CRITICAL COMMENT . . .

J. Parasitol., 93(1), 2007, pp. 216–219

Functional Richness, Functional Evenness, and Use of Niche Space in Parasite Communities

Devon B. Keeney and Robert Poulin, Department of Zoology, University of Otago, P.O. Box 56, Dunedin 9054, New Zealand.
e-mail: robert.poulin@stonebow.otago.ac.nz

ABSTRACT: Most efforts aimed at elucidating the factors responsible for the variation in species richness among different parasite communities have focused on host characteristics such as body mass or diet. Independently of host features, however, the way in which parasites use resources within the host may also affect the species richness of the community. The distribution of parasite individuals or biomass in niche space determines whether host resources are used evenly, or whether there are gaps in resource use, with some parts of the total niche being underutilized. Here, the concepts of functional richness and functional evenness are applied to parasite communities for the first time, using simple indices. Measurements of the distribution of species in niche space within communities, such as mapping the distribution of helminths along the length of the host's intestine, is standard practice in parasitology. In such cases, functional richness is simply the proportion of the total number of intestine sections available that are used by at least 1 worm, whereas functional evenness measures the evenness in the distribution of worm numbers or biomass across all niche sections that are occupied. Data on cestode communities of elasmobranchs are used to illustrate the use of these indices, and to show how important they can be in tests of ecological hypotheses. The indices presented here capture essential features of resource use in parasite communities, and can be useful tools for comparative analyses.

In ecological parasitology, few topics have received more attention than the variation in species diversity among parasite communities from different host species (Poulin, 1997, 1998; Morand, 2000; Poulin and Morand, 2004). Most efforts to date have focused on the search for host characteristics, such as body mass, diet, or geographic range, that may determine the diversification of parasite communities (e.g., Poulin, 1997; Arneberg, 2002; Nunn et al., 2003). Clearly, intrinsic properties of the parasite communities themselves may also influence how many species they can support. Yet this possibility has not been explored, perhaps because the necessary analytical tools are lacking.

Recently, ecologists working on communities of free-living organisms have begun to look at the distribution of individuals (or biomass) in niche space as a determinant of community properties (Petchey and Gaston, 2002; Mason et al., 2005). The total niche space of a community is the multidimensional volume in which different species exist, with each dimension representing a particular resource or abiotic gradient. If individuals or biomass, regardless of species, are evenly distributed throughout niche space, then the entire range of resources available to a community is being used. If, on the other hand, individuals or biomass are unevenly distributed throughout niche space, there will be 'gaps' in resource use. It transpires that a greater evenness of resource use, through a range of mechanisms such as niche complementarity, can affect how many species can coexist and how likely invading species are of becoming established in a community (Tilman et al., 2001; Petchey, 2003). Ecologists are increasingly focusing on functional diversity, i.e., the distribution of individuals of different species along various niche dimensions, as a way to understand community properties (Tilman et al., 1997; Tilman, 2001; Mason et al., 2005; Petchey and Gaston, 2006).

This approach holds much promise for the study of parasite communities. Careful measurement of the distribution of species in niche space within communities has a long history in parasitology (Holmes, 1973). For instance, several investigations of helminth communities in the gastrointestinal tract of vertebrate hosts have mapped the distribution of worms along the length of the host's intestine (e.g., Lotz and Font, 1985; Bush and Holmes, 1986; Stock and Holmes, 1988; Ellis et al., 1999; Vidal-Martinez and Kennedy, 2000). The summarized information that gets published is not always detailed enough, but the raw data obtained in these studies are all that one needs to determine whether resource use is even or not. Of course, the distribution of worms along the length of the intestine is only one facet of their niche, but as argued in the studies cited above and many others, it is one of the most fundamental niche components because it captures both the spatial arrangements of species and the type of nutrients they can use.

Here, we present indices of functional diversity and explain how they can easily be applied to parasite communities. We also illustrate their use with data on cestode communities from the spiral intestines of elasmobranchs, to show how these indices can be used to better understand parasite communities.

