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# Parasite abundance and diversity in mammals: Correlates with host ecology

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**ABSTRACT** **Fecally dispersed parasites of 12 wild mammal species in Mudumalai Sanctuary, southern India, were studied. Fecal propagule densities and parasite diversity measures were correlated with host ecological variables. Host species with higher predatory pressure had lower parasite loads and parasite diversity. Host body weight, home range, population density, gregariousness, and diet did not show predicted effects on parasite loads. Measures of $\alpha$ diversity were positively correlated with parasite abundance and were negatively correlated with $\beta$ diversity. Based on these data, hypotheses regarding determinants of parasite community are discussed.**

Ecological studies on parasite communities of large mammals have been scanty (1) in contrast to those of other vertebrates (e.g., see refs. 2–8). For endangered mammals in protected areas, the only practical alternative to obtaining samples from culled individuals is fecal examination for parasite propagules (9), despite some limitations of this method (10). There have been few attempts to quantify measures of parasite abundance and diversity based on fecal analyses (11). It is also not clear what would be appropriate measures of species richness of parasite communities, and several indices have been used in the past (1, 4, 7, 8, 12). The issue is further complicated by different levels of community organization in parasite communities (13). Similarly, attempts to identify the host ecological factors involved in shaping parasite communities are few and only recent (3, 14–16).

In this paper, we search for quantitative patterns in fecally dispersed parasites in a diverse community of mammalian hosts in Mudumalai Sanctuary, southern India. We first explore various measures of parasite diversity before going on to relate these to their mammalian host ecology. We consider the following host ecological factors that are likely to influence the parasite community.

(*i*) Host population density: Since transmission increases with population density, both parasite loads and diversity are expected to be positively correlated with host density.

(*ii*) Host body size and home range: A large host has higher intake of food and water and a larger home range, thus presumably sampling a higher parasite diversity (16, 17).

(*iii*) Host phylogeny: Since many parasite species can infect more than one species of closely related hosts, host species having more related species at the level of family and order are likely to have greater parasite diversity.

(*iv*) Gregariousness: Gregarious species are expected to show greater parasite loads as well as species richness than solitary species.

(*v*) Anatomical niche diversity: Animals with more complex digestive systems have greater habitat diversity for parasites and therefore may show higher parasite community richness (17).

(*vi*) Host diet: Carnivores are expected to have higher parasite loads and species richness compared to herbivores, as their food contains intermediate hosts of a variety of parasites and also attracts flies and beetles, which are passive carriers of parasite propagules.

(*vii*) Predatory pressures: If predators kill highly parasitized prey individuals in higher proportion, then the infective foci will be continuously removed from the population of the prey species, resulting in reduced transmission. If even moderate parasite loads cause increased susceptibility to predation, then there will be greater selective pressure for parasite resistance. Hence, species with higher predatory pressures are expected to have lower parasite loads.

## MATERIALS AND METHODS

**Study Area, Mammalian Hosts, and Parasite Sampling.** The study was carried out in Mudumalai Sanctuary (11°32′N to 11°43′N and 76°22′E to 76°45′E; average elevation, 900 m above sea level) in southern India. Vegetation varies from tropical moist deciduous forest through dry deciduous forest to dry thorn forest along a rainfall gradient (18). Although the study area contains a variety of mammals characteristic of peninsular India, only 12 species could be sampled sufficiently covering all habitats and seasons. The species selected were taxonomically diverse and included the common langur (*Presbytes entellus*), tiger (*Panthera tigris*), leopard (*Panthera pardus*), sloth bear (*Melursus ursinus*), dhole (*Cuon alpinus*), porcupine (*Hystrix indica*), black-naped hare (*Lepus nigricollis*), Asian elephant (*Elephas maximus*), gaur (*Bos gaurus*), chital or spotted deer (*Axis axis*), sambar (*Cervus unicolor*), and wild boar (*Sus scrofa*).

