

Helminth species diversity of mammals: parasite species richness is a host species attribute

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SUMMARY

Studies investigating parasite diversity have shown substantial geographical variation in parasite species richness. Most of these studies have, however, adopted a local scale approach, which may have masked more general patterns. Recent studies have shown that ectoparasite species richness in mammals seems highly repeatable among populations of the same mammal host species at a regional scale. In light of these new studies we have reinvestigated the case of parasitic helminths by using a large data set of parasites from mammal populations in 3 continents. We collected homogeneous data and demonstrated that helminth species richness is highly repeatable in mammals at a regional scale. Our results highlight the strong influence of host identity in parasite species richness and call for future research linking helminth species found in a given host to its ecology, immune defences and potential energetic trade-offs.

Key words: parasite species richness, helminths, repeatability.

INTRODUCTION

Studies on the variation of parasite diversity among populations of the same vertebrate species have demonstrated the existence of substantial geographical variation in the structure of parasite communities (Fellis *et al.* 2003; Luque and Poulin, 2007). Parasite species richness, which is the number of parasite species found in and on a given host species, has been shown to be variable in space and time at a local (Behnke *et al.* 2004; Calvete *et al.* 2004; Brouat *et al.* 2007), a regional (Krasnov *et al.* 2006; Luque and Poulin, 2007) or even at a latitudinal scale (Guernier *et al.* 2004; Nunn *et al.* 2005).

Most studies have adopted a local approach in their investigations and, consequently, they have focused on parasite infracommunities (all parasites found in an individual host) or parasite component communities (all parasites found in a host population). Parasite species richness was often shown to be highly variable at these local hierarchical scales in fish (Zander, 2007), in birds (Calvete *et al.* 2004) and also in mammals (Behnke *et al.* 2004). These studies strongly suggested a poor repeatability of parasite species richness (i.e. PSR, the total number of parasites found on a host species at a given scale) in space and time (Poulin, 2007*a*) leading to doubts about the existence of strong patterns in parasite

communities at host population or host species levels (Poulin, 2007*b*, but see Morand and Krasnov, 2008).

However, studies that have investigated parasite communities at broader scales (i.e. regional parasite communities or parasitofaunas) have shown the existence of patterns and of some determinants that can explain them (Guégan *et al.* 2005; Nunn *et al.* 2005; Lindenfors *et al.* 2007). One major finding is that parasite assemblages are not the result of random processes but rather the result of the interplays among geographical location, habitat characteristics and host identity (Kennedy and Hartvigsen, 2000; Nelson and Dick, 2002; Calvete *et al.* 2004; Krasnov *et al.* 2005*a*, 2006). In other words, the number and the identity of parasites found in a host species at large scale is determined simultaneously by extrinsic factors that promote variation among host populations (such as climatic factors) and intrinsic host factors that promote stability and so repeatability in parasite communities (Aznar *et al.* 1994; Krasnov *et al.* 2005*a*, 2008). The host factors related to the stability of parasite communities may rely on phylogeny, ecology and immune or behavioural adaptations of species in response to parasite impacts. All these factors determine to some extent the establishment of parasites in hosts (Combes, 2001; Poulin, 2007*a*).

Focusing on mammals, the importance of host identity or host-related factors in shaping macro-parasite assemblages and notably parasite species richness has been intensively investigated. These factors are shown to be related to host morphology (i.e. body size), host ecological traits (density, geographical range) or host life-history traits (longevity,

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Table 1. Summary of the data on mammal parasite species richness for 56 mammal species, with variations in number of populations (minimum-maximum) per mammal species and in host sample size (minimum-maximum)

Mammal group	Number of mammal species	Number of populations per species (mini; maxi)	Host sample size (min-max)	Parasite species richness (min-max)
Chiroptera	2	2	15; 129	3; 22
Carnivora	15	2; 7	12; 1040	3; 32
Cetaceans	2	2	10; 50	5; 10
Ungulates	10	2; 5	5; 215	5; 18
Lagomorpha	7	2; 5	14; 260	3; 15
Marsupiala	3	2; 4	26; 101	7; 39
Rodentia	11	2; 6	25; 557	2; 20
Eulipotyphla	6	2; 6	11; 269	7; 32

