Species accumulation curves and their applications in parasite ecology

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Species accumulation curves (SACs) chart the increase in recovery of new species as a function of some measure of sampling effort. Studies of parasite diversity can benefit from the application of SACs, both as empirical tools to guide sampling efforts and predict richness, and because their properties are informative about community patterns and the structure of parasite diversity. SACs can be used to infer interactivity in parasite infracommunities, to partition species richness into contributions from different spatial scales and different levels of the host hierarchy (individuals, populations and communities) or to identify modes of community assembly (niche versus dispersal). A historical tendency to treat individual hosts as statistically equivalent replicates (quadrats) seemingly satisfies the sample-based subgroup of SACs but care is required in this because of the inequality of hosts as sampling units. Knowledge of the true distribution of parasite richness over multiple host-derived and spatial scales is far from complete but SACs can improve the understanding of diversity patterns in parasite assemblages.

Introduction

Sampling patches of habitat is a necessary evil in ecology because it is rarely possible, practical or desirable to collect every individual of every species in the entire habitat [1]. Replicate samples taken from the same system tend to differ, however, both in species composition and in the relative abundance of member species. Understanding the differences and similarities between samples, their causes and how they vary over multiple scales of organization has helped to spawn the subdiscipline of diversity ecology.

One useful tool in diversity ecology is the species accumulation curve (SAC). SACs chart the accumulation of new species recovered relative to some measure of effort applied during the course of a sampling program [2]. With rare exceptions, they are concave-down curves of ever-decreasing slope and are the embodiment of the law of diminishing returns. SACs have been the subject of considerable literature in ecology and both Colwell and Coddington [2] and Gotelli and Colwell [3] have provided excellent reviews of their nature, applications and implications. One obvious application of such curves is the prediction of species richness based on extrapolations from sampled data. Using richness predictors is especially important for hyperdiverse taxa [2], which include many parasite groups. Despite the simplicity of SACs, they have many interesting properties that can tell researchers far more about a system than a simple extrapolation of how many species are likely to be present.

There are few studies that explicitly address the properties and applications of SACs to studies of parasite diversity and community structure. Parasitologists engaged in field surveys almost certainly apply the principals of SACs intuitively, if not always in practice, to decide when to stop sampling. This review addresses the ways in which SACs can assist parasite ecologists as field and analytical tools and how the properties of SACs relate to existing concepts of parasite community structure. Here, we discuss SACs as empirical tools and investigate the implications of SAC shape for understanding the organization of parasite diversity. Finally, we discuss the shape of SACs in light of a popular conceptual model of parasite community types: the interactive–isolationist continuum of Holmes and Price [4].

Types of SACs

There are two types of SAC [2], both of which have applications in parasitology. The individual-based SAC records the cumulative increase in richness against the number of individual organisms examined. Individual-based SACs are the more fundamental type in that they are based on abundance data of each species. They must, by definition, pass through the data point (1,1) because the first individual examined can only be a member of one species. By contrast, the sample-based SAC records the accumulation of new species against the quantum increases of sampling effort represented by quadrats, transects, grabs or any other collective type of sample; these curves need not pass through (1,1). Sample-based SACs can be derived from individual-based SACs, but not the reverse. In parasitological studies, sample-based SACs dominate, in which individual hosts are used as the unitary measure of sampling effort. Both types of SAC are shown in Figure 1 for parasites of the coral reef fish *Acanthochromis polyacanthus*.

SACs can also be classified by the type of model that fits the data and these models form the basis for subsequent predictions of true species richness using nonlinear regression. Under this scheme, parametric SACs can be asymptotic or nonasymptotic [2] (Figure 2). Asymptotic SACs usually fit the Michaelis–Menten equation (Equation 1a) or negative exponential models (Equation 1b):

(a) $y = ax/(b+x)$ [Eqn 1]

(b) $y = a(1-e^{bx})$

where y is observed richness, x is sample size, a is the asymptote or predicted richness and b is a measure of the

rate at which the curve approaches the asymptote. Nonasymptotic models are often logarithmic forms such as log–log or log–linear [5] but these models are less common in the literature. A range of nonparametric algorithms have found wide application and are discussed in more detail later.

