Ecology, 89(7), 2008, pp. 2043–2051

HIGH INTERVALITY EXPLAINED BY PHYLOGENETIC CONSTRAINTS IN HOST–PARASITE WEBS

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Abstract. The finding of invariant structures in species interaction webs is of central importance for ecology, with the greatest challenge remaining the elucidation of the processes governing these universal web patterns. Here we quantify the degree of intervality of seven fish–metazoan and 33 mammal–flea webs, i.e., the number of irreducible gaps in parasite diets along the host spectrum, and then challenge the idea that some invariant structures may emerge in host–parasite webs. Using a null model of random links between parasite and host species we find that empirical host–parasite webs exhibit a strong bias toward contiguity of parasite diet, i.e., toward intervality. Going one step further, we demonstrate that a null model with phylogenetic constraints on host–parasite links produced webs very similar to empirical ones, particularly when phylogenetic constraints occur at the family level, that is, when two hosts from the same family are more likely to be infected than two random hosts. In addition, we propose a new standardized measure of intervality which describes a novel "facet" of natural networks as it is independent of connectance or web size. We suggest using this measure as a surrogate of web maturity or saturation as phylogenetic constraints can drive webs toward intervality.

Key words: bipartite networks; diet contiguity; fish–metazoan webs; mammal–flea webs; null model; web saturation.

Introduction

Uncovering general and repeatable patterns in species assemblages over space and time has been a major thrust of research in ecology because finding such regularity would suggest that apparently diverse and idiosyncratic assemblages may possess common self-organizing principles. Ultimately the goal of such a comparative approach should be to identify the processes underpinning any observed universal pattern which in turn would provide crucial knowledge allowing advances in conservation and environmental management (Simberloff 2004).

Food web ecology has become a fertile area for discussion about invariant properties in assemblages of interacting species feeding on each other. For instance, predator : prey ratio and connectance in food webs (density of links) have been documented to be scale invariant (Cohen and Briand 1984, Sugihara et al. 1989, Martinez 1992). However, studies exploring this phenomenon have mainly focused on webs where each species can potentially feed on every other species (symmetric webs) through trophic interactions. Asymmetric webs, where one set of species feed on another set of species, have been largely overlooked. Mutualistic networks such as plant–pollinator webs have been studied through the structure of their bipartite graphs summarizing species interactions (e.g., Jordano 1987). Insect parasitoids are also commonly used to investigate the structure of such asymmetric webs (e.g., Lewis et al. 2002). By contrast, host–parasite webs, which are also asymmetric webs, have been mostly neglected (but see Vázquez et al. [2005] or Mouillot et al. [2008]) although parasites constitute a fundamental component of food webs (Marcogliese and Cone 1997, Lafferty et al. 2006). Most species on earth harbor parasites and more than half the known animals can be parasitic at some points of their life cycle (Poulin and Morand 2004). They also influence food web properties by modifying host behavior, community structure, and population dynamics (Thompson et al. 2005). Here we seek invariant patterns in host–parasite webs by estimating their degree of intervality. We do this by borrowing tools developed for the analysis of symmetric food webs and applying them to asymmetric webs, i.e., to host–parasite interaction networks. While recognizing the basic differences between these two types of webs, the use of concepts developed for food web research can still shed new light on the structure of host–parasite webs.

Manuscript received 31 July 2007; revised 18 October 2007; accepted 13 November 2007. Corresponding Editor: K. D. Lafferty.

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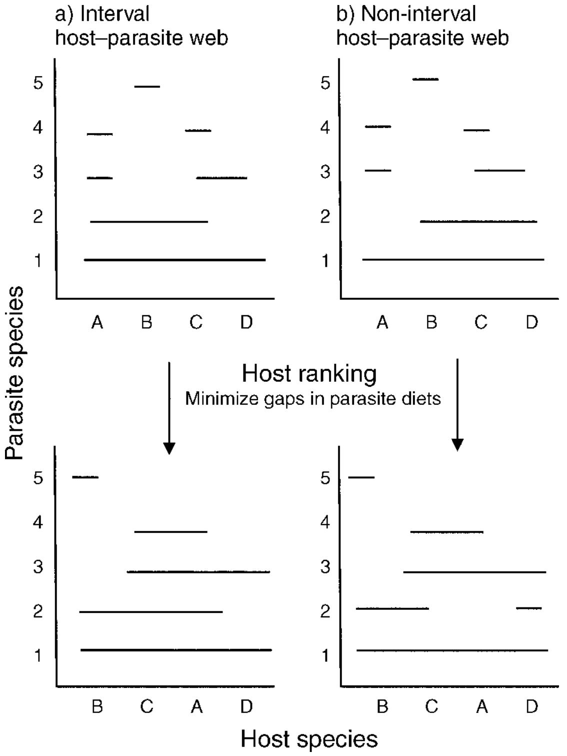

FIG. 1. Illustration of interval and non-interval host–parasite webs. Host species (capital letters) are placed along a single dimension, which is the resource axis, while parasite species are numbers along the y-axis. For each parasite, a line is placed above the hosts it infects. Panel (a) is an interval host–parasite web because there exists a permutation of hosts that makes all parasite diets contiguous (with no gap). By contrast, panel (b) is non-interval because parasite diets cannot be represented as contiguous whatever the host ordering along the resource axis.