basal metabolic rate) (Morand and Harvey, 2000; Arneberg *et al.* 2002; Stanko *et al.* 2002; Ezenwa *et al.* 2006; Lindenfors *et al.* 2007; Korallo *et al.* 2007). Paradoxically, the repeatability of parasite diversity at various geographical scales for various populations of the same host species (i.e. within a host species) has been investigated less in mammals. For gastrointestinal helminths, to our knowledge, there is essentially only a single study concerning 188 populations of 35 species of mammals in North America essentially (Poulin and Mouillot, 2004). This study emphasized that gastrointestinal helminth species richness was too variable across populations of the same host mammal species to be considered as a true host species characteristic. In contrast, recent studies investigating ectoparasite species richness in small mammals have shown that flea and gamasid mite species richness on different populations of the same mammal species were more similar to each other than expected by chance (Krasnov *et al.* 2005a, 2008).

Taken altogether, these contradictory results stress the possibility of a lack of generalization in parasite community ecology, each host-parasite association being particular and unique (Poulin, 2007b). Moreover, these results highlight the need to explore more precisely the importance of host identity as a factor structuring parasite communities among populations of the same host species. As parasite species richness in arthropod ectoparasites seems to be a repeatable host species characteristic at regional scale (Krasnov *et al.* 2005a, 2008), the aim of this study is to reconsider the possibility that helminth species richness is also a repeatable host characteristic. For this, we use a large database including mammal species from various continents.

MATERIALS AND METHODS

Data on parasite species richness

We focused on all helminth taxa (nematodes, cestodes, trematodes and acanthocephalans) and obtained data

on endoparasite species richness from published studies. In order to get homogeneous data, we only used surveys where host sample sizes were given and rejected descriptive parasite reports for a given host species. We retained only surveys for which helminth species were investigated from the whole host body (gastrointestinal tract but also liver, respiratory tract, cardiovascular system ...) and used parasite species richness (PSR) as a measure of parasite diversity.

Comparison of parasite species richness among host species or among host populations may be confounded by uneven sampling effort (the number of hosts examined) and uneven sampling area size (Guégan and Kennedy, 1996; Morand and Harvey, 2000). These introduce major confounding effects in studies investigating parasite community structure and that attempt to identify the structuring processes (Calvete *et al.* 2004; Guégan *et al.* 2005). For a given host species, which was sampled at least twice across its geographical area of distribution, we retained only surveys for which sampling area sizes were comparatively similar among populations of the same host species and controlled for sampling effort. Practically, we retained data in which helminth communities were established at a regional scale in 1 of 3 continents (Europe, America, Australia). There is still no consensus about what exactly a region means for parasite communities (Guégan *et al.* 2005). We therefore followed previous studies where regional community of parasite species for a given mammal species represents the parasite species occurring at the level of a state for North American surveys or at the level of a country for Europe, or in a part of a state for Australia (Krasnov *et al.* 2005a, 2008). We are aware that political divisions may be arbitrary but most parasitological surveys have been done at such geographical scales. The relative homogeneity in sampling area size was then controlled by the number of states or countries included in the survey. As an example, for the mammal species *Sciurus carolinensis*, we retained only 2 surveys which

Table 2. Analysis of variance for helminth species richness, with host species and host group as factor and the number of hosts sampled as covariate

Host effect	Source	Sum of squares	Degree of freedom	F-ratio	P-value
Species	Main effect:	6.17	55	4.38	<0.0001
	Covariate: Host sampling effort	0.669	1	24.75	<0.0001
	Residual	3.081	114		
Group	Main effect:	3.567	7	13.69	<0.0001
	Covariate: Host sampling effort	1.151	1	30.91	<0.0001
	Residual	6.031	162		

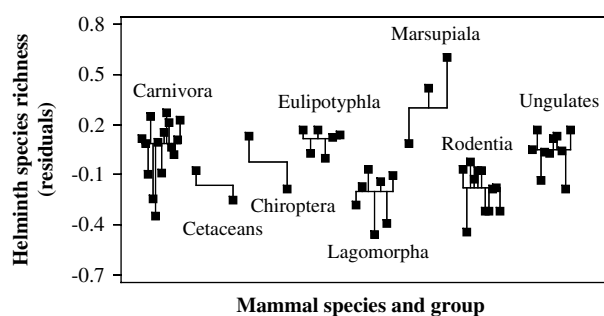


Fig. 1. Variation of parasite species richness (PSR) among mammal species (black squares) and according to mammal group controlling for host sampling (see Tables 2 and 3).

have been both done at the level of a state (Florida and Virginia respectively) and rejected 1 survey representing a sampling area of nearly all the south-east of the United States (with more than 10 states included in the survey).

