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Host introductions and the geography of parasite taxonomic diversity

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Abstract

Aim Geographical variation in parasite diversity is examined among populations of fish in their original heartland and in areas where they have been introduced. The diversity in heartland and introduced populations is contrasted, and also compared with the expectations of a null model.

Location Data on the parasite communities of two salmonid fish species were obtained: the rainbow trout *Oncorhynchus mykiss* in its British Columbia heartland and in introduced populations in North America, Great Britain, South America and New Zealand; and the brown trout *Salmo trutta* in heartland populations from Great Britain, and in introduced populations in North America, South America and New Zealand.

Methods The average taxonomic distinctness and its variance were computed for each parasite community, and used as measures of the taxonomic diversity of parasite species in each fish population. Observed values of taxonomic distinctness were also compared with those expected if each community was a random selection from the world list of parasite species known for each of the two host species.

Results Few parasite communities departed from the expectations of the null model, i.e. few had a taxonomic diversity of parasites greater or lower than that expected from a random selection of parasite species. However, these departures were not more or less likely among heartland fish populations than among introduced ones. In both fish species, parasite communities in introduced populations tended to be a little more taxonomically diverse than in the heartland populations.

Main conclusions Overall, the results suggest that the accumulation of parasite species in introduced hosts over short (ecological) periods of time can result in parasite assemblages that are just as, or even more, taxonomically diverse than those developed over much longer (evolutionary) time frames in the host species geographical heartland. This finding highlights the importance of ecological factors in parasite biodiversity in addition to coevolutionary processes.

Keywords
Taxonomic distinctness, phylogenetic diversity, *Salmo trutta*, *Oncorhynchus mykiss*, helminths.

INTRODUCTION

Recent phylogeographical studies have highlighted the synergy between coevolutionary and historical biogeographical processes in shaping the diversity of parasite assemblages (e.g. Brooks & McLennan, 1993; Hoberg, 1997; Hoberg & Klassen, 2002). Parasites are, to a large extent, closely coupled with their hosts through their shared coevolutionary history, and their geographical distribution often mirrors that of their hosts. Ecological factors also influence parasite biogeography, and especially the local diversity of parasite assemblages (Poulin, 1995, 1998; Rohde, 2002), but the coevolved link between parasites and their hosts always remains strong.

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Recently, the numerous introductions of plants and animals from their area of origin into new geographical regions may have weakened this link, with the distributions of widely introduced host species now far outreaching those of their original parasites. The conventional wisdom is that when a host species is moved out of its area of origin, it leaves behind some if not most of its parasites, possibly gaining new ones in its new habitat. Torchin *et al.* (2002) have recently compiled data from the literature and found that the diversity of parasites in marine hosts is consistently lower in regions where they have been introduced than in their native areas, thus supporting the notion that parasites are lost during an introduction. Kennedy & Bush (1994) have argued that it is the specialist parasites that are lost most easily, the ones that depend on a narrow range of host taxa for their continued transmission. They have shown that the proportion of specialist parasites in the parasite communities of the salmonid fish *Oncorhynchus mykiss* is greatest in the fish heartland, i.e. in the geographical area where the fish evolved and to which it was restricted prior to human intervention, than in areas to which the fish has been introduced. Whereas the species richness of parasite communities did not necessarily decrease with increasing distance from the heartland, the proportion of specialist parasite species in the communities did; an increasing number of generalist species made up the rest of each community (Kennedy & Bush, 1994). Distance from the heartland is a convenient surrogate for the overall differences between the fauna of the heartland and that of the area of introduction; accordingly, the specialist parasite species that require certain intermediate hosts are the first one to disappear as one moves away from the original heartland.