The degree of intervality of a food web is related to the number of trophic dimensions characterizing the possible niches in a community (Cohen et al. 1990, Stouffer et al. 2006). A food web is said to be interval when prey species can be organized along a single dimension in such a way that all predator diets are contiguous (Fig. 1a). Conversely when one cannot find an arrangement of prey species that makes all predator diets contiguous, this food web is classified as non-interval, i.e., some irreducible gaps remain in predators' diets (Fig. 1b). By analogy, the degree of intervality of a host–parasite web would be related to the number of niche dimensions that are necessary to explain patterns of hosts used by parasites. In an interval host–parasite web (no gaps in parasite diets along the host spectrum axis) a single dimension and thus a single niche axis (for instance host body size) is enough to structure host–parasite relationships. This single niche dimension can be the combination of several variables which are highly correlated (host body size, life span, home range size) since more than a single factor is certainly required to sort out the organization of parasite infection along the host spectrum. Alternatively non-interval host–parasite webs would suggest that additional factors (one or several additional niche dimensions) are responsible for the web structure.

Parasites are notoriously host specific, i.e., each parasite species typically only exploits a small subset of the host species potentially available (e.g., Poulin 1997). This subset is generally not a random selection of host species; instead, the hosts used by a parasite often consist of a small set of host species that are more or less closely related phylogenetically (Krasnov et al. 2004, Mouillot et al. 2006). The explanation for this common pattern is that the addition of a new host species to the repertoire of a parasite over evolutionary time is normally only possible when the new host shares traits by descent with the original host species (Poulin and Morand 2004, Poulin et al. 2006). Alternatively, in parasite species with flexible transmission modes and non-specific requirements, the hosts used by a parasite may represent a set of unrelated host species that possess similar ecological or physiological features (Pedersen et al. 2005). The way in which parasites select their hosts may lead to drastic differences in the level of intervality of the host–parasite webs. For instance if parasites infect a random set of hosts some irreducible gaps may appear and then the host–parasite web is expected to be non-interval. Conversely if we can arrange the hosts in a manner that every parasite infects contiguous hosts then the host–parasite web is considered as perfectly interval. We propose that the degree of intervality of a host–parasite web provides a rough index of web saturation: in a perfectly interval web, the potential host spectrum for each parasite may be fully exploited, whereas in webs where gaps remain along the host spectrum, there may be openings left for new species to join the web.

Here, we address the question of the degree of intervality in host–parasite webs using two large databases concerning, respectively, fleas parasitic on small mammals and metazoan parasites of freshwater fish. We hypothesize that host phylogeny will have different effects on the intervality of these different host–parasite webs. For fleas, we expect webs to be non-interval, since one of the main host requirements for a flea is the use of a burrow with constant microclimate that guarantees successful development of pre-imagoes. Use of burrows is a non-phylogenetic trait that is a characteristic of many unrelated small mammal taxa. In contrast, for helminths and most other metazoans parasitic in fish, the webs are expected to be interval, with host phylogeny being the main driver of web structure. The suitability of a host for a helminth depends entirely on physiological and immunological factors strongly associated with phylogeny. We propose two null models to test these predictions and investigate the processes underlying the degree of observed intervality in host–parasite webs. We also present a new standardized index measuring the degree of intervality in asymmetric webs and we challenge the idea that this index provides new information about natural webs and highlights emergent properties such as the scale invariance of intervality.

