REVIEW ARTICLE

Are there general laws in parasite ecology?

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SUMMARY

As a scientific discipline matures, its theoretical underpinnings tend to consolidate around a few general laws that explain a wide range of phenomena, and from which can be derived further testable predictions. It is one of the goals of science to uncover the general principles that produce recurring patterns in nature. Although this has happened in many areas of physics and chemistry, ecology is yet to take this important step. Ecological systems are intrinsically complex, but this does not necessarily mean that everything about them is unpredictable or chaotic. Ecologists, whose grand aim is to understand the interactions that govern the distribution, abundance and diversity of living organisms at different scales, have uncovered several regular patterns, i.e. widely observable statistical tendencies, in the abundance or diversity of organisms in natural ecosystems. Some of these patterns, however, are contingent, i.e. they are only true under particular circumstances; nevertheless, the broad generality of many patterns hints at the existence of universal principles. What about parasite ecology: is it also characterized by recurring patterns and general principles? Evidence for repeatable empirical patterns in parasite ecology is reviewed here, in search of patterns that are consistently detectable across taxa or geographical areas. The coverage ranges from the population level all the way to large-scale patterns of parasite diversity and abundance (or biomass) and patterns in the structure of host-parasite interaction networks. Although general laws seem to apply to these extreme scales of studies, most patterns observed at the intermediate scale, i.e. the parasite community level, appear highly contingent and far from universal. The general laws uncovered to date are proving valuable, as they offer glimpses of the underlying processes shaping parasite ecology and diversity.

Key words: aggregation, biomass, contingency, interaction networks, macroecology, metabolism, scale, species richness.

INTRODUCTION

At some point during the development of a scientific discipline, its practitioners must start asking whether the phenomena they investigate are governed by some deep universal laws. These are generally manifested as recurring and predictable patterns among the possible outcomes of natural events. Only by identifying regularities among the phenomena we observe can we hope to uncover the general processes shaping the natural world. This important step has proven relatively straightforward in some branches of science. In some areas of physics or chemistry, for instance, simple universal laws expressed by simple mathematical equations seem to capture a broad range of natural phenomena, allowing scientists to make robust predictions about further phenomena that have not yet been observed. Finding general predictive laws in ecology has not been this easy, however. Several years ago, Canadian ecologist Rob Peters (1991) delivered a stinging critique of ecology in his widely read book, focusing mainly on ecology's lack of predictive power. He stated: ''Ecology seeks to predict the abundance, distributions and other characteristics of organisms in nature … This book contends that much of contemporary ecology predicts neither the characteristics of organisms nor much of anything else'' (Peters, 1991). Using sharp words, he went on to argue that the main, if not the sole, objective of ecology should be to develop predictive models of nature. I personally believe that there is much more to science than making reasonably accurate predictions about the world at large. Nevertheless, identifying general ecological laws and making full use of their power to predict is of crucial importance to scientists faced with current environmental and conservation issues.

So what is a law? Relevant dictionary definitions include generalization based on recurring events, general principle, and widely observable tendency.

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Here, I use the term as meaning a general principle underpinning recurring patterns or statistical regularities among natural phenomena (see Lawton, 1999). Thus, a law is more than a detectable pattern: it is also the mechanism responsible for the pattern. Of course, the first step in uncovering a law is finding a pattern; this is then followed by hypotheses and tests of possible underlying mechanisms. General laws should apply more or less universally, under almost any set of circumstances, as they involve universal processes that should generate the same patterns repeatedly. In other words, true general laws are not contingent, i.e. they are not restricted to certain taxa or to specific habitats.

Are such general laws possible in ecology? Ecological systems are notoriously complex, with many interacting entities, many scales of observations, and non-linear dynamics (i.e. consequences are not necessarily proportional to their causes). This could make recurring patterns and general mechanisms less likely, or at least more difficult to identify. Yet, not everything in ecology is unpredictable and chaotic. In recent years, macroecology, the branch of ecology focused on large spatial scales, has been remarkably successful at finding highly repeatable patterns from which have emerged general laws (Brown, 1995; Gaston and Blackburn, 2000; Storch and Gaston, 2004). The complex nature of ecological systems does not therefore preclude the existence of universal principles guiding their formation. Uncovering general laws is fundamental to the development and maturation of ecological theory, and represents a major step on the path toward understanding nature (Pickett *et al.* 1994).

Here, I will review the evidence for the existence of general laws applying to the ecology of parasites. Given the breadth of the topic, the scope of the review will be somewhat restricted. Firstly, I will focus on the ecology of macroparasites (helminths and arthropods) in vertebrate hosts. Some of the general laws discussed in the review would no doubt apply to other host-parasite systems, but I will limit my use of empirical examples to metazoans parasitic in vertebrates. Secondly, I will only tackle traditional ecological questions relating to the distribution, abundance and diversity of parasitic species. General laws would surely also apply to the evolution and ecology of parasite virulence or life-history traits, and to other aspects of parasite ecology, but these are not covered here. Finally, general laws can be sought at several hierarchical scales. In this review, I will begin at the parasite population level and scale all the way up to entire parasite faunas and host-parasite interaction networks. In general ecology, this hierarchical progression would involve going from population biology, through community ecology and all the way up to macroecology. This stepwise approach will highlight the scale-dependence of recurring statistical patterns in parasite ecology.

