

How parasites divide resources: a test of the niche apportionment hypothesis

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Summary

1. Modelling species abundance patterns, i.e. the distribution of relative abundance among species within the same community, has become a common framework in community ecology. To describe species abundance patterns several statistical models have been proposed, e.g. the log-normal distribution, but these do not provide an ecological explanation of the underlying processes.

2. Tokeshi introduced (1990) and developed (1993, 1996, 1999) a series of niche-orientated stochastic models to fit species abundance patterns. They suggest that abundance of species are proportional to the resources they apportion. Following this hypothesis, Tokeshi defined some processes in resource partitioning to explain species abundance patterns.

3. To study the rules which govern species assemblages, parasite communities present advantages because each host harbours a replicate community, the total niche is limited to the body of the host and demographic processes are usually similar for all parasite species in a community. Using five Tokeshi models, we searched for common rules structuring the parasite communities of six species of marine fish from the coast of Chile. The biovolume of each parasite species was preferred as a measure of its 'abundance' over actual numerical abundance, to account for the considerable variation in body size among parasite species.

4. The random assortment model, which suggests a lack of competition and interaction and independent apportionment of resources between species in the community, was fitted successfully to the parasite communities of three fish species for both means and variances of abundance ranks using a new Monte-Carlo method.

5. These results are in accordance with current knowledge on parasite coexistence rules, i.e. that most parasite communities appear non-saturated with species, with many empty niches and with interspecific competition not playing a major structuring role.

Key-words: Chile, community structure, marine fishes, parasite biovolume, Tokeshi's models.

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Introduction

The central aim of community ecology has been, and remains, to understand what determines the number of species in an assemblage, and their relative abundance patterns (e.g. May 1975; Pielou 1975; Tokeshi 1999; Weiher & Keddy 1999; He & Legendre 2002). The search for general rules underpinning community structure, how-

ever, is proving difficult (see Lawton 1999). One common problem is the low number of replicate communities available in most tests of community structure, which limits the power of any analysis used to detect existing patterns. Parasite communities have been proposed as model systems for tests of community structure because they alleviate this problem: each host individual can harbour a replicate community, allowing robust statistical testing (Holmes & Price 1986; Naeem & Hawkins 1994). Moreover, the demographic processes giving rise to assemblages of metazoan macroparasites of vertebrate hosts are similar across all the parasite

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species in the community: the population dynamics of macroparasites are open systems driven by recruitment (Poulin 1998). In contrast, in free-living communities, the population dynamics of different organisms will show much more variation.

Over the past decade several studies have used parasite communities in analyses of community structure. In particular many investigators have used presence–absence data to test for patterns of parasite species co-occurrence that depart from various null models (Guégan & Hugueny 1994; Poulin 1996; Worthen & Rohde 1996; Poulin & Valtonen 2001; Gotelli & Rohde 2002). Taken as a whole, these investigations have revealed that departures from random species assembly do occur, but they are the exceptions rather than the norm: most patterns of species co-occurrence are no different from those predicted by null models and in some cases, when a non-random parasite community structure is observed in one host species, it is not necessarily repeatable in space or time, i.e. seen again in the same population at other times, or seen at all in adjacent host populations (Poulin & Valtonen 2002). Analyses based on parasite species abundance (in this study, the term ‘abundance’ is the number of parasites per individual host) rather than mere presence–absence data also failed to reveal general patterns that are applicable to other but similar parasite communities (e.g. Haukisalmi & Henttonen 1998; Dezfuli *et al.* 2001).