MATERIALS AND METHODS

Metazoan–fish webs

Data on host–parasite bipartite interaction networks were obtained from seven Canadian freshwater systems, either large lakes or rivers (Bangham 1955, Dechtiar 1972, Arthur et al. 1976, Chinniah and Threlfall 1978, Leong and Holmes 1981, Arai and Mudry 1983). In each of these seven habitats, all fish species were sampled for parasites; here, though, only fish species for which at least five individuals have been examined per locality were included, because determination of host use by a parasite becomes inaccurate at smaller samples. All species of metazoan parasites, whether internal or external, were included in the analyses. These include the following groups: nematodes, acanthocephalans, cestodes, trematodes, monogeneans, leeches, copepods, and branchiurans. When a species of internal worm occurred among sampled fish as both larval and adult forms, the two forms were treated as functionally distinct species; this is justified because larval and adult worms often have different modes of transmission, infect different fish species, different organs within fish, and so forth. The species composition of both the host and parasite fauna of the different lakes and rivers overlapped to some extent, because several of the species concerned have continental-wide distributions; still, each lake or river can be viewed as an independent system, since patterns of host use will depend on local conditions (local food web, composition of the invertebrate fauna serving as intermediate hosts for the parasites, etc.). The classification of fish species used here largely reflects phylogeny and follows Nelson (2006).

Flea–mammal webs

Data on flea–mammal webs were obtained from published surveys that reported flea distribution and abundance on small mammals (Didelphimorphia, Soricomorpha, Lagomorpha, and Rodentia) in 33 regions. These sources provided data on the number of individuals of a particular flea species found on a number of sampled individuals of a particular host species. Single findings of a flea species on a host species or in a region were considered accidental and were not included in the analysis. In all studies, most species were captured using snap traps; shrews were also captured using pitfall traps, sciurids and lagomorphs were hunted, whereas moles were captured using mole traps. As it was the case with metazoan–fish webs, the species composition of mammals and fleas from some regions overlapped. Nevertheless, we considered each region independently due to the reasons mentioned above. Mammal taxonomy followed Wilson and Reeder (2005). Attribution of a species to a genus or a family in this system fits well with the molecular phylogeny of the four orders.

Null hypotheses for host–parasite web intervality

According to the recent study of Stouffer et al. (2006), we determined the degree of intervality of an entire host–parasite web. To do so, we seek the order of hosts, if any, which would allow all parasite diets to be contiguous along the resource axis, i.e., with a minimum of irreducible gaps. For instance, consider two host–parasite webs with some gaps in parasite diets (Fig. 1). We want all hosts of a given parasite to "appear" as close together as possible on the resource axis. By swapping the hosts' order we can obtain an interval web for case a while some irreducible gaps remain in case b, whatever the host ordering along the resource axis. More formally, we find the most interval host ordering when we minimize the discontinuity of all parasites' hosts which is estimated by the number of gaps in the host–parasite web expressed as

$$G(k) = \sum_{i=1}^{S} \sum_{j=1}^{n_i} g_{ij}^{k}$$

where S is the number of parasite species, n_i is the number of gaps in the diet of parasite i, and g_{ij}^{k} is the number of host species in the jth gap in the diet of parasite species i for a given host ordering k.

Following Stouffer et al. (2006) we found the host ordering $k_{\min}$ that minimizes $G(k)$ using a simulated annealing algorithm, which is a Monte Carlo procedure. Basically we randomly swap the position of two randomly selected hosts to decrease the value of $G(k)$ between two iterations to finally obtain a minimum $G(k_{\min})$, which corresponds to the number of irreducible gaps in the web. The smaller $G(k_{\min})$ is, the more interval the web is. This process yields the best approximation to a host–parasite web where parasite and their diets are organized along a single dimension. We ran the simulated annealing algorithm 10 times on each web using different starting points (different host orders) and we retained the host ordering $k_{\min}$ that minimizes $G(k)$ over the 10 proposed $k_{\min}$. Practically each simulated annealing run yielded the same global minimum.

As pointed out by Stouffer et al. (2006) the value of $G(k_{\min})$ has no ecological significance by itself except when the web is interval ($G(k_{\min}) = 0$). Otherwise the $G(k_{\min})$ observed value has to be compared to simulated values obtained under a null hypothesis with a biological meaning. Indeed we wanted to test whether the degree of intervality that is observed in a host–parasite web can be obtained if we randomly link the parasites and their hosts. In other words, our null models keep the structure of each assemblage in terms of host richness, parasite richness and the number of links between hosts and parasites (connectance), but randomly swap the host–parasite associations.

In our first null hypothesis, we randomly recombine host–parasite links without any constraint. By setting all row sums fixed (the number of hosts infected by each parasite species is assumed to be constant) and all columns fixed (the number of parasite species infecting each host is assumed to be constant) we randomly swapped checkerboard units through the presence/absence matrix summarizing the host–parasite web following the procedure suggested by Gotelli (2000).

In our second hypothesis, we randomly recombined host–parasite links with a phylogenetic constraint. As explained in *Introduction*, parasites often are specific to a few phylogenetically related host species: the host species they use are not a random subset of the locally available species, but rather a phylogenetically constrained one. Basically, we assigned parasites to the host spectrum but this time by constraining infection to host species of the same genus, family or order, until completion. As in the food wed model proposed by Cattin et al. (2004) we imposed a sequence in the attribution of links in such a way that parasite diet depends on the host already infected.