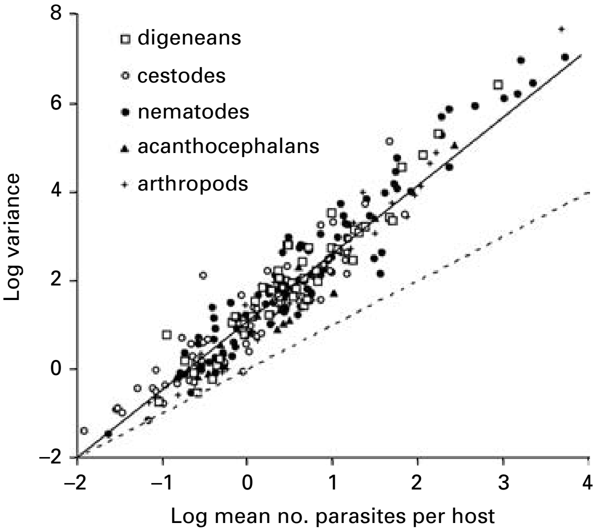

Fig. 1. Relationship between the variance and the mean number of parasites per host across 269 natural populations of metazoan parasites in their vertebrate hosts. The solid line is the fitted regression line ($r^2 = 0{\cdot}87$), and the broken line represents the 1:1 relationship expected if the variance is equal to the mean, i.e. for a Poisson distribution with a variance-to-mean ratio of unity. Data are from Shaw and Dobson (1995).

INFRAPOPULATIONS, POPULATIONS, AND METAPOPULATIONS

In reality, a parasite population consists of all individuals of 1 parasite species, whatever their developmental stage, living in 1 locality and forming a potentially interbreeding group. In practice, however, it is usual to consider only individuals at the same stage of their life-cycle in 1 particular host population, such as adult worms inside their definitive host. The parasite population is broken up into smaller units, or infrapopulations, each consisting of all conspecific parasites inside 1 individual host (Bush *et al.* 1997). One of the simplest questions one might ask about such spatially fragmented populations is whether there exist recurring patterns in the distribution of parasite individuals among host individuals. More than 35 years ago, Crofton (1971) was already proposing that an aggregated distribution pattern was so widely observed among a range of different parasite populations that it should be seen as a defining feature of parasitism.

It turns out that he was absolutely right. In their review of the empirical evidence, Shaw and Dobson (1995) found that aggregation was almost universal among populations of metazoan parasites. In practically all populations surveyed, the variance-to-mean ratio in numbers of parasites per host individual was higher than unity, i.e. higher than expected from a random distribution (Fig. 1). In addition, observed aggregation levels seem to be restricted to a relatively narrow and predictable range. In the regression of variance against mean numbers of parasites per host individual, the points are tightly constrained along the regression line, with the mean explaining almost 90% of the variability in the variance (Fig. 1). Intermediate levels of aggregation may have been favoured by selection, since when aggregation is too high the parasites will incur high mortality resulting from parasite-induced host mortality, and when it is too low mating probability will be low as well. The key point here is that this recurring distributional pattern provides us with our first general law of parasite ecology: within a parasite population, parasites are aggregated among host individuals. Before a new population is sampled for the first time, we can make the safe prediction that the parasites will be aggregated, and using the regression shown in Fig. 1 we can even predict with some confidence the exact level of aggregation that we can expect to observe based on mean abundance. The very rare exceptions to this universal pattern are generally quite informative, because they point to unusual circumstances that can override the general law (Poulin, 2007).

This law of aggregation provides an excellent illustration of how the search for general laws can propel a science forward by fuelling research into processes and mechanisms brought under the spotlight directly because of the discovery of a recurring pattern. It is only after observing repeatable patterns of aggregation in natural parasite populations that research was initiated into the causes of heterogeneities in infection levels among individual hosts. We have now achieved a good understanding of the environmental and genetic components of exposure risk and immunity (Wilson *et al*. 2002; Poulin, 2007); interest in these important issues has been driven mainly by the realization that parasite aggregation, and thus inequalities in infection levels among hosts, are universal phenomena that required explanation.

Are there other general laws at the parasite population level? There are certainly other recurring patterns emerging from the empirical studies available. For instance, the prevalence of infection, or the percentage of host individuals harbouring a parasite species within a locality, is generally positively correlated with the mean number of parasites per host, when one compares different parasite species (e.g. Morand and Guégan, 2000). Parasite species that achieve higher prevalence locally also tend to occur in a greater number of localities within a geographical region (e.g. Barker *et al*. 1996; Cone *et al*. 2006). These patterns may be nothing but epiphenomena of parasite abundance, but they are recurring patterns nonetheless, produced by the same underlying processes, and can thus be considered as general laws.

Parasite populations of the same species do not exist in isolation, but as parts of metapopulations, i.e. interconnected networks of populations (Hanski and Gilpin, 1997). The different parasite populations within a metapopulation are linked by exchanges of individuals via host migration or other dispersal routes. Are there also recurring patterns on this higher scale, such as patterns of gene flow among parasite populations? Answers to this question are now coming from studies of the genetic structure of parasite populations based on mitochondrial or microsatellite DNA markers. These studies indicate that there is much gene flow among parasite populations, even on scales of hundreds or thousands of kilometres (Anderson *et al*. 1998). Two factors that appear important in limiting gene flow between any two parasite populations and in determining the genetic structure of the metapopulation are the geographical distance between populations, and the mobility of the most vagile of the host species used by a parasite for the completion of its life-cycle (e.g. Blouin *et al*. 1995; McCoy *et al*. 2003; Criscione and Blouin, 2004). These studies are still too few, however, to allow anyone to conclude to the existence of predictably recurring patterns, and thus to the operation of general laws, at the metapopulation level.

INFRACOMMUNITIES, COMPONENT COMMUNITIES, AND METACOMMUNITIES

Moving up from parasite populations we reach the level of parasite communities, or the ensembles of parasite populations of different species living in sympatry in a host population. According to some ecologists, when we tackle the community level we enter the realm of messy patterns. In his invited review on the state of ecology, British ecologist John Lawton (1999) said: ''Community ecology is a mess, with so much contingency that useful generalizations are hard to find''. He was of course basing his conclusions on a review of the literature on communities of free-living organisms, but there is no reason to expect anything different with parasite communities.

