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Ecosystem consequences of species richness and composition in pond food webs

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Resolving current concerns about the role of biodiversity on ecosystems calls for understanding the separate roles of changes in species numbers and of composition. Recent work shows that primary productivity often, but not always, saturates with species richness within single trophic levels[1–8]. However, any interpretation of such patterns must consider that variation in biodiversity is necessarily associated with changes in species composition (identity)[9–12], and that changes in biodiversity often occur across multiple trophic levels[13,14]. Here we present results from a mesocosm experiment in which we independently manipulated species richness and species composition across multiple trophic levels in pond food webs. In contrast to previous studies that focused on single trophic levels, we found that productivity is either idiosyncratic or increases with respect to species richness, and that richness influences trophic structure. However, the composition of species within richness levels can have equally or more marked effects on ecosystems than average effects of richness *per se*. Indirect evidence suggests that richness and associated changes in species composition affect ecosystem attributes through indirect effects and trophic interactions among species, features that are highly characteristic of natural, complex ecosystems.

The role of biodiversity in ecosystems is important both because it can reveal basic insights into the functioning of ecosystems, and because it has implications for how humans respond to current losses in global biodiversity. In a given situation, changes in biodiversity will influence local ecosystems depending on the identity[5,15–18] and number[4,6,8,18,19] of species going extinct. The effects of biodiversity on ecosystems may also depend on whether declines in biodiversity occur at a single trophic level compared with multiple trophic levels[13] when ecosystem processes are influenced by the complex set of species and trophic interactions in communities[1,20]. Here we ask how changes in species composition and richness affect ecosystems when they occur across multiple trophic levels. We focus our analysis on ecosystem attributes that indicate the importance of indirect effects of species in ecosystems.

We tested the effects of species composition and species richness in selected trophic functional groups of pond communities—macrophytes, benthic (bottom-dwelling) grazers and carnivorous predators—while holding functional group diversity constant in field mesocosms. These functional groups were chosen because they are dominant functional groups in fishless ponds, they represent three different trophic levels, and they can be experimentally manipulated with little threat of contamination. The mesocosms also contained decomposers, phytoplankton, periphyton and zooplankton, which together with the manipulated functional groups account for the dominant functional groups in aquatic systems[21]. Although natural ponds differ from the mesocosms in some respects, the mesocosms were subject to natural fluctuations in light, temperature and rainfall, and should represent better analogues of natural systems than more controlled laboratory situations.

The experiment was designed to examine the impacts of declining richness while simultaneously estimating the relative impact of random compositional changes that are associated with biodiversity loss. To disentangle effects of richness from composition, we nested species composition treatments within diversity treatments (see Methods for details). First, we created three species richness treatments with one, three or five species per functional group. Second, within each level of richness, we nested and replicated seven unique species compositions (particular combinations of species). Testing for the effects of all possible combinations is experimentally prohibitive; however, we tested for the effects of seven random draws of species compositions from a fixed species pool within each richness level, providing an unbiased sample of possible species combinations. To draw attention to the effects of composition *per se* rather than the effects of extinction-prone species, we treat all manipulated species equally. Thus our approach does not consider how likely each of the manipulated species is to go extinct, and we emphasize that in situations of environmental concern, compositional effects will depend on additional factors that determine which species are most likely to go extinct[13,22]. We also recognize that as a greater number of species are lost from a community, the number of possible species combinations changes and the proportional similarities between combinations may decrease.

We monitored ecosystem attributes other than the manipulated species in order to capture the importance of trophic interactions and indirect effects of the manipulated species in ecosystems. Specifically, we measured decomposition rates, and phytoplankton, periphyton and zooplankton biomass, all of which are primarily measures of the activities or abundances of unmanipulated functional groups. For example, predators consume zooplankton and benthic grazers. Zooplankton and benthic grazers in turn consume phytoplankton, periphyton, and decomposers. The ecosystem response variables also included ecosystem productivity and respiration, as calculated from diurnal oxygen cycles[23]. In our system, ecosystem productivity and respiration are determined primarily by periphyton, phytoplankton and microbes (based on allometric calculations involving the metabolism and biomass of these organisms), providing a broad measure of collective metabolic activity in the larger community primarily involving trophic groups that were not manipulated.

