A comparison of Passalidae (Coleoptera, Lamellicornia) diversity and community structure between primary and secondary tropical forest in Los Tuxtlas, Veracruz, Mexico

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Abstract. Comparison of the diversity and community structure of Coleoptera (Passalidae) collected in Los Tuxtlas, Veracruz, Mexico, in primary and secondary tropical forest has been carried out. The saproxylophagous beetles studied can be differentiated according to their presence in three distinct microhabitats of rotting logs: underbark, sapwood–heartwood and microhabitat generalists. Over the 2-year study period, 12 passalid species were recorded (six Passalini and six Proculini) represented by a total of 2971 individuals, collected from 234 rotting logs. The rarefaction method, the lognormal species–abundance relationship, and the nonparametric jackknife method were used to compare species richness between the habitats. The data were also fitted to log series, truncated lognormal, geometric, and broken-stick species abundance models to detect changes in community structure. The community composition of Passalidae in Los Tuxtlas did not differ ostensibly between the primary and secondary forests. Neither the mean number of individuals nor the biomass per log differed significantly. Furthermore, there were no significant differences between the two habitats in terms of the number of underbark, sapwood/heartwood, and microhabitat generalist species. Different richness estimators indicated that the primary forest community is only slightly richer. The slight decrease in richness of the secondary forest is related to a decrease in dominance by certain species, as well as to a more balanced abundance distribution, which is adequately described by the broken-stick model. Complementary explanations for this pattern may be: (1) that logging reduces the abundance of dominant species, thus preventing competitive exclusion in the secondary forest; and (2) that passalid diversity is not regulated by the diversity of tree species.

Introduction

The chemical and morphological heterogeneity of tropical trees can affect the species richness of some insect groups (Huston 1994). In these circumstances, insect species richness would be causally related to tree species richness, so that logging and forest clearance would have a direct impact on insect diversity (Holloway et al. 1992; Kremen et al. 1993; Samways 1994; Basset et al. 1998). Different groups of tropical insects respond in different ways to the same type of disturbance, but frequently insect species peak over intermediate disturbance levels (Petraitis et al. 1989; Spitzer et al. 1997).

Passalidae are a group of Coleoptera with pantropical distribution (Reyes-Castillo 1970; Boucher 1986; Fonseca 1988; Bührnheim and Aguiar 1991; Mouzinho and Fonseca 1998). Their entire life cycle occurs within logs, where they feed on rotting wood. Although it is known that these Coleoptera are responsible for processing almost a third of the dead wood in some tropical forests (Rodríguez 1985), we have no data on how disturbance in arboreal vegetation influences their communities (Schuster 1978; Castillo 1987). To estimate if coexisting passalid trunk consumers are influenced by forest disturbance, the variation in species richness and community composition between undisturbed (primary) and disturbed (secondary) Mexican tropical forests has been examined. Using several species richness estimators (Colwell and Coddington 1995) as well as species–abundance models (Magurran 1988) the present research addresses this subject for the first time. Models that examine the relationship between number of species and number of individuals allow us to hypothesize about the biological characteristics of communities and the ecological processes that operate in them (Pielou 1975). However, questions about the underlying ecological processes that generate species–abundance models, and the efficiency of these models in detecting insect responses to tropical forest disturbance, are still not satisfactorily answered (see May 1975; Sugihara 1980; Tokeshi 1993; Hill et al. 1995; Basset et al. 1998; Hill and Hamer 1998; Nummelin 1998). Causes must be inferred from patterns with caution when using species–abundance models. In this paper we use species–abundance models to describe diversity patterns, and to provide a first approximation to the underlying causal mechanism due to forest disturbance that may modify passalid diversity and composition.

Materials and methods

Study area

This study was carried out in Los Tuxtlas, Veracruz, at the Estación de Biología Tropical (18°34′–18°36′ N and 95°04′–95°09′ W), which belongs to the Universidad Nacional Autónoma de México. The predominant vegetation is primary tropical evergreen forest, while secondary vegetation grows in the surrounding areas. Altitude ranges from 150 to 530 m (Lot-Helgueras 1976), and the climate is warm and humid with a mean annual temperature of 23.2 °C and mean annual rainfall of 4725 mm (Ibarra and Sinaca 1987). Research was carried out in preserved areas of primary tropical evergreen and secondary forest. The former is characterized by trees that reach a height of 30–40 m and include Leguminosae, Moraceae, and Lauraceae among the most important plant families. Secondary forest areas have pioneer plant species, quick-growing heliophiles, and some softwood trees such as *Heliocarpus appendiculatus* Turcz. and *Cecropia obtusifolia* Bertol.