We computed 999 null host–parasite webs for each null hypothesis (random, genus, family, and order) and we estimated $G(k_{\min})$ for each of them. Then we compared observed and simulated $G(k_{\min})$ values to determine whether our observed degree of intervality differed from those obtained under the null hypothesis (Manly 1998).

A new standardized index of intervality in host–parasite webs

As the number of gaps is related to the number of host and parasite species (a larger web is more likely to show irreducible gaps [Cohen and Palka 1990]), we propose a new standardized measure of host–parasite intervality. This measure allows different webs to be compared with one another and some invariant scaling properties of this index can be investigated. Let L be the number of realized connections (links) between P parasite species and H host species. Then the number of empty cells in the interaction matrix (no link) between P parasites and H hosts is $H \times P - L$; this value corresponds to the maximum number of gaps in host spectra thus giving $G(k_{\min}) \leq H \times P - L$. The degree of intervality (DI) was quantified as

$$\mathrm{DI} = 1 - \frac{G(k_{\min})}{H \times P - L}.$$

This index is based on the proportion of irreducible gaps out of the potential number of gaps in the interaction matrix. When the web is interval (i.e., has no gap $[G(k_{\min}) = 0]$) we have $\mathrm{DI} = 1$ whatever the number of potential gaps ($H \times P - L$). Since $G(k_{\min}) \leq H \times P - L$, we have $\mathrm{DI} \geq 0$. DI tends to zero when $G(k_{\min})$ tends to $H \times P - L$, i.e., when the number of irreducible gaps approaches the potential number of gaps. Accordingly, this index ranges between 0 and 1 and is proportional to the degree of intervality independently of the web size.

This new index is only relevant if it adds new information compared to classical measures of web interactions. We tested the relationship between DI and the connectance, the size, and the number of realized links in host–parasite webs using the Pearson correlation coefficient. By analogy to food webs, the connectance in a host–parasite web (C) is simply defined as the ratio between realized connections and total number of potential connections. Thus we have

$$C = \frac{L}{H \times P}.$$

We also tested the similarity in DI values between fish–metazoan and mammal–flea webs using an ANOVA test after verifying the homogeneity of variances and residuals normality.

RESULTS

We studied 40 host–parasite webs and not a single one was perfectly interval, with the number of irreducible gaps varying between one (for the flea–mammal web of southwest California) to 305 (for the metazoan–fish web of Lake of the Woods; Table 1).

In 33 cases out of 40, the observed minimum number of gaps in the host–parasite web ($G(k_{\min})$) is lower than expected by chance when host–parasite links are randomly drawn without any constraint (Table 1), i.e., empirical host–parasite webs are more interval than random webs. For instance, as illustrated in Fig. 2a the observed number of irreducible gaps in the Lake Huron metazoan–fish web is 158 while the null model predicts a median value of 347 gaps with the lowest simulated value being 293 gaps.

Overall the degree of intervality in host–parasite webs is well explained by phylogenetic constraints on host–parasite associations. We obtained no significant difference between observed and simulated $G(k_{\min})$ values in 18 cases out of 40 for phylogenetic constraints at the genus level, in 30 cases out of 40 for phylogenetic constraints at the family level, and in 11 cases out of 40 for phylogenetic constraints at the order level. A phylogenetic constraint at the host family level generates the values of intervality closest to the one observed in nature. For instance the observed number of irreducible gaps in the Lake Huron metazoan–fish web (158) is significantly lower and higher than expected for, respectively, the null models imposing phylogenetic constraints at the genus and the order levels (Fig. 2b, d). Conversely the observed $G(k_{\min})$ value does not differ from the null model imposing phylogenetic constraints at the family level (Fig. 2c).

The new intervality measure (DI) ranged between 0.76 and 0.99 (Table 1). Moreover the new index is independent from the connectance ($r = 0.10$, $P = 0.515$), web size ($r = -0.10$, $P = 0.519$), and the number of realized links ($r = -0.21$, $P = 0.182$) while connectance

TABLE 1. Numbers of host and parasite species for each of the 40 host–parasite webs (seven metazoan–fish webs and 33 flea–mammal webs).

