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The predictability of helminth community structure in space: a comparison of fish populations from adjacent lakes

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Abstract

Patterns in helminth community structure can suggest that various processes are acting to shape parasite communities into organised, non-random assemblages of species. It is not clear, however, whether a pattern observed in one host population at one time would be observed again at another time, or at the same time in a different but comparable host population. Here, we test the repeatability of parasite community structure in space, and to a lesser extent time, with data on helminth parasites of two fish species, perch *Perca fluviatilis* and roach *Rutilus rutilus*, collected in different seasons from four adjacent lakes in Central Finland. Since populations of the same fish species harbour the same parasite species and were sampled in the same way, we would expect similar patterns in the structure of their helminth parasites if the same structuring processes are acting in all lakes. We found that no pairwise association between the most common helminth species were observed consistently between seasons within lakes, or among lakes during the same season. Similarly, nested subset patterns of species assembly were observed in some samples, but not consistently between seasons or among lakes. The lack of repeatability in space and between seasons shown by these analyses indicates that although helminth community structure often departs from randomness, it does not do so in a consistent and predictable manner. There may be some general, large-scale processes acting to structure helminth communities, but local or seasonal influences can often either mask their action, or play more important roles themselves.

Keywords: Helminth communities; Interspecific associations; Nestedness; *Perca fluviatilis*; Predictability; *Rutilus rutilus*

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1. Introduction

The past decade has seen much progress toward a synthetic understanding of the forces shaping parasite community structure (Esch et al., 1990; Sousa, 1994; Simberloff and Moore, 1997; Poulin, 1998, 2001). Much of the evidence available to date, however, comes from studies that lack replication in either space or time. Typically, a non-random association of parasite species among hosts in a sample is almost never validated by comparisons with other independent samples from another host population, or from another season. The potential for spatio-temporal variation in community structure, and the importance of short-term or very local processes, are usually ignored. We generally have no idea whether or not an observed pattern is found at several different scales. The lack of replication can also lead to an underestimation of the importance of stochastic factors in determining parasite community structure.

Null models of species association, either borrowed from studies of free-living organisms or developed specially for parasite communities, have proven powerful in detecting patterns and suggest the action of several structuring processes (Poulin, 1998, 2001). They can be used to assess the repeatability (defined here as consistency between independent results) of community structure in both space and time. In this paper we focus on two commonly studied aspects of parasite community organisation and how they differ between adjacent populations of the same host species. Our analysis provides a crucial test of the underlying assumption behind any ecological generalisation, i.e. that it applies everywhere as long as the conditions remain the same.

First, we look at the repeatability of nested patterns in parasite community organisation. After showing their worth in the study of insular or fragmented communities of free-living organisms (Patterson and Atmar, 1986; Worthen, 1996; Wright et al., 1998), nestedness analyses have

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recently proven useful in detecting non-random patterns of species co-occurrences in parasite communities (Guégan and Hugueny, 1994; Poulin, 1996; Worthen and Rohde, 1996; Rohde et al., 1998; Poulin and Guégan, 2000; Poulin and Valtonen, 2001). In the context of parasite communities, a nested subset pattern occurs when the parasite species found in depauperate infracommunities (sensu Bush et al., 1997) represent non-random subsets of progressively richer ones; it implies that the distributions of different parasite species among host individuals are not mutually independent. Significant nestedness has been observed in parasite communities of fish, though it has not been found in all of the host species studied (Guégan and Hugueny, 1994; Worthen and Rohde, 1996; Rohde et al., 1998; Poulin and Guégan, 2000; Poulin and Valtonen, 2001). Is nestedness a feature of all parasite communities in a given host species, or only a characteristic of certain communities at specific times and places? With only one exception (see Carney and Dick, 2000), no previous study has examined the repeatability of nestedness in space or time.

