The decay of similarity with geographical distance in parasite communities of vertebrate hosts

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Abstract

Aim The rate at which similarity in species composition decays with increasing distance was investigated among communities of parasitic helminths in different populations of the same host species. Rates of distance decay in similarity of parasite communities were compared between populations of fish and mammal hosts, which differ with respect to their vagility and potential to disperse parasite species over large distances.

Location Data on helminth communities were compiled for several populations of three mammalian host species (*Ondatra zibethicus*, *Procyon lotor* and *Canis latrans*) and three fish host species (*Perca flavescens*, *Catostomus commersoni* and *Esox lucius*) from continental North America.

Methods Distances between localities and similarity in the composition of helminth communities, the latter computed using the Jaccard index, were calculated for all possible pairs of host populations within each host species. Similarity values were then regressed against distance to see if they decayed at exponential rates, as reported for plant communities; the significance of the regressions was assessed using randomization tests.

Results The number of hosts examined per population did not correlate with the number of helminth species found per population, and thus sampling effort is unlikely to have confounded the results. In four (two mammals and two fish) of the six host species, similarity in helminth communities decayed exponentially with distance. When the log of similarity is plotted against untransformed distance, the slopes obtained for the two fish species are lower than those obtained for the two mammalian host species.

Main conclusions Similarity in the composition of parasite communities appears to decay exponentially with increasing distance in some host species, but not in all host species. The rate of decay is not necessarily associated with the vagility of the host. Although distance decay of similarity is generally occurring, it seems that other ecological processes, related either to the host or its habitat, can obscure it.

Keywords
Dispersal, distance decay, geographical range, internal helminths, Jaccard similarity index, parasite biodiversity.

INTRODUCTION

The proportion of species shared by two plant or animal communities often decreases as the distance between them increases. This simple observation is an expected outcome of most ecological or evolutionary phenomena shaping spatial patterns in biodiversity and biogeography (Hengeveld, 1990;

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Huston, 1994; Rosenzweig, 1995; Brown & Lomolino, 1998; Hubbell, 2001). The rate at which biological similarity decays with increasing distance can shed light on some of the processes acting on it. Nekola & White (1999) produced one of the first quantitative analyses of distance decay rates in natural communities. Using large data sets on the plant communities of North American spruce-fir forests, they compared the distance decay of similarity for various categories of plants. Their findings showed that both the decrease in environmental similarity with increasing distances and limits to dispersal affect rates of distance decay in

biological similarity (Nekola & White, 1999). We currently lack quantitative estimates of distance decay rates for other types of biological communities; such estimates would be useful, as they would allow us to determine how variable rates of decay are among different types of organisms, and to formulate general laws of distance decay of similarity.

Parasite communities represent good models for investigations of distance decay rates. They have often been well censused, i.e. their moderate species richness makes it possible for all species to be enumerated. There also exist considerable data on the parasite communities from several populations of the same host species across large geographical areas, providing sufficient material for analyses of distance decay rates. Finally, there is already evidence that distance between host populations affects similarity in the species composition of parasite communities. In multivariate analyses of habitat characteristics that relate with similarity of parasite communities, distance between sampling localities usually emerges as the best predictor of similarity (Poulin & Morand, 1999). However, the rate at which similarity among parasite communities decays with distance has never been quantified.

As a rule, the potential for parasite propagules to disperse in space is much lower than the dispersion potential of their hosts. The vagility of the host species may thus be a key determinant of the spread or exchanges of parasite species among host populations on geographical scales. We might expect rates of distance decay of similarity to be lower among parasite communities of vagile host species than those of parasite communities in hosts with limited dispersal abilities. Typically, among vertebrate host species, values of similarity indices among parasite communities of coastal marine fish, which live in a continuous habitat without real barriers, are the highest recorded, followed by those of parasite communities in birds and mammals (Poulin, 1997). Parasite communities of freshwater vertebrate hosts such as fish and amphibians have the lowest similarity values (Poulin, 1997). The latter hosts live in isolated habitats (lakes, rivers, ponds) separated by terrestrial environments; exchanges of parasite species among freshwater host populations are possible via several routes (Esch et al., 1988), but they should be less frequent than those among host populations not physically constrained to particular locations. We might thus expect the rates of distance decay to be higher among parasite communities of, say, freshwater fish, than among those of more vagile hosts such as terrestrial mammals.