SACs are useful in enabling field biologists to decide when to stop sampling: the majority of system diversity is likely to have been recovered when the curve has flattened off. SACs can also be used to estimate, based on early samples, the total richness of the system being sampled. In both applications and for both individual-based and sample-based curves, the value of SACs is greatly improved by iterative randomization of the order in which individuals or samples are added to the curve (Figure 3); this is also known as rarefaction [2] but we use the more intuitive term 'randomization'. Randomization smoothes out the influence of intersample heterogeneity and improves the model fit in nonlinear regressions. The freeware program EstimateS (Version 7.5, R.K. Colwell; http://purl.oclc.org/estimates) enables the easy generation of such randomized SACs.

Richness estimation

The data necessary to produce simple SACs also have substantial power to produce estimates of the total richness in the system. For parametric curve models, this is achieved through the fitting of nonlinear regression models to randomized data, to generate the asymptote term for the best-fitting model. (A simple program for randomizing richness data is available from the author on request and a range of commercial nonlinear regression packages is available for curve fitting.) EstimateS provides several different nonparametric algorithms for richness estimation. In an assessment of the performance of these methods when applied to parasite assemblages, Walther and Morand [6] concluded that the Chao2 and Jackknife1 algorithms converged on observed component community richness faster than other estimators, for both real and simulated datasets. Zelmer and Esch [7] also found the Jackknife estimator to be robust. Given these observations, some discussion of the relative values of these algorithms is warranted.

Both Chao2 and Jackknife1 produce estimates of undiscovered richness based on the presence of rare species, specifically singletons and doubletons. For sample-based curves, singletons means species that only occur in one sample (in the parasitological case, one host), whereas in individual-based curves, it means species that are represented by a single individual. Doubletons are similar but present exactly twice. Jackknife1 generates estimates based only on the frequency of singletons in the dataset. Chao2 generates estimates based on the numbers of both singletons and doubletons. Both of these algorithms predict that if there are some rare species in the sample, then others probably remain in the system that have not been discovered. The most recent version of EstimateS includes a 'bias-corrected' version of Chao2, wherein some of the influence of sample size is corrected to prevent overestimation of richness.

The Jackknife 1 predictor is affected only by singletons and, as the sample size gets larger, the estimate of undiscovered richness becomes progressively bigger (although it does so by ever-decreasing increments, never quite reaching 1). In both Chao2 and Chao2 bias-corrected,

the positive effect of singletons on the estimate of undiscovered species is reduced by doubletons. Thus, in a sample of 20 host animals, the change from three singleton and two doubleton parasite taxa to the reverse will reduce the Chao2 estimate dramatically by 1.58 and the Chao2 bias-corrected by 0.712. Moving from two singletons and two doubletons to two singletons and three doubletons drops the total estimate by 0.33 and 0.08 respectively. Interestingly, there seems to be an anomaly in both estimators. If one of the doubleton species mentioned earlier was found three times instead of twice, then it would have no effect on the estimate, thus increasing the estimate of richness accordingly. This is a necessary side effect of reclassifying these species from the group that is 'useful for richness prediction' (singletons and doubletons) to the group 'core, uninformative richness'. In other words, these estimators can predict more undiscovered richness if the parasites are distributed bimodally (i.e. some common, others rare) than if there is a continuum of prevalences in the sample.

The typical behavior of these estimators along the x axis is that they will initially rise much faster than observed richness, then overshoot the eventual asymptote before converging on the true richness asymptote (Figure 4). The best predictors will achieve this convergence as early as possible in a sample series. The bias-corrected Chao2 estimator seems to perform best under many circumstances.

How well do these estimators reflect the reality of what is going on biologically in parasitological systems? Superficially, it is difficult to see how the presence of a rare species would imply the likelihood that there are more rare species. However, the fact that various simulations have shown that they are effective suggests that this is precisely the case. Species estimation is really all about finding and coping with the rare species because the common ones will almost always be found. Thus, if a standard parasitological sample of 30 individuals reveals five rare (singleton) species, then perhaps the interpretation should be that this kind of animal is susceptible to infrequent parasites. Given that a sample of 30 only gives 95% confidence of discovering parasites present at 10% prevalence, the evidence suddenly becomes compelling that a further search needs to be done.