Sampling design and statistical considerations

A total of 15 sampling periods were interspersed between May 1984 and October 1986. In each sampling period one man worked during 4 days to extract beetles manually from randomly selected rotting logs in primary and in secondary forest sites. The number of logs sampled during each period was chosen taking into account the available logs with an adequate decomposition degree. This number varied from 4 to 30, with a mean of 15.6 (± 2.0 SE) logs per sampling period. A total of 234 rotten logs belonging to 45 different plant species were examined. The various passalid species were divided into three groups according to the microhabitat that each prefers (Castillo 1987; Lobo and Castillo 1997): underbark inhabitants (U), sapwood/heartwood inhabitants (S), and microhabitat generalist species (G). Fresh body weight, body length and body width were measured for each species (sample sizes varied from 7 to 36). The passalid material was deposited in the Instituto de Ecología in Xalapa, Veracruz.

Since sampling period effort differed, the data were standardized to number of individuals per log. Thus, the mean abundance of each species was the arithmetic mean of the standardized number of individuals for the 15 sampling periods. As counts of species in a locality generally underestimate the true number of species, the rarefaction method (Hurlbert 1971), the estimation of the total number of species in a community or the area under the lognormal curve (Fagan and Kareiva 1997), and the jackknife procedure (Krebs 1989) were used to calculate complementary species richness scores (Colwell and Coddington 1995). The Shannon index of diversity (H') and the evenness measure based on this index (H'/H_{max}) were also calculated (Magurran 1988).

Rank abundance and biomass plots were constructed and the data were fitted to log series, truncated lognormal, geometric series and broken stick species–abundance models (Magurran 1988; Krebs 1989). Abundance of species was grouped in classes or 'octaves' according to Preston's original method (Lobo and Favila 1999). We used the Kolmogorov–Smirnov one-sample with Lilliefor's corrected critical values (Legendre and Legendre 1983), to compare the expected with the observed patterns of species–abundance distributions. This test is more powerful than the χ^2-test and it can be applied to very small samples (Siegel and Castellan 1988; Tokeshi 1993). The nonparametric Wilcoxon matched pairs test for dependent samples was employed to compare standardized abundances (Snedecor and Cochran 1967).

Results

Twelve species (six Passalini and six Proculini) and a total of 2971 individuals were collected (Table 1). The number of Passalini per log was higher than the number of Proculini (Wilcoxon test, $z = 2.84$, $P = 0.005$; $n = 15$) in primary forest ($z = 2.44$, $P = 0.01$), but not in secondary forest ($z = 1.02$, NS) (see Table 2). In both habitats, the number of individuals classified as microhabitat generalists was notably higher than the numbers of underbark species ($z = 2.48$, $P = 0.01$ in primary forest and

Table 1. Abundance per log of Passalidae species at Los Tuxtlas tropical forest for each of the 15 sampling periods (mean abundance per log). U = underbark inhabitants, S = sapwood/heartwood species, and G = microhabitat generalists.