The first goal of this study was to determine if the similarity in the species composition of helminth parasite communities tends to decay exponentially with increasing distance among host populations in continental North America. Nekola & White (1999) observed exponential rates of decay among plant communities, and a comparison with parasite communities would be informative. The second goal of the study was to determine whether the rate of decay was different between parasite communities in mammal hosts and those in freshwater fish hosts whose geographical dispersal may be more constrained. The helminth communities in mammals and fish consist of the same four taxonomic groups

(trematodes, cestodes, nematodes and acanthocephalans), and are thus comparable in this respect. The results of this study provide a test of the spatial dispersal potential of parasites, and of how it is affected by the type of host they exploit.

METHODS

Data on the species composition of helminth communities in different populations of vertebrate hosts were obtained from the parasitological literature. The three mammalian host species chosen are among the best-studied in North America: the muskrat *Ondatra zibethicus*, the raccoon *Procyon lotor*, and the coyote *Canis latrans*. The total numbers of helminth species observed in these hosts, from all populations pooled, were 35, 47 and 37, respectively. All species of endoparasitic helminths in these hosts were considered since published surveys included both enteric parasites and those found in other tissues. As the number of hosts examined in a survey is an important determinant of how many of the less common parasite species are found (see Walther et al., 1995), only data from surveys that examined at least 30 individual hosts per population were included. Except for data on two raccoon populations presented in the same report, data on each of the host populations came from different surveys (Table 1).

The three fish host species chosen are also well-studied, and come from distinct higher taxa; they are the yellow perch *Perca flavescens*, the white sucker *Catostomus commersoni*, and the pike *Esox lucius*. Data on the helminth communities of perch were obtained from the appendix of Carney & Dick's (1999) paper, which compiled information from numerous surveys carried out throughout North America; these included only the enteric helminths of perch, for a total of 38 species across all host populations included here. Data on the composition of helminth communities in different populations of sucker and pike came from several different surveys (Table 1), and included all internal helminths, i.e. adult worms in the gastrointestinal tract as well as larval forms in other tissues. The latter can mature in hosts, such as birds, that can disperse parasites quickly and over large distances. The inclusion of such allogenic parasites with the autogenic parasites (that mature locally in fish) for the computation of similarity values can affect the results (see Esch et al., 1988). However, excluding the few allogenic species (five of a total of 34 helminth species in sucker, six of 32 in pike) had no influence on the results, and all parasites are therefore included in the analyses that follow. As with mammalian hosts, data were only included if at least 30 individual hosts per population have been examined in a survey; because of the low number of host populations available, however, a population of suckers where only 22 fish have been examined, and one of pike where 23 fish were examined, were exceptionally included in the analysis. In any event, it was verified whether host sample size covaried significantly with the number of helminth species found in a population, across all host populations of the same species.

Table I Summary of the parasite community data used in the analysis of distance decay in similarity

Host species	No. of host populations	Average distance (km)	Parasite species richness (range)	Average similarity	Sources
Mammals					
Ondatra zibethicus	8	2243	5–18	0.312	1–8
Procyon lotor	8	1066	6–33	0.284	9–15
Canis latrans	7	1609	5–20	0.288	16–22
Fish					
Perca flavescens	21	1138	2–15	0.193	23
Catostomus commersoni	6	1470	2–21	0.128	24–28
Esox lucius	6	2008	4–14	0.207	26–31