The null models used in these earlier studies may be wrong, which would explain the lack of consistent results. Alternatively, general patterns may exist but not be apparent in analyses based on either the presence or abundance of parasite species. The biomass of different parasite species in a community is likely to be a better measure of their apportionment of available resources than relative abundance (Poulin 1998). In this study, we used total parasite volume instead of the ‘abundance’ of parasites species. In ecology, the term species ‘abundance’ is often used as if synonymous with the number of individuals per unit area or volume, i.e. density. For example, in work on the relative abundance distributions of free-living animals, density is used almost exclusively (Tokeshi 1993). Where individual body size is constant within a species, the expression of abundance in terms of density is justified. However, when individual body size varies greatly within a species, the estimation of species abundance becomes problematic, and this is the case in parasite communities. It is misleading to use density when this implies that an individual weighing a few micrograms has the same importance as an individual of several grams. This is particularly true when we use niche-orientated models to explain the relative abundance distribution, because it seems more relevant to consider the relation between the resource apportioned and the species biomass instead of the species density. One approach to this problem has been to use a composite ‘importance’ index, combining measures such as cover, frequency and density (Curtis 1947; Whittaker 1965). The central aim remains to choose

an ‘abundance metric’ in relation with the ecological process or the functional explanation of the process (Camargo 1996; Guo & Rundell 1997; Chiarucci *et al.* 1999; Mouillot *et al.* 2001). In our study parasite volume, which is proportional to biomass, seems the best ‘abundance metric’; this choice assumes that the total resource is divided continuously rather than discretely among species.

Traditionally, species abundance patterns or ‘abundance distributions’ have been fitted by either niche-orientated models or statistically orientated models (Pielou 1975; Engen 1978; Frontier 1985; Wilson 1991; Tokeshi 1999; Mouillot *et al.* 2000; Engen *et al.* 2002). The latter models, like the lognormal model (Preston 1948, 1962), test more the probability distributions of species than any ecological hypothesis (Pielou 1975). To overcome this statistical interpretation, McArthur (1957) proposed ecological mechanisms, based on niche-division (of a total resource represented by a one-dimensional stick) that produce abundance patterns. Generally, can we expect niche partitioning models to explain community structure, and can we find rules predicting how species divide resources (Sugihara 1980, 1989; Harvey & Godfray 1987)?

Recently, Tokeshi (1990, 1993, 1996, 1999) developed a series of niche-orientated models to provide mechanistic explanations of species abundance patterns. Although designed originally for analyses of patterns in the relative abundance of species, they can be used with biomass data (Fromentin *et al.* 1997). The models are each based on the total niche, or total resource, being broken into smaller subunits as new species are added to a community, but the way in which the division occurs differs among models. If we consider an individual host as a resource for the parasite community that it harbours, then the relative biomass of the different parasite species reflect how this resource is partitioned among species. Even if the total resource provided by the host is not used by the parasite community, we can consider that the total niche in the hosts is the niche occupied by the parasite community, i.e. the one that the community can apportion. With each individual host harbouring a replicate community, we can compare the average partitioning of the total parasite biomass among ranks of parasite species with the predictions derived from Tokeshi’s models. If one model in particular fits the observed data consistently, we might obtain an insight into some general rules of parasite community structure.

Here, we confront the predictions of five models of resource apportionment (Tokeshi 1990, 1993, 1996, 1999) with biomass data on the metazoan parasite communities of six species of marine fishes with a new fitting procedure based on species ranks. The use of relative biomass data allows us to quantify resource use more appropriately than in earlier studies based strictly on species abundance data, and a comparison of the results obtained for different host fish species will reveal the existence of general patterns, if any.

Materials and methods

DATA COLLECTION

Adult fishes of six marine species were sampled off the coast of Chile. They were: *Brama australis* (Bramidae & Valenciennes 1837), *Cilus gilberti* (Sciaenidae & Abbot 1899), *Dissostichus eleginoides* (Nototheniidae & Smitt 1898), *Seriola violacea* (Centrolophidae & Guichenot 1848), *Pinguipes chilensis* and *Prolatilus jugularis* (Pinguipedidae & Valenciennes 1837). The number of individual fish examined for each species were, respectively, 26, 29, 49, 20, 29 and 35, and the total number of metazoan parasite species found in or on each fish species were, respectively, 16, 23, 11, 11, 13 and 14. Basic parasitological information on the first three fish species has been published elsewhere (Rodriguez & George-Nascimento 1996; Garcías, Mendoza & George-Nascimento 2001; George-Nascimento, Garcías & Muñoz 2002), whereas information on the latter three has not (George-Nascimento, unpublished data).