Second, we quantify associations between pairs of common parasite species (e.g. Moore and Simberloff, 1990; Lotz and Font, 1991, 1994; Haukisalmi and Henttonen, 1993). No association indicates that two parasite species are randomly distributed among hosts, whereas positive or negative associations between parasite species suggest a departure from random co-occurrence. Although they represent a very basic null model approach, pairwise associations nevertheless serve to identify non-random patterns, whose repeatability in space can then be assessed across similar host populations. If two common parasite species are associated significantly in one host population, but not in another, as is sometimes the case (e.g. Dezfuli et al., 2001), the importance of this association for parasite community structure may vary in space. Like other departures from randomness, pairwise associations between parasite species need to be examined across locations and/or seasons to assess their generality.

Here, using these two approaches (pairwise associations between species and nestedness), we examine the repeatability in space of parasite community structure in two freshwater fish species from four more or less interconnected lakes in Central Finland. The lakes are remnants of Lake Ancylus, a postglacial lake that still existed around 6000 BC; thus, the four lakes have the same origin, as well as the same recent geological history. The only differences among them arose recently because they have been increasingly isolated in the past 50 years by the building of dams, and because they have been subjected to different levels of eutrophication and pollution. Still, all four lakes are inhabited by the same fish species, including the two focal species of this study, perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*). An earlier study revealed that the species composition of the helminth communities of these two fish species were remarkably similar among lakes, with some minor differences in parasite abundance being attributed to eutrophication or pollution (Valtonen et al., 1997). Still, the similarities between lakes allow for comparisons of parasite community structure in space, i.e. among host populations. A secondary objective of the study was to examine the repeatability of parasite community structure in time as well, i.e. between seasons within lakes, to determine how seasonal colonisation of hosts by parasites can affect community patterns.

2. Methods

The four lakes sampled were: (1) Lake Peurunka, 6.5 km^2, oligotrophic and relatively unpolluted, and now isolated from the others by a dam; (2) Lake Vatia, 5.5 km^2, eutrophic and polluted, also isolated from the others by rapids; (3) Lake Saravesi, 4.7 km^2, moderately polluted, eutrophic and connected to other lakes; and (4) Lake Leppavesi, 36 km^2, eutrophic and slightly polluted, and isolated from others by dams. All lakes are ice covered from late November through mid-May, and stratified during the summer, with the highest temperatures reached in July and August. Detailed information about the lakes is given in Valtonen et al. (1997).

Perch and roach were sampled from each lake by angling throughout 1986. Fish were returned alive in lake water to the laboratory, where they were killed by severing the spinal cord. All fish included in the study were adults; their total length was recorded prior to dissection. Our study focused exclusively on gastrointestinal helminths acquired by ingestion because they form a spatially cohesive assemblage that is more likely to be a true community than the ensemble of all parasite species found anywhere in a fish. The gastrointestinal tract was taken out of each fish and cut into pieces; each was examined for large parasites. In addition, the mucosa of each piece was scraped, and both the scrapings and the gut wall were examined under the microscope for smaller helminths. All helminths were identified and counted (see Valtonen et al., 1997 for details).

Fish taken during cold or winter months (November, February, April) were pooled into winter samples, and those taken during warm months (June, July, August and September) formed summer samples. The biological reason behind this pooling is that there is very little parasite multiplication or recruitment during cold months; most of it takes place in summer months. There is thus an ecological difference between winter and summer with respect to parasite communities. We therefore obtained eight distinct samples (four lakes × two seasons) of both fish species.

We used two-way analysis of variances (ANOVAs), with lake and season as main factors, to compare the total length of fish from the different samples. Pairwise associations among the most common helminth species were computed within each sample using Spearman's rank correlation coefficient, excluding fish that did not harbour at least one of the two species in a pair. Spearman's rank correlations were also used to assess the relationship between fish length and total abundance of all helminths combined.

For the parasite community in each fish sample, we computed the index of nestedness, N, first proposed by Patterson and Atmar (1986). This index corresponds to the sum, across all parasite species, of the instances where a parasite species is absent from infracommunities richer than the most species-poor one in which it occurs. For each fish sample, the observed N value was compared with the N values of 1000 randomly generated presence/absence matrices, produced using the algorithm RANDOM1 of Patterson and Atmar (1986). In these Monte Carlo simulations, the probability of each parasite species of being included in an infracommunity was set equal to its observed prevalence in the fish sample being considered. The proportion of simulated N values that were lower than or equal to the observed N value gave the RANDOM1 P-value, which was used as a measure of departure from the structure expected from random assembly (Guégan and Hugueny, 1994; Hugueny and Guégan, 1997). When the RANDOM1 P-value is ≤ 0.05, the infracommunities are significantly nested; when the P-value is ≥ 0.95, they also show a significant departure from randomness, known as an anti-nested pattern (Poulin and Guégan, 2000). Both significant nestedness and anti-nestedness were considered as departures from a random assemblage.