SACs as empirical tools

It is extremely simple to plot the cumulative number of new species recovered from a sequential sample of hosts in the order examined (i.e. without randomization), and this might be sufficient in the field to make a decision about when the costs of further sampling could outweigh the benefits. There are, however, several issues that can shape SACs generated in this fashion and thereby influence sampling decisions.

First, the decision about what sort of SAC to plot is not as simple as it might seem. There is a prevalent notion that individual hosts represent statistically equivalent replicates of parasite assemblages, so it might seem logical to treat them as quadrats and generate a sample-based SAC. We argue, however, that individual hosts should not be uncritically treated as equivalent sampling units because, unlike quadrats (which have a fixed size and properties), hosts in a population differ in any number of ways including size, age, diet and behavior. This is well illustrated by abundant published evidence for

relationships between parasite richness and host size (see Refs [8,9]). It can be convenient to overlook these differences during ecological studies but to do so is to risk spurious conclusions. Some interhost differences (size, age) can be controlled by using residuals (see Ref. [10] for free-living examples) but it is much harder to control for other differences (diet, behavior). Furthermore, hosts cannot be regarded as statistically independent replicates because of the tendency of parasites to aggregate in host individuals and populations [11], and the tendency of hosts themselves to behave in nonindependent fashions (e.g. schooling, territoriality). This nonindependence represents a type of dynamic spatial autocorrelation, the nature of which is poorly understood and the implications of which have not been explored for parasite communities. One possible solution is to abandon, analytically, the borders between individual hosts and generate individual-based SACs. Producing individual-based SACs involves more intensive sampling because it requires full counts of all parasite individuals rather than presence–absence data. Like sample-based curves, it requires randomizing but can avoid the inequalities of hosts as sampling units by using parasite individuals as the sample unit instead. The authors are aware of only one study that has used this approach; Miura *et al.* [12] used sample-based and individual-based SACs to draw inferences about the presence of undetected cryptic trematode species in an intertidal ecosystem. The other possible solution is to proceed with the analysis using hosts as sampling units and to discuss limitations or situations in which differences between hosts could have influenced the outcome.

Second, heterogeneity in parasite composition among hosts can radically alter the shape of the accumulation curve, just as heterogeneity between quadrats can affect SACs in free-living species [13]. The aggregation of parasite individuals and species in a relatively small proportion of the host population is a dominant pattern in nature; although much of it can derive from the intrinsic differences between host individuals (see earlier), some of it might also be stochastically generated. Strong aggregation of parasite richness (i.e. strongly skewed frequency distributions with many zeroes and with few large numbers) can cause substantial problems for the simple manual plotting of SACs (Figure 3). For example, if an unusually rich host is not encountered until late in the series, then the curve will jump at that point, which makes the decision about when sampling benefit is tailing off much more difficult. This will also cause poor model fit in nonlinear regressions if randomization is not used to generate a smoothed curve. A more serious problem, perhaps, is that if the series is not continued long enough to encounter such a host (i.e. sample size is too small), then a potentially spurious conclusion could be made (i.e. that the host population has a species-poor parasite fauna). Ultimately, this is a problem that nonrandomized SACs cannot solve.

Third, the differences in SAC shape among different types of communities have implications for the selection of target sample sizes. For example, communities represented by SACs with steep initial slopes and early asymptotes require smaller sample sizes to recover the major portion of richness in the system, whereas for SACs with shallow slopes, even with the same asymptote,

recovery of a similar portion might not be possible, practical or likely in a permitted sample size. This influence of community structure on effective sample size challenges the notion of 'magic cutoff' sample sizes like $n = 30$, the number required to detect a parasite of 10% prevalence with 95% confidence [14]. If the aim of the study is to recover the majority of parasite richness, then the sample size necessary will differ among host species depending on the distribution of parasite diversity within and between hosts.

SACs and hierarchical scale effects

Ecological communities can be delineated at several hierarchical scales of organization. In free-living systems, the most common hierarchy is spatial, in which local, regional and global scales are recognized [15]. In parasite community ecology, an additional and important hierarchical scale is recognized, which derives from the organization of hosts into individuals, populations and communities [16–18]. SACs are influenced by scale effects and, conversely, much can be inferred about scale-dependent effects from the shape of empirically generated SACs. Therefore, they are potentially useful tools in diversity ecology.