If we regard hosts as repositories of parasite biodiversity, we might ask what role introduced hosts play as habitats for diverse assemblages of parasites. Hosts that were introduced completely free of parasites into new areas are essentially empty habitats awaiting colonization by parasites. In their heartland, these hosts harboured a fauna of parasites with which they had coevolved over long periods of time. In their new surroundings, introduced hosts are often colonized by novel parasites over short periods of time. Their fauna in those new surroundings is the product of ecological rather than evolutionary processes. Will this limit the diversity of their new parasite fauna compared with that in their heartland? The concept of phylogenetic diversity (Faith, 1992; Humphries *et al.*, 1995; Barker, 2002) provides a useful framework in which to address this question and ask related ones. Regardless of how many of their parasites are specialists as opposed to generalists, are the parasite communities harboured by introduced hosts more or less diverse, phylogenetically, than those of their conspecifics back in the species heartland? In other words, do introduced hosts provide a habitat to a broader or narrower spectrum of parasite taxa than they did prior to their introduction?

In this paper, we compare the diversity of parasite communities found in introduced and heartland populations of two salmonid fish species, the rainbow trout *O. mykiss* Richardson, 1836 (formerly *Salmo gairdneri*) and the brown trout *Salmo trutta* Linnaeus, 1758. The former originates along the Pacific coast of North America and eastern Asia, and has been introduced to other parts of North America, and to Europe, South America, Japan, Australia and New Zealand, among other places (MacCrimmon, 1971). The latter originates from Eurasia, and was translocated from its native Great Britain to several new areas, including North and South America and New Zealand (MacCrimmon & Marshall, 1968). These fish were introduced as either fry or eggs (e.g. Lever, 1977), and therefore free of parasites: whatever parasite species now exploit them in their new habitats were acquired following the fishes, introduction. This provides a great opportunity to compare parasite communities assembled over ecological time with those assembled in the same host species over much longer, evolutionary time. These may include specialist salmonid parasites, if other salmonid fish occur locally as a source of infection, or parasites acquired from totally unrelated fish species.

In most ecological studies, the measures of diversity of communities most often used are either the number of species present, i.e. species richness, or diversity indices (see Magurran, 1988). However, these measures are dependent of sample size (Frontier, 1985; Price *et al.*, 1999) and do not take into account differences between species (morphological, functional, phylogenetic or taxonomic) (Purvis & Hector, 2000; Shimatani, 2001). In the past few years, Warwick & Clarke (1995, 1998) and Clarke & Warwick (1998, 1999, 2001) have proposed new diversity indices that take into account the phylogenetic or taxonomic differences between species. These indices seem to be independent of sample size and appropriate to assess differences between communities (Rogers *et al.*, 1999; Clarke & Warwick, 2001; Warwick *et al.*, 2002). We apply the indices of taxonomic distinctness developed by Clarke & Warwick (1998, 1999, 2001) to data on the parasite communities of the two salmonid hosts; these allow easy quantification of the taxonomic or phylogenetic disparity of the parasite species infecting the different populations of fish. To our knowledge, this is the first use of these indices for measurements of parasite biodiversity.

Our study has two specific aims. First, we determine whether each fish population harbours a parasite community with a taxonomic diversity different from that expected had the community been drawn at random from the global parasite species list known from the host species. Secondly, we compare the taxonomic diversity of parasite communities in introduced populations with those from the heartland. Our results will shed light on the geographical patterns of parasite biodiversity created by large-scale translocations of their animal hosts.

METHODS

Data on the parasite species exploiting both fish species in their heartland and in introduced populations were obtained from the literature. For *O. mykiss*, parasitological data were available for the heartland, i.e. coastal British Columbia, and for several areas where the fish was introduced in North

Table 1 Summary of the parasite species richness in populations of rainbow trout, *Oncorhynchus mykiss*, from different regions, in increasing distance from the host's heartland (the latter in bold)

Region	No. fish examined	No. of trematodes	No. of cestodes	No. of nematodes	No. of acanthocephalans	Total	Source
British Columbia	696	3	4	6	2	15	1
Canadian Rockies	49	2	2	3	0	7	2
Manitoba	43	4	0	0	1	5	3
Lake Huron	15	1	3	1	2	7	4
Michigan	24	0	0	0	2	2	5
New Mexico	94	1	0	1	0	2	6
Newfoundland	27	1	2	0	1	4	7
England-1	42	4	3	1	1	9	8
England-2	89	5	3	1	1	10	9
Scotland	55	5	0	1	0	6	10
Chile	242	2	2	2	2	8	11, 12
Argentina	137	0	1	1	2	4	13, 14, 15
New Zealand	?	0	0	2	0	2	16
World-wide		15	10	15	9	49	