We gathered data for 171 populations representing 56 mammal species in various groups including Cetartiodactyla, Chiroptera, Carnivora, Didelphimorphia, Diprodontia, Lagomorpha, Rodentia and Eulipotyphla (Table 1).

Statistical analyses

To determine whether species richness of helminth assemblages is invariant of geographical locality, we performed a repeatability analysis. We only retained mammal species that had been investigated at least twice in its geographical area. We analysed the variation in number of helminth species using a one-way ANOVA in which host species and host group were the independent factor, and the number of hosts sampled a covariate. We performed a variance component analysis. The variance of helminth species richness was divided into 2 components: host species and host group with host species was nested in host group. The number of hosts sampled remained a covariate.

Table 3. Variance components analysis for helminth species richness, with mammal group and mammal species as factors, and the number of hosts sampled as covariate

(The factor mammal species is nested in the factor mammal group.)

Source	Sum of squares	Degree of freedom	Percent of variance
Mammal group	2.970	7	18.22
Mammal species	3.431	48	20.23
Error	3.751	115	51.56

RESULTS

There was a significant correlation between helminth species richness and host sample size ($P=0.002$, $F_{1,170}=9.935$) although the variance explained is low ($R^2=0.055$).

The repeatability analysis showed that helminth species richness was repeatable within host species (Table 2). The number of helminth species on the same host populations was more similar to each other than expected by chance, and varied significantly among mammal species (Table 2, $P<0.0001$, Fig. 1), taking into account a significant effect of host sampling effort (Table 2, $P<0.0001$). Helminth species richness was also repeatable within mammal groups (Table 2, $P<0.0001$).

The variance component analysis showed that 18% of the variance in helminth species richness was explained by mammal groups and 20% of the variance by mammal species (Table 3).

DISCUSSION

Our study has focused on all helminth species whereas only gastrointestinal helminths were taken into account in the study of Poulin and Mouillot (2004), with a larger data set with 56 mammal species in our study compared to the 35 mammal species in Poulin and Mouillot's study (2004). Moreover, we have

considered variation in helminth species richness at a more comparable scale, i.e. regional scale.

We are then able to show that regional helminth species richness is repeatable within a mammal host species despite the undeniable and well-demonstrated effects of biotic and abiotic factors (Fellis *et al.* 2003; Thieltges *et al.* 2008). In relation to recent results on fleas and gamasid mites, our results reinforce the importance of host identity in structuring helminth community at larger scales in mammals. Moreover, the validity of parasite species richness (PSR) as an estimator of parasite diversity is reinforced as PSR seems to be a true attribute of a host mammal species.

The results obtained in arthropod communities (Krasnov *et al.* 2005a, 2008) and helminth communities (here) strongly suggest that certain intrinsic properties of mammal species may affect parasite species richness. From this perspective, our study and those of Krasnov *et al.* (2005a, 2008) are relevant for the investigation on the determinants and causes of the observed heterogeneity in parasite diversity across species (Poulin and Morand, 2004), but also to investigate the covariation in species diversities of different parasite taxa found in the same host species (Krasnov *et al.* 2005b).

Why some mammal species harbour comparatively more parasites than others may find the answer in the possibility that some parasite taxa may facilitate the installation of other species or groups of parasites (Krasnov *et al.* 2005b; Graham, 2008). However, many causes and potential mechanisms, not mutually exclusive, may also play a role. Phylogeny and factors linked to host ecology or physiology (i.e. body size, feeding activity, habitat preference, geographical distribution, solitary versus social behaviour) may explain why some host species are more prone to encounter and accumulate a higher diversity of parasites in comparison to other host species (Aznar, 1994; Krasnov *et al.* 2006; Klimpel *et al.* 2007; Bordes *et al.* 2007). By exploring the variance of PSR among host species and among host groups, our analysis highlights the importance of host phylogeny. We were able to establish that the percentage of the total variance of PSR was largely dependent on host species, but also on host group (i.e. rodents, carnivores ...).