Species	Sampling period															Mean
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Passalini																
Paxillus leachi Mac Leay (U)	0	0.27	0	8.33	1.28	4.75	5.41	2.14	0	0.78	2.73	0.06	0	0.25	0	1.73
Passalus caelatus Erch (G)	1.73	0	1.50	1.25	1.44	0	0	2.71	1.50	0	1.00	1.71	1.75	0.92	3.75	1.28
P. inops Truqui (S)	0	0	0	0.33	0	0	0	0	0	0.11	0	0.06	0.06	0	0	0.04
P. punctatostriatus Percheron (G)	2.20	7.47	1.00	5.08	5.83	6.63	1.48	8.86	3.19	5.11	1.09	5.18	2.19	4.83	4.40	4.30
P. interstitialis Eschsholtz (U)	0	0	0	0.75	0	0	0.52	0	0.15	7.00	0	0	0	0	0	0.56
P. punctiger Lep. & Serv. (G)	0.03	0.60	0	19.80	0.11	1.50	0	0	0	27.00	0.27	0	0.06	4.42	0	3.58
Proculini																
Spurius bicornis (Truqui) (S)	0	0.07	0	0	0	0	0	0	0.12	0	0	0	0	0	0	0.01
Popilius mysticus (Bates) (S)	0	0	0	0	0.22	0	0	0	0	0	0	0	2.19	0	0	0.16
Odontotaenius striatopunctatus (Percheron) (S)	0	0.87	0	0	0.11	0	0	8.14	0	0	0	0	0.38	0	0	0.63
Heliscus tropicus (Percheron) (S)	0	0	0	0	0	1.75	0	0	0	0	0	0	0	0	0	0.12
Verres corticicola (Truqui) (G)	0.23	4.47	7.00	2.00	3.33	0.38	1.48	3.43	1.77	0.89	2.00	2.88	0.06	3.42	1.60	2.33
V. cavicollis Bates (S)	0.37	0	0.50	0	0.94	0.25	0.76	0.14	0	0	0	0	0.06	5.08	0	0.54
Mean abundance per tree	4.57	13.73	10.00	37.50	13.28	15.25	9.66	25.43	6.73	40.89	7.09	9.29	6.75	18.92	9.75	15.26
Underbark-inhabitant species	0	0.27	0	9.08	1.28	4.75	5.93	2.14	0.15	7.78	2.73	0.06	0	0.25	0	2.30
Sap/heartwood-inhabitant species	0.37	0.93	0.50	0.33	1.28	2.00	0.76	8.29	0.12	0.11	0	0.06	2.69	5.08	0	1.50
Microhabitat generalist species	4.20	12.53	9.50	28.10	10.70	8.50	2.97	15.00	6.46	33.00	4.36	9.76	4.06	13.60	9.75	11.50
Passalini	3.97	8.33	2.50	35.5	8.67	12.90	7.41	13.71	4.85	40.00	5.09	7.00	4.06	10.42	8.15	11.50
Proculini	0.60	5.40	7.50	2.00	4.61	2.38	2.24	11.71	1.88	0.89	2.00	2.88	2.69	8.50	1.60	3.79
Number of trees (total)	30	15	4	12	18	8	29	7	26	9	11	17	16	12	20	234
Number of Passalidae (total)	137	206	40	450	239	122	280	178	175	368	78	168	108	227	195	2971

Table 2. Mean abundance per log (±SE) according to type of microhabitat exploited and taxonomic group for both primary and secondary forest. U = underbark inhabitants, S = sapwood/heartwood species, and G = microhabitat generalists.

	Microhabitat groups			Taxonomical groups		Total
	U	S	G	Passalini	Proculini	
Primary forest						
Number of species	2	6	4	6	6	12
Mean abundance/log	2.05 ± 1.09	1.34 ± 0.93	8.75 ± 2.07	9.45 ± 2.50	2.68 ± 0.97	12.13 ± 2.31
Secondary forest						
Number of species	2	4	4	6	4	10
Mean abundance/log	5.99 ± 3.83	2.19 ± 1.13	21.23 ± 10.79	22.86 ± 14.63	6.55 ± 2.28	29.41 ± 14.35
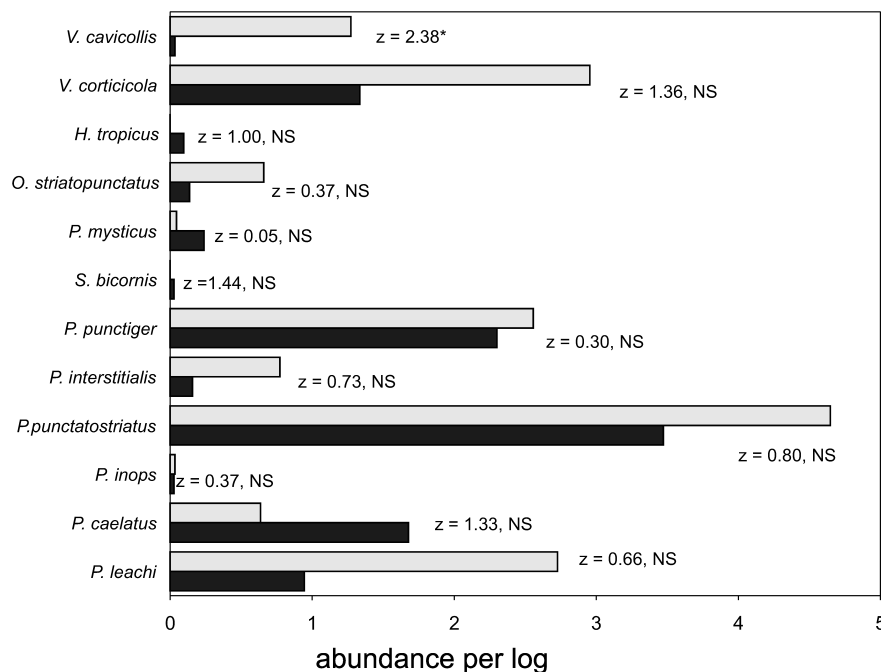
Figure 1. Comparison of the number of individuals per log between primary (black bars) and secondary forest (gray bars) for each of the species studied. Z is the value of the nonparametric Wilcoxon matched pairs test (Snedecor and Cochran 1967). NS = non-significant difference; * significant difference at $P < 0.05$.