	Richness (no. species)				Null model: phylogenetic constraint			
Web type and location	Host	Parasite	No. gaps	Intervality, DI	None	Genus	Family	Order
Metazoan–fish webs								
Lake of the Woods	31	144	305	0.93	Inf	Sup	Sup	Sup
McGregor River	15	51	21	0.97	Inf	Inf	×	Sup
Smallwood reservoir	6	25	4	0.96	Inf	Inf	×	×
Parsnip River	17	53	30	0.96	Inf	Inf	×	×
South Bay-Lake Huron	33	97	158	0.95	Inf	Inf	×	Sup
Cold Lake	10	40	12	0.96	Inf	Inf	×	×
Aishihik Lake	7	29	2	0.98	Inf	Inf	×	×
Flea–mammal webs								
Adzharia	15	20	22	0.90	×	×	Sup	Inf
Akmolinsk	19	26	24	0.93	Inf	×	×	Inf
Barguzin	17	29	26	0.94	Inf	Inf	×	Inf
Brazil	16	10	9	0.93	Inf	×	×	×
Central California	19	22	30	0.91	Inf	×	×	×
Central Yakutia	9	18	15	0.88	×	×	×	×
Dzhungarskyi	15	22	17	0.93	Inf	Inf	×	Inf
East Balkhash	22	37	54	0.92	Inf	×	Sup	Inf
Gissar	8	25	8	0.94	Inf	Inf	×	Inf
Idaho	15	29	16	0.96	×	×	Sup	×
Kabarda	13	21	17	0.92	×	×	×	Inf
Amur	9	22	8	0.94	Inf	Inf	×	Inf
Khasan	9	12	3	0.96	×	×	×	Inf
Kustanai	17	19	18	0.92	Inf	×	Sup	Inf
Central Khangay	9	21	2	0.98	Inf	Inf	×	Inf
Northwestern Khangay	21	44	67	0.91	Inf	Inf	×	Inf
Moyynkum	18	31	30	0.93	Inf	Inf	×	Inf
Negev	13	11	3	0.97	Inf	×	×	Inf
New Mexico	29	34	54	0.94	Inf	×	×	Inf
Magadan and Tchukotka	15	16	6	0.96	Inf	×	×	×
Kyrgyz	16	35	34	0.93	Inf	×	Sup	Inf
Novosibirsk	34	28	188	0.76	Inf	Sup	Sup	Sup
Pavlodar	16	15	12	0.94	×	×	Sup	×
Selenga	9	13	6	0.93	×	×	×	Inf
Slovakia	19	22	14	0.96	Inf	×	×	×
Southwestern Azerbaijan	14	23	9	0.97	Inf	Inf	×	Inf
Southwestern California	9	17	1	0.99	Inf	Inf	Inf	Inf
Tarbagatai	23	35	37	0.95	Inf	×	Sup	Inf
Turkmenistan	18	42	51	0.90	Inf	Inf	×	Inf
Tuva	13	28	25	0.89	Inf	Inf	×	Inf
Ussury	9	21	13	0.89	Inf	Inf	×	Inf
Volga Kama	30	35	62	0.92	Inf	Inf	×	Inf
West Sayan	15	29	19	0.94	Inf	Inf	×	Inf

Notes: The degree of intervality is presented as both the number of irreducible gaps (No. gaps) after optimizing the hosts along the resource axis to make parasite diets the most contiguous possible, and in terms of standardized degree of intervality, DI. Results of tests comparing the observed degree of intervality (number of gaps in the web) with those simulated by randomly linking parasites to hosts (random) and by constraining host–parasite relationships at the genus, family, and order level, respectively, are also shown. "Inf" and "Sup" mean that the observed sum of gaps is significantly lower or higher than expected, respectively; × means that the observed sum of gaps is not significantly different from the null model.

is significantly and negatively related to both web size ($r = -0.598$, $P < 0.001$) and the number of realized links ($r = -0.441$, $P = 0.004$). The ANOVA test revealed that the standardized degree of intervality (DI) was not significantly different between fish–metazoan and mammal–flea webs (df = 1, 38, $F = 3.71$, $P = 0.062$) even if DI was higher for fish–metazoan webs (0.96 ± 0.02 [mean ± SD]) than for mammal–flea webs (0.93 ± 0.04).

DISCUSSION

Parasites and their hosts form bipartite networks of interactions, and the underlying structure of these networks has generated much interest. However, previous research on assembly rules in parasite communities has focused almost exclusively on the number of links per species and/or the distribution of these numbers of links across all species in a network. For instance, earlier studies of interaction networks between fish and metazoan parasites have examined the hypothesis that specialist parasites, i.e., those with few links, are more frequently associated with hosts that harbor many parasite species, i.e., hosts with many links, and vice versa (Poulin 1997). This asymmetric arrangement of specialization has been shown to be common in host–parasite webs (Vázquez et al. 2005), as in other bipartite interaction networks such as plant–pollinator networks