As with populations, parasite communities are organized in a hierarchical manner, with infracommunities consisting of all parasites of all species found together in 1 individual host, and the component community representing the sum of all infracommunities, i.e. all parasites of all species found within a host population (Bush *et al*. 1997). A range of patterns could be sought at these levels to detect the operation of general laws, but here I'll focus on just two of them, to illustrate the sort of results that are typical at the community scale. Firstly, are there universal patterns in the observed limits on species richness of infracommunities across several comparable component communities? And secondly,

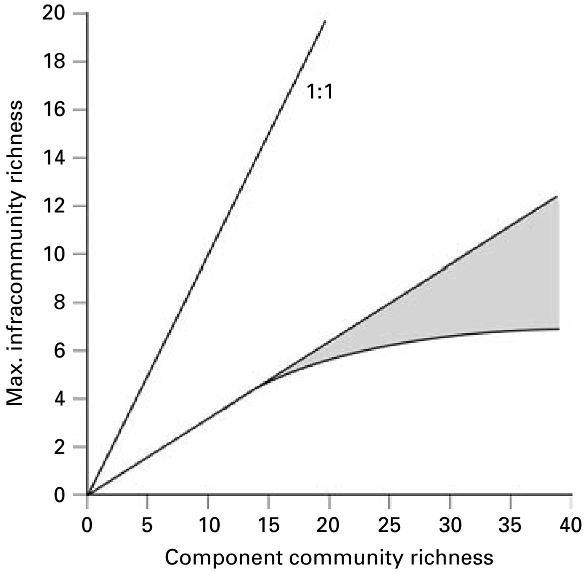

Fig. 2. Possible relationships between the maximum (or mean) infracommunity species richness and the richness of the component community, across different but comparable component communities. The 1 : 1 line represents the hypothetical case in which all species in a component community occur within individual infracommunities, regardless of how many species there are. The other two lines, i.e. the bounds of the shaded area, encompass the range of relationships that are actually observed. At the upper end are linear relationships, where infracommunity richness increases proportionately with the richness of the component community, usually with a maximum of 30–50% of the species in the component community potentially co-occurring in the same infracommunity. At the lower end is a curve with an asymptote, indicating that infracommunities become saturated with species, i.e. that there is a ceiling to how many species can 'fit' in an infracommunity.

are there recurring patterns of non-random associations among parasite species in component communities?

The first question addresses the possibility that there is an upper limit, or a ceiling, on how many parasite species can coexist in an infracommunity. The most common approach to this question is to quantify the relationship between the maximum observed richness of infracommunities and the richness of the component communities to which they belong. This can be done among different host species or, preferably, among component communities in different populations of the same host species. In principle, the observed relationships can range between two extremes (Cornell and Lawton, 1992). At one extreme, the relationship can be linear, indicating that the maximum number of species seen in an infracommunity is some fixed proportion of the number of species available from the component community (Fig. 2). At the other extreme, the relationship can be curvilinear, such that infracommunity richness becomes increasingly independent of component community richness as the latter increases, eventually levelling off at some maximum value (Fig. 2). Curvilinear relationships between infracommunity richness and component community richness suggest that infracommunities become saturated with species when the local species pool is large enough, though other explanations are also possible (Srivastava, 1999; Hillebrand, 2005). Available evidence from parasite communities indicates that the full gamut of possible relationships is observed. For instance, of 2 studies on component communities of intestinal helminths in eels, *Anguilla anguilla*, across the United Kingdom, one reported a curvilinear relationship between maximum infracommunity richness and component community richness (Kennedy and Guégan, 1996), whereas the other reported a strong linear relationship (Norton *et al*. 2004*b*). The full range of possible relationships, from linear to curvilinear, is also seen from other host-parasite systems (e.g. Poulin, 1996; Calvete *et al*. 2004; Krasnov *et al*. 2006). Whatever these may tell us about the importance of resource competition or other limiting factors in parasite communities, there is clearly no evidence for a general law governing the species richness of infracommunities across all component communities.

The second question asked above concerns the existence of structure in the composition of infracommunities, and whether or not there are recurring and repeatable patterns of non-random associations among parasite species. The distribution of parasite species among infracommunities can range from completely random to highly structured (Poulin, 2005). In a 'random' scenario, the probability of occurrence of any parasite species in a host individual is equal to its prevalence in the host population, and is totally independent of the presence of other parasite species. The most basic departure from randomness consists of positive or negative associations between pairs of parasite species, i.e. pairs of species that co-occur in the same infracommunities more or less often than expected by chance. Any significant association between 2 parasite species is a sign that the composition of infracommunities is not random. A more powerful approach is to look at the entire set of parasite species rather than tackling them 1 pair at a time. One can compare the observed pattern of parasite occurrences among host individuals with that expected under random assembly of infracommunities. Various null models have been proposed to generate expected random patterns, and these, if appropriate and chosen with care, can provide a solid baseline for comparisons with observed patterns (Gotelli and Graves, 1996). The most common application of this approach to parasite communities has involved testing for the presence of nested species subsets, a pattern often seen in communities of free-living animals (Patterson and Atmar, 1986; Worthen, 1996; Wright *et al*.

1998). Although the theory underpinning nested subsets is more applicable to patterns of presence-absence of parasite species in different host populations or localities than to their presence-absence in individual hosts (González and Poulin, 2005), the search for nested subsets has been intense at the parasite component community level. In a parasite component community, a nested pattern would imply that the species forming species-poor infracommunities are distinct subsets of progressively richer infracommunities. In other words, in a nested pattern, parasite species with high prevalences are found in all sorts of infracommunities, whereas rare parasite species only occur in species-rich infracommunities. To determine if there is a significant nested subset pattern in a parasite component community, the observed pattern is tested against the expectations derived from a null model based on each species' prevalence.