$z = 2.78$, $P = 0.005$ in secondary forest) and sapwood/heartwood species ($z = 2.54$, $P = 0.01$ in primary forest and $z = 3.24$, $P = 0.001$ in secondary forest; Table 2).

Twelve species were collected from primary forest and 10 species from secondary forest (Table 2). No species were observed to be exclusive to secondary forest, while two species were found to be restricted to primary forest: *Spurius bicornis* (0.01 individuals per log) and *Heliscus tropicus* (0.12 individuals per log). All other species were found in both habitats. Species composition is quite similar among primary and secondary forest, as reflected in both standardized abundances and presence–absence data. The Bray–Curtis percentage of dissimilarity between inventories of the two habitats was rather low (0.32), while the Jaccard index of similarity is very high (0.83) (Ludwig and Reynolds 1988). Only one species, *Verres cavicollis*, which predominated in secondary forest, is significantly more abundant in one habitat than in the other (Figure 1).

The total abundance per log (Table 2) of the two habitats (Wilcoxon test, $z = 0.97$, NS, $n = 15$) was not significantly different, nor did biomass per log (mean $\pm$ SE) differ significantly from primary to secondary forest; 10.71 ± 3.56 g in the former and 36.52 ± 21.19 g in the latter ($z = 1.25$, NS). Furthermore, significant differences cannot be established between the two habitats in terms of the number

Table 3. Species abundance data are fitted to the four models selected according to the methods of Magurran (1988) and Krebs (1989). Preston's method of octave construction has been used. D is the value of the Kolmogorov–Smirnov one-sample test with Lilliefor's corrected critical values (Legendre and Legendre 1983) used to compare the observed and expected values of species–abundance distributions. S = number of species, S_T = estimate of total number of species in the community or area under the log normal curve (Magurran 1988; Fagan and Kareiva 1997), S^* = estimate of the total number of species in the community using the jackknife technique (Krebs 1989). $S_{(1000)}$ = calculation of the number of species expected in a sample of 1000 individuals using the rarefaction method (Hurlbert 1971). H' is the Shannon index of diversity and H'/H_{max} is the evenness measure based on this index (Magurran 1988).

	Species abundance models			
	Broken stick	Truncated log normal	Log series	Geometric series
Primary forest	$D = 0.294$	$D = 0.219$	$D = 0.256$	$D = 0.083$
	$0.05 > P > 0.01$	$0.3 > P > 0.2$	$P = 0.05$	$P > 0.3$
Fit models	No	Yes	No	Yes
Secondary forest	$D = 0.153$	$D = 0.180$	$D = 0.431$	$D = 0.200$
	$P > 0.3$	$P > 0.3$	$P < 0.01$	$P > 0.3$
Fit models	Yes	Yes	No	Yes

	Species richness measures				Diversity indices	
	S	S_T	S^*	$S_{(1000)}$	H'	H'/H_{max}
Primary forest	12	12.1	13.9 ± 1.3	12.0 ± 0.2	2.56	0.714
Secondary forest	10	10.0	11.9 ± 1.3	9.9 ± 0.2	2.72	0.819

of Passalini per log ($z = 0.06$, NS), the number of Proculini ($z = 1.31$, NS), the number of underbark species ($z = 0.62$, NS), the number of sapwood/heartwood species ($z = 0.73$, NS), and the number of generalist species ($z = 0.74$, NS) (Table 2).