Sources: (1) Gilford (1954), (2) Ball (1952), (3) Beckett & Gallicchio (1967), (4) Senger & Neiland (1955), (5) McKenzie & Welch (1979), (6) MacKinnon & Burt (1978), (7) Rigby & Threlfall (1981), (8) Abram (1969), (9) Jordan & Hayes (1959), (10) Bafundo *et al.* (1980), (11) Harkema & Miller (1964), (12) Hoberg & McGee (1982), (13) Smith *et al.* (1985), (14) Snyder & Fitzgerald (1985), (15) Price & Harman (1983), (16) Butler & Grundmann (1954), (17) Franson *et al.* (1978), (18) Ameel (1955), (19) Holmes & Podesta (1968), (20) Pence & Windberg (1984), (21) Samuel *et al.* (1978), (22) van den Bussche *et al.* (1987), (23) Carney & Dick (1999), (24) Amin (1974), (25) Arai & Mudry (1983), (26) Bangham (1955), (27) Dechtiar (1972), (28) Leong & Holmes (1981), (29) Arthur *et al.* (1976), (30) Chinniah & Threlfall (1978), (31) Watson & Dick (1980).

For each host species, similarity in helminth species composition and geographical distance were computed for all possible pairs of host populations. The Jaccard similarity index was used because of its simplicity, widespread use, and reliance on presence/absence data. Put simply, it is the number of helminth species shared by two host populations divided by the total number of helminth species found in the two host populations put together. It ranges from zero (no species in common between two host populations) to one (the two host populations have exactly the same helminth species). Distance between pairs of host populations was calculated as the linear distance between sampling localities, obtained from a map. The scale of the map was 1 cm = 92.4 km, and the precision of each measurement of distance was to within 1 mm or 9 km, when sampling localities were specified with accuracy. When only a larger area was given as the sampling site, the centre of this area was used, and the precision of the distance measurement was therefore more variable; given that typical distances between localities are in the order of 10^2 and 10^3 km, this imprecision is probably insignificant.

Jaccard similarity values were ln-transformed [or $\ln(x + 1)$-transformed if there were Jaccard values of zero]; linear regressions of the transformed similarity values against untransformed distance values provided the best overall fit to the data (see Results). As the pairwise similarity values and distances are not truly independent in a statistical sense (each host population is used in more than one pairwise comparison), and as there were slight deviations from normality for certain variables, the significance of each regression model was tested using a randomization approach (Manly, 1997). This was achieved using the RT 2.1 program (B. Manly, Centre for Applications of Statistics and Mathematics, University of Otago, New Zealand). All regression probabilities are based on 10,000 permutations.

RESULTS

Among conspecific populations of mammalian hosts, there was no relationship between the number of hosts examined per population and the number of helminth species found (on ln-transformed values: *O. zibethicus*, $r = 0.463$, $n = 8$, $P = 0.248$; *P. lotor*, $r = 0.578$, $n = 8$, $P = 0.132$; *C. latrans*, $r = -0.401$, $n = 7$, $P = 0.375$). Sampling effort and helminth species richness were also not correlated when all mammalian populations were pooled, irrespective of what host species they represented ($r = 0.194$, $n = 23$, $P = 0.376$). The same pattern was observed for fish hosts, whether host species were treated separately (*P. flavescens*, $r = 0.269$, $n = 21$, $P = 0.239$; *C. commersoni*, $r = -0.440$, $n = 6$, $P = 0.382$; *E. lucius*, $r = 0.028$, $n = 6$, $P = 0.958$) or together ($r = 0.025$, $n = 33$, $P = 0.889$). There is thus no reason to believe that inadequate sampling effort resulted in a systematic error in the lists of helminth species from the various host populations, or in artefacts in the following results.

Similarity in helminth communities decreased with distance in two of the three mammalian host species (Fig. 1, Table 2). A linear regression in a semi-log plot provided a good fit to these data, implying an exponential rate of distance decay. The slopes for both *P. lotor* and *C. latrans* are very similar, around a value of 0.50. The scatter of points for *C. latrans*, however, suggests that similarity decays more rapidly at first, and more slowly as distances between host populations become larger (Fig. 1); such an effect is not apparent for *P. lotor*.