Sources: (1) Bangham & Adams (1954), (2) Mudry & Anderson (1977), (3) Szalai & Dick (1988), (4) Bangham (1955), (5) Muzzall (1984), (6) Wier *et al.* (1983), (7) Sandeman & Pippy (1967), (8) Kennedy *et al.* (1991), (9) Wootten (1973), (10) McGuigan & Sommerville (1985), (11) Torres *et al.* (1991), (12) Torres (1995), (13) Ubeda *et al.* (1994), (14) Revenga *et al.* (1995), (15) Rauque *et al.* (2003), (16) Hewitt & Hine (1972).

America (alpine lakes in the Rockies, Manitoba, Lake Huron, Michigan, New Mexico and Newfoundland), Europe (two localities in England and one in Scotland), South America (Chile and Argentina), and New Zealand (Table 1). For *S. trutta*, data were available from ten lakes in the heartland, i.e. Great Britain, and from areas where the fish was introduced in North America (two localities in Newfoundland, Michigan and New Mexico), Chile and New Zealand (Table 2).

For each fish population, the total number of fish examined for parasites, if given, and the total number of parasite species (i.e. parasite species richness) found were recorded. The number of hosts examined, or sampling effort, is often a key determinant of the number of parasites found in a survey (Walther *et al.*, 1995), and must therefore be included as a potential confounding variable. We only included species of parasitic helminths (trematodes, cestodes, nematodes and acanthocephalans).

Table 2 Summary of the parasite species richness in populations of brown trout, *Salmo trutta*, from different regions, in increasing distance from the host's heartland (the latter in bold)

Region	No. fish examined	No. of trematodes	No. of cestodes	No. of nematodes	No. of acanthocephalans	Total	Source
Great Britain-1	?	4	4	5	1	14	1
Great Britain-2	?	4	4	4	3	15	1
Great Britain-3	?	4	3	3	3	13	1
Great Britain-4	?	2	2	1	2	7	1
Great Britain-5	?	2	0	1	1	4	1
Great Britain-6	?	1	0	1	1	3	1
Great Britain-7	?	2	0	2	0	4	1
Great Britain-8	?	2	0	1	0	3	1
Great Britain-9	?	2	2	1	1	6	1
Great Britain-10	56	4	3	2	1	10	2
Newfoundland-1	22	1	0	0	1	2	3
Newfoundland-2	23	2	2	1	1	6	4
Michigan	281	1	1	0	3	5	5
New Mexico	29	1	0	1	0	2	6
Chile	348	1	0	2	1	4	7, 8
New Zealand	103	5	1	5	1	12	9
World-wide		16	9	14	9	48	

Sources: (1) Kennedy (1978), (2) Wootten (1973), (3) Threlfall & Hanek (1970), (4) Sandeman & Pippy (1967), (5) Muzzall (1984), (6) Wier *et al.* (1983), (7) Torres *et al.* (1991), (8) Torres *et al.* (1992), (9) Dix (1968).

For the computations of taxonomic distinctness (see below), we used the proposed phylogenetically based taxonomy of trematodes of Brooks & McLennan (1993), and the taxonomies of Khalil *et al.* (1994) for cestodes, Anderson (2000) for nematodes and Amin (1985) for acanthocephalans.