3. Results

A total of eight helminth species was found in the intestine of perch, and eight in the intestine of roach. These were not always present in all lakes or in both winter and summer. Except for the cestode *Eubothrium* sp. in perch, all helminths recovered were in the adult stage.

3.1. Community structure in perch

Total length of perch varied among samples (Fig. 1). Both the lake from which they were collected (two-way ANOVA, $F_{3,353} = 19.79$, $P = 0.0001$) and the season in which they were collected ($F_{1,353} = 53.76$, $P = 0.0001$) influenced the length of perch. There was also a significant interaction between lake and season ($F_{3,353} = 4.46$, $P = 0.0043$). Although length of perch varied among lakes, the range of values obtained was relatively narrow (Fig. 1), making the lakes comparable.

Four helminth species were generally more abundant than others in all perch samples, and could be used for pairwise association tests. The abundance of these helminths varied among lakes, and not surprisingly, it also varied between seasons within lakes (Table 1). The abundance of the cestode *Proteocephalus percae* tended to be higher in winter, whereas that of other helminths generally peaked in summer. Interspecific associations between pairs of species were only computed for helminth species harboured by at least five fish in a sample, so that association between certain pairs could not be evaluated in all samples. Nine of the 10 significant pairwise associations observed were negative (Table 2). Some associations were observed in one season and not in the other within the same lake, and, more importantly, in one lake but not in another during the same season, despite good sample sizes providing sufficient statistical power. No single significant association could be detected in all lakes or seasons.

Departures from random assembly were also not found in all samples using nestedness analyses. Significant nested subset patterns were observed in lakes Peurunka and Saravesi, whereas a significant anti-nested pattern was found during summer in lake Leppavesi (Table 3). Significant relationships between fish length and total helminth abundance were found in these three lakes, but not in lake Vatia, the only lake in which helminth species assemblages did not depart from randomness in any way according to the nestedness analyses (Table 3).

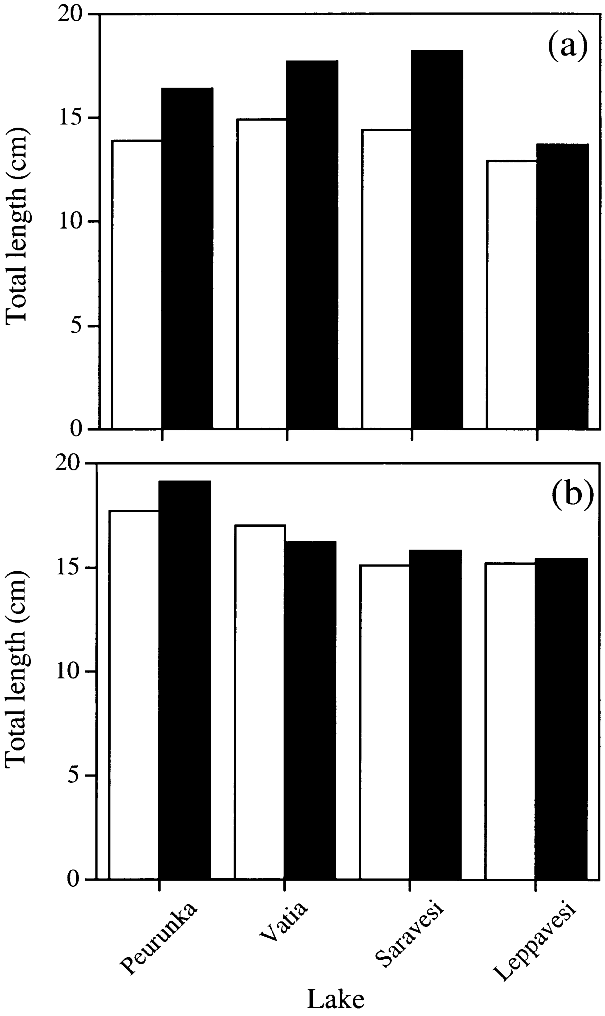

Fig. 1. Mean total length of (a) perch *Perca fluviatilis* and (b) roach *Rutilus rutilus*, caught in winter (white bars) and summer (black bars) samples from four lakes in Central Finland. Standard errors are not shown but were very small (between 0.3 and 0.6 for perch, and 0.2 and 0.4 for roach).