The scores of truncated lognormal estimates (S_T) and jackknife richness estimations (S^*) for both habitats are very similar to the total number of observed species (Table 3), suggesting that collections during the sampling periods represented a large proportion of the species actually present in the two zones. The various measurements of richness employed all indicate that the primary forest community is only slightly richer than the secondary forest, while its evenness is lower (Table 3). However, rank abundance plots (Figure 2) show that in secondary forest, more species' abundance and biomass are intermediate, and fewer species' biomass and abundance are relatively low, when compared to those in primary forest. Therefore, values for diversity and evenness indices (which incorporate species proportional abundance information) are higher for secondary forest (Table 3). The truncated lognormal and geometric models fit the pattern of species abundance in the two habitats well. In primary forest, species abundance approaches a log series distribution, while secondary forest data are described by the broken-stick model, not the log series model.
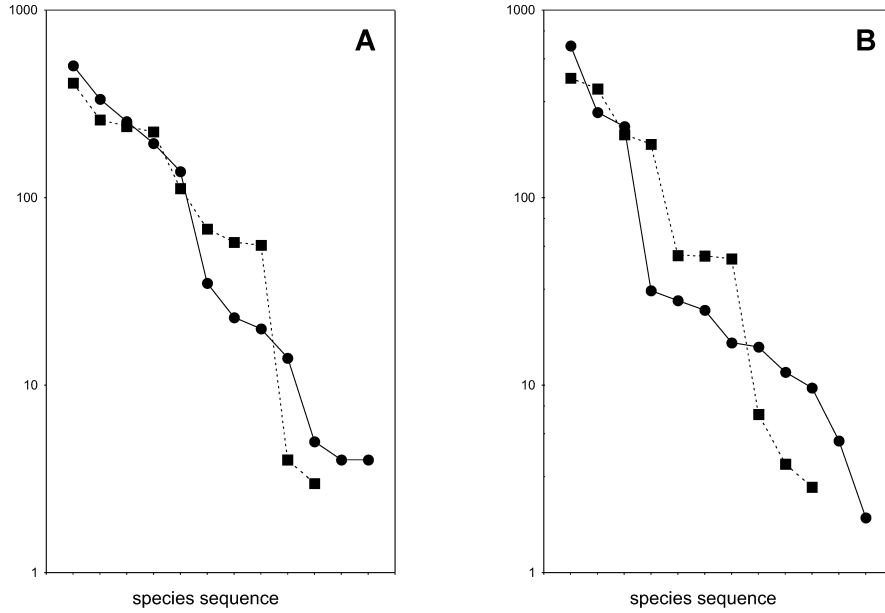
Figure 2. Rank abundance (A) and biomass (B) plots in primary (continuous line with black circles) and secondary forest (broken line with black squares).
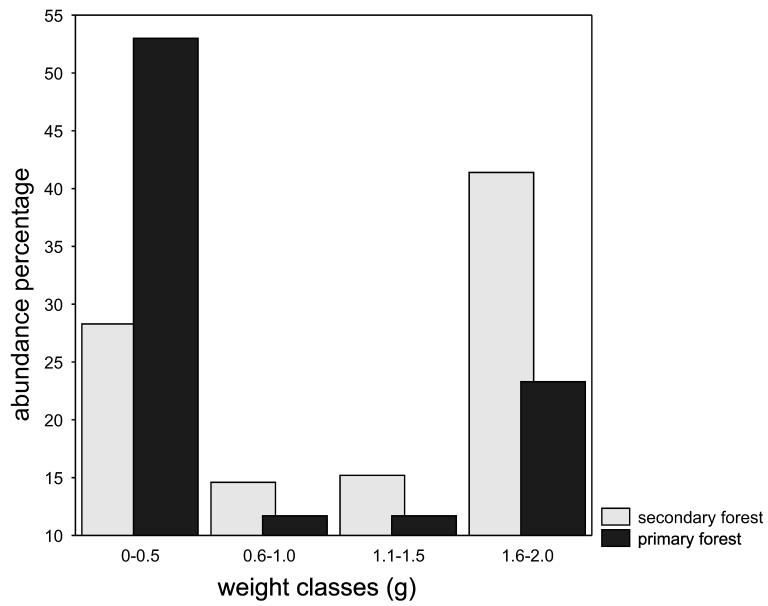

Figure 3. Percentage of total abundance captured per body weight category for both habitats.