For each of the two fish species, a world list of parasite species was constructed using the lists for individual populations from both the heartland and areas where the fish has been introduced. The original authors' identification of parasite species was taken as valid, with synonymous names checked using the taxonomic references above. Then, for each fish population and for the world lists of parasites of both fish species, we computed the average taxonomic distinctness (Δ^+) and the variance in taxonomic distinctness (Λ^+) of the parasite species included. When parasite species are placed within a taxonomic hierarchy, based on the Linnean classification into kingdom, phyla, classes, orders, families, genera and species, the average taxonomic distinctness, Δ^+, is simply the mean number of steps up the hierarchy that must be taken to reach a taxon common to two parasite species, computed across all possible pairs of parasite species (Clarke & Warwick, 1998, 1999; Warwick & Clarke, 2001). Thus, if two species are congeners, one step (species-to-genus) is necessary to reach a common node in the taxonomic tree; if the two species belong to different genera but the same family, two steps will be necessary (species-to-genus, and genus-to-family); and so on, with these numbers of steps averaged across all species pairs. For any given species pair, the number of steps corresponds to half the path length connecting two species in the taxonomic tree, with equal step lengths being postulated between each level in the taxonomic hierarchy. Step lengths are standardized so that the distinctness of two species connected at the highest taxonomic level is set equal to 100 (Clarke & Warwick, 1999); with six levels above the species in the taxonomy we used, each step length was thus equal to 16.67. The greater the taxonomic distinctness between parasite species, the higher the number of steps needed, and the higher the value of Δ^+. A high value means that on average the parasites in a host population are not closely related. Formally, Δ^+ is computed as follows (see Clarke & Warwick, 1998):

$$\Delta^+ = 2\frac{\sum\sum_{i<j}\omega_{ij}}{s(s-1)},$$

where s is the number of parasite species, the double summation is over the set $\{i = 1,\ldots s;\ j = 1,\ldots s$, such that $i < j\}$, and ω_{ij} is the taxonomic distinctness between parasite species i and j, or the number of taxonomic steps required to reach a node common to both.

The index Δ^+ measures the average taxonomic distinctness between species, and does not capture all of the taxonomic structure of a set of parasite species. It is possible to have two host populations, each harbouring the same number of parasite species and each characterized by an identical value of Δ^+, but with one host population clearly supporting a broader taxonomic range of parasites. Asymmetries in the taxonomic distribution of species across higher taxa can sometimes be missed by Δ^+, which is only the average taxonomic distinctness; in these situations complementary information can be obtained by examining the variance in taxonomic distinctness (see Clarke & Warwick, 2001 or Warwick & Clarke, 2001):

$$\Lambda^+ = \frac{\sum\sum_{i\neq j}\left(\omega_{ij} - \varpi\right)^2}{s(s-1)},$$

where $\bar{\omega}$ is simply the average taxonomic distinctness, or Δ^+. The variance Λ^+ conveys separate information of how much taxonomic heterogeneity there is among a group of parasite species. Note, however, that Λ^+ can only be computed when at least three parasite species are found in a host population (it always equals zero with two species).

We tested the null hypothesis that the taxonomic distinctness of a parasite community is no different from that of a random subset of the host fish world parasite list. To do this, for each fish population, we generated 10,000 random selections of parasite species from the world list, each selection having the same number of species as that found in the host population. Average taxonomic distinctness and its variance were computed for each random subset. Observed values of Δ^+ and Λ^+ were then compared with the null distributions of these random subsets; the probability that the observed values depart from the null distribution is equal to the proportion of simulated values that are greater (or lower) than the observed ones. To calculate the indices and to run the simulations, a computer program was developpped using borland C++ Builder 5.0.

RESULTS

Parasite diversity in *O. mykiss*

We obtained data on the helminth parasites of *O. mykiss* from thirteen regions or populations, one from the fish heartland in British Columbia and the rest from areas where the fish has been introduced (Table 1). Overall, the parasite species from these different regions contributed to a global world list of forty-nine helminth species (Table 1). Parasite species richness was clearly highest in the heartland, although this is also where the most fish were examined for parasites. There was, however, no relationship between the number of fish examined and parasite species richness across all regions (Spearman rank correlation: $r_s = 0.32$, $n = 12$, $P = 0.2887$).

The average taxonomic distinctness, Δ^+, of the parasites in the heartland was almost identical to that of the world list, and it did not differ from what would be expected if the parasite species in the heartland were a random selection from the world list (Fig. 1). In one of the areas where *O. mykiss* has been introduced (New Mexico), the value of Δ^+ is higher than expected under our null hypothesis (Fig. 1);