Table 1
Abundance (mean number of parasites per host, range in parentheses) of four common helminths in perch, *Perca fluviatilis*, from four lakes in Central Finland[a]

Helminth species	Lake Peurunka		Lake Vatia		Lake Saravesi		Lake Leppavesi	
	Winter ($n = 44$)	Summer ($n = 59$)	Winter ($n = 16$)	Summer ($n = 42$)	Winter ($n = 43$)	Summer ($n = 62$)	Winter ($n = 42$)	Summer ($n = 53$)
Trematoda								
Bunodera luciopercae	15.4	36.9	6.7	6.2	9.6	30.15	3.1	3.1
	(0–90)	(0–200)	(0–24)	(0–45)	(0–61)	(0–675)	(0–36)	(0–32)
Cestoda								
Proteocephalus percae	**5.2**	**0.7**	0.1	0.1	**0.6**	**0.1**	**0.9**	**0.1**
	(0–34)	(0–13)	(0–1)	(0–1)	(0–5)	(0–3)	(0–11)	(0–2)
Nematoda								
Camallanus lacustris	–	0.3	0.8	1.1	**3.7**	**7.5**	**0.3**	**1.2**
		(0–10)	(0–5)	(0–6)	(0–51)	(0–42)	(0–3)	(0–12)
Acanthocephala								
Acanthocephalus lucii	**0.6**	**4.5**	1.4	2.2	0.4	1.2	**0.1**	**2.4**
	(0–11)	(0–30)	(0–10)	(0–16)	(0–7)	(0–13)	(0–2)	(0–20)

[a] Pairs of values in bold indicate seasonal differences, Mann–Whitney *U*-test, $P < 0.005$.

Table 2
Matrix of pairwise associations between the intensity of infection of the four most common helminths in perch, *Perca fluviatilis*, from four lakes in Central Finland[a]

	Camallanus lacustris	*Proteocephalus percae*	*Bunodera luciopercae*	*Acanthocephalus lucii*
Lake Peurunka				
Camallanus lacustris	×	–	–	–
Proteocephalus percae	–	×	−0.335* (47)	−0.040 (44)
Bunodera luciopercae	–	−0.014 (44)	×	−0.150 (57)
Acanthocephalus lucii	–	0.010 (30)	0.077 (43)	X
Lake Vatia				
Camallanus lacustris	×	–	−0.340 (34)	−0.316 (31)
Proteocephalus percae	–	×	–	–
Bunodera luciopercae	0.121 (13)	–	×	0.039 (36)
Acanthocephalus lucii	−0.722* (11)	–	−0.674* (15)	×
Lake Saravesi				
Camallanus lacustris	×	–	0.142 (57)	−0.407** (55)
Proteocephalus percae	−0.217 (27)	×	–	–
Bunodera luciopercae	0.573** (38)	0.009 (37)	X	−0.016 (50)
Acanthocephalus lucii	−0.471* (23)	−0.742** (20)	−0.078 (36)	×
Lake Leppavesi				
Camallanus lacustris	×	–	−0.452** (42)	−0.234 (39)
Proteocephalus percae	−0.755** (17)	×	–	–
Bunodera luciopercae	0.082 (24)	−0.058 (24)	×	−0.416* (41)
Acanthocephalus lucii	–	–	–	×

[a] Fish not harbouring worms from at least one of the two species in a pair (i.e. double zeros) were excluded; actual sample sizes are shown in parentheses. Associations in summer samples are shown above the diagonal, and those in winter samples are shown below. *$P < 0.05$; **$P < 0.005$.