Of the many indices of functional diversity proposed recently (e.g., Petchey et al., 2004), we chose those proposed by Mason et al. (2005). It is not possible to sum up all aspects of functional diversity in a single number (see Mouillot et al., 2005). Thus, Mason et al. (2005) decomposed functional diversity into 2 basic components: functional richness and functional evenness. Importantly, these 2 components are orthogonal to each other, i.e., they vary independently of each other, and they are both also independent of species richness (Mason et al., 2005). They can be computed along more than 1 niche dimension (see Mason et al., 2005), but for the sake of simplicity, here we deal only with univariate niche space such as the position of worms along the roughly linear host intestine.

Functional richness is defined as the amount of niche space occupied by species in the community. This amount must be standardized to allow comparisons among different communities. When niche space can be divided into discrete sections, the standardization is simple, i.e., the number of sections occupied is expressed as a proportion of the total number of sections available. For helminth communities living in the gut of vertebrates, the gut can be naturally or arbitrarily divided into sections; in such cases, functional richness is the proportion of the total number of gut sections that are occupied by at least 1 worm of any species (see Fig. 1). Values of functional richness, therefore, range from 0 to 1, with low values indicating that some of the resources potentially available to the community are unused.

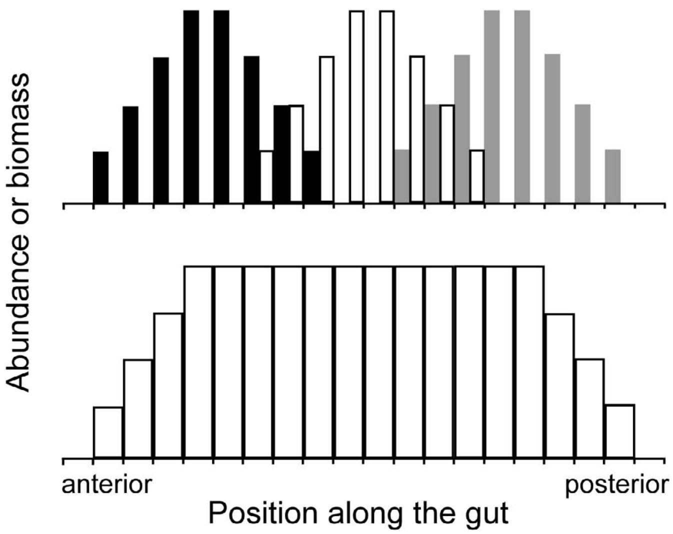
In contrast, functional evenness is the degree to which the organisms in a community are distributed in niche space to allow the effective utilization of the entire range of resources available. It measures the evenness in the distribution of organisms across all niche sections that are occupied, excluding empty niche sections (Fig. 1). It is comparable to species evenness, which measures the evenness in the distribution of organisms across all species present in a community. Thus, both functional evenness and species evenness can be computed using the same indices. Any of those recommended by Smith and Wilson (1996) or Mouillot and Wilson (2002) would do. Here, we have used E_{var}:

$$E_{\mathrm{var}} = 1 - \frac{2}{\pi} \arctan\left\{ \frac{\sum_{s=1}^{S} \left[\ln(x_s) - \sum_{s=1}^{S} \ln(x_s)/S \right]^2}{S} \right\}$$

where arctangent provides an angle in radians, S is the number of niche sections occupied by at least 1 parasite, and x_s represents the abundance of parasites in the sth niche section. Although daunting at first glance, the formula for E_{var} is based on the variance in abundance across niche sections, an intuitive way to measure evenness (see Smith and Wilson, 1996). It is taken on log-transformed abundance values to emphasize proportional differences, and to make the index independent of the units used. The index ranges from 0 (minimum evenness) to 1 (maximum evenness), with increasing values indicating an increasingly even distribution of parasites in niche space.