In helminth communities from fish hosts, similarity also decreases with increasing geographical distance between host populations for two of the three host species investigated (Fig. 2, Table 2). In the two fish species for which this applies, excluding Jaccard values of zero (i.e. pairwise
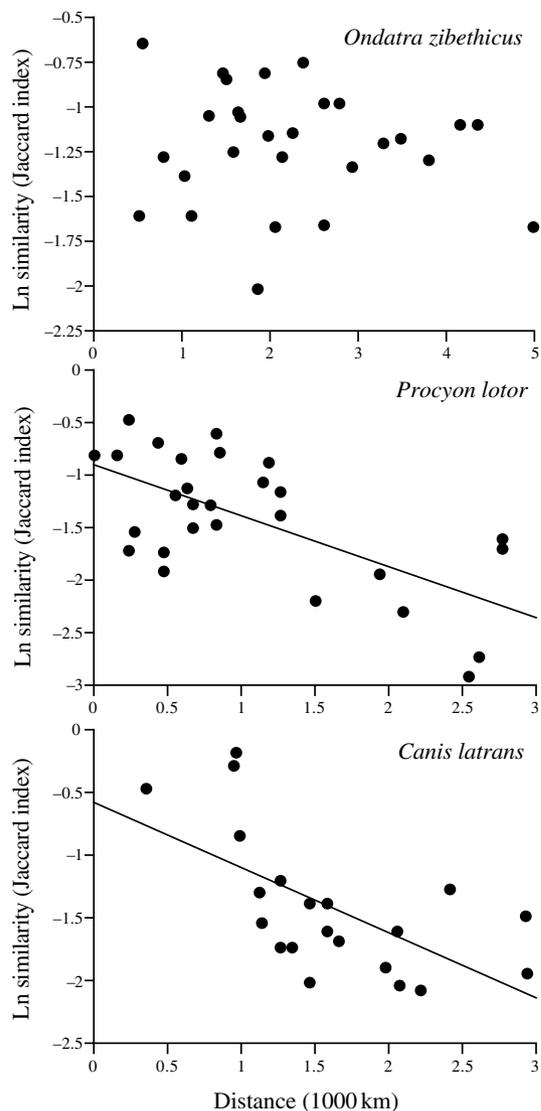
Figure 1 The ln-transformed similarity plotted against distance for all pairwise comparisons of helminth communities in three species of mammalian hosts. Lines indicate that there is a significant relationship between the two variables (see Table 2).

comparisons between fish populations that do not share any helminth species) had no important impact on these results (Table 2). The slopes of the regression in the semi-log plots for fish hosts were lower than those for mammal hosts (Table 2), but still indicate an exponential decay of similarity with distance. However, it is how *P. flavescens* and *E. lucius* differ from one another that is interesting. The scatter of points for *P. flavescens* is roughly triangular (Fig. 2). This suggests that although the maximum similarity between any two helminth communities tends to decrease with the distance between their localities, low similarity or even complete dissimilarity is relatively common regardless of distance, i.e. even between adjacent communities. In contrast, the points for *E. lucius* form a tight pattern

Table 2 Regression statistics for the decay of similarity with distance in helminth parasite communities. The sample size (n) is the number of similarity values and distances in each analysis, i.e. the number of pairwise contrasts between host populations. Intercepts are in units of ln(similarity), and slope values are in units of ln(similarity) per 1000 km distance

Host species	n	Intercept	Slope	r^2	P
Mammals					
Ondatra zibethicus	28	−1.148	−0.028	0.01	0.6109
Procyon lotor	28	−0.902	−0.485	0.42	0.0002
Canis latrans	21	−0.579	−0.520	0.38	0.0029
Fish					
Perca flavescens	210	0.223	−0.048	0.07	0.0012
*Perca flavescens**	159	0.273	−0.046	0.12	0.0005
Catostomus commersoni	15	0.133	−0.012	0.01	0.6850
*Catostomus commersoni**	11	2.030	0.117	0.04	0.5765
Esox lucius	15	−0.896	−0.383	0.69	0.0001

*Including only pairs of helminth communities with at least one species in common.

along the regression line, indicating a much more important determining role for geographical distance.