Richness partitioning explores how species richness is quantitatively and qualitatively distributed among sampling units and between scales of organization [19–24]. It evolved from the recognition by R.H. Whittaker [25] that total richness in a system can be split into two components. The first is richness due to the number of species that occur in a given sampling unit, or α richness. The second is richness due to the presence of different species in different samples or hosts, or β richness. β richness is also sometimes described as 'spatial species turnover' or 'differentiation diversity' [10]. The functional relationship between α and β diversity was initially considered multiplicative but is now known to be additive [10]. Total richness (γ) is mean α richness plus β richness (Equation 2):

$$\gamma = \alpha_\mu + \beta \qquad [Eqn\ 2]$$

This method of analyzing richness is termed the Cody tier system and is one of several partitioning schemes reviewed by Whittaker *et al.* [10]. α and γ richness are obtained empirically, and from these, β richness can be deduced by subtraction. In parasitology terminology, α richness is the same as mean infracommunity richness and γ richness is component community richness, whereas β richness remains a measure of parasite species turnover between hosts.

Communities can be α or β dominated [22]. In α-dominated communities, richness is concentrated at the individual sample level. In other words, any individual sample (or individual host) contains the majority of the richness that exists at the next hierarchical level. In β-dominated communities, individual samples (or hosts) tend to be dissimilar and, therefore, more of the total richness exists as species turnover among samples (or hosts). In this case, communities are said to be 'enriched' by the regional pool of species [26]. These patterns are associated with specific shapes of SAC; α-dominated systems produce steep initial slopes that rapidly reach asymptote, whereas β-dominated systems produce gradual slopes and late asymptotes.

To illustrate richness partitioning and its effects on the SAC, two hypothetical host populations of five individuals can be considered, each with a component community richness of five (Figure 5). In one population each host harbors all five species. In the other, each host harbors one species and they are all different. Despite having the same total or γ richness (five), the two host populations have different α and β richness. For the first component community: $\gamma = 5$, $\alpha_\mu = 5$ and therefore $\beta = 0$; for the other community, $\gamma = 5$, $\alpha_\mu = 1$ and therefore $\beta = 4$. By partitioning richness in this way and relating the values of α and β richness to each other and to total richness, the distribution of parasite species richness in the host population can be better characterized. To our knowledge, this method has not been applied to host–parasite systems but we predict that it will prove valuable in the exploration of patterns of parasitism associated with different types of host–parasite systems.

Two other aspects of richness partitioning deserve comment. The first is that β richness can be related to community similarity indices [23]. These indices have long been used to describe the similarity of community species composition, which is essentially the same as species turnover between sampling units. The second is that both the β-by-subtraction and the β-by-similarity indices rank taxonomic differences among species in a sample equally. Izsak and Price [21] recently derived a β index using presence–absence data that incorporates a measure of taxonomic distance. In other words, the difference between two species in their contribution to β can be weighted by their relatedness. As a parasitological example, if two parasite species that occur in two different infracommunities are in the same genus, they would contribute less to the β richness component than two parasites that are not in the same genus. This weighting continues in increasing increments up the taxonomic hierarchy. Although Izsak and Price [21] recognized that higher taxa are inherently (partly) subjective units, they considered that important information about species turnover is not incorporated by β components that ignore taxonomic contributions. We tend to agree, although this can have no bearing on the shape of SACs.

The interactive–isolationist continuum

Holmes and Price [4] first proposed the concept of an interactive–isolationist continuum of parasite community structure. Briefly, interactive infracommunities are considered to be composed of species with high transmission rates, engaged in strong interspecific interactions, leading to predictable infracommunity structure and high similarity among infracommunities. Isolationist infracommunities, by contrast, are considered to be composed of species with low transmission rates, engaged in few or weak interspecific interactions, leading to unpredictable infracommunity structure and low similarity between infracommunities. In other words, stochasticity plays the dominant part in their assembly.

There are clear parallels between this conceptual framework and the richness partitioning and community similarity patterns discussed in the preceding section. Clearly, interactive communities will generate α-dominated patterns of steep initial slope and early asymptote due to their high similarity, whereas isolationist communities will have the β-dominated

pattern of gentle slope and late asymptote due to their diminished and stochastic nature.