Our results show that ecosystem productivity is greatest at the highest richness level (Fig. 1b and Table 1). Treatments with three and nine species had very similar and slower rates compared with the most diverse communities of 15 species. Unlike previous studies, we found that effects of species richness on productivity and respiration did not saturate and were synergistic[3], enhanced in only the most diverse communities, at least over this range of richness levels. Patterns for respiration are similar but not quite significant (Fig. 1c and Table 1). Richness also influences the partitioning of plankton biomass within the ecosystems (Fig. 1d–f and Table 1). Phytoplankton biomass increased and zooplankton and periphyton biomass decreased with richness. In contrast, species richness did not significantly alter the total biomass of any of the manipulated functional groups (macrophytes, $F = 0.15$,

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$P = 0.86$; grazers, $F = 1.7$, $P = 0.21$; predators, $F = 0.40$, $P = 0.673$; degrees of freedom (d.f.) = 2,18 in all cases, analysis of variance (ANOVA)). This result suggests that there was compensation among species within functional groups as diversity increased.

In contrast to richness, species composition did not significantly affect phytoplankton, periphyton and zooplankton biomass, but had significant and equally variable or more variable effects on productivity, respiration and decomposition rates, compared with richness (Fig. 2 and Table 1). Furthermore, in contrast to richness, the biomass of all the manipulated functional groups varied with composition (macrophytes, $F = 49.7$, $P < 0.001$; grazers, $F = 6.31$, $P < 0.001$; predators, $F = 6.24$, $P < 0.001$; d.f. = 18,42 in all cases, ANOVA). The effects of species composition on productivity, respiration, and decomposition rates were at least as large or larger in magnitude than the average effects of species richness (Fig. 2). Although some of these effects might be related to changes in similarity among communities, we found no relationship between pairwise compositional similarity and similarity of ecosystem functioning in this experiment (A.L.D. and J. T. Wootton, manuscript in preparation).

A central debate surrounding 'diversity–ecosystem functioning' relationships is whether effects of diversity are due to the presence of one or a few species with strong and direct effects on ecosystems (that is, the sampling effect)[9,11,24], or if the effects are due to diversity *per se*, involving more complex interactions between species including resource complementarity, species interactions, and indirect effects[8,20,25]. Our data provide evidence indicating that the manipulated species are largely influencing ecosystem properties indirectly by altering abundances of other species with strong effects, and are probably not modifying ecosystem processes solely though the direct effects of a few species. First, the absence of an effect of richness on the biomass of manipulated functional groups provides no evidence for the sampling effect. Second, many of the ecosystem responses are primarily measures of unmanipulated functional groups such as phytoplankton, periphyton, zooplankton and microbes. Macrophytes, periphyton grazers and predators are known to influence ecosystem dynamics including nutrient recycling dynamics, grazing rates and predation rates[26,27], consequently altering the biomass of unmanipulated functional or trophic groups through an abundance of direct and indirect effects. Our results suggest that not only the presence of these functional groups but also their composition and diversity may alter ecosystem functioning.

Even ecosystem productivity was probably controlled mostly by phytoplankton in our experiment, rather than the manipulated macrophyte species, which probably contributed proportionately little to oxygen dynamics. Although macrophyte biomass contributed strongly to total community biomass (42% or 2,654 ± 315 mg dry weight, standard error (SE)) it did not vary with species richness. In contrast, periphyton and phytoplankton biomass changes were related to species richness (Fig. 1 and Table 1) even though they contributed much less on average to community biomass (1% or 65.0 ± 4.7 mg dry weight, SE, for periphyton, and 8.7% or 553.1 ± 105.5 mg dry weight, SE, for phytoplankton). However, the effects of changes in plant biomass on ecosystem production also depend on productivity to biomass (P/B) ratios of these groups. Average macrophyte P/B ratios in the literature range between 1 and 5, whereas average phytoplankton and periphyton P/B ratios generally exceed 100 (ref. 21). Using these rough calculations, we estimate that phytoplankton contributed approximately an order of magnitude more than periphyton or macrophytes to overall productivity in these mesocosms. Consequently, the effects of species richness on productivity are much more likely to involve indirect effects of the species on phytoplankton biomass (known to vary appropriately) or phytoplankton composition, rather than on the direct effects of macrophytes on productivity.