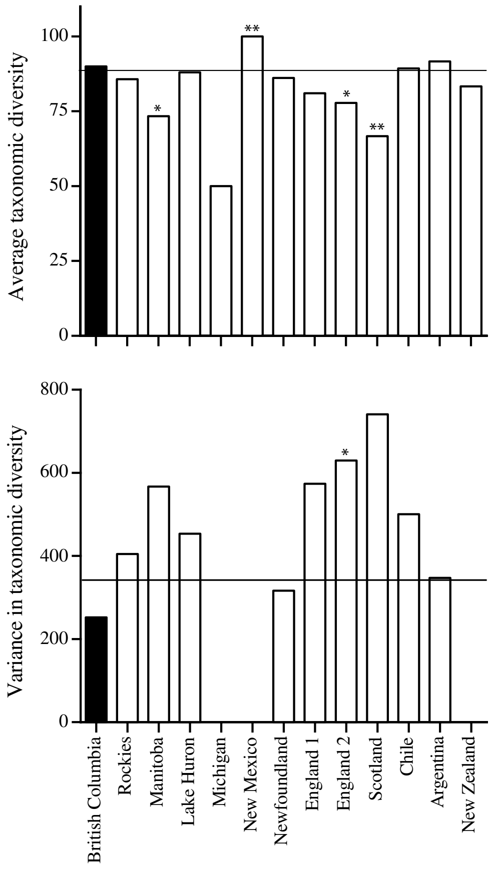

Figure 1 Average, Δ^+, and variance, Λ^+, in taxonomic distinctness of helminth parasite assemblages in populations of rainbow trout, *Oncorhynchus mykiss*, from its original heartland (black bar) and in regions where it has been introduced (open bars). The line represents the value of Δ^+ or Λ^+ computed for the world list of helminths parasitizing this fish. Asterisks indicate significant departures between the observed value and that expected from assemblages of identical species richness drawn at random from the world list ($*P < 0.05$; $**P < 0.005$). Note that variance in taxonomic distinctness, Λ^+, was not computed for the three regions (Michigan, New Mexico and New Zealand) with only two helminth species.

there are only two parasite species recorded in that area, however, and the usefulness of Δ^+ in such circumstances is questionable. In three other areas, where parasite species richness is higher, the values for Δ^+ were significantly lower than those generated by our null model (Fig. 1). In general, Δ^+ can be considered as a measure of diversity independent from parasite species richness, as the two are not correlated ($r_s = 0.039$, $n = 13$, $P = 0.8931$). However, there is a weak tendency for Δ^+ to increase with the number of fish examined ($r_s = 0.545$, $n = 12$, $P = 0.0704$).

The variance in taxonomic diversity, Λ^+, of the parasite species in the heartland was lower than in any other area, although not significantly lower than expected under our null hypothesis (Fig. 1). The generally higher values of Λ^+ in areas where *O. mykiss* has been introduced suggest that the parasite assemblages in these new areas consist of a more heterogeneous group of helminth taxa than in the heartland. The observed value of Λ^+ was significantly higher than those of our null model in only one locality, however (Fig. 1). Across all regions, Λ^+ was not correlated with either the number of fish examined ($r_s = -0.127$, $n = 10$, $P = 0.7026$) or parasite species richness ($r_s = 0.152$, $n = 10$, $P = 0.6474$); however, Λ^+ and Δ^+ were negatively related to one another ($r_s = -0.794$, $n = 10$, $P = 0.0172$).

Parasite diversity in *S. trutta*

We gathered data on the helminth parasites of *S. trutta* from sixteen regions or populations, including ten British lakes where the fish is native, and six areas where it has been introduced (Table 2). The world list of parasite species of this fish totalled forty-eight species. Among the few populations for which data were available (Table 2), there was no relationship between the number of fish examined and parasite species richness ($r_s = 0.288$, $n = 7$, $P = 0.4801$). Some of the highest values of parasite species richness were observed in the British heartland; however, there was no difference in parasite species richness between native and introduced populations of *S. trutta* (Mann–Whitney *U*-test: $Z = 1.254$, $n_1 = 10$, $n_2 = 6$, $P = 0.2099$).