3.2. Community structure in roach

As with perch, total length of roach varied among samples (Fig. 1). The lake from which they were collected influenced the length of roach (two-way ANOVA, $F_{3,374} = 53.31$, $P = 0.0001$) and, to a much lesser extent, so did the season in which they were collected ($F_{1,374} = 3.78$, $P = 0.0525$). There was also a significant interaction between lake and season ($F_{3,374} = 4.11$, $P = 0.0069$). The length of roach, although it differed among lakes, was still quite comparable across all four lakes (Fig. 1).

Five helminth species were generally common enough in all roach samples to be used for pairwise association tests. The abundance of these helminths varied among lakes and, in some instances, between seasons within lakes (Table 4). When significant differences between seasons were observed, the abundance of helminths tended to be higher in winter than in summer (Table 4). As for perch, interspecific associations between pairs of species were computed only for helminth species harboured by at least five fish in a sample, so that no pairwise association was evaluated in all samples. All five significant pairwise associations observed between helminth species were negative (Table 5). Again, some associations were observed in one season and not in the other within the same lake, or in one lake but not in another during the same season, although some sample sizes limited the power of the analyses. Also, no single significant association could be detected in all lakes or seasons.

Table 3
Nestedness and correlation between fish length and total helminth abundance (Spearman's rank correlation coefficient, all species combined) in helminth communities of perch, *Perca fluviatilis*, from four lakes in Central Finland[a]

Lake	Nestedness, *N* (no. species)		Length-abundance correlation (r_s)	
	Winter	Summer	Winter	Summer
Peurunka	3* (3)	60 (7)	0.322*	0.389**
Vatia	9 (4)	50 (5)	−0.134	0.054
Saravesi	24* (5)	64* (6)	0.592**	0.341*
Leppavesi	13 (4)	54** (4)	0.312*	0.389*

[a] Sample size (number of fish included) are as in Table 1. *$P < 0.05$, **$P < 0.005$ (or $P > 0.95$ and $P > 0.995$, respectively, in the case of nestedness).

Departures from random assembly among helminth parasites of roach were not found in all samples using nestedness analyses. Significant anti-nested patterns were observed in winter in lakes Vatia and Saravesi; no other significant patterns were found (Table 6). Significant relationships between fish length and total helminth abundance were found in at least one season in all lakes except lake Saravesi (Table 6).

4. Discussion

The search for patterns in community ecology is only

Table 4
Abundance (mean number of parasites per host, range in parentheses) of five common helminths in roach, *Rutilus rutilus*, from four lakes in Central Finland[a]

Helminth species	Lake Peurunka		Lake Vatia		Lake Saravesi		Lake Leppavesi	
	Winter ($n = 45$)	Summer ($n = 63$)	Winter ($n = 19$)	Summer ($n = 59$)	Winter ($n = 44$)	Summer ($n = 60$)	Winter ($n = 45$)	Summer ($n = 47$)
Trematoda								
Allocreadium isosporum	0.8 (0–7)	2.7 (0–40)	–	–	**1.6** (0–20)	**0.3** (0–13)	0.11 (0–3)	–
Sphaerostoma globiporum	–	–	–	–	0.3 (0–4)	0.2 (0–3)	**2.1** (0–16)	**0.3** (0–5)
Cestoda								
Caryophyllaeus fennica	0.3 (0–9)	0.1 (0–2)	0.2 (0–3)	0.1 (0–5)	0.1 (0–2)	0.1 (0–1)	0.1 (0–1)	0.1 (0–1)
Acanthocephala								
Neoechinorhynchus rutili	1.2 (0–14)	0.3 (0–5)	**1.1** (0–5)	**0.3** (0–5)	0.3 (0–10)	0.1 (0–2)	0.3 (0–3)	0.1 (0–2)
Acanthocephalus anguillae	–	–	–	0.2 (0–3)	0.1 (0–1)	0.1 (0–3)	0.1 (0–2)	0.2 (0–4)

[a] Pairs of values in bold indicate seasonal differences, Mann–Whitney *U*-test, $P < 0.005$.