DISCUSSION

The diminishing proportion of shared species between two communities with increasing geographical distance is an obvious feature of natural systems, but the exact rate at which similarity decays with distance is an aspect of this phenomenon that has only recently received attention. Nekola & White (1999) found that a simple negative exponential function provided the best fit to the distance decay of similarity in plant communities. In the four host species where similarity in parasite communities decreased with distance, an exponential function also fits the observed pattern. Exponential decay can have many explanations. For instance, it is consistent with Hubbell's (2001) recent neutral theory of biodiversity and biogeography, based on ecological drift coupled with random speciation and dispersal. Regardless of its cause, exponential decay of similarity implies a constant proportional reduction in similarity per unit distance. Except for the slope value for perch (*P. flavescens*) populations, which is rather low, the exponential decay in similarity of parasite communities in the other three vertebrate host species is very similar to the values for plant communities obtained by Nekola & White (1999). This suggests that despite the biological differences between spruce-fir forest communities and helminth communities in vertebrates, the distance decay of similarity may be similar among these communities.

Two aspects of the present results require an explanation. First, why was an exponential decay of similarity with distance observed among the parasite communities of only four of the six host species investigated? One possible reason may be that there was some taxonomic uncertainty in the data; in particular there may have been some errors in the published
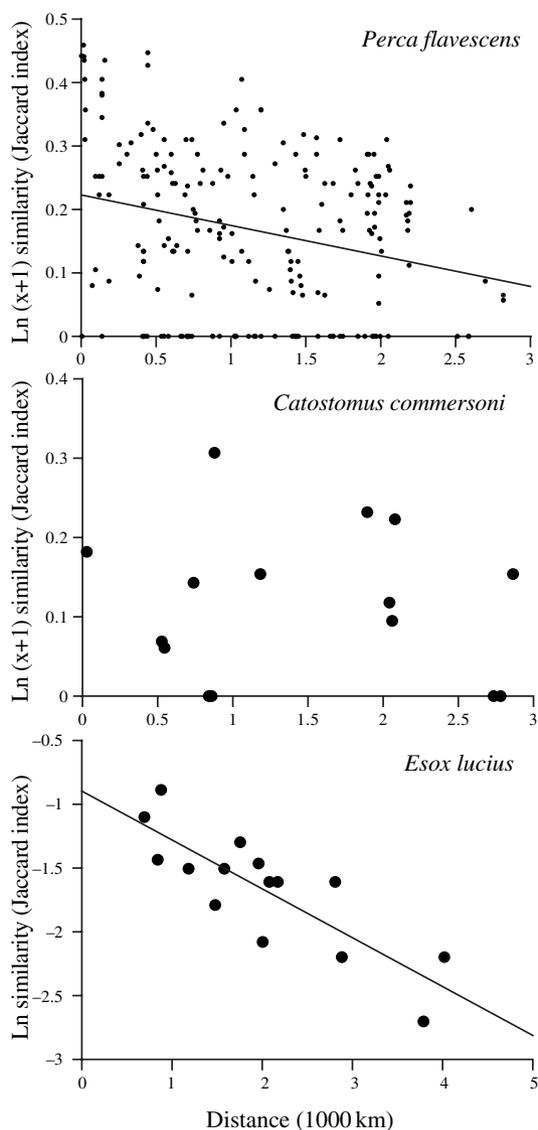
Figure 2 The ln-transformed similarity plotted against distance for all pairwise comparisons of helminth communities in three species of fish hosts. Lines indicate that there is a significant relationship between the two variables (see Table 2).

lists of helminth species used to assemble the data base. The identification of helminth species by the original authors of the parasite surveys had to be taken as accurate in this study, as there was no way to have all the specimens examined by a single person. An error or two could have a big impact on the computation of the Jaccard index of similarity. Another explanation may be that some host species possess traits that are capable of neutralizing any distance effect on similarity of parasite communities. For instance, populations of muskrat (*O. zibethicus*) were separated by greater distances than those of the other two mammal species in this study, and yet their parasite communities were on average more similar to each other (Table 1). There was no distance decay

in similarity among parasite communities in muskrat populations. Perhaps the semi-aquatic habits, or some other feature, of this host species has favoured the dispersal of its parasites over greater distances, resulting in greater homogeneity among the parasite communities, and blurring the effect of distance. Whatever the explanation, it appears that exponential distance decay of similarity is not a universal property of parasite communities.