The average taxonomic distinctness, Δ^+, of the parasite species in both native and introduced populations of *S. trutta* were generally very close to that of the world list. The three cases (one native and two introduced) in which Δ^+ values were significantly higher than those predicted by our null model are all regions where only two or three parasite species have been recorded (Fig. 2). Overall, Δ^+ values in areas where *S. trutta* was introduced were marginally higher than in populations from the heartland ($Z = 1.961$, $n_1 = 10$, $n_2 = 6$, $P = 0.0499$). Again, Δ^+ can be considered as a measure of diversity independent from parasite species richness, as the two are not correlated ($r_s = -0.404$, $n = 16$, $P = 0.1178$). Unlike the results for *O. mykiss*, there was no correlation between Δ^+ and the number of fish examined across *S. trutta* populations ($r_s = -0.327$, $n = 7$, $P = 0.4227$).

The variance in taxonomic diversity, Λ^+, of the parasite species in the heartland populations was more variable than in other areas, sometimes significantly different from that expected under our null hypothesis (Fig. 2). In general, values of Λ^+ in the heartland did not differ from those in areas where *S. trutta* has been introduced ($Z = 1.131$, $n_1 = 10$, $n_2 = 4$, $P = 0.2579$). Across all regions or fish populations, Λ^+ was not correlated with either the number of fish examined ($r_s = -0.301$, $n = 5$, $P = 0.5485$) or parasite species richness ($r_s = 0.252$, $n = 14$, $P = 0.3631$); however, as in the case for *O. mykiss*, Λ^+ and Δ^+ were negatively related to one another ($r_s = -0.896$, $n = 14$, $P = 0.0012$).

DISCUSSION

The parasitological literature conveys a clear message regarding the origin of communities of parasite species

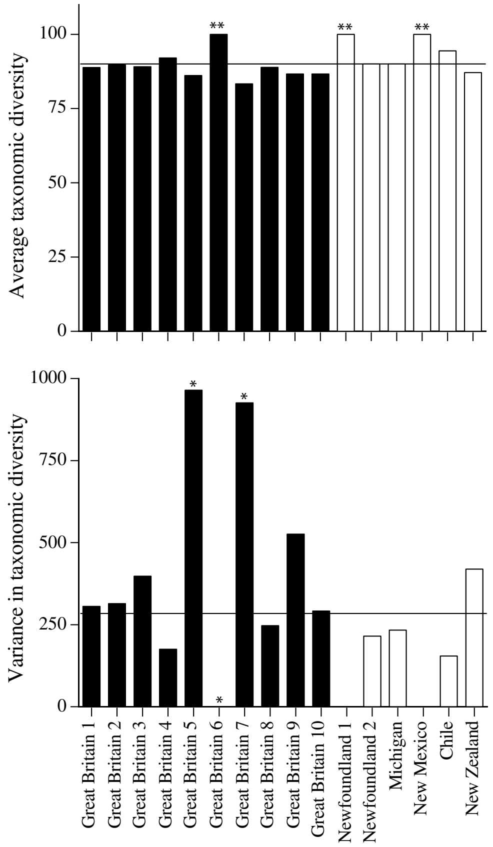

Figure 2 Average, Δ^+, and variance, Λ^+, in taxonomic distinctness of helminth parasite assemblages in populations of brown trout, *Salmo trutta*, from its original heartland (black bars) and in regions where it has been introduced (open bars). The line represents the value of Δ^+ or Λ^+ computed for the world list of helminths parasitizing this fish. Asterisks indicate significant departures between the observed value and that expected from assemblages of identical species richness drawn at random from the world list (*$P < 0.05$; **$P < 0.005$). Note that variance in taxonomic distinctness, Λ^+, was not computed for the two regions (Newfoundland 1 and New Mexico) with only two helminth species, but that it equals zero in Great Britain 6.

exploiting a given host species: these communities are mainly assembled over evolutionary time, with parasite lineages acquired by descent across host generations (Brooks & McLennan, 1993; Hoberg, 1997; Hoberg & Klassen, 2002). Host switches, i.e. transfers of parasite species from one host species to another, do occur from time to time, but they are not frequent enough to allow a diverse community of parasites to be assembled over a short period of time (Poulin & Morand, 2000). The results of our study, however, challenge these ideas.