If pond food webs are highly connected and interdependent[28], changes in richness or composition would alter the abundance or diversity of other, unmanipulated species or functional groups in the community through a complex set of direct and indirect effects[29]. Theory indicates that if these species or functional groups further proceed to have strong ecosystem impacts, then originally small shifts in species composition or species richness could translate into large effects on ecosystem functioning[30]. For example, in our experiment the effects of species richness

Table 1 Effects of species diversity and composition on ecosystem function

		Ecosystem rate					
Source of variation	d.f.	Productivity		Respiration		Decomposition	
		m.s./m.s.e.	*F*	m.s./m.s.e.	*F*	m.s./m.s.e.	*F*
Diversity	2	0.0240	4.84*	0.0114	2.90§	0.0790	0.03
	18	0.0049		0.0039		2.3100	
Time × diversity	10	0.0006	0.36	0.0002	0.27	0.4277	0.74
	90	0.0015		0.0006		0.5770	
Composition	18	0.0049	2.59†	0.0039	5.10‡	2.3102	2.02*
	42	0.0019		0.0008	1.1460		
Time x composition	90	0.0059	4.83*	0.0006	1.40*	0.5772	1.07
	210	0.0012		0.0004		0.5390	

		Trophic functional group						
Source of variation	d.f.	Periphyton biomass¶		Phytoplankton biomass¶		d.f.	Zooplankton biomass¶	
		m.s./m.s.e.	*F*	m.s./m.s.e.	*F*		m.s./m.s.e.	*F*
Diversity	2	1.478	6.06‡	1.914	8.12†	2	1.163	5.42*
	18	0.244		0.236		18	0.214	
Time × diversity	10	0.069	1.32	0.070	0.65	4	0.250	1.17
	90	0.052		0.108		36	0.213	
Composition	18	0.244	0.59	0.236	0.99	18	0.214	1.17
	42	0.412		0.238		42	0.184	
Time × composition	90	0.052	0.81	0.108	0.66	36	0.213	1.54‖
	210	0.064		0.164		84	0.138	

Univariate repeated measures ANOVA results are reported for among the group effects diversity and composition. Significance values for within-group effects time × diversity and time × composition are adjusted using the Greenhouse-Gelser correction for degrees of freedom (d.f.). m.s./m.s.e.—the mean square (m.s.) and mean square error (m.s.e.) are shown as the first and second entry respectively for each source of variation. A significant time by treatment interaction corresponds to different temporal patterns between treatments.
*$P < 0.05$; †$P < 0.01$; ‡$P < 0.001$; §$P = 0.08$; ‖$P = 0.06$.
¶ Data were log-transformed to better meet the assumption of normality.

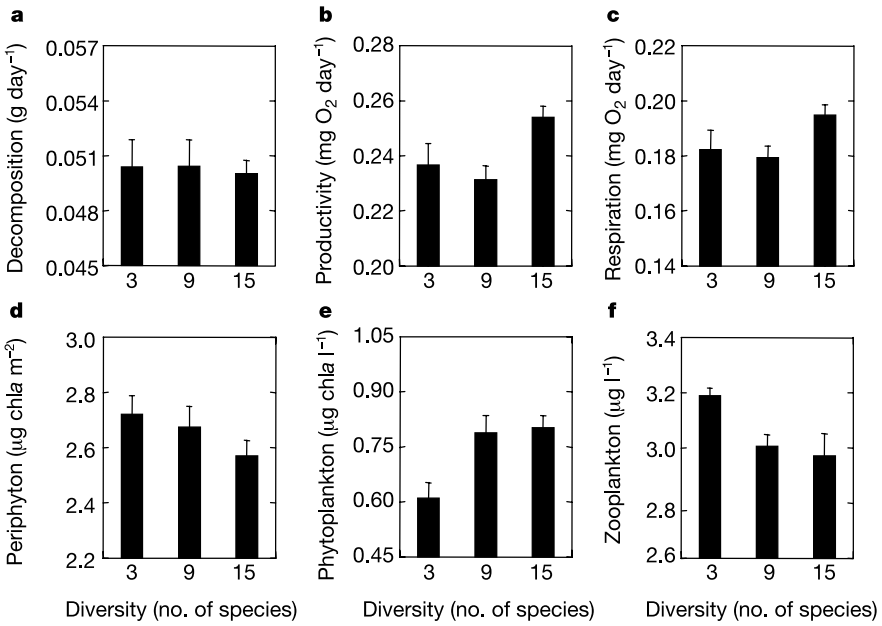

Figure 1 The response of ecosystem rates and trophic structure to species diversity. **a**–**c**, Ecosystem rates of decomposition (**a**), productivity (**b**) and respiration (**c**). **d**–**f**, Response of indicated functional group (log values): periphyton (**d**), phytoplankton (**e**) and zooplankton (**f**). Mean values for each diversity level are calculated from the seven means of each composition level nested within diversity, averaged with respect to replicates and time. These values correspond to the main effects of the repeated measures ANOVA found in Table 1. Error bars depict standard error among the seven composition means nested within each level of diversity. Chl*a*, chlorophyll *a*.