The interactive–isolationist continuum has a central place in the theory of parasite community ecology [27]. Methods to assess objectively the placement of a given community on this continuum were lacking, however, which resulted in a degree of controversy [28,29] until Dove [30] proposed an index of interactivity. This index is derived from a negative exponential equation for SACs. By relating the component community richness (SAC asymptote, γ richness, or a term of Dove [30]) to the b term that describes the slope of the SAC (β richness), the index enables comparison of interactivity between hosts of different total richness.

More recently, Poulin and Luque [31] proposed an easier, nonparametric method for assessing interactivity. They suggested ranking infracommunities from poorest to richest and then counting hosts until 50% of the component community richness had been reached. This point was termed CC_{50} and was considered to represent the position of that community on the interactive–isolationist continuum. Interactive communities should have a low CC_{50}, whereas isolationist communities should have a high CC_{50}. An advantage of this method lies in avoiding the necessity for randomizing; however, Poulin and Luque [31] recognized that the method does have an inherent sensitivity to sample size. This is because the 50% point to be reached is not of the total component community richness but the sample component richness, which is a subset of total richness and a direct function of sampling effort.

Importantly, these methods do not measure interactivity directly. Rather, they serve to condense several properties of parasite communities into a single number that is likely to be strongly correlated with interactivity [31]. Neither method has been rigorously tested for several large datasets nor has any comparative analysis of their performance been carried out. However, methods now exist for estimating interactivity objectively while accounting for effects such as sample size, infracommunity heterogeneity and differences in total component community richness. Interesting explorations of Holmes' and Price's idea surely await among some existing ecological datasets.

Figure 6 illustrates two forms of SAC and how they relate to several ecological axes, some of which have been previously discussed, such as the interactivity continuum and richness partitioning patterns. The fact that SACs can reflect so many recognized ecological axes underscores their usefulness but also indicates that these ecological continuums are probably intimately related. The core-satellite concept of Hanski [32] was involved in the genesis of the interactive–isolationist continuum but the relationship of these parasitological concepts to others in ecology [such as local versus regional enrichment and niche versus dispersal (neutral) assembly] need to be formalized and explored. This should be a fertile area of research in parasite ecology in the future (Box 1).

Concluding remarks

We argue that richness, sampling effort, hierarchical scales (both spatial and host-derived) and community assembly are interrelated concepts in parasite community ecology that deserve an integrated approach. SACs provide a simple and direct entry into the exploration of these

issues and a useful practical tool for application in the field. They can be used to estimate richness in ecological systems, to make pragmatic decisions about the application of sampling effort and to draw inferences about parasite community structure and assembly rules. Two extremes of SAC shape – steep slope with early asymptote and gentle slope with late asymptote – can be related to a range of ecological continuum concepts and express many properties of parasite assemblages that are of interest to parasite ecology researchers. The properties of nonasymptotic SACs are more mysterious and deserve closer investigation. Much research remains to be done on the properties and applications of these useful curves in the burgeoning field of parasite ecology.

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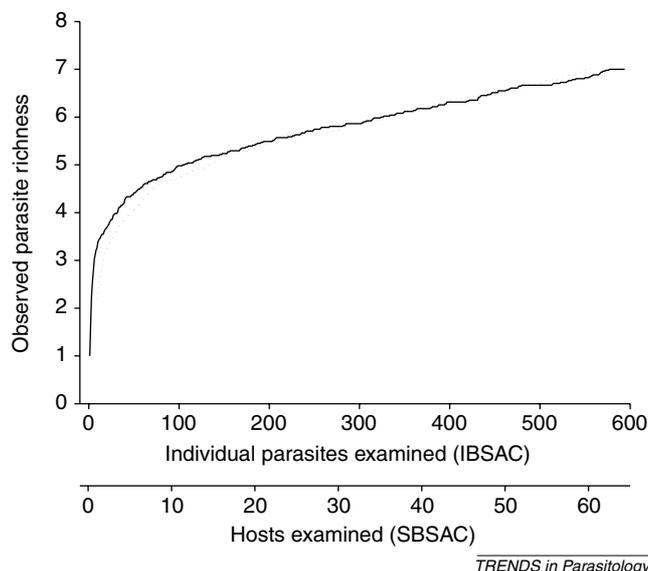
Figure 1. Individual-based (IBSAC, solid line) and sample-based (SBSAC, broken line) species accumulation curves for parasites of the coral reef fish *Acanthochromis polyacanthus* from the Great Barrier Reef. Both curves have similar form (in this case a nonasymptotic form) but in the IBSAC, the unit of effort is the individual parasite and the