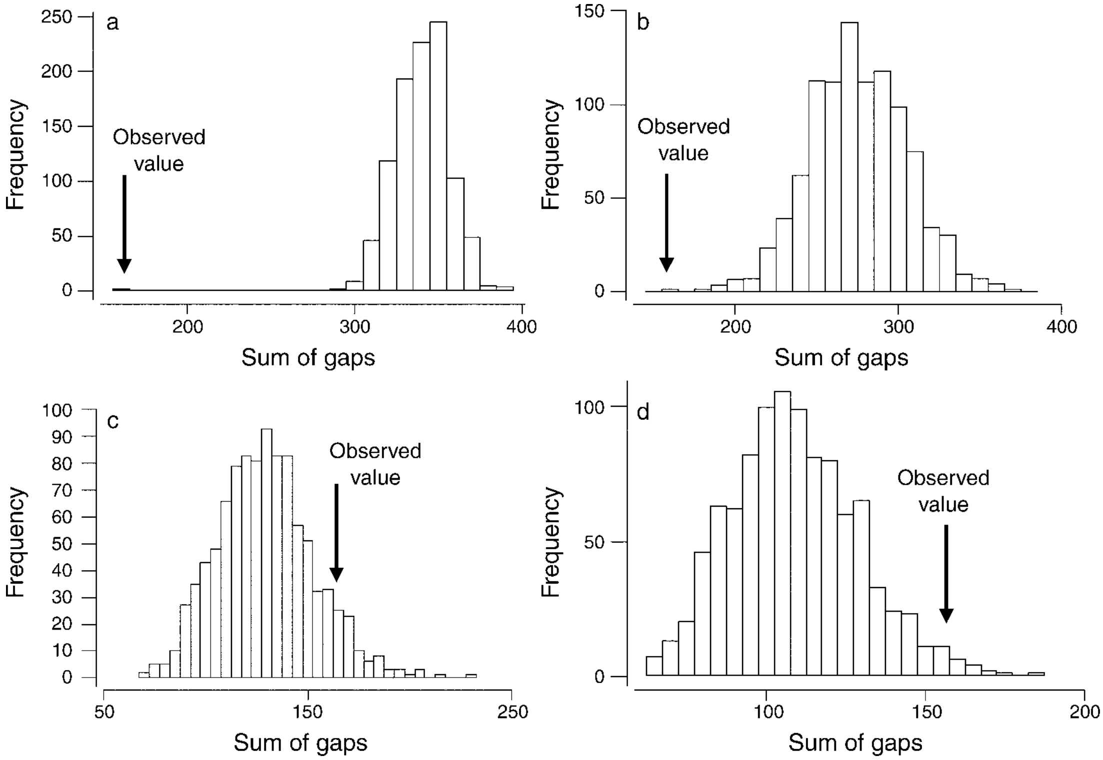

FIG. 2. Sum of gaps distributions for the metazoan–fish web of Lake Huron under four null models: (a) the random swap model vs. the phylogenetically constrained models at the (b) genus, (c) family, and (d) order levels. The observed value, with 158 gaps for the web, is not significantly different from the sum of gaps obtained using the phylogenetically constrained null model at the family level, while the observed value is significantly lower than expected by chance for two models (a and b) and significantly higher than expected for the last null model (d).

(Bascompte et al. 2003, Vázquez and Aizen 2003). Still, there have been very few attempts to elucidate the processes underlying these patterns. By considering the potential role of phylogenetic constraints in structuring host–parasite webs, our study reinforces the finding of Rezende et al. (2007) to suggest that phylogenetic relationships among species matter in interaction networks, at least to predict the number and nature of interactions and the degree of intervality.

While the extent and scale of our data sets allow comparisons as well as the detection of any general and repeatable pattern, one may still question their quality. The main issue possibly open to debate concerns the fact that some parasite species occurring at very low prevalence on a particular species may have been missed during sampling. We argue that the quality of our data is comparable to, if not better than, that of most food web studies. For instance, food web data often rely on analysis of stomach contents; prey items are not only transient inside a predator gut, but they also are partially digested and often difficult to identify. In contrast, intestinal parasites reside within host guts for long periods, and are intact at sampling, providing reliable data on host–parasite associations.