Samples were collected by following animals (elephant, chital, sambar, gaur, langur, wild boar, and dhole) during the day and collecting fresh defecations. For the relatively nocturnal species (all others), samples were collected by searching commonly used animal trails in the morning. The minimum sample required for inclusion in the analysis was at least 15 independently collected positive samples (i.e., samples with a detectable number of parasite propagules) or at least 30 independently collected samples if the total parasite prevalence was low, and the sum total of parasite propagules detected from all samples should be at least 100.

**Detection and Characterization of Parasites.** The sedimentation flotation technique was modified to quantify parasites in fecal samples (10, 19). One gram of fecal sample was weighed, after mixing 15–20 g of the collected sample, and subjected to centrifugation and the zinc sulfate flotation technique. The contents of the surface layer were transferred to a slide for observation and all parasite propagules were counted.

The propagules were photographed and classified into operational taxonomic units (OTUs) based on qualitative as well as quantitative features. In cases where the differentiation was

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Abbreviation: OTU, operational taxonomic unit.

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based only on size, a distinct bimodality in the size distribution was interpreted as two different OTUs. A taxonomic list of parasite species identified is available elsewhere (10, 19). We have considered the helminths separately and also pooled helminths and protozoans for parallel analysis where appropriate. Some of our definitions differ from those of Margolis *et al.* (20) because of differences in the methods used. We use the term prevalence to indicate the percentage of samples in which propagules were detected and fecal propagule density as a measure of abundance or intensity of infection.

**Measures of Parasite Community Variables.** (*i*) Parasite loads. Two measures of parasite loads were used for the analysis. (*a*) Parasite prevalence or percentage of samples found positive. (*b*) Median standardized propagule output, defined as median total output of parasite propagules per day per unit host weight for a given host species. This was equal to

$$\frac{\text{median propagule density} \times \text{mean adult daily fecal output}}{\text{mean adult body weight}}.$$

Estimates of the daily fecal outputs were obtained from the field, zoo animals, and available literature (10, 21, 22). This transformation was necessary because the fecal propagule densities can be influenced by the food turnover and animals with different diets have different food turnover rates. However, the ranks before and after transformation were highly correlated (for helminths, Kendall's $\tau = 0.91, P < 0.001$; for all parasites, $\tau = 0.85, P < 0.001$).

(*ii*) Parasite species diversity. Of the several measures of species diversity used (1, 4, 7, 8, 12), we considered the following indices in order to choose the appropriate ones for further analyses. Since the terms species diversity, species richness, etc., are well established we will not replace them by OTU diversity or OTU richness. (*a*) Number of species per individual (sp/ind): The mean number of OTUs detected in 1 g of fecal sample. This represents the mean infracommunity richness. (*b*) Number of species observed in $n$ randomly selected individuals (sp/$n$ ind). This was computed by repeated simulated subsampling with replacement taking $n = 15$ for all species. (*c*) Number of species observed in 100 parasite propagules, each randomly selected from a randomly selected host individual (sp/100 par), computed by repeated simulated subsampling. (*d*) Mean percentage similarity (persim) between 100 randomly chosen pairs of individuals. (*e*) Component community evenness index (compeven) based on Shannon–Weiner index (23) considering the cumulative total abundances of parasite species in all samples. (*f*) Bootstrap estimate (spboot) of total number of parasite species including the estimated number of undetected species by repeated bootstrap sampling and estimating the extrapolated species richness using the Smith and van Belle equation (23). (*g*) Species area curve parameters: The species area curves are well known and extensively used in community ecology (24). For the parasite communities we fitted the function $s = cA^z$, where $s$ is the number of parasite species, $A$ is the number of individuals examined, $c$ is a constant denoting the species richness per individual host, and z is a function of faunal dissimilarities between hosts.

The parasite OTU versus host individual curves were obtained by simulated subsampling with 15 repetitions. A log–log transform was used to linearize the above equation. The intercept $c$ and the slope $z$ of the log–log plot were used as indices of species diversity.