The second intriguing aspect of the present results is the difference in rates of decay between parasite communities in fish and mammal hosts. Contrary to what had been expected, similarity apparently decreases at a higher rate in mammal hosts than in fish hosts (Table 2); for a given distance, decay rates in mammals were approximately 1.3 times higher than in pike *E. lucius*, and 10 times higher than in perch *P. flavescens*. This is not compatible with the idea that host (and parasite) dispersal over geographical distance is more constrained in freshwater fish than in terrestrial mammals, because the former live in physically isolated habitats. This pattern remains the same if the very few all-ogenic parasite species that mature in birds are excluded from the analyses involving helminth communities of pike. Clearly, host vagility is not the main determinant of the similarity among parasite communities and its decay with distance.

One possible explanation for the lower exponential decay of similarity in communities of fish parasites may be that parasite communities of fish hosts are saturated with species (see Kennedy & Guégan, 1994). A limit on the number of locally coexisting parasite species could lead to greater homogeneity in species composition, regardless of distance, by preventing rare parasite species not specialized on the host from successfully invading a community. Another possibility may be that the freshwater habitats of fish tend to be rather predictable, at least on a continental scale, in terms of the composition of food webs and the main trophic relationships in which fish take part (see Carney & Dick, 1999; Nelson & Dick, 2002). If the same fauna of invertebrates, which serve as intermediate hosts of helminth parasites, occurs in all freshwater habitats occupied by a given species of fish host, then we may expect distance effects to be attenuated by the ecological stability of these habitats. This would result in lower rates of decay among parasite communities of fish than mammal hosts, but only if the habitats of mammals display greater variability with respect to the availability of intermediate hosts. Having said this, it must be pointed out that stochastic events, such as chance colonization or extinction, are believed to play an important role in the evolution of local parasite assemblages of freshwater fish, especially with respect to parasites disseminated by fish or mammal definitive hosts (Esch *et al.*, 1988; Kennedy, 1990). Clearly, the predictability of many ecological features of freshwater habitats is no guarantee of the presence of specific parasite species. The data on helminth communities of perch support the idea that stochastic events may be important in the assembly of parasite communities. Many pairs of helminth communities in perch do not share a single species (Fig. 2), and this is true regardless of the

distance separating them. Another possibility, of course, is that local habitat effects determine the pattern observed for perch, with the ecological similarity between two near habitats being less predictable than the dissimilarity between distant habitats.

The present analyses focused on assemblages of parasites found in the same host population, and ignored whether these parasites were specialists or generalists. Some parasite species are specialists exploiting only one host species, or a small group of closely related host species, whereas others can parasitize unrelated host species. There is no reason to believe that host specificity limits spatial dispersal, although generalist parasite species may have more opportunities to expand their geographical range. The parasite species exploiting host populations on the fringes of a host species geographical range typically include few specialist species (Kennedy & Bush, 1994). The results of the present analyses may be different if ectoparasite species were included, as ectoparasites of both fish and mammals are typically highly host-specific (see Poulin, 1998).

In summary, the results of this study show that similarity in the composition of parasite communities decays exponentially with increasing distance in some, but not all host species, and that the rate of decay is not necessarily associated with the expected vagility of the host species. The results, while compatible and similar to those of Nekola & White (1999) on plant communities, demonstrate that the biogeography of parasite species does not follow simple rules: distance matters, but it is not always the key determinant of similarity.

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REFERENCES

Abram, J.B. (1969) Some gastrointestinal helminths of *Ondatra zibethicus* Linnaeus, the muskrat in Maryland. *Proceedings of the Helminthological Society of Washington*, **36**, 93–95.

Ameel, D.J. (1955) Parasites of the coyote *Canis latrans* Say, in Kansas. *Journal of Parasitology*, **41**, 325.

Amin, O.M. (1974) Intestinal helminths of the white sucker, *Catostomus commersoni* (Lacépède), in SE Wisconsin. *Proceedings of the Helminthological Society of Washington*, **41**, 81–88.