Functional evenness can be computed using abundance data, i.e., numbers of individuals in each niche section. Ideally, however, it would be computed using biomass data, because the total biomass in a given

(a) High functional evenness



(b) Lower functional evenness

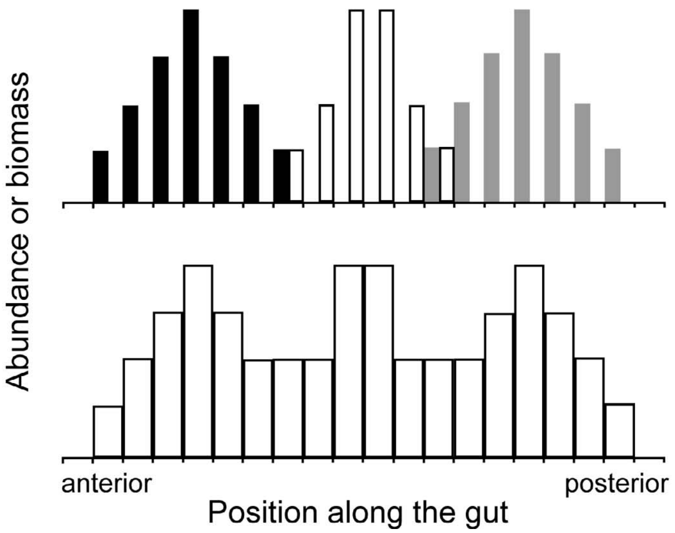


FIGURE 1. Two hypothetical frequency distributions of individual helminths, or helminth biomass, along the length of the host intestine, one with high functional evenness (**a**) and one with lower functional evenness (**b**). The number of gut segments, species richness, and functional richness are the same in both cases, with values of 20 segments, 3 species, and 0.9, respectively. Thus, in both examples, 3 species of parasites occupy 18 out of 20 segments, with only the most anterior and the most posterior segments left empty. The top graph in each example shows the frequency distribution of each helminth species along the intestine, with each species represented by a different shading; in these examples, there are no more than 2 species per segment. The bottom graph displays the frequency distribution for the whole community, which consists of the sum of the abundances or biomass of all species for each segment. Note that small differences in the distributions of individual species can have major repercussions on the overall distribution of abundance or biomass.

niche section is a better indicator of resource use in that section than is the number of individuals. This is particularly true in the case of gastrointestinal helminth communities where some species are orders of magnitude larger than others. Whether abundance or biomass data are used, lower values of functional evenness indicate that some parts of niche space, although occupied, are underutilized. Because functional evenness has no a priori relationship with either species richness or functional richness, any correlation that may be observed between the 3 measures would be an ecological feature and not a mathematical artifact (Mason et al., 2005).

We collected published data on the frequency distributions of cestode parasites in the spiral intestines of elasmobranch hosts. This was not meant to be an exhaustive survey of the literature, but only a source of data to illustrate the use of functional diversity measures. The data set included 4 cestode communities (Table I), comprising species from the Trypanorhyncha and Tetraphyllidea. For each community, functional richness was measured as the number of spiral intestine chambers occupied by at least 1 worm divided by the total number of chambers.

Measuring functional evenness requires information on the numbers of individuals of each species in each spiral intestine chamber. For 2 communities, the raw data were available (McVicar, 1979; Keeney, 1999; Keeney and Campbell, 2001); for the other 2, the data had to be read from histograms showing the frequency distributions of the different cestode species among the different chambers (Cislo and Caira, 1993; Friggens and Brown, 2005). Histograms were magnified and numbers of worms per chamber were obtained by averaging the values of 3 independent readings. The small error (much less than 5% variation among readings) associated with this procedure does not affect our results, and is insignificant given that the data are here used for illustrative purposes only. Functional evenness was first calculated by adding up the abundances of the different species in each intestine chamber, and using these values in the formula for E_{var}, as shown above. In addition to abundance data, we obtained a surrogate of biomass by multiplying the number of worms of a given species in a spiral intestine chamber by the average body length of that species. This was repeated for each species and each chamber, providing 'biomass' values for each species that were added up to give the total 'biomass' per chamber. Body length of cestodes is influenced by the developmental stage of the worms; sufficient information on size variability among developmental stages was provided for 1 community (Keeney, 1999) to allow a corrected average biomass to be computed for some species that takes into account developmental stage. Functional evenness was then computed again for each of the 3 communities for which parasite length data were available, using these 'biomass' values in the formula for E_{var}.