Repeatability in parasite species richness may suggest that the existence of thresholds beyond hosts may not be able to cope with multiple parasite attacks without strong effects on their survival or reproductive success. As it is established that immunity is an energetically and nutritionally demanding process (Lochmiller and Derenberg, 2000; Zuk and Stoehr, 2002; Hanssen *et al.* 2004), interactions between parasites and several physiological tasks (reproduction, survival ...) may be mediated through immunity. The great heterogeneity in parasite species richness among host species and the finding that this

diversity is an attribute of host species may be linked to the level of immune investment at species level resulting from evolutionary trade-offs with other physiological tasks. Facing multiple parasitic attacks may force hosts to maintain a performing immune system against all parasite species at the expense of reproduction or even survival or to tolerate parasite accumulations with some levels of detrimental effects and/or negative effects on host energy balance.

Energetic budget and nutritional status are then expected to explain heterogeneity in parasite diversity and potentially covariation among various parasite taxa.

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REFERENCES

- Arneberg, P.** (2002). Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. *Ecography* **25**, 88–94.
- Aznar, F. J., Balbuena, J. A. and Raga, J. A.** (1994). Helminth communities of *Pontoporia blainvillei* (Cetacea: Pontoporiidae) in Argentinian waters. *Canadian Journal of Zoology* **72**, 702–706.
- Behnke, J. M., Barnard, C. J., Bajer, A., Bray, D., Dinmore, J., Frake, K., Osmond, J., Race, T. and Sinski, E.** (2004). Variation in the helminth community structure in spiny mice (*Acomys dimidiatus*) from four montane wadis in the St Katherine region of the Sinai Peninsula in Egypt. *Parasitology* **129**, 379–398.
- Bordes, F., Blumstein, D. T. and Morand, S.** (2007). Rodent sociality and parasite diversity. *Biology Letters* **3**, 692–694.
- Brouat, C., Kane, M., Diouf, M., Bâ, K., Sall-Drame, R. and Duplantier, J. M.** (2007). Host ecology and variation in helminth community structure in *Mastomys* rodents from Senegal. *Parasitology* **134**, 437–450.
- Calvete, C., Blanco-Aguiar, J. A., Virgos, E., Cabezas-Diaz, S. and Villafuerte, R.** (2004). Spatial variation in helminth community structure in the red-legged partridge (*Alectoris rufa* L.): effects of definitive host density. *Parasitology* **129**, 101–113.
- Combes, C.** (2001). *Parasitism. The Ecology and Evolution of Intimate Interactions*. University of Chicago Press, Chicago, USA.
- Ezenwa, V., Price, S. A., Altizer, S., Vitonen, N. D. and Cook, C.** (2006). Host traits and parasite species richness in even and odd-toed hoofed mammals, Artiodactyla and Perissodactyla. *Oikos* **115**, 526–537.
- Fellis, K. J., Negovetich, N. J., Esch, G. W., Horak, I. G. and Boomker, J.** (2003). Patterns of association, nestedness and species co-occurrence of helminth parasites in the greater Kudu, *Tragelaphus strepsiceros*, in the Kruger National Park, South Africa, and the Etosha National Park, Namibia. *Journal of Parasitology* **89**, 899–907.
- Graham, A. L.** (2008). Ecological rules governing helminth-microparasite coinfection. *Proceedings of the National Academy of Sciences, USA* **105**, 566–570.