Nestedness has been investigated extensively in communities of ecto- and endoparasites of fish hosts. Although significant nested patterns have been observed in the parasite communities of some fish species, overall nestedness is not a common pattern in these communities, occurring only in about one third of them (Worthen and Rohde, 1996; Rohde *et al*. 1998; Poulin and Valtonen, 2001). The possibility exists also that significant nested subsets are merely artefacts of heterogeneity in age or size among host individuals in a sample, such that nestedness would result from ontogenetic changes in parasite acquisition rather than from intrinsic community processes (see Guégan and Hugueny, 1994; Poulin and Valtonen, 2001; Zelmer and Arai, 2004). Another departure from random assembly, qualitatively opposite from nestedness and dubbed anti-nestedness, is seen in another 30% or so of parasite communities of fish (Poulin and Guégan, 2000; Poulin and Valtonen, 2001). Thus, the absence of any detectable structure is a common pattern observed in these communities, suggesting that structuring forces are only occasionally responsible for the distribution of parasite species among infracommunities (see also Gotelli and Rohde, 2002). Any pattern in the structure of parasite communities appears to be contingent on the host species involved.

The contingency of community structure runs even deeper: when searching for nested patterns within the same parasite component community but in different years, or within component communities in different populations of the same host species, there is little apparent repeatability of patterns across space or time. For instance, among samples of red grouper, *Epinephelus morio*, collected along the southeastern coast of Mexico, highly significant nested patterns were observed in some localities but not in others, despite the species composition of the various parasite component communities being roughly the same among samples (Vidal-Martínez and Poulin, 2003). Similarly, significant nested patterns were only found in some of the distinct populations of a pelagic fish, the anchovy *Engraulis anchoita*, sampled in the South West Atlantic (Timi and Poulin, 2003). In contrast, Carney and Dick (2000) observed consistent nested subset patterns in the composition of metazoan infracommunities of perch, *Perca flavescens*, across lakes and years. The vast majority of other studies, however, showed that community structure is not repeatable in space or time within otherwise similar parasite communities (see Poulin and Valtonen, 2002; Calvete *et al*. 2004; Norton *et al*. 2004*a*). Non-random patterns of parasite community structure are therefore found in only some host fish species, and only in some populations of these host species or during certain years. The idiosyncratic nature of parasite community structure is in itself informative, because it points to the predominance of local or seasonal factors over universal processes. Nothing here suggests the existence of general laws applying to the structure of parasite communities: at this level, contingency rules supreme.

The inherent properties of parasite communities can make it difficult to use them as models for testing theoretical predictions (see Dove, 2006). A change of direction will be necessary for parasite ecologists to uncover the general laws, if any, operating at the parasite community level. New information on parasite communities is accumulating rapidly, but most of it consists of descriptive surveys of the parasites in previously unstudied host populations or species. These surveys, which in the end are merely lists of parasite species in component communities, fill the pages of many second- and third-tier parasitology journals. They contribute useful data for studies of parasite metacommunities and parasite faunas (see below), but on their own they add nothing to our understanding of parasite community structure. This incremental, theory-free expansion of our knowledge of parasite biodiversity is what some refer to as stamp collecting; if driven by hypothesis-testing, this same work could achieve so much more.

Not all parasite surveys are merely lists of species. The application of certain ecological concepts to parasite systems has become common practice in parasite community ecology. For instance, the core and satellite species concept (Hanski, 1982) is now part of the traditional tool kit of parasite community ecologists. Early users of the core and satellite species idea (e.g. Bush and Holmes, 1986) actually derived new insights into parasite community structure from the application of the concept to parasite prevalence values. Over the years, however, the trend has been to use core and satellite species as mere descriptive labels, and to pigeonhole parasite species within a community into either category based on some arbitrarily chosen threshold prevalence value. This fails to address the key questions. For example, are there general patterns across different communities in the shape of the frequency distribution of species prevalence values? Other traditionally popular concepts in parasite community ecology, such as the distinction between interactive and isolationist communities (Holmes and Price, 1986), are also now mostly used in a descriptive context. Beyond trivial patterns, this approach has not uncovered the existence of fundamental and universal processes. Of course species interactions are more important in some communities than in others (see Poulin and Luque, 2003); the real issue is what determines the variation in interaction strength among different communities. If there are general laws of parasite community structure, and if we are to find them, we will need to replace the detailed single-community descriptive approach that currently dominates the field, with a multi-community comparative approach.

Parasite communities can also be examined at a slightly larger spatial scale. Just like parasite populations of the same species do not exist in isolation, but as parts of metapopulations, parasite communities in the same host species also form interconnected networks of component communities. The different component communities within a 'metacommunity' are linked by movements of individual hosts between host populations or via other dispersal routes. We might expect recurring patterns on this higher scale, such as patterns in the similarity of component communities within a metacommunity. If the similarity between pairs of component communities is measured as the proportion of shared species, i.e. with the Jaccard index, and plotted against the geographical distance between them, a negative relationship would be expected (Poulin and Morand, 1999). Among communities of terrestrial plants, similarity between communities decreases exponentially with distance, with slopes roughly consistent across different plant types (Nekola and White, 1999). Is the same true for parasite component communities? Well, the available evidence suggests that observed patterns are contingent on the host species or type of parasites studied (Poulin, 2003; Krasnov *et al.* 2005; Oliva and González, 2005). Even among intestinal helminth communities in similar host species and within the same geographical area, different patterns emerge, ranging from strong decreases in similarity with distance all the way to non-significant effects of distance (Fig. 3). A greater consistency among the results from different metacommunities might be achieved by focusing on distinct subsets of parasite species rather than on all species, for instance by analysing only species with similar opportunities for dispersal among component communities (Karvonen and Valtonen, 2004; Fellis and Esch, 2005). Also, repeatable patterns depend on the host species that are compared being sampled across most if not all of their geographical range (Oliva and González, 2005). Still, to date, there is no convincing evidence that a general law controls the relationship between community similarity and spatial distance. As for other aspects of parasite community ecology, contingent patterns predominate.