All the above indices were subjected to computation of Pearson's product moment correlations with each other in order to study their interrelationships and to choose the appropriate ones for further analyses.

**Measures of Host Ecological Variables.** Ecological information on the host species in the study area was obtained from earlier studies of mammals in Mudumalai and nearby regions (21, 25–32). Some of the host ecological variables such as weight and population density can be expressed quantitatively (e.g., weight, population density) while others (e.g., diet) are qualitative. Because of natural variations or errors in estimation, the use of ranks was preferred while using quantitative variables (Table 1).

Table 1. Host ecological factors in mammalian species

| Species | pd | od | bw | pi | hr | so | gc |
|---|---|---|---|---|---|---|---|
| Hare | 10 | 6 | 1 | 8 | 1 | 1 | 5 |
| Chital | 12 | 9.5 | 6 | 11 | 2 | 12 | 8 |
| Elephant | 7 | 1 | 12 | 6 | 12 | 1 | 5 |
| Gaur | 6 | 9.5 | 11 | 9 | 11 | 12 | 8 |
| Langur | 11 | 7 | 2 | 7 | 4 | 3 | 8 |
| Leopard | 2 | 3.5 | 5 | 2.5 | 6 | 15 | 4 |
| Porcupine | 8 | 12 | 3 | 5 | 7 | 11 | 5 |
| Sambar | 9 | 9.5 | 10 | 12 | 5 | 12 | 8 |
| Bear | 3 | 3.5 | 8 | 2.5 | 8 | 15 | 4 |
| Tiger | 1 | 3.5 | 9 | 2.5 | 9 | 15 | 4 |
| Boar | 5 | 9.5 | 7 | 10 | 3 | 12 | 5 |
| Dhole | 4 | 3.5 | 4 | 2.5 | 10 | 15 | 4 |

The population density of host species (pd), population density at the level of order (od), host body weight (bw), home range size (hr), and predation index (pi) are ranked in ascending order. The two other columns give the number of species in a given host's order (so) present in the study area and the number of distinct anatomical compartments in the gut (gc) counted from the esophagus to the large intestine.

For predatory pressure, an index based on analysis of hair in the scats of the three large carnivores (all of them given equal weighting) was defined as the relative percentage representation in carnivore scats divided by the population density of the prey species.

## RESULTS

**Parasite Loads, Diversity, and Their Correlations.** Host species differed widely in their parasite loads (Table 2). When the indices of parasite species diversity (Table 2) were subjected to computation of Pearson's product moment correlations with each other, an interesting pattern emerged (Table 3). The sp/ind, $c$, and sp/$n$ ind formed one intercorrelated group. The $z$, persim, evenness, and sp/100 par formed another intercorrelated group. Correlations between members of these two groups were poor. The bootstrap estimate (spboot) was poorly correlated with all other indices except sp/100 par, and hence it can be treated as a third group. Given the three distinct groups, we selected one index each ($c$, $z$, and spboot) from these groups for further correlation analyses between parasite species diversity and host ecological variables.

**Correlation Between Parasite Diversity and Host Ecology.** The following patterns emerged from the correlation matrix using Kendall's $\tau$. The patterns within helminth parasites alone and all parasites combined are almost identical and therefore we report results only for the latter.

(*i*) Host body size and home range size are not correlated significantly with any of the parasite load or species diversity measures and therefore hypotheses related to these factors can be rejected. The prediction of positive correlation between host population densities at species or higher taxonomic levels and parasite loads and species diversity is rejected. In fact, the correlations are negative (Fig. 1*A*) and individually significant at $P < 0.05$ but not significant when the Bonferroni test of tablewide significance is applied.