curve passes through (1,1), whereas in the SBSAC, the unit of effort is the individual host and the curve might not pass through (1,1). In systems in which abundance within hosts is high, SBSAC often looks different from IBSAC.
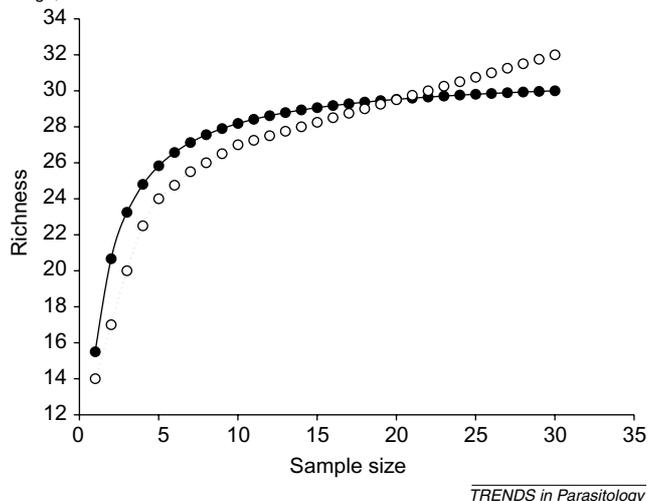

TRENDS in Parasitology

Figure 2. Asymptotic (filled circles) and nonasymptotic (open circles) species accumulation curves. Asymptotic models follow negative exponential or Michaelis–Menten forms, whereas nonasymptotic models are typically logarithmic and often involve large contributions from rare species.