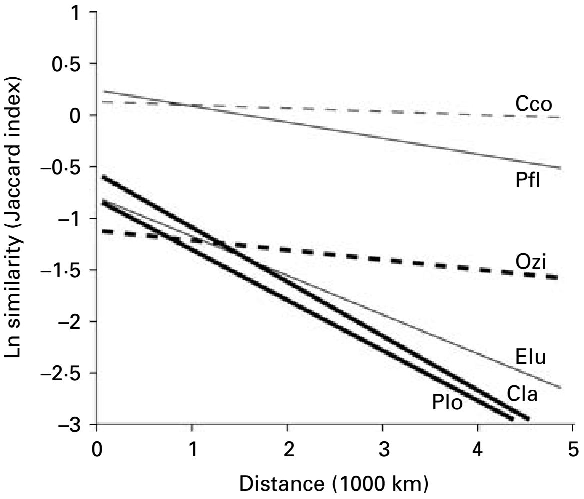

Fig. 3. Relationship between the similarity in the species composition of helminth component communities (measured using the Jaccard index) and the distance between them. The relationships were computed across all pairwise comparisons between different host populations, though only the slopes are shown here, separately for 3 species of North American mammal hosts (thick lines) and 3 species of North American fish hosts (thin lines). Solid lines indicate statistically significant relationships, and broken lines indicate non-significant relationships. Host species are: Ozi, *Ondatra zibethicus*; Cla, *Canis latrans*; Plo, *Procyon lotor*; Cco, *Catostomus commersoni*; Pfl, *Perca flavescens*; Elu, *Esox lucius*. The summarized results are from Poulin (2003).

PARASITE FAUNAS IN DIFFERENT HOST SPECIES

There are at least two ways of scaling up from the parasite community level. The first is to consider entire parasite faunas, i.e. the sets of all parasite species exploiting given host species. Some of the general patterns and laws existing at this higher macroecological scale have been discussed elsewhere (Guégan *et al.* 2005); here, I will focus on patterns of variation in species richness and total biomass between the parasite faunas of different host species.

It has become clear to parasitologists that different host species, even closely related ones, often harbour different numbers of parasite species. Many parasite species belonging to the same parasite fauna have likely been inherited by their current host from its distant ancestors. Thus, shortly after they split, 2 sister host lineages issued from the same ancestor probably harbour very similar parasite faunas. Over evolutionary time, however, parasite faunas gain new parasite species and lose old ones, as the consequence of various evolutionary events (Paterson and Gray, 1997; Vickery and Poulin, 1998; Poulin and Morand, 2004). There are two main ways in which a fauna can lose species. First, a parasite lineage may go extinct in a host lineage. Extinction of parasites can result from the host evolving resistance to a particular parasite, from other hosts necessary for the completion of the parasite's life-cycle becoming scarce, or from environmental changes leading to inhospitable conditions for the free-living stages of the parasite. Second, because of the aggregated distribution of parasites among host individuals in a population, the part of the ancestral host population splitting off to give rise to a new host species may harbour no parasites during speciation. A founder host population may thus be free of certain parasite species, or contain too few individual parasites to allow the parasite species to survive. There are also 2 main ways in which new parasite species can be acquired by parasite faunas. First, hosts can be colonized by new parasite species. This involves host-switching, i.e. parasites moving in from other sympatric host species provided that the new hosts are compatible with the parasites. The second way in which new parasites can be acquired by a parasite fauna involves intra-host parasite speciation. It happens when parts of the parasite population become genetically isolated without gene flow being interrupted between parts of the host population. The rate at which parasite faunas acquire or lose parasite species over evolutionary time may be related to the ecological characteristics of the host species or of the environment in which it lives. In the context of general laws, there is an obvious question that one can ask: across different types of hosts and parasites, are there recurring patterns of associations between host-related or environmental characteristics and the richness of parasite faunas?

Three major theoretical frameworks have been used to generate testable predictions concerning the diversity of parasite faunas (Poulin and Morand, 2004; Poulin, 2004, 2007). First, the well-documented latitudinal gradients in the diversity of plants and animals (see Rohde, 1992; Rosenzweig, 1995; Gaston and Blackburn, 2000) have prompted the search for similar patterns in parasite faunas. Second, MacArthur and Wilson's (1967) classical theory of island biogeography has proven influential. Just as island features are predicted to influence the rate at which its fauna diversifies, host characteristics such as body size and geographical range are expected to determine the rate at which parasite species join or leave parasite faunas (Kuris *et al*. 1980). Third, epidemiological models originally constructed to explain and predict the spread and maintenance of parasites in host populations (Anderson, 1993; Diekmann and Heesterbeek, 2000) have been applied to parasite communities to predict how many parasite species can coexist at equilibrium in a host population (Dobson and Roberts, 1994; Roberts *et al*. 2002). Host features such as population density play key roles in epidemiological models; they are predicted to determine whether or not parasites can persist in host populations, and by extrapolation they are predicted to affect the species richness of parasite faunas.

Several relationships between host-related or environmental characteristics and the richness of parasite faunas are predicted by the above 3 frameworks. These have been the impetus for many studies, on a range of host and parasite taxa, and using increasingly sophisticated comparative methods. Many of these studies have found statistically significant relationships between the richness of parasite faunas and other ecological variables. Taken as a whole, however, these results not only fall short of suggesting the existence of general laws, but they are also rather disappointing. There are several reasons for this (Poulin, 2004; Poulin and Morand, 2004). To begin with, the predictions derived from the theory are only qualitative, not quantitative. In other words, the predictions are limited to the direction of the relationship, i.e. positive or negative, but say nothing about its slope. For example, from island biogeography theory, one might predict that if the body mass of host species A is 3 orders of magnitude larger than that of host species B, then A should harbour more parasite species than B, but exactly how much more cannot be predicted. Even in hindsight, looking back at all the published slope values between a particular host characteristic and parasite species richness across different host species, there does not appear to be any slope value around which published values are clustered. This is the second major disappointing aspect of these results: there is little or no consistency among the results (see reviews in Poulin, 1997, 2007; Morand, 2000; Poulin and Morand, 2004). For every positive relationship between a host trait and parasite species richness currently published, one can find a negative relationship and some non-significant relationships between the same trait and parasite richness in other studies. Investigations of parasite diversity as a function of latitude illustrate this lack of universal pattern: relative ectoparasite diversity (i.e. species richness per host species) on marine fish hosts peaks in tropical waters, whereas relative endoparasite diversity in marine fish does not vary with latitude, and relative parasite diversity in freshwater fish peaks in temperate areas (Rohde and Heap, 1998; Choudhury and Dick, 2000; Poulin, 2001). Other problems plague these studies of parasite biodiversity. For instance, statistically significant relationships between host traits and parasite species richness typically have low predictive power, i.e. the regressions are characterized by low r^2 values. Also, since these are essentially correlations, the direction of causality is not always clear. Overall, even the most optimistic researcher would admit that general laws are unlikely to emerge from these studies into parasite biodiversity.