Arai, H.P. & Mudry, D.R. (1983) Protozoan and metazoan parasites of fishes from the headwaters of the Parsnip and McGregor Rivers, British Columbia: a study of possible parasite transfaunations. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 1676–1684.

Arthur, J.R., Margolis, L. & Arai, H.P. (1976) Parasites of fishes of Aishihik and Stevens Lakes, Yukon Territory, and potential consequences of their interlake transfer through a proposed water diversion for hydroelectrical purposes. *Journal of the Fisheries Research Board of Canada*, **33**, 2489–2499.

Bafundo, K.W., Wilhelm, W.E. & Kennedy, M.L. (1980) Geographic variation in helminth parasites from the digestive tract of Tennessee raccoons, *Procyon lotor*. *Journal of Parasitology*, **66**, 134–139.

Ball, L. (1952) Notes on helminth parasites of muskrats from western Colorado. *Journal of Parasitology*, **38**, 83–84.

Bangham, R.V. (1955) Studies on fish parasites of Lake Huron and Manitoulin Island. *American Midland Naturalist*, **53**, 184–194.

Beckett, J.V. & Gallicchio, V. (1967) A survey of helminths of the muskrat, *Ondatra z. zibethica* Miller, 1912, in Portage County, Ohio. *Journal of Parasitology*, **53**, 1169–1172.

Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*, 2nd edn. Sinauer Press, Sunderland, MA.

van den Bussche, R.A., Kennedy, M.L. & Wilhelm, W.E. (1987) Helminth parasites of the coyote (*Canis latrans*) in Tennessee. *Journal of Parasitology*, **73**, 327–332.

Butler, J.M. & Grundmann, A.W. (1954) The intestinal helminths of the coyote *Canis latrans* Say, in Utah. *Journal of Parasitology*, **40**, 440–443.

Carney, J.P. & Dick, T.A. (1999) Enteric helminths of perch (*Perca fluviatilis* L.) and yellow perch (*Perca flavescens* Mitchill): stochastic or predictable assemblages? *Journal of Parasitology*, **85**, 785–795.

Chinniah, V.C. & Threlfall, W. (1978) Metazoan parasites of fish from the Smallwood Reservoir, Labrador, Canada. *Journal of Fish Biology*, **13**, 203–213.

Dechtiar, A.O. (1972) Parasites of fish from Lake of the Woods, Ontario. *Journal of the Fisheries Research Board of Canada*, **29**, 275–283.

Esch, G.W., Kennedy, C.R., Bush, A.O. & Aho, J.M. (1988) Patterns in helminth communities in freshwater fish in Great Britain: alternative strategies for colonization. *Parasitology*, **96**, 519–532.

Franson, J.C., Jorgenson, R.D., Boggess, E.K. & Greve, J.H. (1978) Gastrointestinal parasitism of Iowa coyotes in relation to age. *Journal of Parasitology*, **64**, 303–305.

Gilford, J.H. (1954) A survey of muskrat helminths in Illinois. *Journal of Parasitology*, **40**, 702–703.

Harkema, R. & Miller, G.C. (1964) Helminth parasites of the raccoon, *Procyon lotor*, in the southeastern United States. *Journal of Parasitology*, **50**, 60–64.

Hengeveld, R. (1990) *Dynamic biogeography*. Cambridge University Press, Cambridge.

Hoberg, E.P. & McGee, S.G. (1982) Helminth parasitism in raccoons, *Procyon lotor hirtus* Nelson and Goldman, in Saskatchewan. *Canadian Journal of Zoology*, **60**, 53–57.

Holmes, J.C. & Podesta, R. (1968) The helminths of wolves and coyotes from the forested regions of Alberta. *Canadian Journal of Zoology*, **46**, 1193–1204.

Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.

Huston, M.A. (1994) *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.

Jordan, H.E. & Hayes, F.A. (1959) Gastrointestinal helminths of raccoons (*Procyon lotor*) from Ossabaw Island, Georgia. *Journal of Parasitology*, **45**, 249–252.

Kennedy, C.R. (1990) Helminth communities in freshwater fish: structured communities or stochastic assemblages? *Parasite communities: patterns and processes* (ed. by G.W. Esch, A.O. Bush and J.M. Aho), pp. 131–156. Chapman & Hall, London.