In each of the six fish species, each individual fish was dissected and searched for metazoan ecto- or endoparasites using standard procedures. The volumetric abundance (volume of all parasite species per host, in mm^3) was used as a surrogate for biomass. The body volume of each taxon was approximated using either of the following methods. For the small parasites, body volume was determined by measuring maximum length and diameter, and computed assuming a regular body shape for the parasite (e.g. cylindrical for nematodes and

acanthocephalans, ellipsoid for digeneans and some cestodes, cylindrical with an ovoid base for other cestodes, etc.). For large-sized parasites or those of irregular shape, body volume was determined by volume displacement in a graduated container. The body volume of each parasite individual was measured for most taxa, as most of them were rare. In more common and abundant taxa, the subsample consisted of at least 30 specimens. Body sizes in parasites inhabiting more than one host species were measured separately in each host species. From these measures of volume and the data on numbers of individual parasites of each species in individual fish, we computed the total volume of each parasite species per host for all fish in the samples.

MODELS

In this study, we used five niche-orientated models of Tokeshi introduced in 1990 and developed in 1993, 1996 and 1999: Dominance decay (DD), MacArthur fraction (MF), random fraction (RF), random assortment (RA) and dominance pre-emption (DP) models. These models are based on the assumption that the abundance/biomass of species are proportional to the fraction of the total niche apportioned to them (Tokeshi 1993, 1996, 1999). A description of each model can be found in Tokeshi's papers (1990, 1993, 1996, 1999), in Laird (2002) or in Mouillot & Wilson (2002); apportionment rules for each model are summarized in Table 1. The five models, for a theoretical community of 15 species, are presented in Fig. 1.

Table 1. Niche apportionment rule for a new species joining a community in a niche filling process for the five Tokeshi models (1990, 1993, 1996, 1999)

Model	Niche apportionment rule for a new species
Dominance decay (DD)	Largest niche space invaded
MacArthur fraction (MF)	Niche/species invaded chosen at weighted random
Random fraction (RF)	Niche/species invaded randomly chosen
Random assortment (RA)	Carve out an arbitrary proportion of the remaining niche
Dominance pre-emption (DP)	Smallest niche space invaded

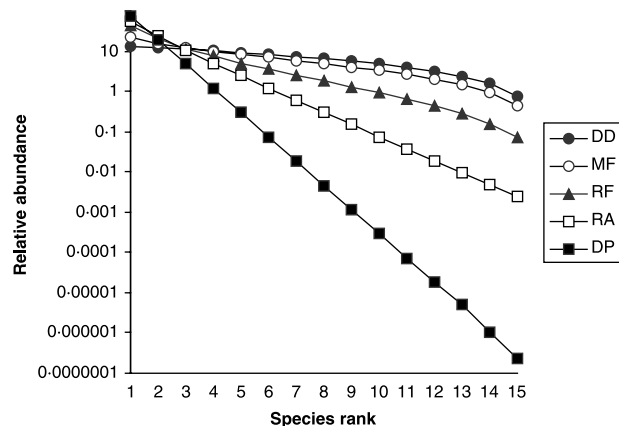


Fig. 1. Mean relative abundance/biomass distributions, plotted as dominance/diversity curves, of 15-species communities expected for the five Tokeshi (1990, 1993, 1996, 1999) models: dominance decay (DD), MacArthur fraction (MF), random fraction (RF), random assortment (RA) and dominance pre-emption (DP) models.