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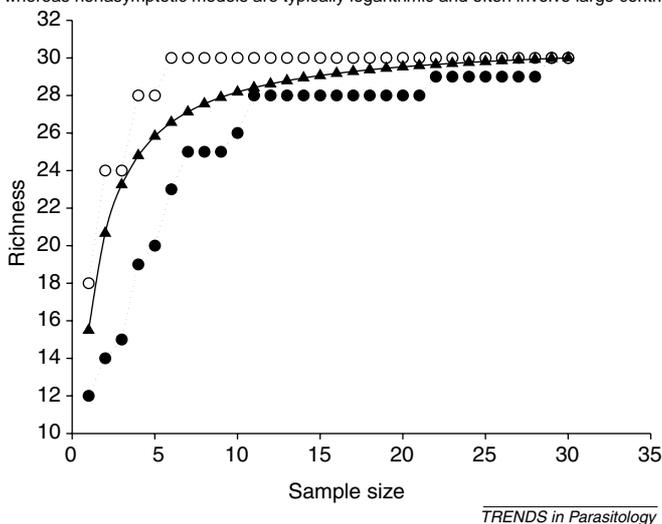
Figure 3. Two sample-based species accumulation curves from the same population (filled and open circles) and their associated randomized curve (filled triangles). The randomized curve smoothes the effects of spatial heterogeneity or differences in richness between hosts, facilitating better fits in nonlinear regression models and, thus, more robust estimates of total richness in asymptotic models.
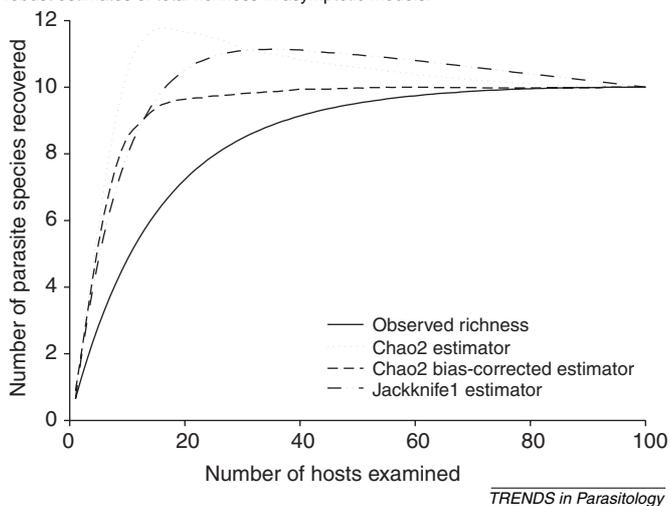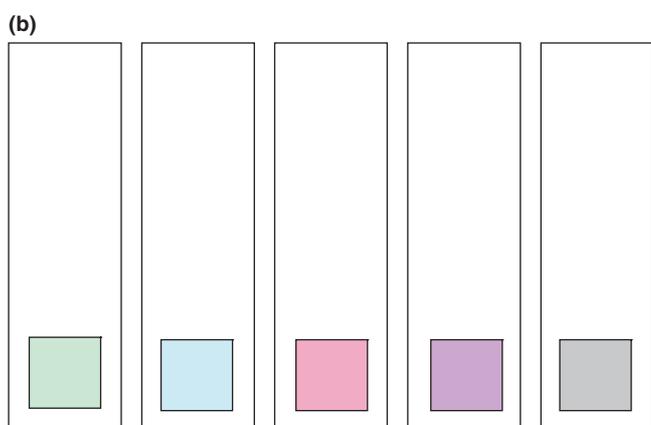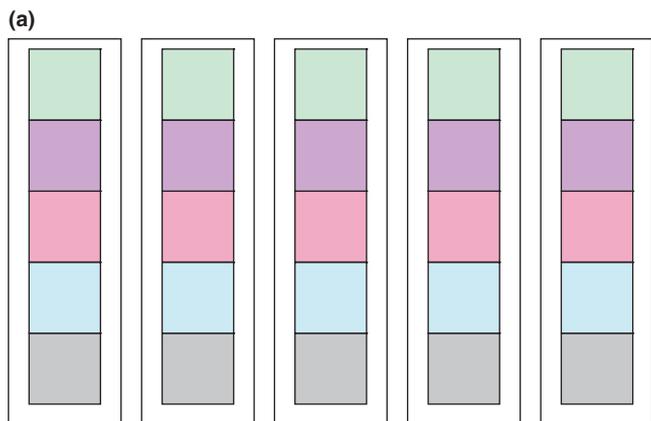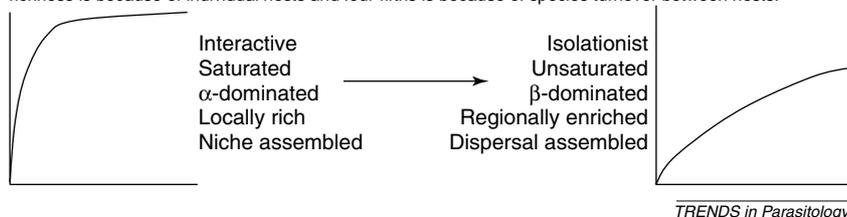

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Figure 4. Relative performance of different richness estimators. The bias-corrected Chao2 estimator approaches asymptotic richness early without overshooting; it therefore seems to be the best estimator of true species richness.

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Figure 5. Richness partitioning more fully characterizes diversity distribution among hosts (unfilled long boxes). Both population **(a)** and population **(b)** have the same total richness of five parasite species (colored squares). In population (a), however, all richness is because of richness in individual hosts, whereas in population (b), only one-fifth of richness is because of individual hosts and four-fifths is because of species turnover between hosts.

Figure 6. Species accumulation curves (SACs) can reflect ecological continuums. The two extreme forms of SACs, steep slope with early asymptote (left) and gentle slope with late asymptote (right), can be related to a suite of interrelated ecological concepts including dispersal modes, interactivity and richness partitioning. They might, therefore, be useful tools in a wide range of ecological studies.

Box 1. Outstanding questions

(i)   What are the relative contributions of host-derived and spatially derived scale effects on parasite community composition?

(ii)   Is parasite diversity typically dominated by α richness (within host) or β richness (species turnover between hosts)?

(iii)   Are parasite infracommunities enriched top-down by higher spatial or host hierarchy scales, or are they limited by internal niche processes? In other words, are they more dispersal assembled or niche assembled?

(iv)   How much has global parasite richness been underestimated by sampling inappropriately?

(v)   Is the interactive–isolationist continuum still a useful model of parasite community composition or is it just another expression of the assembly rule debate?