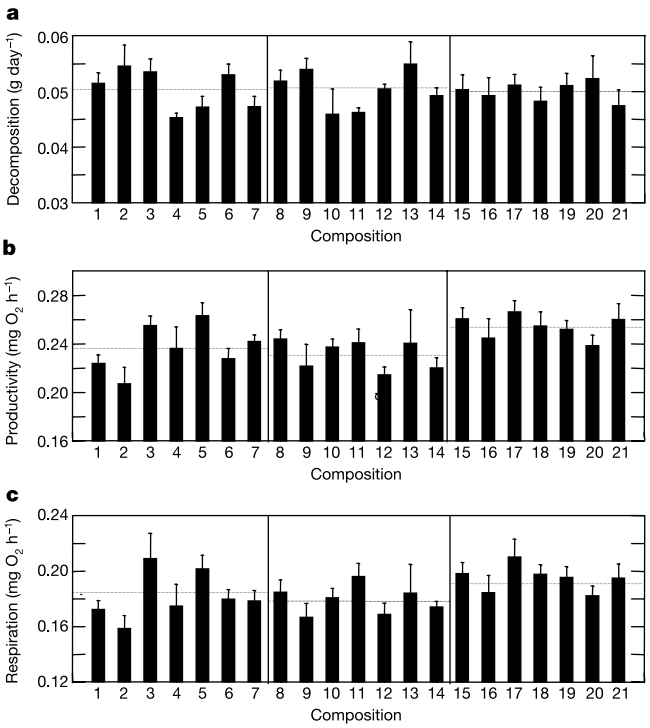

Figure 2 The response of ecosystem rates to species composition nested in species diversity. Ecosystem rates of decomposition (**a**), productivity (**b**) and respiration (**c**) are shown. Bars represent the means and standard error of the four replicates of each composition treatment averaged over time. The horizontal dotted lines indicate the overall mean for each of the three diversity levels (left, middle and right sections, respectively), corresponding the to the means shown in Fig. 1a–c. All 21 unique species combinations are shown. To compare the variability in ecosystem response due to composition versus diversity, we calculated bootstrapped estimates of variance in the means of composition treatments by randomly sampling three composition treatments (equivalent to three diversity treatments) from the seven treatments nested within each level of diversity. We calculated the mean of 150 bootstrapped estimates of variance due to composition (50 estimates within each level of diversity) to arrive at a variance estimate for each variable. Composition had equal or more variable effects than diversity on ecosystem responses, however only decomposition was significantly greater as determined by an F_{max} test (decomposition: diversity variance = 0.000000039, composition variance = 0.00000917, $F = 238$, d.f. = 2, $P < 0.01$; respiration: diversity variance = 0.000048, composition variance = 0.000135, $F = 2.8$, d.f. = 2, $P > 0.05$; productivity: diversity variance = 0.000114, composition variance = 0.000211, $F = 1.85$, d.f. = 2, $P > 0.05$).

and composition on productivity may have involved indirect mechanisms mediated through the phytoplankton assemblage. Importantly, as the potential number and types of direct and indirect effects increases rapidly with species richness, the balance of interactions may be more easily disrupted in complex food webs relative to single trophic level systems, potentially explaining our observation that species richness can have synergistic effects on productivity. (We recognize that the synergisms we see at these levels of richness may show an asymptotic relationship at yet higher levels, or may also be consistent with the 'idiosyncratic' hypothesis.) Intriguingly, results from the first major study that manipulated diversity across entire food webs in terrestrial systems also suggest an accelerating, 'synergistic' relationship between diversity and respiration[19].

Our results demonstrate that both composition and species richness can alter ecosystem attributes in food webs with many trophic levels. Species richness effects appear to be synergistic or idiosyncratic, perhaps because of the greater likelihood of indirect effects than in previous studies involving single trophic levels. Additionally, our results indicate that not all ecosystem attributes respond similarly to richness and composition. Compositional effects can be as large or larger than the effects of species richness *per se*. The application of these results to environmental concerns about losses of biodiversity is incomplete because we describe ecosystem responses to random compositional change. Nevertheless, we suggest that the consequences of biodiversity loss might be complex and difficult to predict without also accounting for compositional changes that will largely depend on the factors generating non-random extinctions in nature[22]. □

Methods

Mesocosms

Polyethylene tanks (300 l) were filled with sand substrate and nutrient-poor well water enriched to average nitrogen and phosphorus concentrations found in local, natural ponds. We inoculated mesocosms with diverse mixtures of zooplankton, phytoplankton and periphyton from local ponds. Fibreglass screen lids prevented unwanted colonization and escape of aquatic species.