Notwithstanding the fact that it is not the purpose of this paper to discuss the validity of the different niche orientated models, we review briefly here past models and justify our use of Tokeshi's models. The first model which was assimilated to a niche-orientated process is the geometric series model (Motomura 1932), although it was developed originally with the aim of providing only a statistical description. The parameter of this model is difficult to interpret in an ecological way, and Tokeshi (1990) denounced a lack of consistency of this parameter among replicates. The first 'true' niche-orientated model was the broken stick model (McArthur 1957), but this model deals more with the 'niche fragmentation' process (related to community evolution) than with the 'niche filling' process (sequential colonization). For parasite communities, with a relatively short history of species accumulation, we chose to focus on the latter. Based on the same niche division rules, others (Sugihara 1980; Gray 1987) proposed models that produce patterns conforming to the lognormal model; however, this last model can be considered a special case of the random fraction model (Tokeshi 1993, 1999) and we chose not to consider it in this study despite its ecological value and the fact it was one of the first models proposed in the literature. The composite (Tokeshi 1993), the power fraction (Tokeshi 1996) and the dominance assortment models (Fesl 2002) are not included in this study because of the difficult interpretation of their hypotheses.

FITTING PROCEDURE

To fit these models, a procedure was first proposed by Tokeshi (1993). However, this procedure does not allow the rejection of communities whose variance is larger than the one expected from the model, and it is sensitive to the number of species or ranks. Bersier & Sugihara (1997) introduced a Monte-Carlo test to overcome these problems, which was improved upon by Cassey & King (2001). In their paper, Cassey & King (2001) calculated the mean and variance of abundance for each species and ranked species by their mean abundance to fit the models. This procedure implies that the species are equivalent and that the ranks are consistent among replicates, which is not the case in ecology and particularly for parasite communities. This leads to an over-estimation of rank variances, as can be observed in Cassey & King (2001). The new procedure we propose

in this study is based on the relative abundance of ranks among replicates and is detailed in 10 steps below:

1. For each fish (host) species, calculate the relative biomass of each species (parasite) in each replicate (fish).
2. Rank the species in each replicate.
3. Calculate the mean and variance of each rank j in our data set to, respectively, obtain M_{j0} and V_{j0} . If we have some zeroes (this occurs when the number of species is different among replicates), they are included in the mean and variance estimation.
4. Produce x simulations of each replicate for each model, retaining the number of ranks present in each replicate; x being 9999 in our study.
5. For each model, calculate the mean and variance of ranks j in each simulation i to obtain, respectively, M_{ji} and V_{ji} .
6. Estimate the two-tailed probability ($p_j(m)$) that an observed mean abundance/biomass of rank j is predicted by a particular model by inspecting its position in the distribution of M_{ji} with $p_j(m) = 2 \min[s_j/(x+1), l_j/(x+1)]$, s_j and l_j being, respectively, the number of simulated means (M_{ji}) smaller and larger than the observed data mean (M_{j0}).
7. Repeat this procedure for the variances to estimate $p_j(v)$.
8. Calculate T observed to summarize the $p_j(m)$ and $p_j(v)$ over all ranks as:

$$T_{Mo} = -2 \sum \ln p_j(m) \text{ for the mean and } T_{vo} = -2 \sum \ln p_j(v)$$

for the variance.

9. Compare T_o to the distribution of $T_1 \dots T_x$ calculated by applying steps 6–8 to the x simulations.
10. The final P -value, for the test that the model fits the data, is given as: $p = l/(x+1)$ where l is the number of simulated T -values greater than T_o .

More details on this procedure are provided by Bersier & Sugihara (1997) and Cassey & King (2001); our method differs only by assuming no consistency of species ranks across replicates.

