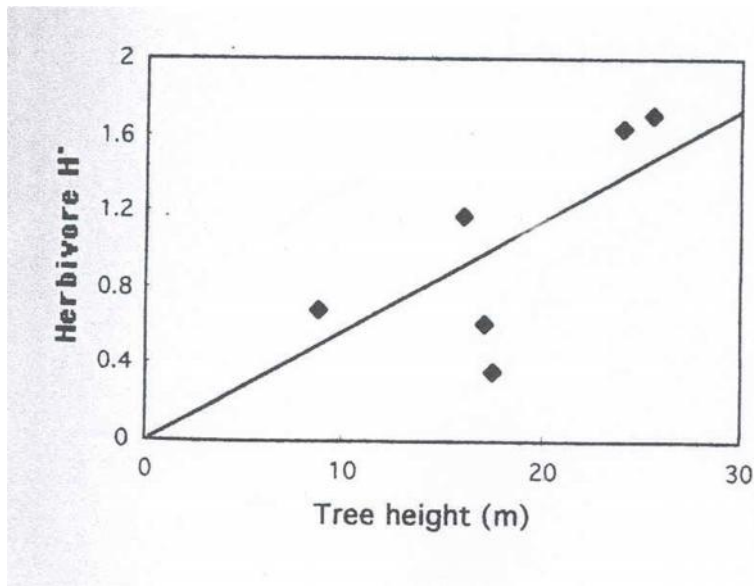


Figure 4. An example of a trend between diversity and size: H' versus height for the herbivore community. $P = 0.0729$.

Appendix 1.

Taxon, trophic classification, and relative abundance for all morphospecies found. Insects were categorized as being parasitoids (P), predators (Pr), scavengers (S), herbivores (H), fungivores (F), parasites (Pa), and fig interlopers (I).

Taxon	Trophic group	Relative Abundance	Taxon	Trophic group	Relative Abundance
Blatodea	S	0.0027	Hymenoptera		
			Chalcidoidea		
Coleoptera	H	0.0055	Agaonidae	H	0.0989
Coleoptera	H	0.0027	Agaonidae	H	0.0137
Coleoptera	H	0.0027	Agaonidae	H	0.011
Coleoptera	H	0.0027	Agaonidae	H	0.0082
Coleoptera	H	0.0027	Bethylidae	p	0.0082
Coleoptera	H	0.0027	Bethylidae	p	0.0027
Coleoptera	H	0.0027	Bethylidae	p	0.0027
Coleoptera	H	0.0027	Encyrtidae	p	0.0027
Coleoptera	Pr	0.0027	Eupolmidae	p	0.0027
			Eulophidae		
Coleoptera			Entedoninae	p	0.0027
Curculionidae	H	0.3846	Entedoninae	p	0.0027
Curculionidae	H	0.0027	Entedoninae	p	0.0027
Curculionidae	H	0.0027	Tetrastichinae	p	0.0027
Curculionidae	H	0.0027	Tetrastichinae	p	0.0027
Curculionidae	H	0.0027	Mymaridae	p	0.0055
			Pteramalidae	p	0.0055
Diptera			Pteramalidae	p	0.0027
Rhagionidae	Pr	0.0027	Pteramalidae	p	0.0027
Rhagionidae	Pr	0.0027	Pteramalidae	p	0.0027
Sciaridae	F	0.0055	Pteramalidae	p	0.0027
Sciaridae	F	0.0027	Signiphoridae	p	0.0027
Sciaridae	F	0.0027	Tanaostigmatidae	H	0.0027
Simulidae	B	0.0027	Tetrastichinae	P	0.0027
Hemiptera	H	0.0467	Ichneumoidea	P	0.0027
Hemiptera	H	0.0412			
Hemiptera	H	0.0055	Proctotrupoidea	P	0.0027
Hemiptera	H	0.0027	Proctotrupoidea	p	0.0027
			Proctotrupoidea	p	0.0027
			Proctotrupoidea	p	0.0027
Hymenoptera					
Formicidae	S	0.0357			
Formicidae	S	0.0110	Larva	H	0.1346
Formicidae	S	0.0082	Larva	H	0.0027
Formicidae	S	0.0027	Larva	H	0.0027
Hymenoptera	I	0.0110	Mantoidea	Pr	0.0027
Hymenoptera	I	0.0027			
Hymenoptera	I	0.0027	Mycoptera	Pr	0.0055
Hymenoptera	I	0.0027			
Hymenoptera	I	0.0027	Orthoptera	H	0.0027
Hymenoptera	I	0.0027	Orthoptera	H	0.0027
Hymenoptera	I	0.0027			
			Psocoptera	H	0.0110