(*ii*) The host variables most strongly and consistently correlated with parasite loads/diversity are predatory pressure (Fig. 1*B*) and gut complexity. The correlations between gut complexity and diversity index $c$ are, however, negative against the expectation. The only two correlations that are significant at the $\alpha/k$ level by the Bonferroni test are between prevalence

Table 2. Parasite abundance and estimated measures of parasite diversity from feces of mammalian species

| Species | Samples examined | % infected | | Median propagule density/g | | Median propagule output per day per kg of body weight | | spboot | Evenness | sp/15 ind | sp/ind | sp/100 par | persim | c | z |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | A | B | A | B | A | B | | | | | | | | |
| Hare | 29 | 64 | 72 | 4 | 41 | 80 | 82 | 16.61 | 0.452 | 9.9 | 2.1 | 7.2 | 13.2 | 0.466 | 0.480 |
| Chital | 292 | 59 | 60 | 1 | 1 | 15 | 15 | 4.0 | 0.733 | 7.8 | 0.9 | 16.0 | 16.0 | 0.246 | 0.576 |
| Elephant | 184 | 92 | 92 | 10 | 10 | 300 | 300 | 6.02 | 0.140 | 3.1 | 1.7 | 3.9 | 85.1 | 0.306 | 0.250 |
| Gaur | 37 | 30 | 43 | 0 | 0 | 0 | 0 | 21.26 | 0.535 | 6.9 | 1.0 | 8.3 | 15.4 | 0.191 | 0.590 |
| Langur | 26 | 77 | 77 | 2 | 2 | 40 | 40 | 12.73 | 0.603 | 5.6 | 1.1 | 8.3 | 11.5 | 0.228 | 0.490 |
| Leopard | 16 | 100 | 100 | 16 | 23 | 112 | 161 | 19.91 | 0.506 | 7.5 | 2.6 | 6.3 | 48.1 | 0.389 | 0.506 |
| Porcupine | 17 | 100 | 100 | 33.5 | 33.5 | 670 | 670 | 21.0 | 0.611 | 12.4 | 3.4 | 10.6 | 25.2 | 0.566 | 0.457 |
| Sambar | 42 | 48 | 55 | 0 | 1 | 0 | 15 | 31.05 | 0.780 | 9.5 | 0.9 | 15.1 | 2.5 | 0.314 | 0.577 |
| Bear | 47 | 89 | 94 | 59 | 122 | 1180 | 2440 | 20.54 | 0.401 | 12.2 | 3.9 | 9.2 | 48.3 | 0.633 | 0.393 |
| Tiger | 19 | 100 | 100 | 532 | 641 | 2660 | 3205 | 31.15 | 0.464 | 17.7 | 5.7 | 11.2 | 26.0 | 0.832 | 0.410 |
| Boar | 30 | 60 | 71 | 2 | 2 | 40 | 40 | 16.97 | 0.730 | 8.1 | 1.3 | 10.9 | 11.6 | 0.360 | 0.487 |
| Dhole | 168 | 72 | 89 | 6 | 222 | 54 | 1998 | 27.11 | 0.094 | 7.1 | 2.3 | 5.5 | 62.9 | 0.423 | 0.368 |

See text for explanation of the various indices used. A, helminths only; B, all parasites.

(all parasite species) and predation index and between $c$ (only helminths) and gut compartments.

(*iii*) Herbivores have lower parasite loads and low $\alpha$ diversity (Wilcoxon two-sample rank test, $t = 24$, $P < 0.05$) compared to all other species. Contrary to the expectation, solitary species have significantly greater parasite outputs ($t = 18$, $P < 0.05$) and $\alpha$ diversity ($t = 17$, $P < 0.01$) than do the gregarious species.

(*iv*) All the variables that correlate positively with $c$ or $\alpha$ diversity correlate negatively with $z$ or $\beta$ diversity. The bootstrap species richness is not correlated with any of the host variables except marginally with the number of taxonomically related species. These correlations become insignificant when a tablewide test of significance is applied.

## DISCUSSION

We have tried to establish rational means of expressing parasite species diversity. The three groups that emerge from the correlational analyses can be treated as measures of $\alpha$ (within individual hosts), $\beta$ (differences between individual hosts), and $\gamma$ (host population level) diversity (33), respectively.