Results

On average, individual fish of the six species harboured similar numbers of parasite species, i.e. they had similar parasite species richness (Table 2). However, the total volume of all parasites per individual fish varied by

Table 2. Mean (standard deviation) of parasite species richness and volume per individual host fish

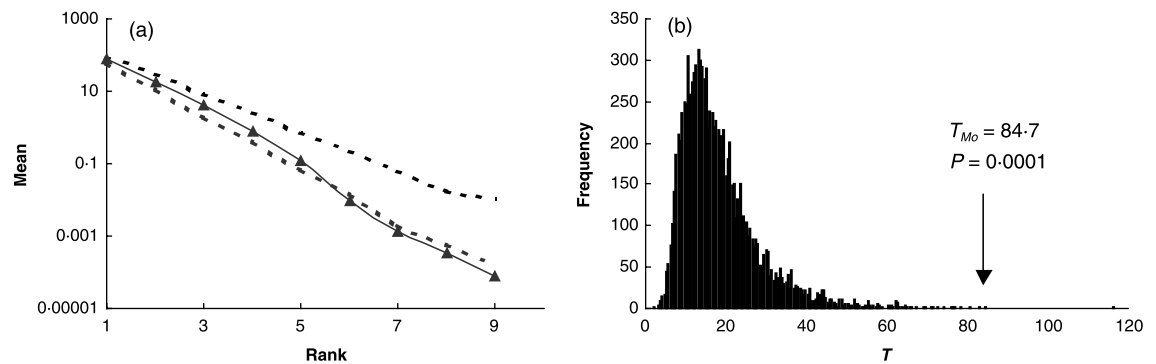
Species	Fish sizes (cm)	Parasite richness	Total biovolume (mm ³)
<i>Prolatilus jugularis</i>	28.37 (2.49)	4.28 (1.58)	25.59 (18.23)
<i>Cilus gilberti</i>	53.42 (11.14)	8.90 (2.50)	466.11 (314.34)
<i>Serirolella violacea</i>	60.94 (5.41)	4.60 (1.54)	3864.53 (4092.43)
<i>Pinguipes chilensis</i>	38.29 (3.45)	5.41 (1.45)	111.55 (53.06)
<i>Brama australis</i>	41.76 (3.80)	4.38 (1.60)	741.74 (555.80)
<i>Dissostichus eleginoides</i>	108.02 (20.87)	6.49 (1.63)	1203.99 (1292.17)

Table 3. *P*-values for a fitting attempt based on the mean of ranks of parasite communities of six fish species to the five Tokeshi models described in Table 1 and Fig. 1. Models not rejected are in bold

	Model				
	DD	MF	RF	RA	DP
<i>Prolatilus jugularis</i>	*	*	*	0.056	*
<i>Cilus gilberti</i>	*	*	*	0.119	*
<i>Seriolella violacea</i>	*	*	*	0.001	*
<i>Pinguipes chilensis</i>	*	*	*	0.090	*
<i>Brama australis</i>	*	*	*	*	0.0001
<i>Dissostichus eleginoides</i>	*	*	*	*	*

P* < 0.00001.Table 4.** *P*-values for a fitting attempt based on the variance of ranks of parasite communities of six fish species to the five Tokeshi models described in Table 1 and Fig. 1. Models not rejected are in bold

	Model				
	DD	MF	RF	RA	DP
<i>Prolatilus jugularis</i>	*	*	*	0.598	*
<i>Cilus gilberti</i>	*	*	*	0.129	*
<i>Seriolella violacea</i>	*	*	*	0.067	*
<i>Pinguipes chilensis</i>	*	*	*	0.210	*
<i>Brama australis</i>	*	*	*	*	0.055
<i>Dissostichus eleginoides</i>	*	*	*	*	*

P* < 0.00001.Fig. 2.** Observed relative biomass means for the parasite species of *Brama australis* ranked in decreasing abundance (solid triangles) and the range of dominance pre-emption (DP) model means (dashed lines) (a). Frequency distribution of the *T*-values for the means of the DP model; the observed T_{Mo} value is significantly higher for the parasite community of *Brama australis* (b), so the model is rejected.

two orders of magnitude across the six host species (Table 2).

We tested the goodness-of-fit of the six parasite communities to the five models using a Monte-Carlo procedure. We performed 9999 simulated communities for each replicate for each model and computed the means and variances for each rank of the 9999 theoretical samples.