- Guernier, V., Hochberg, M. E. and Guégan, J. F.** (2004). Ecology drives the worldwide distribution of human infectious diseases. *Plos* **2**, 740–746.
- Guégan, J. F. and Kennedy, C. R.** (1996). Parasite richness/sampling effort/host range: the fancy three-piece jigsaw puzzle. *Parasitology Today* **12**, 367–369.
- Guégan, J. F., Morand, S. and Poulin, R.** (2005). Are there general laws in parasite community ecology? The emergence of spatial ecology and epidemiology. In *Parasitism and Ecosystem* (ed. Thomas, F., Renaud, F. and Guégan, J. F.), pp. 22–42. Oxford University Press, Oxford, USA.
- Hanssen, S. A., Haselquist, D., Folstad, I. and Erikstad, K. E.** (2004). Costs of immunity: immune responsiveness reduces survival in a vertebrate. *Proceedings of the Royal Society of London, B* **271**, 925–930.
- Kennedy, C. R. and Hartvigsen, R. A.** (2000). Richness and diversity of intestinal metazoan communities in brown trout *Salmo trutta* compared to those of eels *Anguilla anguilla* in their European heartlands. *Parasitology* **121**, 55–64.
- Klimpel, S., Förster, M. and Schmahl, G.** (2007). Parasites of two abundant sympatric rodent species in relation to host phylogeny and ecology. *Parasitology Research* **100**, 867–875.
- Korallo, N. P., Vinarski, M. V., Krasnov, B. R., Shenbrot, G. I., Mouillot, D. and Poulin, R.** (2007). Are there general rules governing parasite diversity? Small mammalian hosts and gamasid mite assemblages. *Diversity and Distribution* **13**, 353–360.
- Krasnov, B. R., Shenbrot, G. I., Mouillot, D., Khokhlova, I. S. and Poulin, R.** (2005a). Spatial variation in species diversity and composition of flea assemblages in small mammalian hosts: geographical distance or faunal similarity. *Journal of Biogeography* **32**, 633–644.
- Krasnov, B. R., Mouillot, D., Khokhlova, I. S., Shenbrot, G. I. and Poulin, R.** (2005b). Covariance in species diversity and facilitation among non-interactive parasite taxa: all against the host. *Parasitology* **131**, 557–568.
- Krasnov, B. R., Stanko, M., Miklisova, D. and Morand, S.** (2006). Habitat variation in species composition of flea assemblages on small mammals in central Europe. *Ecology Research* **21**, 460–469.
- Krasnov, B. R., Korallo-Vinarskaya, N. P., Vinarski, M. V., Shenbrot, G. I., Mouillot, D. and Poulin, R.** (2008). Searching for general patterns in parasite ecology: host identity versus environmental influence on gamasid mite assemblages in small mammals. *Parasitology* **135**, 229–242.
- Lindenfors, P., Nunn, C. L., Jones, K. E., Cunningham, A. A., Sechrest, W. and Gittleman, J. L.** (2007). Parasite species richness in carnivores: effects of host body mass, latitude, geographical range and population density. *Global Ecology and Biogeography* **1**, 1–14.
- Lochmiller, R. L. and Deerenberg, C.** (2000). Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos* **88**, 87–98.
- Luque, J. L. and Poulin, R.** (2007). Metazoan parasite species richness in Neotropical fishes: hotspots and the geography of biodiversity. *Parasitology* **134**, 865–878.
- Morand, S. and Harvey, P. H.** (2000). Mammalian metabolism, longevity and parasite species richness. *Proceedings of the Royal Society of London, B* **267**, 1999–2003.
- Morand, S. and Krasnov, B. R.** (2008). Why apply ecological laws to epidemiology? *Trends in Parasitology* **24**, 304–309.
- Nelson, P. A. and Dick, T. A.** (2002). Factors shaping the parasite communities of troutperch, *Percopsis omiscomaycus* Walbaum (Osteichthyes: Percopsidae), and the importance of scale. *Canadian Journal of Zoology* **80**, 1986–1999.
- Nunn, C., Altizer, S., Jones, K. E., Sechrest, W. and Cunningham, A. A.** (2005). Latitudinal gradients of parasite species richness in primates. *Diversity and Distribution* **11**, 249–256.
- Poulin, R. and Morand, S.** (2004). *Parasite Biodiversity*. Smithsonian Institution Press, Washington, DC, USA.
- Poulin, R. and Mouillot, D.** (2004). The evolution of taxonomic diversity in helminth assemblages of mammalian hosts. *Evolutionary Ecology* **18**, 231–247.
- Poulin, R.** (2007a). *Evolutionary Ecology of Parasites (2nd Edn)*. Princeton University Press, Princeton, USA and Oxford, UK.
- Poulin, R.** (2007b). Are there general laws in parasite ecology? *Parasitology* **134**, 763–776.
- Stanko, M., Miklisova, D., Goüy De Bellocq, J. and Morand, S.** (2002). Mammal density and patterns of ectoparasite species richness and abundance. *Oecologia* **131**, 289–295.
- Thieltges, D. W., Jensen, K. T. and Poulin, R.** (2008). The role of biotic and abiotic factors in the transmission of free-living endohelminth stages. *Parasitology* **135**, 407–426.
- Zander, C. D.** (2007). Parasite diversity of sticklebacks from the Baltic Sea. *Parasitology Research* **100**, 287–297.
- Zuk, M. and Stoehr, A. M.** (2002). Immune defence and host life history. *American Naturalist* **160**, 9–22.