Kennedy, C.R. & Bush, A.O. (1994) The relationship between pattern and scale in parasite communities: a stranger in a strange land. *Parasitology*, **109**, 187–196.

Kennedy, C.R. & Guégan, J.-F. (1994) Regional versus local helminth parasite richness in British freshwater fish: saturated or unsaturated parasite communities? *Parasitology*, **109**, 175–185.

Leong, T.S. & Holmes, J.C. (1981) Communities of metazoan parasites in open water fishes of Cold Lake, Alberta. *Journal of Fish Biology*, **18**, 693–713.

McKenzie, C.E. & Welch, H.E. (1979) Parasite fauna of the muskrat, *Ondatra zibethica* (Linnaeus, 1766), in Manitoba, Canada. *Canadian Journal of Zoology*, **57**, 640–646.

MacKinnon, B.M. & Burt, M.D.B. (1978) Platyhelminth parasites of muskrats (*Ondatra zibethica*) in New Brunswick. *Canadian Journal of Zoology*, **56**, 350–354.

Manly, B.F.J. (1997) *Randomization, bootstrap and Monte Carlo methods in biology*, 2nd edn. Chapman & Hall, London.

Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, **26**, 867–878.

Nelson, P.A. & Dick, T.A. (2002) Factors shaping the parasite communities of trout-perch, *Percopsis omiscomaycus* Walbaum (Osteichthyes: Percopsidae), and the importance of scale. *Canadian Journal of Zoology*, **80**, 1986–1999.

Pence, D.B. & Windberg, L.A. (1984) Population dynamics across selected habitat variables of the helminth community in coyotes, *Canis latrans*, from South Texas. *Journal of Parasitology*, **70**, 735–746.

Poulin, R. (1997) Species richness of parasite assemblages: evolution and patterns. *Annual Review of Ecology and Systematics*, **28**, 341–358.

Poulin, R. (1998) *Evolutionary ecology of parasites: from individuals to communities*. Chapman & Hall, London.

Poulin, R. & Morand, S. (1999) Geographical distances and the similarity among parasite communities of conspecific host populations. *Parasitology*, **119**, 369–374.

Price, R.L. & Harman, D.M. (1983) Helminths from the raccoon, *Procyon lotor litoreus* Nelson and Goldman 1930, on St. Catherines Island, Georgia. *Proceedings of the Helminthological Society of Washington*, **50**, 343–344.

Rigby, M.D. & Threlfall, W. (1981) Helminth parasites of the muskrat (*Ondatra zibethica* (L.)) in Newfoundland. *Canadian Journal of Zoology*, **59**, 2172–2176.

Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.

Samuel, W.M., Ramalingam, S. & Carbyn, L.N. (1978) Helminths in coyotes (*Canis latrans* Say), wolves (*Canis lupus* L.), and red foxes (*Vulpes vulpes* L.) of southwestern Manitoba. *Canadian Journal of Zoology*, **56**, 2614–2617.

Senger, C.M. & Neiland, K.A. (1955) Helminth parasites of some fur-bearers of Oregon. *Journal of Parasitology*, **41**, 637–638.

Smith, R.A., Kennedy, M.L. & Wilhelm, W.E. (1985) Helminth parasites of the raccoon (*Procyon lotor*) from Tennessee and Kentucky. *Journal of Parasitology*, **71**, 599–603.

Snyder, D.E. & Fitzgerald, P.R. (1985) Helminth parasites from Illinois raccoons (*Procyon lotor*). *Journal of Parasitology*, **71**, 274–278.

Walther, B.A., Cotgreave, P., Price, R.D., Gregory, R.D. & Clayton, D.H. (1995) Sampling effort and parasite species richness. *Parasitology Today*, **11**, 306–310.

Watson, R.A. & Dick, T.A. (1980) Metazoan parasites of pike, *Esox lucius* Linnaeus, from Southern Indian Lake, Manitoba, Canada. *Journal of Fish Biology*, **17**, 255–261.

BIOSKETCH

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