Experimental design

The species diversity treatment consisted of three, nine and 15 species evenly distributed across three functional groups: macrophytes, periphyton grazers and invertebrate predators. Seven unique species compositions were nested in each of the three levels of diversity through random draws of one, three or five species per functional group, for a total of 21 unique species composition treatments. Each composition was replicated four times (see Supplementary Information for specific species combinations for each treatment). Half of the experiment was subjected to a pulse acidification event part way through the experiment to explore the effects of pH changes on ecosystem stability, however the results of this treatment will be discussed elsewhere. Species were added in a replacement design, keeping total number of individuals (wet weight for macrophytes) in each functional group constant across diversity levels; 60 g total wet weight macrophyte biomass, 90 individual benthic grazers, and 24 individual carnivorous predators. The number of individuals per each functional group was chosen to approach species densities found in natural ponds while ensuring enough individuals of each species for reproduction. All species manipulated were observed to reproduce successfully in the mesocosms, with the exception of tadpoles and macrophytes, which exhibited growth responses. In experiments we have conducted testing for effects of starting densities on final species biomass, differences in biomass generally disappear within 8 weeks of the experiment due to reproduction, mortality, or growth of the pond biota (see Supplementary Information). Treatments were established over a six-week period, beginning with macrophyte species, followed by grazers, and lastly predators.

Ecosystem response variables

Ecosystem variables were measured six times over the course of the experiment, except zooplankton biomass, which was measured three times. We took measurements approximately every two weeks (four weeks for zooplankton) for 12 weeks, beginning four weeks after treatments were established. Ecosystem productivity and respiration rates were calculated as the difference between the maximum and minimum oxygen concentrations over a 24-h period taken with an oxygen probe. Productivity rates are the net gain of oxygen between dawn and dusk, and respiration rates are the net loss between dusk and dawn[23]. We calculated decomposition rates as the loss of dry mass per day of sugar maple leaves enclosed in mosquito netting. Phytoplankton and periphyton biomass were determined from chlorophyll *a* extraction, and converted into dry weight. Zooplankton were sieved through an 80-μm mesh filter and transferred to a pre-weighed glass fibre filter for dry weight determination. To correct for phytoplankton biomass, a subsample of each zooplankton sample was analysed for chlorophyll, which was then converted into dry weight of phytoplankton and subtracted from the zooplankton sample. All manipulated species were counted and weighed at the end of the experiment, and converted to dry weight based on length–weight regressions or direct weighing. Mean biomass and mean number of individuals of each species for each composition treatment at the termination of the experiment can be found in the Supplementary Information. Community biomass was calculated as the total biomass of the manipulated species in addition to phytoplankton, periphyton and zooplankton biomass. The average biomass of periphyton, phytoplankton and zooplankton biomass per tank was calculated by using the appropriate conversion factors (total surface area available for periphyton growth, and total volume of water per mesocosm for zoopankton and phytoplankton) to convert biomass per area or volume to biomass per mesocosm.

Statistical analyses

Statistical analyses use the appropriate error terms for the full experimental design, although the results of the acidification treatment are not reported here. Data were analysed using mixed model, repeated measures ANOVA, where species composition is a random effect nested in species diversity, which is a fixed effect. Levene's test confirmed that variances were homogeneous across diversity treatments for all response variables except zooplankton biomass ($P = 0.03$), where variance increased as the mean decreased and as compositional similarity presumably increased within the high richness treatment.

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Low host specificity of herbivorous insects in a tropical forest

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Two decades of research[1–4] have not established whether tropical insect herbivores are dominated by specialists or generalists. This impedes our understanding of species coexistence in diverse rainforest communities. Host specificity and species richness of tropical insects are also key parameters in mapping global patterns of biodiversity[1,4,5]. Here we analyse data for over 900 herbivorous species feeding on 51 plant species in New Guinea and show that most herbivorous species feed on several closely related plant species. Because species-rich genera are dominant in tropical floras, monophagous herbivores are probably rare in tropical forests. Furthermore, even between phylogenetically distant hosts, herbivore communities typically shared a third of their species. These results do not support the classical view that the coexistence of herbivorous species in the tropics is a consequence of finely divided plant resources; non-equilibrium models of tropical diversity[6] should instead be considered. Low host specificity of tropical herbivores reduces global estimates of arthropod diversity from 31 million (ref. 1) to 4–6 million species. This finding agrees with estimates based on taxonomic collections, reconciling an order of magnitude discrepancy between extrapolations of global diversity based on ecological samples of tropical communities with those based on sampling regional faunas[7,8].