Combined all together our results show that empirical host–parasite webs are significantly more interval than expected by chance, albeit not fully interval (Table 1). In addition, we demonstrate that a simple null model based on phylogenetic constraints at the family level simulates host–parasite webs very closely, generating patterns very similar to real data for both metazoan–fish and mammal–flea webs. For instance, we found that the observed metazoan–fish web of Aishihik Lake has only two irreducible gaps (Fig. 3) which is much fewer than expected by chance (Table 1). However this degree of intervality is not significantly different from those simulated using constrained null models at the family and order levels (Table 1). In this web we have 29 parasite species sharing seven host species. These host species belong to seven different genera but to four different families and orders (four species belonging to family Salmonidae). Of 12 parasite species infecting at least four host species, 10 infect the four Salmonidae species (83.3%). The two irreducible gaps correspond to the other two species (*Piscicola milneri* and *Capillaria salvelini*) that infect more than three hosts but not all Salmonidae. This is a clear example of the host specificity of parasites which tend to infect closely related host species. Consequently our algorithm which seeks the host order minimizing the number of gaps in parasite diets places hosts belonging to the same family as contiguous. We obtained the same results for

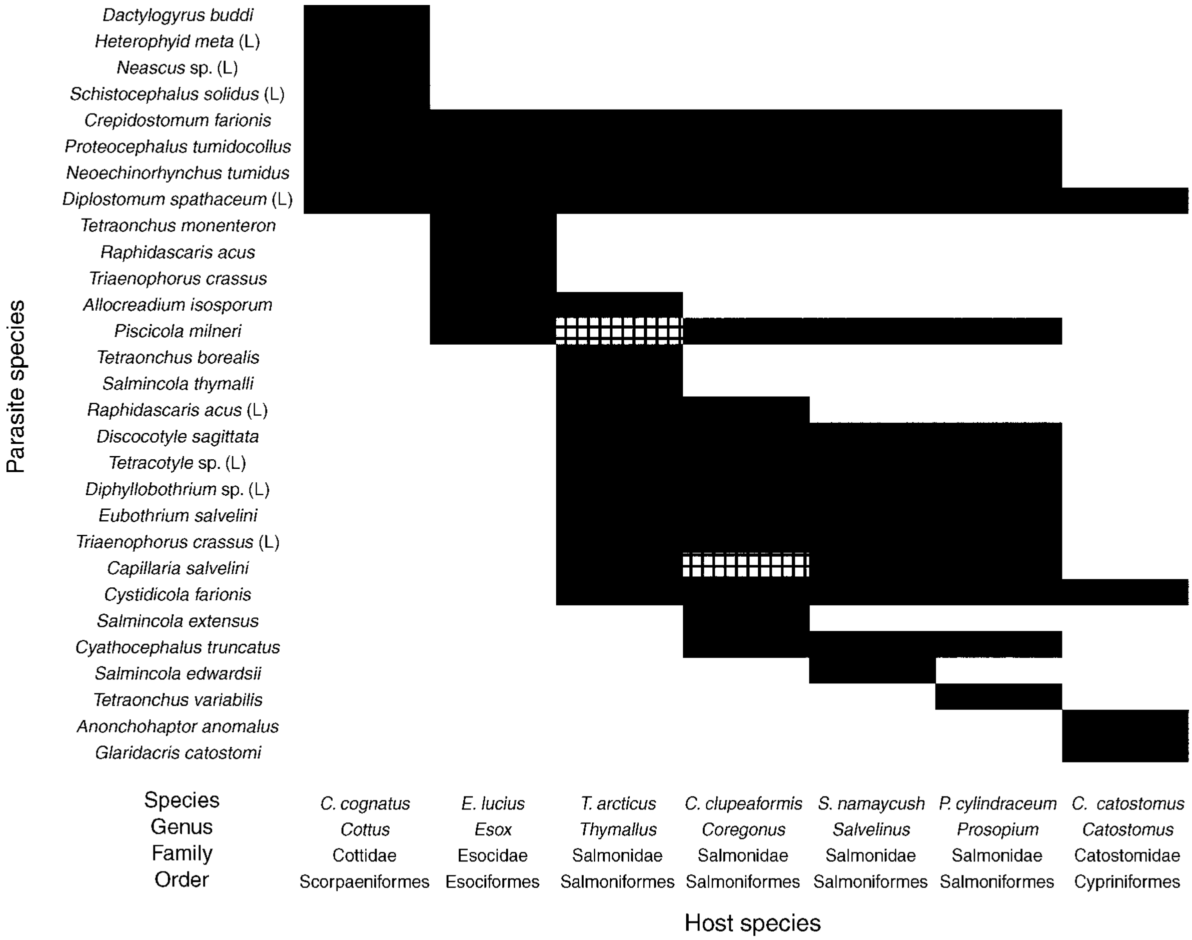

FIG. 3. Metazoan–fish web for Aishihik Lake. For each parasite species (y-axis), a black rectangle is placed above the hosts (x-axis) it infects. This web is non-interval with two irreducible gaps (checkered areas), i.e., all parasite diets cannot be contiguous along the resource axis, with two parasites (*Piscicola milneri* and *Capillaria salvelini*) each having one irreducible gap.

phylogenetic constraints occurring at the order level because, in this particular case, the different families correspond to different orders (Fig. 3). It must be pointed out that in this and other metazoan–fish webs, the fish are not the only host taxa used by the parasites: many helminths have complex life cycles also involving invertebrate intermediate hosts. Here, we have only considered fish hosts, and it would be interesting to look at intervality in use of invertebrate hosts as well. Still, the strong signal we obtain indicates that at least for fish hosts, phylogeny explains web structure. In turn, this would suggest that biological traits, with a strong phylogenetic conservatism at the family level, matter in host–parasite interaction patterns.