Table 5
Matrix of pairwise associations between the intensity of infection of the five most common helminths in roach, *Rutilus rutilus*, from four lakes in Central Finland[a]

	A. isosporum	*S. globiporum*	*N. rutili*	*A. anguillae*	*C.fennica*
Lake Peurunka					
Allocreadium isosporum	X		−0.116 (16)		−0.748** (18)
Neoechinorhynchus rutili	−0.857** (21)		X		−0.361 (11)
Caryophyllaeus fennica	–		–		X
Lake Vatia					
Neoechinorhynchus rutili			X	−0.803** (15)	
Acanthocephalus anguillae			–	X	
Lake Saravesi					
Allocreadium isosporum	X	−0.915** (12)			
Sphaerostoma globiporum	−0.225 (16)	X			
Lake Leppavesi					
Sphaerostoma globiporum		X	–	−0.437 (10)	–
Neoechinorhynchus rutili		0.098 (25)	X	–	–
Acanthocephalus anguillae		–	–	X	–
Caryophyllaeus fennica		0.156 (22)	−0.653** (12)	–	X

[a] Fish not harbouring worms from at least one of the two species in a pair (i.e. double zeros) were excluded; actual sample sizes are shown in parentheses. Associations in summer samples are shown above the diagonal, and those in winter samples are shown below. $^{*}P < 0.05$; $^{**}P < 0.005$.

worthwhile if general patterns, which show both consistency and predictability, can be found (Strong et al., 1984; Weiher and Keddy, 1999). Otherwise, the myriad of factors needed to explain highly variable patterns would preclude us from identifying any general rules of species assembly. Others (e.g. Kennedy, 1978; Holmes, 1990) have pointed out that local effects can determine whether given parasite species are present or not in a given host population, but here we focused on general structural patterns of the entire helminth community across lakes where species composition and environmental conditions were highly comparable. We did not find a single departure from random species assembly that could be observed repeatedly between similar and nearby helminth communities in the same season. This was true of helminth communities in two different host species, perch and roach, suggesting that the lack of repeatability in helminth community structure is a general feature. The differences between seasons within the same lake reflect seasonal colonisation patterns by parasites rather than true temporal unpredictability in parasite community structure, which would only become apparent if year-to-year variation was found. Nevertheless, the seasonal effect emphasises the dynamic nature of parasite communities over time.

We compared fish populations from different lakes that were adjacent, more or less interconnected, and inhabited by the same fish species. Still, one could argue that there were some differences among the lakes that limit their use in a comparative study like the present one. First, the lakes varied with respect to levels of eutrophication and pollution. From the perspective of the species composition of these helminth communities, minor differences can be attributed to either pollution or eutrophication (see Valtonen et al., 1997). From the perspective of community structure, however, our analyses focused mainly on the common species found in all lakes. The discriminant analyses of Valtonen et al. (1997) that found differences in the parasite faunas of the lakes were influenced by differences in larval helminths and ectoparasites, and here we focus on adult endohelminths found in perch and roach, a group that

Table 6
Nestedness and correlation between fish length and total helminth abundance (Spearman's rank correlation coefficient, all species combined) in helminth communities of roach, *Rutilus rutilus*, from four lakes in Central Finland[a]

Lake	Nestedness, *N* (no. species)		Length-abundance correlation (r_s)	
	Winter	Summer	Winter	Summer
Peurunka	41 (7)	40 (6)	0.245	0.454**
Vatia	3** (3)	13 (6)	0.688**	0.285*
Saravesi	11** (6)	31 (8)	0.045	−0.103
Leppavesi	33 (7)	25 (7)	0.535**	0.033

[a] Sample sizes (number of fish included) are as in Table 4. $^{*}P < 0.05$, $^{**}P < 0.005$ (or $P > 0.95$ and $P > 0.995$, respectively, in the case of nestedness).

showed no consistent differences between lakes with respect to pollution or eutrophication. In any event, whereas water quality can determine whether a parasite species is present in a given lake, it is less likely to determine how it is distributed among host individuals. Besides, no two lakes, or no two host populations, are identical with respect to all biotic and abiotic variables; at least our study lakes were of similar origins, harboured identical fish faunas, and were exposed to identical climatic conditions. The general community assembly rules that parasite ecologists are looking for should overcome these minor local influences. Second, it must be pointed out that fish length differed significantly among lakes, for both perch and roach. These differences were not large, and probably reflect the different growth of fish in the different lakes (because of lake trophic status). The fish examined were of the same age classes, which is probably more relevant to a study on parasite communities in which accumulation of parasites is time-dependent.