All communities had high functional richness (Table I), indicating that all or most spiral intestine chambers were occupied. However, there was considerable variation among communities in functional evenness (Table I). Two patterns deserve mention. First, functional evenness scores based on biomass data were higher than those derived from abundance data. This suggests that the use of resources, in this case attachment space, by the whole cestode community is more even when biomass is considered than when mere numbers of worms are used. Spiral intestine chambers with many worms thus tend to contain relatively small worms, whereas those with fewer worms tend to contain relatively large worms. Abundance may be an easier parameter to obtain, but in studies of resource use and niche partitioning, it can obscure the relevant patterns and is no substitute for biomass. Using estimates of biomass in functional analyses will always be a major improvement over using abundance itself; massive size differences among different cestode species make it unjustifiable to simply use raw numbers of individuals.

As an aside, it must be pointed out that our biomass estimates may not reflect true relationships among cestode species because biomass is not necessarily proportional to length. For example, some short cestode species may be thicker than long species. However, sufficient data for calculating accurate biomass estimates are rarely published, highlighting the need for detailed studies when applying diversity indices to parasite communities. If biomass is to be informative in comparative analyses, it must be estimated in a standard manner across all communities.

The second interesting pattern seen in Table I is that functional evenness appears to increase with species richness, i.e., with the number of species in the community. The formula for E_{var} is completely independent of species richness, so this is not merely a mathematical artefact. Although we do not have sufficient communities in our data set to

TABLE I. Summary data for 4 cestode communities in elasmobranch hosts.

Host species	No. of hosts examined	No. of spiral valve chambers	Species richness	Functional richness	Functional evenness (abundance)	Functional evenness (biomass)	Source
Bathyraja spp.*	27	12	6	0.83	0.357	0.475	Keeney (1999)
Leucoraja naevus	204	9	5	1.00	0.254	—	McVicar (1979)
Urobatis halleri†	28	11	9	1.00	0.580	0.688	Friggens and Brown (2005)
Mustelus canis	49	8	4	0.88	0.354	0.446	Cislo and Caira (1993)

* Includes 3 congeneric and sympatric skate host species sharing the same cestode species.

† Excludes rare cestode species with <10% prevalence.

determine if this is a statistically robust pattern, it does suggest that new parasite species join a community by filling gaps in niche space, leading to a more even use of resources when more species are present.

We have presented here an approach to community analysis, recently developed by ecologists working on free-living organisms, and illustrated how it can be applied to parasite communities. Based on the functional roles of species in the community, and thus on their distribution in niche space and use of resources, measures of functional diversity reduce several fundamental aspects of community structure down to a couple of numbers. This makes them highly suitable for comparative analyses, in which they could be related to other basic community properties, such as species richness, across host species. A couple of issues require some discussion, however.

First, although the position of helminths along the length of the host's digestive tract is easy to quantify, it only represents 1 niche dimension. It seems to correlate well with other important variables, however. For instance, the distribution of cestodes within elasmobranch intestines may be influenced by changes in host mucosal morphology along the intestine (e.g., Williams, 1960; Borucinska and Caira, 1993; Keeney and Campbell, 2001), as well as the quality and quantity of nutrients available for cestodes (Williams et al., 1970; McVicar, 1979; Curran and Caira, 1995). Therefore, the position of a cestode along the host's intestine may indicate more than its spatial location in the gut habitat and focusing on a single niche dimension will not fully quantify resource use by helminths. However, features such as mucosal morphology or concentrations of various nutrients, as well as other properties of the gut, tend to follow unidirectional gradients along the length of the intestine. The position of a worm in the intestine, therefore, single-handedly captures its position along more than 1 niche dimension, making this possibly the most relevant parameter to include in studies of functional diversity.

What if independent data are available for multiple traits, i.e., for more than 1 niche dimension? The indices can relatively easily be used in a multivariate context by averaging the index values obtained for each of the different traits or niche dimensions (Mason et al., 2005). Although this approach is overly simplistic, in the absence of a priori information on which characters should be given greater weight, it allows a rough estimation of multidimensional functional diversity. In practice, however, given that a parasite's position is often the only niche parameter that can be determined, and given that position along the gut correlates with other variables, this single niche dimension can still provide much information on resource use.