We divided the species into four categories according to fresh body weight (from 0 to 0.5, 0.6 to 1, 1.1 to 1.5, and 1.6 to 2 g) and examined the relationship between mean abundance per log for each category and habitat type (primary forest versus secondary forest) using a contingency table. A significant association between the two classifications ($\chi^2 = 2.45$, df $= 3$, $P \sim 0.5$) does not exist. However, the mean fresh weight of an individual captured in secondary forest (0.954 g) was significantly higher than that of an individual captured in primary forest (0.859 g) ($d = 4.57$; $P < 0.001$). Primary forest species of lower weight and size made up a larger percentage of total individuals, while in secondary forest heavier individuals contributed more to the total abundance (Figure 3).

Discussion

The faunistic composition of Los Tuxtlas passalid communities does not differ between primary and secondary forest. Only 2 of the 12 species collected showed a significant preference for one or the other type of habitat. *Passalus caelatus* preferred primary forest and *V. cavicollis* preferred secondary forest. Hence, the disturbance of primary forest reduces passalid richness only slightly and hardly changes the community composition. Additional sampling, both manually and with light traps, increased the passalid inventory by only one species in secondary forest and by three species in the primary forest (Castillo and Reyes-Castillo 1997). These new species were, furthermore, rare or are not generally associated with rotting logs.

It is well established that the diversity and richness of various tropical biological groups can remain unaltered or even increase with a certain degree of environmental disturbance (Connell 1978; Janzen 1988; Holloway et al. 1992; Spitzer et al. 1997). In Los Tuxlas, a similar pattern has been observed through research on groups of insects directly linked to vegetation, such as Lepidoptera and Melolonthidae (Raguso and Llorente 1990; Lobo and Morón 1993). This could be due to an increase in the diversity of certain plant species associated with canopy gaps (Dirzo et al. 1992) or an increase in heterogeneity and the edge effects. Passalids, however, depend on rotting, standing or fallen trees, a resource which is lower in variety and abundance in secondary forests (Ibarra and Sinaca 1987). It seems contradictory, therefore, to conclude that the decomposition of arboreal vegetation might have had so slight an effect on the Passalidae, when this group of insects is known to be dependent on rotting organic matter. Complementary explanations for this result may be: (1) that there was less competition among species that fed on rotting logs in the secondary forest; and/or (2) that the type of tree is not a determinant key factor of the community structure.

Logging can reduce the abundance of dominant species, preventing competitive exclusion and increasing diversity (Huston 1994). Some of our results indicate that this process might occur in passalid communities. The slight decrease in richness of secondary forest is related to a decrease in dominance by certain species, as well as to a more balanced abundance distribution. The lower dominance of secondary
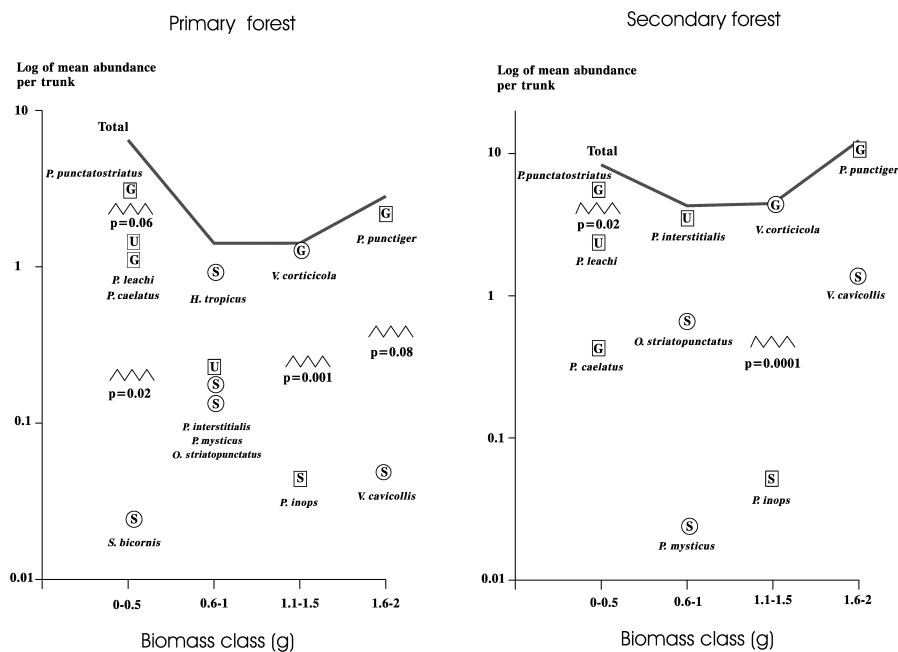
Figure 4. Mean abundance per log, body weight category, systematic position (($\square$) Passalini, ($\bigcirc$) Proculini), and microhabitat preference (U = underbark species, S = sapwood/heartwood inhabitants, G = microhabitat generalists) for all species collected in both types of habitat. The line indicates a statistically significant difference in abundance according to the nonparametric Wilcoxon matched pairs test and *P* represents the associated probability (Snedecor and Cochran 1967).