Almost all significant pairwise associations, and most of the non-significant ones, were negative (see Tables 2 and 5). At a glance, this finding suggests that some form of antagonistic interaction, possibly competition, is taking place between many pairs of helminths in the intestine of perch and roach. Given that positive associations are usually easier to detect for a range of reasons (Lotz and Font, 1994; Haukisalmi and Henttonen, 1998), the excess of negative associations reinforce the suggestion that competitive interactions are common. The fact that less than one third of the pairwise tests showed a statistically significant association suggests that patterns in species co-occurrences are erratic and unpredictable. It must be pointed out that prevalence and intensity of infection affect the magnitude and direction of pairwise associations, as well as how easy they are to detect (see Lotz and Font, 1994; and Appendix in Vickery and Poulin, 2002), so that their interpretation must be made with care. Still, not a single pairwise association was observed consistently in all seasons or all lakes, indicating that local factors or short-term influences can mask or eliminate any negative or competitive interaction. For instance, the mean abundance of one or both parasites in a pair of species, or the seasonal sequence in which one or the other species infects the host, could determine whether or not they will be negatively associated. These and other factors will vary among lakes. Dezfuli et al. (2001) also found that pairwise associations between gastrointestinal species of the brown trout, *Salmo trutta*, varied unpredictably between localities. Taken together, these results mean that associations between species are subject to a wide range of local or temporal effects, and that results from one sample cannot say anything reliable about the generality of the association. It is also very likely that pairwise associations between helminth species in fish are simply transferred from existing associations in intermediate hosts, and that they have nothing to do with interspecific interactions occurring in the fish host (see Vickery and Poulin, 2002). Again, variation in time or space in the relative availability of different intermediate host species can result in differences in species associations among helminths in the definitive host. Although testing for associations between pairs of helminth species is a method widely used to assess departures from random assembly in communities of gastrointestinal helminths of vertebrates (e.g. Moore and Simberloff, 1990; Lotz and Font, 1991, 1994; Haukisalmi and Henttonen, 1993), it cannot be used to infer the operation of competition or other structuring processes at scales larger than that of the local host population.

The other approach we followed to detect departures from random species assembly was to look for nested (or anti-nested) subset patterns in the helminth communities of perch and roach. This method has been used widely in studies of fish parasite communities (Guégan and Hugueny, 1994; Worthen and Rohde, 1996; Rohde et al., 1998; Poulin and Guégan, 2000; Poulin and Valtonen, 2001). Here, we found evidence for either nestedness or anti-nestedness in some of our samples, but never the same pattern in both seasons in the same lake (with one exception, i.e. perch in lake Saravesi; see Table 3), or in all lakes in the same season. Poulin and Valtonen (2001) have shown that nested subset patterns are more likely to be observed in host samples in which parasite abundance is correlated with host size. For perch, the only lake (lake Vatia) in which fish size did not correlate with helminth abundance was indeed the only one where nestedness was not observed. However, this pattern is not seen in analyses of roach populations. There must therefore be other forces affecting the assembly of helminth species in these fish, and it is impossible to use results from one sample to predict what sort of nested subset pattern will be found in another sample of the same fish species. Only one other study has investigated the repeatability of nested patterns across time and space. Carney and Dick (2000) found that helminth communities of yellow perch, *Perca flavescens*, were nested in five populations, and in two consecutive summers in one of those populations. In this fish species, nestedness appears to be a repeatable feature of helminth communities. It is not clear why nested patterns are more or less predictable in time and space in *P. flavescens* but not in its congener *P. fluviatilis*; the two groups have similar parasite faunas in terms of species richness and the representation of major helminth taxa. Clearly, we need to explore the repeatability of helminth community structure in more host species to determine which of these two perch species is the exception.

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