Second, the measures of functional diversity presented here are not solely relevant to gastrointestinal helminth communities. Relevant data are often collected for other types of parasite communities. For example, gill ectoparasites of teleost fishes use slightly different microhabitats, and several investigations have mapped the exact distributions of different species of ectoparasites (monogeneans or copepods) across different gill regions (e.g., Geets et al., 1997; Bagge et al., 2005). In this context, the measurement of functional richness and evenness also becomes not only readily feasible, but also relevant to understanding community properties. In principle, functional diversity is applicable to any parasite community, as long as the distribution of its component species along some niche dimension is possible.

Functional diversity is seen as a key feature of biological assemblages, proving to be a key predictor of many ecosystem processes (e.g., Tilman et al., 1997; Petchey et al., 2004; Petchey and Gaston, 2006). What can functional diversity tell us about parasite communities? To date, host characteristics have proven rather poor predictors of species richness in parasite communities, in terms of the amount of variance they explain (Poulin and Morand, 2004). Our findings based on just a few cestode communities of elasmobranchs suggest that evenness in resource use might be related to parasite species richness, independently of host features. Could functional diversity, and what it measures in terms of the full utilization of resources and niche space, turn out to be a better correlate of species diversity than host-related factors? Incorporating measures of functional diversity in comparative studies should provide answers.

D. Keeney is supported financially by the Marsden Fund, New Zealand.

LITERATURE CITED

ARNEBERG, P. 2002. Host population density and body mass as determinants of species richness in parasite communities: Comparative analyses of directly transmitted nematodes of mammals. Ecography **25:** 88–94.

BAGGE, A. M., P. SASAL, E. T. VALTONEN, AND A. KARVONEN. 2005. Infracommunity level aggregation in the monogenean communities of crucian carp (*Carassius carassius*). Parasitology **131:** 367–372.

BORUCINSKA, J., AND J. N. CAIRA. 1993. A comparison of mode of attachment and histopathogenicity of four tapeworm species representing two orders infecting the spiral intestine of the nurse shark, *Ginglymostoma cirratum*. Journal of Parasitology **79:** 238–246.

BUSH, A. O., AND J. C. HOLMES. 1986. Intestinal helminths of lesser scaup ducks: An interactive community. Canadian Journal of Zoology **64:** 142–152.

CISLO, P. R., AND J. N. CAIRA. 1993. The parasite assemblage in the spiral intestine of the shark *Mustelus canis*. Journal of Parasitology **79:** 886–899.

CURRAN, S., AND J. N. CAIRA. 1995. Attachment site specificity and the tapeworm assemblage in the spiral intestine of the blue shark (*Prionace glauca*). Journal of Parasitology **81:** 149–157.

ELLIS, R. D., O. J. PUNG, AND D. J. RICHARDSON. 1999. Site selection by intestinal helminths of the Virginia opossum (*Didelphis virginiana*). Journal of Parasitology **85:** 1–5.

FRIGGENS, M. M., AND J. H. BROWN. 2005. Niche partitioning in the cestode communities of two elasmobranchs. Oikos **108:** 76–84.

GEETS, A., H. COENE, AND F. OLLEVIER. 1997. Ectoparasites of the whitespotted rabbitfish, *Siganus sutor* (Valenciennes, 1835) off the Kenyan coast: Distribution within the host population and site selection on the gills. Parasitology **115:** 69–79.

HOLMES, J. C. 1973. Site segregation by parasitic helminths: Interspecific interactions, site segregation, and their importance to the development of helminth communities. Canadian Journal of Zoology **51:** 333–347.

KEENEY, D. B. 1999. A study of the cestode faunas of skates from the North Pacific Ocean: Systematics, ecology and biogeography. M.S. Thesis. University of Massachusetts, Dartmouth, Massachusetts, 218 p.