The indices $c$ and sp/$n$ ind are measures of $\alpha$ diversity or infracommunity species richness. The sp/$n$ ind is an index expected to reflect two components, the species per individual and the faunal differences between individuals. However, as seen from the correlations, it is dominated by the former. This index has been used as a measure of component community richness (12), which may not be appropriate given that it is dominated by the infracommunity richness. The indices $z$ and the persim, or rather its counterpart the percentage dissimilarity (100 − persim), are measures of faunal differences or $\beta$ diversity. The compeven and sp/100 par are well correlated with $\beta$ rather than with $\alpha$ diversity. Finally, the bootstrap estimate (spboot) can be treated as a measure of $\gamma$ diversity or the component community richness. Because of the discrete levels of community organization in parasites (13), no single measure is adequate. The three levels of measuring diversity need not necessarily be correlated; in our data, the measures of $\alpha$ and $\beta$ diversity are actually negatively correlated. For a complete description of parasite diversity, it would be necessary to specify all three measures.

**Relationship Between Parasite Loads and Diversity with Host Ecology.** (*i*) Host population density: The apparently negative correlations of host population density with prevalence/abundance of parasites are counterintuitive. Such a relationship can result for several reasons. Carnivores always have low population densities and high parasite loads. A positive correlation exists between population density and predatory pressure (Kendall's $\tau = 0.49$, $P = 0.016$) and a negative correlation exists between predatory pressure and parasite loads. Species normally reaching high population densities may have greater selective pressures for parasite resistance since escalation to disastrous epidemics is more probable. If the three obligate carnivores are removed, the correlations cease to be significant. Furthermore, if only the herbivores with substantial predatory pressures are considered, the trend is apparently positive (Fig. 1*a*), although the sample size becomes too small to show statistical significance.

(*ii*) Gregariousness: Here again, contrary to expectation, the solitary species have higher parasite loads than do gregarious species. Explanations similar to those relating to population density can be sought. However, in this case, removal of the obligate carnivores or the species without predators does not destroy the trend. Among the three obligate carnivores, the social dholes have the lowest prevalence of parasites. Dholes also have lower helminth outputs, although the coccidial

Table 3. Pearson's product moment correlation matrix for measures of species diversity

| | sb | Even | sp/15 | sp/ind | sp/100 | ps | c |
|---|---|---|---|---|---|---|---|
| Even | 0.39 | | | | | | |
| sp/15 | 0.41 | 0.20 | | | | | |
| sp/ind | 0.08 | −0.29 | 0.83* | | | | |
| sp/100 | 0.76* | 0.82* | 0.40 | −0.09 | | | |
| ps | −0.37 | −0.87** | −0.29 | 0.24 | −0.71* | | |
| c | 0.12 | −0.21 | 0.88** | 0.97 | 0.01 | 0.14 | |
| z | 0.50 | 0.82** | 0.05 | −0.42 | 0.65* | −0.84** | −0.40 |

sb, spboot; Even, evenness; sp/15, sp/15 ind; sp/100, sp/100 par; ps, persim.
*, $P < 0.05$; **, $P < 0.01$; in all other cases $P > 0.05$.