Contrary to our initial predictions, intervality driven by host phylogeny is a feature of not only webs involving metazoan parasites and fish hosts, but also of flea–mammal webs. This result suggests that with respect to host–parasite interaction webs, inherited similarities between hosts in terms of physiology, immunology, or ecology are much more important than other traits shared following convergent evolution, such as burrowing in mammals, or diet in fish. For example, Goüy de Bellocq et al. (2006) found two types of temporal pattern of cell-mediated immune response in desert rodents. The prompt but relatively weak response was characteristic mainly of murine rodents, whereas the delayed but relatively strong response was typical of gerbilline rodents. This suggested that the two types of responses represent different anti-parasitic strategies and are associated with some properties inherited from common ancestors. A similar conclusion is often reached by cophylogenetic studies that map the evolutionary history of parasites on that of their hosts (Poulin and Morand 2004). It is therefore reasonable to assume that phylogeny-based intervality would also characterize other types of host–parasite webs involving other host or parasite taxa.

Finally our study shows that, as in symmetric food webs, there is some degree of determinism in the structure of host–parasite webs. Indeed, using the same method, our results converge with those obtained by

Stouffer et al. (2006): both asymmetrical and symmetrical webs show a high degree of intervality without being perfectly interval. Going a step further, using a new index of standardized intervality, we demonstrate that intervality is a complementary "facet" of the description of natural networks in addition to connectance or web size. Furthermore this index appears scale invariant and as such reveals an emergent property of host–parasite webs which deserves to be tested on other webs: the number of irreducible gaps increases proportionally with the number of potential gaps. Thus, we support the prediction of Cohen and Palka (1990) who suggested that large webs should be less likely of being interval, although we found that the size of the web has no influence on the standardized intervality.

The estimation of the intervality level of any host–parasite web may provide information about the completeness of the links between parasite and host species. Indeed, because host phylogeny appears to tightly constrain host–parasite links, we may expect phylogenetically driven contiguity between hosts. Conversely, when the web is not interval (ID < 1), some irreducible gaps remain for links which would be filled in case of web completeness. For instance, the two parasite species (*Piscicola milneri* and *Capillaria salvelini*) that lack one salmonid species in their host spectrum prevent the metazoan–fish web of Aishihik Lake from being perfectly interval (Fig. 3). Hence this web would be interval if and when *Piscicola milneri* and *Capillaria salvelini* infect the whole spectrum of salmonid fish species. Using the same reasoning we could also predict the next links occurring in a host–parasite web, the ones that would decrease the number of irreducible gaps and thus increase the intervality level. This prediction deserves to be tested using host–parasite webs where host species have been introduced accidentally. The change of intervality during the completion of the host–parasite web would be of great interest. Thus, instead of the degree of connectivity (connectance) which is scale dependent for asymmetric webs such as plant-pollinator mutualistic networks (Olesen and Jordano 2002) and host–parasite webs (Mouillot et al. 2008), we suggest to use the intervality level, which is independent of web size, as a surrogate of web maturity.

Beyond providing descriptive tools, the challenge of our study was to achieve a better understanding of the processes driving these non-interval empirical webs. In accordance with the study of Cattin et al. (2004) we found that a simple rule, positing that any parasite diet is the consequence of phylogenetic constraints, is mostly responsible for structuring assemblages as complex as host–parasite webs over very different ecosystems. Indeed we got similar results at a community scale within a region for fishes and at a regional scale within continent for mammals which reinforce the generalization of our conclusions. Our study also suggests that historical contingency, habitat characteristics (productivity), biogeography and species functional groups are all of secondary importance in explaining host–parasite web structures when compared with phylogeny.

ACKNOWLEDGMENTS

This study was partly supported by the Israel Science Foundation (Grant no. 249/04 to B. R. Krasnov). This is publication no. 239 of the Ramon Science Center and no. 588 of the Mitrani Department of Desert Ecology. We thank two anonymous reviewers for their comments and constructive criticisms on our manuscript.

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