Why have universal patterns not been found in such studies? One possible reason might be that parasite assemblages come with evolutionary baggage. Unlike true islands, host species are not devoid of parasites at their origin, but instead they inherit parasites from their ancestors, mostly independently of their body size, population density, or other characteristics. Thus, even with proper statistical corrections, inherited parasite species might create enough background noise to mask any underlying association between host traits and parasite diversity. A more important problem plaguing any attempt to find universal relationships between host ecology and parasite diversity comes from the marked inequalities in body sizes, and therefore in resource use, among parasite species within the same parasite fauna. It is not unusual to observe variation over 2 or 3 orders of magnitude in the body mass of parasite species living alongside each other, such as small trematodes and huge cestodes sharing the same intestine. Most theoretical predictions make the tacit assumption that different species are roughly equivalent to one another; this assumption is severely violated in parasite communities and parasite faunas. Because different parasite species are not using the host to the same degree, predicting how many parasite species can exploit a particular host species become impossible. What may be predictable, though, is the total amount of parasite biomass that can be supported by a given host. Total parasite biomass takes into account the different sizes of parasites by pooling them all into a combined measure of total parasite tissue per host. It has taken a while, but the attention of parasite ecologists is finally turning toward parasite biomass (George-Nascimento *et al.* 2004). In our search for general laws, it may prove more rewarding to ask not how many parasite species can exploit a host, but instead how much parasite biomass can be supported by that host.

It is even possible to derive quantitative predictions from existing theory regarding parasite biomass. The supply of energy and nutrients should ultimately determine how much biomass can be sustained; for parasites, therefore, host metabolic rate should be a key determinant of total biomass. That is because metabolism controls the rate at which resources are taken up, transformed and allocated to various functions within the host. The combined parasites inside a host can be seen as just another function competing for metabolic products. Thus, the amount of energy and resources available to sustain parasite biomass should depend directly on host metabolism. In recent years, the metabolic theory of ecology has emerged as a general explanation for many phenomena and patterns in nature (Allen *et al.* 2002; Brown *et al.* 2004). It is founded on well-established empirical relationships between body size, temperature and metabolic rate. Like other characteristics of organisms, metabolic rate scales allometrically with body mass. Whole-organism metabolic rate scales as $H^{3/4}$, i.e. on a log-log plot metabolic rate increases with increasing body mass, H, with a slope of 0·75 (Gillooly *et al.* 2001; Savage *et al.* 2004). At the same time, metabolic rate and other rates of biological activity also increase exponentially with temperature, as described by the Boltzmann factor $e^{-E/kT}$, where E is the activation energy (in electron volts), k is Boltzmann's constant, and T is absolute temperature in K (see Gillooly *et al.* 2001; Brown *et al.* 2004). It captured quite well the temperature dependence of whole-organism metabolic rate across all taxa and all sizes (Gillooly *et al.* 2001). Thus, the joint effect of body size and temperature on individual metabolic rate, I, can be described as:

$$I \propto H^{3/4} e^{-E/kT}$$

Using the value of $E = 0{\cdot}63$ eV obtained by Brown *et al.* (2004), metabolic rate can be temperature-corrected to isolate the effect of body mass. This relationship should also apply to other biological rates. Organisms devote some fraction of their metabolism to the production of new biomass for growth and reproduction. Empirically, rates of whole-organism biomass production should be proportional to $H^{3/4}e^{-E/kT}$ (Brown *et al.* 2004). This suggests that a constant fraction of metabolism is allocated to biomass production. Brown *et al.* (2004) found that, across a wide range of eukaryotic plants and animals, the log-log relationship between temperature-corrected rates of whole-organism biomass production and body mass had a slope of almost exactly 0·75, with all values clustering tightly around the regression line. Biomass production within an organism is not limited to the organism itself: its parasites 'steal' a portion of the metabolic products that would otherwise be allocated to host growth or other functions, and use it for the production of parasite biomass. The rate of conversion of host resources into parasite biomass may thus follow the same scaling rules and constraints that apply to the production of host biomass. The parasite biomass, P, supported by a host organism would therefore scale as:

$$P \propto H^{3/4} e^{-E/kT}$$

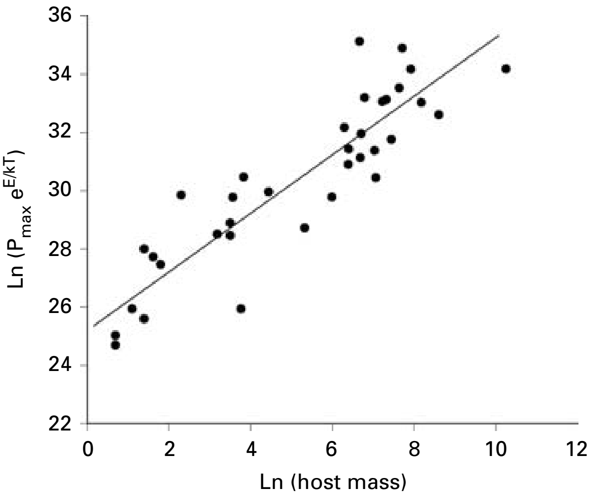

Fig. 4. Relationship between temperature-corrected maximum parasite biomass, $P_{\max}$, and host mass, across 35 species of marine fish hosts. The maximum parasite biomass represents the maximum total biomass of all endo- and ectoparasitic metazoans that was actually found in an individual host. The regression line has a slope of 0·98 ($r^2=0{\cdot}79$). Data are from Poulin and George-Nascimento (2007).