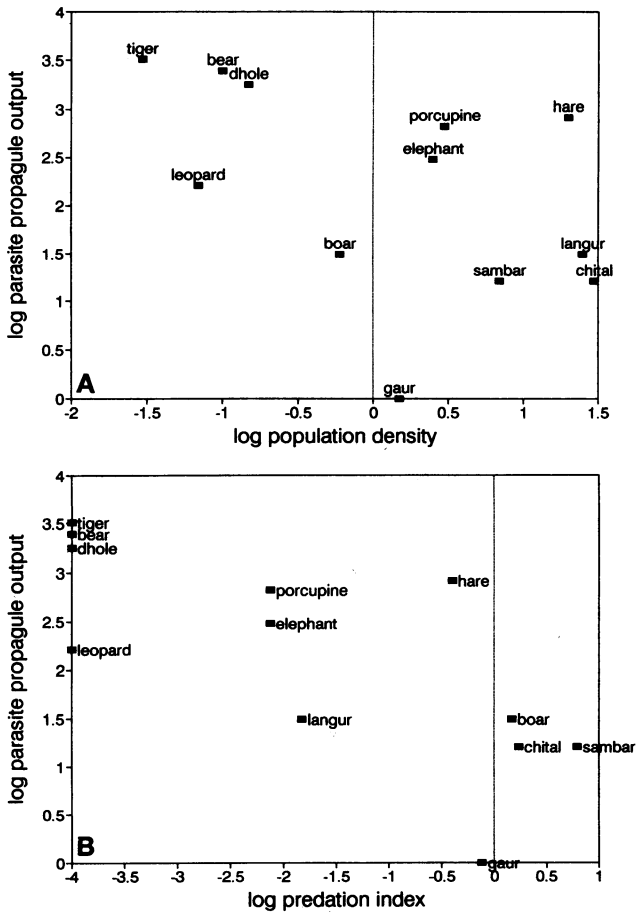


FIG. 1. (*A*) Plot of $\log_{10}$ host population density ($km^{-2}$) versus log parasite propagule output in 12 mammalian host species. Correlation is negative against the expectation. However, removal of carnivores destroys the relationship. (*B*) Plot of $\log_{10}$ host predatory pressure index versus $\log_{10}$ parasite propagule output in the host species. Relationship is robust and does not collapse after removing carnivores.

output is considerable. Among herbivores the solitary black-naped hare and the porcupine have higher prevalences and outputs than all other species. A possible explanation could be that the gregarious species need to evolve higher parasite resistance than would the solitary species.

(*iii*) Host diet: The obligate herbivores have lower outputs than the opportunistic and obligate carnivores but this relationship is fragile. It crucially depends on the inclusion of the porcupine as an opportunistic scavenger. Although porcupines gnaw at bones, evidence for active scavenging on meat is scanty. If the porcupine is listed as a herbivore or is excluded from the analysis, then no significant difference remains. The differences between the three obligate carnivores and all other species are not significant. Furthermore, the predominant parasite species of tiger and leopard are not the ones contracted through consumption of prey species (10, 19). The predominant parasite (*Sarcocystis sp.*) of dhole has a predator–prey cycle. The hypothesis that carnivores have higher parasite loads because they acquire parasites from their prey is not supported in our case.

(*iv*) Gut complexity (anatomical habitat diversity): Contrary to the expectation of niche diversity, the relationship between gut complexity and parasite $\alpha$ diversity is negative. It is not clear why animals with more complex digestive tracts should have fewer parasite species per individual. Gut complexity bears highly significant positive correlation with predation index (Kendall's $\tau = 0.682$, $P < 0.001$) and predation index is negatively correlated with parasite prevalence abundance and $\alpha$ diversity, which may explain the apparent relationship.

(*v*) Predatory pressure: The predation index is highly and consistently negatively correlated with the prevalence, output, and $\alpha$ diversity of all parasites as well as helminths only. The correlation between predation index and the prevalence of all parasites is significant by the Bonferroni test of tablewide significance. The significance is maintained even after removal of the order Carnivora.

The following mechanisms may be responsible for the negative relationship between predatory pressure and parasite loads. All depend on the assumption that prey individuals with higher parasite loads are more susceptible to predation (34–36). Chital killed by dhole in the study area had significantly higher parasite loads (10). In such a case, by selectively removing highly parasitized individuals, the infective foci are constantly being removed from the population. Because of susceptibility to predation, the selective pressure for parasite resistance will also be greater in host species with predators than in those without them.

The negative relationship between predatory pressure and parasite loads may be more general. Among reptiles that have generally depauperate communities, turtles and crocodilians having low predatory pressures have rich and complex helminth communities (2). Also among amphibians, species with antipredator defenses (e.g., skin toxicants, mimicking noxious insects) have greater helminth community complexity (2).