Table 3 presents the *P*-values to reject the models tested for the means of ranks. The random assortment (RA) model was not rejected for three parasite communities: *C. gilberti*, *P. chilensis* and *P. jugularis*. For these three species, we also cannot reject the RA model on the rank variance criterion (Table 4).

We can notice that the rank variances were not significantly different from the RA model for *P. chilensis* and not significantly different from the dominance pre-emption (DP) model for *B. australis*. To illustrate these results we chose to present data for *B. australis* and the DP model, for both the means (Fig. 2) and the variances (Fig. 3).

Discussion

In this study, we attempted to find evidence of underlying rules in the parasite community structure of six species of host fishes. For this, we used five niche-orientated models with different resources apportionment

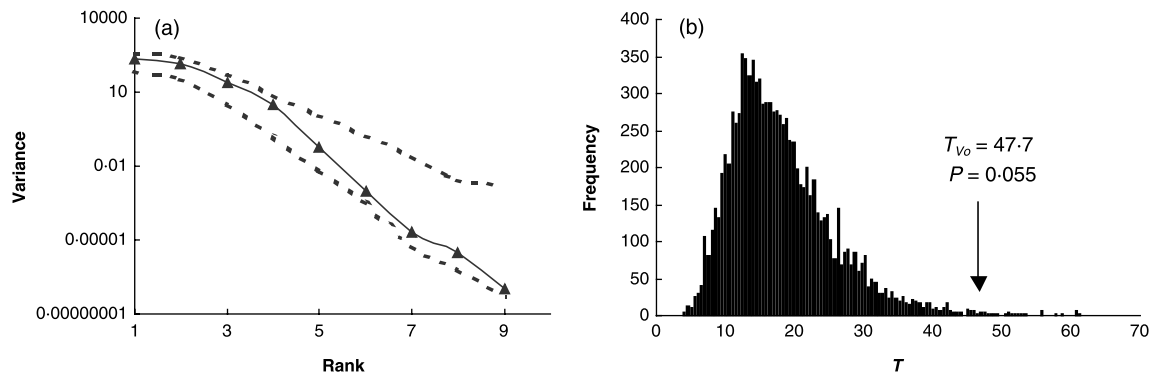


Fig. 3. Observed relative biomass variances for the parasite species of *Brama australis* ranked in decreasing abundance (solid triangles) and the range of dominance pre-emption (DP) model variances (dashed lines) (a). Frequency distribution of the T -values for the variances of the DP model; the observed T_{vo} value is not significantly higher for the parasite community of *Brama australis* (b), so the model is not rejected.

mechanisms. For three fish species (*C. gilberti*, *P. chilensis* and *P. jugularis*), the RA model was not rejected ($P > 0.05$) for both the means and variances of parasite species ranks. This means that the ecological hypothesis associated with the RA model cannot be rejected as an explanation of the parasite community structure, whereas ecological processes associated with the four other models can be rejected for these communities (Tables 3 and 4). Tokeshi described this RA model as referring to a situation where abundances of different species vary independently of each other. For example, this model seems to fit chironomid assemblages (Tokeshi 1990; Schmid 1997; Fesl 2002). Even if this model does not fit all the parasite assemblage structures of all six host species, it is important to discuss what this study can tell us about how parasites divide resources or about the rules of coexistence in parasite communities. Beyond the RA model, the process suggests 'a limit in total resources while at the same time allowing the maximum level of independence of niches' (Tokeshi 1999). This process appears in agreement with the dynamic of parasite communities because the total niche is always subjected to temporal variation, leading to limited species interactions and a lack of time for resource-based competition to develop. Indeed, several earlier workers, using mainly data on presence/absence but also sometimes on relative numerical abundance of different species, have emphasized that most parasite communities appear non-saturated with species, with many empty niches and with interspecific competition not playing a major structuring role (e.g. Rohde 1991; Poulin 1996; Morand *et al.* 1999; Gotelli & Rohde 2002). A recent study (Rohde 2001) of relative species body sizes in parasite communities also supports this view. There are therefore several lines of evidence suggesting that parasite communities are unsaturated with species and not shaped by interspecific competitive processes. Our results provide some of the strongest support for this position for at least three reasons. First, they are based on biomass data (or volumetric abundance), probably the best measure of a parasite species' presence in a community (Poulin 1998). Secondly, they could not reject the