The mass-specific parasite biomass, P/H, or the parasite biomass per gram of host, would scale as:

$$P/H \propto H^{-1/4}e^{-E/kT}$$

When P and P/H are temperature-corrected, and plotted against host mass on a log-log plot, we would expect slopes of 0·75 and −0·25, respectively. These provide testable predictions, and baselines for comparisons should the observed relationships deviate from these values.

The above predictions derived from the metabolic theory of ecology apply to the *maximum* parasite biomass that can be sustained by a host, or the highest value for combined biomass of all parasite species found in an individual host, and not to the *mean* parasite biomass per host. The latter includes data from uninfected individuals, and thus underestimates how much parasite biomass an animal can actually support. Data on metazoan parasites of marine fish indicate that maximum parasite biomass, not surprisingly, correlates strongly and positively with host mass (Poulin and George-Nascimento, 2007). In a log-log plot, the slope of this relationship is approximately 1, however, clearly higher than the value of 0·75 expected if parasites grew merely as host tissues (Fig. 4). This may indicate that parasites apportion a greater amount of host resources than their 'fair' share, converting host metabolic products into parasite biomass at a higher rate than host tissues. The maximum mass-specific parasite biomass, P/H, did not change with increasing host mass, having a slope of about zero (Poulin and George-Nascimento, 2007). These log-log slopes indicate that maximum parasite biomass per gram of host is independent of host mass, i.e. larger hosts can potentially support the same parasite biomass per gram as small hosts. Data on other taxa of hosts and parasites will be necessary before we can speak of these patterns as general laws. Still, these early results show that the search for universal patterns in parasite biomass may prove more successful than that for patterns in parasite diversity.

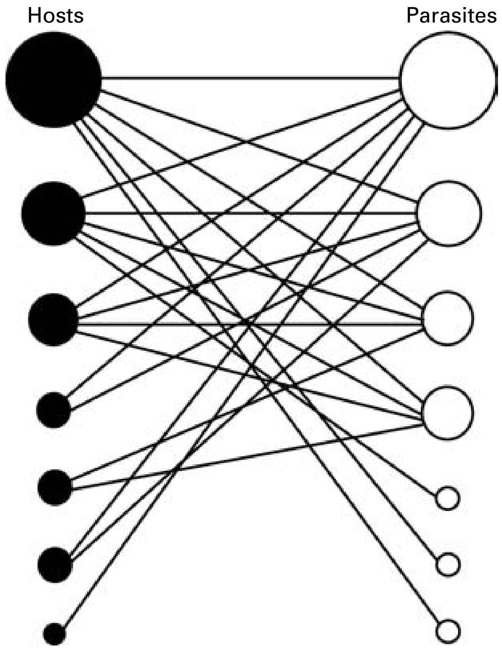

Fig. 5. Hypothetical network of interactions between host species (black circles) and parasite species (open circles) in a given ecosystem. Lines connecting different species represent the network links, i.e. they indicate which parasite species is found on which host species. Host and parasite species are ranked from those involved in the most links to those involved in the fewest links, as indicated by circle diameter.

HOST-PARASITE INTERACTION NETWORKS

As stated above, there are two ways of scaling up from the level of the parasite community. The first is to consider entire parasite faunas, and the second is to focus instead on local interaction networks between host and parasite species. A network consists of all links, or actual associations, between the host and parasite species in a given ecological system, such as a lake or a patch of forest (Fig. 5). It is often easier to consider parasites at only 1 stage in their lives and hosts of 1 large taxon only, such as adult helminths in fish within a lake, rather than all parasites and hosts. Still, this hierarchical level is roughly equivalent to the compound community or supracommunity level of the parasitology literature (Bush *et al.* 1997). These higher scales of study are often considered too complex for simple patterns to be found, and yet if one asks the right questions, order emerges from apparent complexity.

The simplest question one might ask when looking at several host-parasite interaction networks is what influences the number of links in each network. Not all possible links are realised in actual networks (Fig. 5). There are host-specific parasite species that only infect a small number of the available host species. Similarly, there are host species that only harbour a small fraction of the parasite species present locally. Thus, only a proportion of the possible links are actually realised in any given network. This proportion is called the connectance of the network, and across comparable host-parasite networks, connectance tends to decrease exponentially with increasing number of host or parasite species per network (Mouillot *et al.* manuscript submitted). The available data are limited, but they suggest that this applies more or less universally; examples for networks involving helminths parasitic in fish and fleas parasitic on mammals are shown in Fig. 6. Therefore, in species-poor networks a large fraction of possible links is actually realised, whereas in species-rich networks this fraction is very small (Fig. 6). This pattern suggests that networks become richer by adding new parasite species that are very host-specific, and new host species that will only harbour few parasites. Whatever the underlying mechanisms, the recurring pattern suggests the existence of another general law, this one acting on network connectance.