Within a century following their introduction as eggs, i.e. completely free of helminth parasites, salmonids can accumulate communities of parasites just as diverse, if not more so, as those they harbour in their geographical areas of origin. In other words, the communities of helminth parasites assembled over ecological time in new areas are just as diverse as those assembled over evolutionary time in the host's heartland. The diversity we refer to here is not simply species richness, but the taxonomic (or phylogenetic) diversity of the parasite assemblage (Clarke & Warwick, 1998, 1999, 2001; Warwick & Clarke, 2001). The measures of taxonomic distinctness used quantify the taxonomic disparity among a group of species: four completely unrelated species will thus obtain higher scores of average taxonomic distinctness and its variance, Δ^+ and Λ^+, than four congeneric species. These measures emphasize the phylogenetic origins of species rather than their mere numbers. Our results show that in its heartland, *O. mykiss* harbours a parasite community with a lower Λ^+ than in any of its populations introduced to new areas. This means that the parasites it harbours outside of its heartland area have more disparate phylogenetic origins than in the heartland. Similarly, the Δ^+ values of the parasite assemblages of *S. trutta* tend to be higher in areas where the fish has been introduced than in its heartland. In other words, the taxonomic or phylogenetic relatedness of the parasite species in fish populations outside the heartland tends to be lower than within the British part of the fish heartland.

In addition, parasite communities in introduced fish populations were not obviously more (or less) likely than communities in the fish heartland to have taxonomic distinctness values that departed from those expected under our null model. The subsets of species from the world list found in each population were occasionally more or less taxonomically diverse than expected, but these differences had no clear connection with fish introductions.

Therefore introduced fish rapidly accumulate an assemblage of parasite species with a taxonomic diversity at least as great as what they harboured back in their heartland. But what kinds of parasite species do they acquire following their introduction? As shown by Kennedy & Bush (1994), these are mainly generalist parasites capable of infecting a wide range of host species. If other salmonid fish occur in the area, they may serve as the source of parasite species. If no related fish species is found in the new area, broad generalist parasites can transfer from native fishes. The potential for rapid host switching has been documented in other studies of either host or parasite introductions into new geographical areas (Dove, 1998; Font, 1998). There were native salmonids in all areas where *O. mykiss* and *S. trutta* were introduced except South America and New Zealand; in the latter areas, both *O. mykiss* and *S. trutta* acquired parasite assemblages as diverse as those they harbour in other areas, a good illustration of how generalist parasites can easily colonize distantly related hosts.

The fact that introduced fish become hosts for native parasites does not necessarily mean that they begin playing major ecological roles in the life cycles and transmission of these parasites. Although a parasite species is found in an introduced fish population, it may not be capable of reproducing successfully within the exotic fish. For instance, the acanthocephalan *Pomphorhynchus patagonicus* is one of the helminths parasitizing *O. mykiss* in Argentina. Although the prevalence (percentage of infected fish) and intensities of infection (mean number of worms per fish) are often very high in introduced trout populations, very few worms successfully attain sexual maturity inside trout as compared with their success in native atherinid and galaxiid fishes (Trejo, 1992; Ubeda *et al.*, 1994). In many other cases, however, the introduced fish proved a better, more suitable host for its newly-acquired parasites. The important point is that although the introduced fish population may harbour a considerable diversity of parasites, it may not be necessary resource for the maintenance of all these parasite species.

Regardless of these compatibility issues, our results show that introduced fish can rapidly accumulate new parasite species, soon harbouring communities just as, and sometimes more, taxonomically diverse as those in the fish original heartland. As a result, the world list of parasites for *O. mykiss* has more than tripled in length, and that of *S. trutta* has more than doubled. This study illustrates that potential for host species to rapidly build up new parasite faunas following their translocation to new geographical areas, more than compensating for the original parasite species left behind in the heartland. It also highlights the importance of ecological processes in the formation of parasite communities (Brooks & McLennan, 1993; Poulin, 1995, 1998; Hoberg, 1997; Hoberg & Klassen, 2002; Rohde, 2002). As with other kinds of species assemblages (see Janzen, 1980, 1985), a long period of coevolutionary interactions between hosts and parasites is not necessary for the establishment of a diverse set of parasite species in a host population, and ecological forces should be considered in any study of parasite biodiversity and biogeography.

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