possibility of a fit between observed and predicted patterns in three of six host species, using a model designed for completely different types of organisms and communities. Thirdly, for the three other fish species, all five models can be rejected with a very high significance. This result could be interpreted in various ways. The most common interpretation is that these parasite communities are structured by other assembly rules. We can also hypothesize a mixture of niche apportionment models for several groups of parasite species but this kind of pattern remains very difficult to fit. A species abundance pattern can be seen in a dynamic form and we can suggest that if a strong interaction occurs between species, the community structure is expected to be robust through time. In the case of parasite communities submitted to high temporal variation, a niche apportionment model can be transient, the community being ruled successively by different processes leading to an absence of structure at the time the host is killed.

Whether the RA model would provide a good fit to parasite communities in general remains to be seen. There are possible limitations to the generality of our findings. For instance, our study and most other studies cited earlier on parasite community ecology have been performed on parasite communities of fish. It is unlikely that parasite communities in other groups of vertebrate hosts are greatly different from those in fish (but see Kennedy, Bush & Aho 1986), but studies on these other animals would be useful. There have been several studies, mainly experimental, on helminth parasites of mammals in which relatively strong competitive interactions have been documented (e.g. Holmes 1961; Silver, Dick & Welch 1980; Dash 1981; Holland 1984; Patrick 1991). These studies, however, were performed under unnatural conditions where the likelihood of detecting interspecific competition may have been enhanced artificially. Typically, these studies focused on simple systems with two parasite species only, using unnaturally high intensities of infection. In natural parasite communities of vertebrate hosts, where different parasite species rarely co-occur at high

intensities in the same host individual, these interspecific interactions are less likely and the RA model may provide a good description of abundance (or biomass) patterns. The situation may be very different in communities of larval helminth parasites in invertebrates, where competitive interactions can be very strong (e.g. Kuris & Lafferty 1994).

Some theoretical work is certainly needed to allow niche apportionment models to be fitted and discriminated. Indeed, no statistical power is associated with the goodness-of-fit proposed here or in previous studies (Tokeshi 1990, 1993; Bersier & Sugihara 1997; Cassey & King 2001). One great drawback is the lack of a discrimination procedure for Tokeshi's models; this would be useful when more than one model are not significantly rejected. Bersier & Sugihara (1997) argue that the best fit is obtained with the lowest *P*-value, but this is not a correct method to discriminate among models; a separate procedure must be proposed based on a likelihood criterion. Tokeshi's models are also based on some contentious assumptions, such as a single axis representing the total resource or an orientated invasion during the niche filling process (how could a species choose to compete always with the most abundant one?). Nevertheless, the hypothesis behind these models (McArthur 1957; Sugihara 1980; Tokeshi 1990) remains very attractive as an explanation of species abundance patterns, and they are certainly the first models of a long series. We suggest that future studies should include functional trait attributes of species in new niche orientated models, because these traits govern resource apportionment rules.

In our study, biomass patterns of parasite communities fit the predictions of the RA niche partitioning model for three host fish species of the six species we investigated. This result means that we cannot reject the species coexistence rules of the RA model as an explanation of the relative distribution of parasite biomass. This result is in accordance with the study of Naeem & Hawkins (1994) on parasitoids, which concluded that parasitoid communities are minimally structured with only a minor influence of competition in coexistence rules. Nevertheless, we need further theoretical and experimental investigations to uncover the processes that could explain the observed structure of parasite communities. For such purposes, resource apportionment models can provide fruitful insights because they are derived from clear ecological hypotheses, a niche-orientated approach, and stochastic processes that most probably govern community structure, and particularly parasite assemblages.

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