The identity of the realised links is an even more interesting property of interaction networks than connectance, as it determines the basic structure of the networks. For instance, a highly host-specific parasite may participate in only one link within a network, but this could be with a host species harbouring numerous other parasite species, or with one having no other parasites. The arrangement of links within a host-parasite interaction network may be random, but it could also follow a predictable structure. An analysis of 7 helminth-fish networks, each from a different lake, and 25 flea-mammal networks, each from a different geographical area, shows that the structure of host-parasite interaction networks is far from random, and highly predictable (Vázquez *et al.* 2005). The analysis used null models based on real data on parasite specificity and component community richness to generate random networks of associations between hosts and parasites. In the simulated networks, the specificity of a parasite did not affect which type of component community it would be found in (Vázquez *et al.* 2005). In all cases, observed networks were significantly more asymmetrical than the expectations of the null model, with specialist parasites occurring in rich component communities (i.e. hosts with many other parasites) more often, and generalists occurring in poor communities more often, than expected by chance. The similarity of these findings from vastly different host-parasite systems hints at common ecological processes shaping the structure of interaction networks within a locality, with consequences for the composition of component communities. The association between specialist and generalist parasites on the one hand, and hosts with few or many parasites on the other hand, is also strikingly similar to the patterns of distribution of specialization reported for mutualistic association networks, such as those involving pollinators and flowering plants

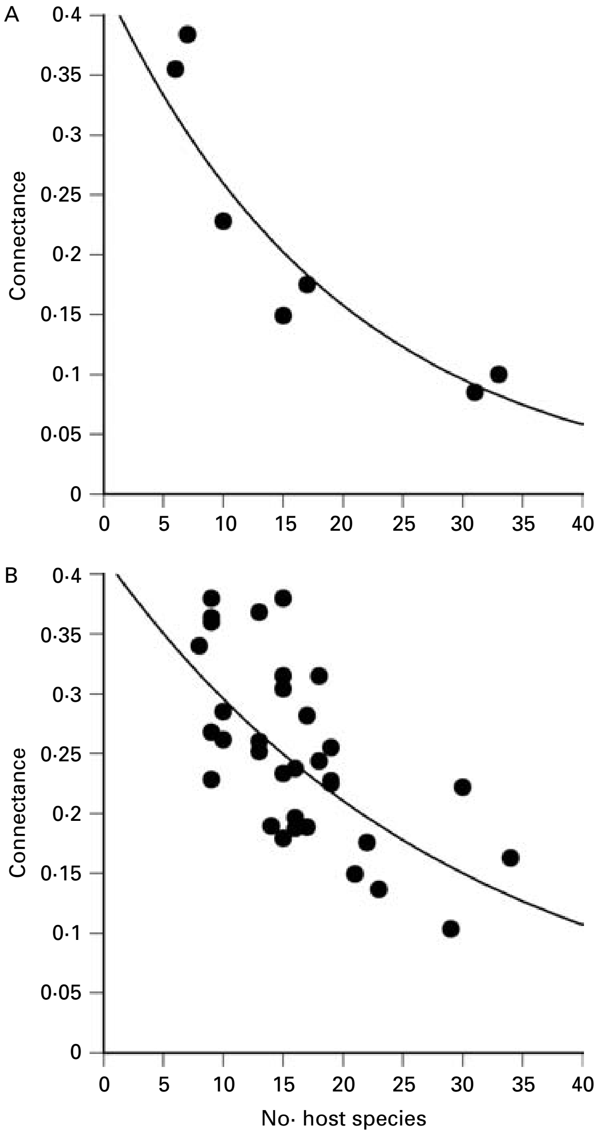

Fig. 6. Exponential decrease in connectance, i.e. the proportion of realised links within a network, as a function of increasing host species richness across different host-parasite interaction networks. The data are shown separately for (A) networks involving helminths parasitic on fish in 7 Canadian freshwater bodies, and (B) networks involving fleas ectoparasitic on small mammals in 33 localities across the Palaearctic and Nearctic, with each point representing a distinct local network. Helminth data are from Poulin (unpublished) and flea data from Mouillot *et al.* (manuscript submitted).

(Bascompte *et al.* 2003; Vázquez and Aizen, 2003). Thus, there may be universal laws acting on interaction networks, whether the associations are parasitic or not. Beyond confirming the existence of these general laws in other kinds of host-parasite associations, the next step will be to elucidate the processes underlying them.

CONCLUSIONS

At the population level, the lowest study scale considered here, general laws apply to the distribution of parasites among their hosts, and to the relationships between parasite abundance, prevalence and occurrence on geographical scales. At the highest scales of study, general laws are also apparent, in the structure of host-parasite interaction networks, and possibly in patterns of variation in parasite biomass among different host species. It is at intermediate scales of study, those relevant to parasite community ecology, that we observe only contingent or 'messy' patterns, to use Lawton's (1999) expression. In fact, in his assessment of the state of ecology, Lawton (1999) went on to make the following recommendation: "To discover general patterns, laws and rules in nature, ecology may need to pay less attention to the 'middle ground' of community ecology, relying less on reductionism and experimental manipulations but increasing research efforts into macroecology".

Other commentators, such as Simberloff (2004), are not so quick at dismissing community ecology, and I tend to agree with them. There is no doubt that the large-scale macroecological approach has proven successful and furthered our understanding of ecological systems. But we should not neglect community ecology simply because it has not yet delivered universal laws. The more complex a system, the less likely we are to achieve quantitatively accurate predictions and to find general laws (Kauffman, 1993). Parasite communities are complex systems and they exist in non-equilibrium conditions, a situation where contingencies should be predominant (see Rohde, 2005). Nevertheless, to me the lack of clear general patterns coming out of parasite community ecology research to date is not a reason to despair, but a challenge to parasite ecologists. If robust patterns have emerged from the level below (populations) and that above (faunas and interaction networks), surely there is a clear signal somewhere in the chaotic noise that comes out of parasite communities. It is possible that we have been asking the wrong questions. To date, parasite community ecology has focussed on the determinants of species richness and composition of parasite assemblages. Perhaps looking at other aspects, such as the relative abundances of different parasite species in a community, maybe using a different measure of abundance, such as biomass instead of numbers of individuals, would yield more promising results (see Mouillot *et al.* 2003; Muñoz *et al.* 2006). The search for general laws in parasite community ecology must go on, because our understanding of these communities depends on it.

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