———, AND R. A. CAMPBELL. 2001. *Grillotia borealis* sp. n. (Cestoda: Trypanorhyncha) from five species of *Bathyraja* (Rajiformes: Arhynchobatidae) in the North Pacific Ocean with comments on parasite enteric distribution. Folia Parasitologica **48:** 21–29.

LOTZ, J. M., AND W. F. FONT. 1985. Structure of enteric helminth communities in two populations of *Eptesicus fuscus* (Chiroptera). Canadian Journal of Zoology **63:** 2969–2978.

MASON, N. W. H., D. MOUILLOT, W. G. LEE, AND J. B. WILSON. 2005. Functional richness, functional evenness and functional divergence: The primary components of functional diversity. Oikos **111:** 112–118.

MCVICAR, A. H. 1979. The distributions of cestodes within the spiral intestine of *Raja naevus* Muller & Henle. International Journal for Parasitology **9:** 165–176.

MORAND, S. 2000. Wormy world: Comparative tests of theoretical hypotheses on parasite species richness. *In* Evolutionary biology of host-parasite relationships: Theory meets reality, R. Poulin, S. Morand, and A. Skorping (eds.). Elsevier Science, Amsterdam, The Netherlands, p. 63–79.

MOUILLOT, D., N. W. H. MASON, O. DUMAY, AND J. B. WILSON. 2005. Functional regularity: A neglected aspect of functional diversity. Oecologia **142:** 353–359.

———, AND J. B. WILSON. 2002. Can we tell how a community was constructed? A comparison of five evenness indices for their ability to identify theoretical models of community construction. Theoretical Population Biology **61:** 141–151.

NUNN, C. L., S. ALTIZER, K. E. JONES, AND W. SECHREST. 2003. Comparative tests of parasite species richness in primates. American Naturalist **162:** 597–614.

PETCHEY, O. L. 2003. Integrating methods that investigate how complementarity influences ecosystem functioning. Oikos **101:** 323–330.

———, AND K. J. GASTON. 2002. Functional diversity (FD), species richness and community composition. Ecology Letters **5:** 402–411.

———, AND ———. 2006. Functional diversity: Back to basics and looking forward. Ecology Letters **9:** 741–758.

———, A. HECTOR, AND K. J. GASTON. 2004. How do different measures of functional diversity perform? Ecology **85:** 847–857.

POULIN, R. 1997. Species richness of parasite assemblages: Evolution and patterns. Annual Review of Ecology and Systematics **28:** 341–358.

———. 1998. Evolutionary ecology of parasites. Chapman and Hall, London, U.K., 212 p.

———, AND S. MORAND. 2004. Parasite biodiversity. Smithsonian Books, Washington, D.C., 216 p.

SMITH, B., AND J. B. WILSON. 1996. A consumer's guide to evenness indices. Oikos **76:** 70–82.

STOCK, T. M., AND J. C. HOLMES. 1988. Functional relationships and microhabitat distributions of enteric helminths of grebes (Podicipedidae): The evidence for interactive communities. Journal of Parasitology **74:** 214–227.

TILMAN, D. 2001. Functional diversity. *In* Encyclopedia of biodiversity, S. A. Levin (ed.). Academic Press, New York, New York, p. 109–120.

———, J. KNOPS, D. WEDIN, P. REICH, M. RITCHIE, AND E. SIEMANN. 1997. The influence of functional diversity and composition on ecosystem processes. Science **277:** 1300–1302.

———, P. B. REICH, J. KNOPS, D. WEDIN, T. MIELKE, AND C. LEHMAN. 2001. Diversity and productivity in a long-term grassland experiment. Science **294:** 843–845.

VIDAL-MARTINEZ, V. M., AND C. R. KENNEDY. 2000. Potential interactions between the intestinal helminths of the cichlid fish *Cichlasoma synspilum* from southeastern Mexico. Journal of Parasitology **86:** 691–695.

WILLIAMS, H. H. 1960. The intestine in members of the genus *Raja* and host-specificity in the Tetraphyllidea. Nature **188:** 514–516.

———, A. H. MCVICAR, AND R. RALPH. 1970. The alimentary canal of fish as an environment for helminth parasites. Symposia of the British Society for Parasitology **8:** 43–77.