Host specificity is difficult to measure, and the limitations of existing studies include sampling only certain taxonomic groups rather than entire guilds, or sampling limited numbers of host plant species and lineages. Studies are often of insufficient duration, producing samples too small for quantitative analysis, or insects are sampled destructively, which precludes feeding experiments and the study of immature stages. Further, previous studies[2] failed to consider the phylogenetic relationships of host plants by using measures of host specificity that relied on counts of higher plant taxa (for example, genera or families). This approach can be misleading when taxonomic ranks are not commensurate with plant lineages. We examined the impacts of sampling bias and phylogenetic effects on estimates of host specificity by analysing the largest available data set of its kind. The leaf-chewing insect community on 51 plant species was characterized by using a sample

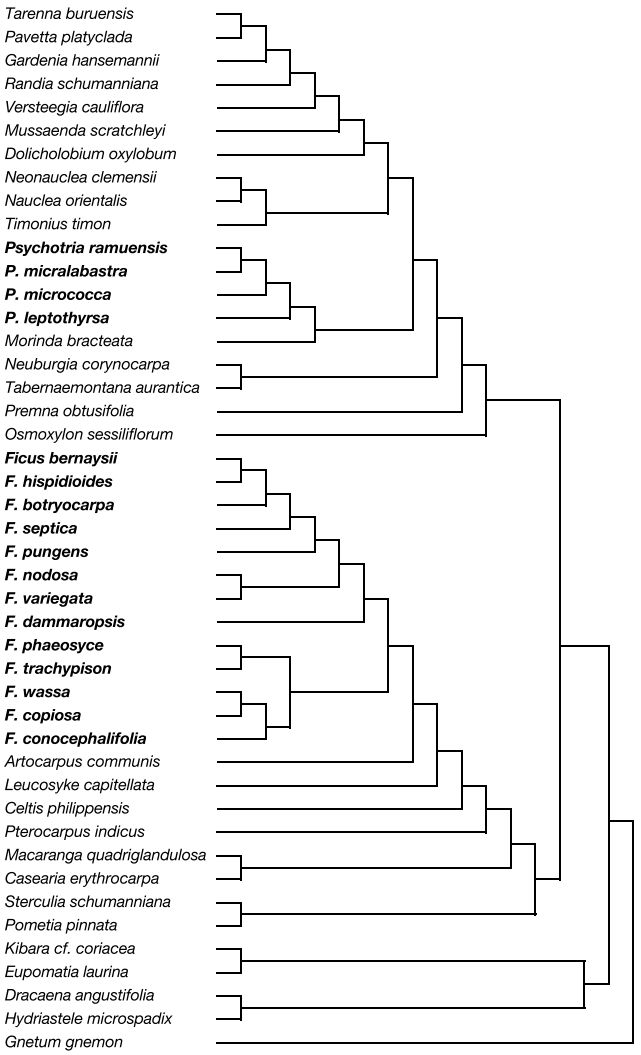

Figure 1 Phylogenetic relationships of host plants included in the study.

Table 1 Overlap between leaf-chewing communities from closely and distantly related host plants

Host plant	Herbivores	*r*	*So* (mean ± s.e.m.)
Ficus spp.	Coleoptera	−0.182	0.51 (±0.008)
	Lepidoptera	**− 0.274**	0.52 (±0.010)
	Orthopteroids	**− 0.267**	0.48 (±0.019)
	Total	**− 0.370**	0.51 (±0.007)
Psychotria spp.	Coleoptera		0.58 (±0.020)
	Lepidoptera		0.57 (±0.059)
	Orthopteroids		0.54 (±0.076)
	Total		0.57 (±0.029)
Plant genera	Coleoptera	**− 0.237**	0.45 (±0.006)
	Lepidoptera	**− 0.328**	0.09 (±0.005)
	Orthopteroids	0.018	0.53 (±0.007)
	Total	**− 0.165**	0.37 (±0.004)

r, Spearman correlation between the phylogenetic distance of plants and the overlap of their herbivore communities measured by the Sorensen index. Significant values ($P < 0.05$, Mantel test) are in bold; data for *Psychotria* were too limited for calculation. *So*, average value of the Sorensen index for all pairwise comparisons between communities from different hosts.