forest and its broken-stick species abundance distribution may be functionally related results. Although conclusions should be viewed with caution (Wilson 1993), good fits to the broken-stick model seem to be found in narrowly defined communities of related organisms where resources are evenly distributed among species (Magurran 1988). The truncated lognormal model fits well for both habitats, indicating a large and varied natural community (May 1975; Magurran 1988). Contrariwise, the primary forest community data fit a log series model, showing that fewer species dominate the primary forest community (Magurran 1988).

The equilibrium competition theory predicts that mobile organisms with a high frequency of competitive interactions will have: (1) low species diversity, and (2) a large niche separation among species (Hutchinson 1959; Grant and Schluter 1984). The passalid communities are not species-rich but seem to be well structured. Body weight, abundance, systematic position and microhabitat specialization make the segregation possible of practically all Los Tuxtlas species, both in the primary and secondary forest (Figure 4). Microhabitat generalist species dominate these communities and are found evenly distributed throughout the different body weight

categories. Furthermore, species within each body weight category tend to show significant differences in the mean number of individuals per log. When this is not the case, they adopt various strategies to exploit the microhabitat, or else they belong to a different tribe (Figure 4).

As the species abundance distribution is well fitted by the truncated lognormal models and approaches the log series model, it is not expected that many environmental variables could influence the Passalidae community in the primary forest. An even lower number of variables appears to influence the secondary forest communities where, due to its higher evenness, the species–abundance distribution is adequately described by the broken-stick model (Magurran 1988). The number of tree species is one of the variables expected to influence passalid richness because it allows an increase in the opportunity of feeding niches. However, though there is no experimental evidence, passalid diversity seems not to be regulated by the variety of tree species. It is usually accepted that the Passalidae do not select specific tree types (MacVean and Schuster 1981), although they are more likely to be found in certain species, while they are never found in others (Castillo 1987). Los Tuxtlas primary forest disturbance seems to produce a decrease in dominant populations of passalid species and the disappearance or decrease of certain rare species. Thus, the response of the passalids would be similar to that of animals of higher trophic levels, which are more strongly influenced by the primary productivity than by plant species diversity (Huston 1994). Therefore, while a certain degree of arboreal clearance in tropical forest may not be a key factor in establishing community structure, it can reduce the survival of individuals belonging to lower demographic capacity species.

The secondary forest passalid community is distinguished by two other characteristics: a greater number of large individuals and an increase in the mean abundance of Proculini when compared to Passalini. These results may be related. Passalini include species that dominate the South American communities of Passalidae (Reyes-Castillo 1973; Boucher 1986; Fonseca 1988; Bührnheim and Aguiar 1991; Mouzinho and Fonseca 1998). This may also be the case in the Los Tuxtlas primary forest. However, mean abundance per log is not significantly different between the two tribes in the secondary forest. In this habitat, pantropical Passalini are generally less dominant than Proculini. The latter are more characteristic of the Mexican Transitional Zone and cloud forest (Reyes-Castillo and Halffter 1978). The larger mean size of individuals captured in the secondary forest could be due quite simply to the greater size and mean body weight of the Proculini (mean $\pm$ SE; 31.04 mm $\pm$ 4.84, 1.24 g $\pm$ 0.45) compared with the Passalini (25.49 mm $\pm$ 6.65, 0.78 g $\pm$ 0.56) or, on the contrary, the manifestation of an adaptive advantage relating to size (Brown and Maurer 1986).

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