Our results differ from those obtained or predicted by several others (3, 14–16, 37) in that we did not observe any correlations with body size and related factors. This could be because our measure of parasite loads is expressed per unit host weight. Significant correlations may be obtained if it is expressed as total daily outputs or total worm numbers. This we think is a trivial result. Larger species eat more food and therefore have higher chances of engulfing infective propagules and different species. Larger animals can also probably accommodate and tolerate more worms. For a fair interspecific comparison, the parasite loads should be expressed per unit host weight. The host diet, vagility, and other factors thought to be important by Kennedy *et al.* (17) did not seem to be important. It is possible that factors that were found to be important in comparisons across taxa (fishes versus birds in ref. 17) are different than those operating within taxa (mammals only in our case).

**What Shapes Parasite Communities?** A study of the interrelationships between parasite community variables (Tables 4 and 5) shows that the prevalence and outputs are highly

Table 4. Parasite community parameters and their correlates (Kendall's $\tau$) with host ecological variables

| | pd | od | bw | so | pi | gc | hr |
|---|---|---|---|---|---|---|---|
| Preval | −0.41* | −0.40* | −0.14 | 0.17 | −0.70** | −0.60** | 0.17 |
| Output | −0.40* | −0.44* | −0.15 | 0.15 | −0.61** | −0.64** | 0.21 |
| spboot | −0.10 | 0.18 | 0.15 | 0.41* | 0.10 | −0.05 | −0.10 |
| *c* | −0.42* | −0.20 | −0.20 | 0.30 | −0.46* | −0.62** | −0.10 |
| *z* | 0.24 | 0.49* | 0.10 | −0.02 | 0.50* | 0.50* | −0.33 |

Preval, prevalence; other abbreviations are as in Table 1.
*, $P < 0.05$; **, $P < 0.01$; in all other cases $P > 0.05$.

Table 5. Correlations between measures of parasite loads and parasite diversity

| | % infected | Output | spboot | $c$ |
|---|---|---|---|---|
| Output | 0.621** | | | |
| spboot | −0.106 | 0 | | |
| $c$ | 0.531 | 0.727** | 0.121 | |
| $z$ | −0.469* | −0.636** | 0.182 | −0.455* |

Values represent Kendall's $\tau$.
*, $P < 0.05$; **, $P < 0.01$; in all other cases $P > 0.05$.

correlated, the infracommunity richness $c$ is strongly correlated with both prevalence and output, while the $c$ and $z$, measures of $\alpha$ and $\beta$ diversity, respectively, are negatively correlated. Based on these results one can try to reconstruct the processes that shape parasite communities. The component community species richness is probably affected more by phylogenetic, regional, and historical processes than by local ecological processes at the level of host species. The bootstrap estimate of component community richness is not correlated with any of the local ecological factors at the level of individual species but is correlated with the number of species in the order of the host. This is consistent with the suggestion of Stock and Holmes (38) that species richness is enhanced not by a high degree of specificity to a single host species but by a lower degree of specificity, which allows exchange among related host species. Ricklefs (39) identified the importance of regional and historical processes in community diversity. Cornell and Lawton (40) suggested that the principal direction of species richness is from regional to local and that community richness is more historical. We have not examined the effects of historical and regional processes for lack of adequate data. It is likely, however, that the geographical distribution of the host in the past, the host as well as parasite corridors, in case the distribution was patchy, may have played a role in determining the total parasite species pool from which an individual can sample.

An individual host samples from a pool of parasite species that can infect the host species (7). The more the individual samples, the more species it is likely to acquire. For a given pool of parasite species, the more the number of parasite species acquired by each individual host, the less the difference in the parasite species composition of two host individuals. Such a process can lead to a negative correlation between $\alpha$ and $\beta$ diversity. Thus, two factors can be said to affect mainly the parasite communities—the regional and phylogenetic processes that influence the component community richness and the rate of successful invasion of individuals by parasites. Local ecological factors such as predatory pressure influence the latter process and thereby affect $\alpha$ and $\beta$ diversity indirectly.

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