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Phylogenetically related and ecologically similar carnivores harbour similar parasite assemblages

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Summary

1. Most parasites infect multiple hosts, but what factors determine the range of hosts a given parasite can infect? Understanding the broad scale determinants of parasite distributions across host lineages is important for predicting pathogen emergence in new hosts and for estimating pathogen diversity in understudied host species.

2. In this study, we used a new data set on 793 parasite species reported from free-ranging populations of 64 carnivore species to examine the factors that influence parasite sharing between host species.

3. Our results showed that parasites are more commonly shared between phylogenetically related host species pairs. Additionally, host species with higher similarity in biological traits and greater geographic range overlap were also more likely to share parasite species.

4. Of three measures of phylogenetic relatedness considered here, the number divergence events that separated host species pairs most strongly influenced the likelihood of parasite sharing. We also showed that viruses and helminths tend to infect carnivore hosts within more restricted phylogenetic ranges than expected by chance.

5. Overall, our results underscore the importance of host evolutionary history in determining parasite host range, even when simultaneously considering other factors such as host ecology and geographic distribution.

Key-words: biological similarity, disease sharing, geographic overlap, host phylogenetic clustering, host–parasite interactions, wild carnivores, wildlife conservation, wildlife disease

Introduction

One of the most pressing issues in host–parasite ecology and evolution is identifying factors that determine the range of host species that a parasite can infect. Indeed, reports of novel pathogen introductions in humans and wildlife underscore the importance of a broad-scale framework for predicting parasite occurrence across multiple host species (Fenton & Pedersen 2005; Keesing *et al.* 2010). Two factors that have been suggested as predictors of parasite sharing among host species (and hence might limit the range of hosts a parasite can infect) are the extent of geographic range overlap among host species and host phylogenetic relatedness (Pfennig 2000; Antonovics, Hood & Partain 2002; Ricklefs & Fallon 2002; Poulin 2003). In terms of geographic constraints, parasites can only exist where their hosts exist (Poulin 1997; Harris & Dunn 2010), and overlap among host species' ranges provides greater ecological opportunities for hosts to share parasite species compared to hosts with non-overlapping ranges (Antonovics, Hood & Partain 2002; Poulin 2003; Streicker *et al.* 2010). In diverse host communities where many species overlap, more abundant host species can serve as maintenance hosts, allowing parasites to reach relatively high prevalence in other host species that might already suffer from low population densities or population declines (Cleaveland *et al.* 2007; Altizer & Pedersen 2008; Hampson *et al.* 2008).

Host phylogenetic relatedness has been proposed as a second key predictor of parasite sharing among host species (Gilbert & Webb 2007; Davies & Pedersen 2008; Streicker *et al.* 2010). Phylogeny might be important for at least two reasons. First, closely related host species that have gone through fewer divergence (i.e. speciation)

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events might share a higher proportion of their parasite species assemblages through common descent (Ricklefs & Fallon 2002). This is because each time a host lineage diverges, both descendants could maintain a portion of the parasites infecting the ancestral host, while other parasite species are lost from one or the other lineage (i.e. parasites might be 'missing the boat', Page 2003). Secondly, host species that are separated by greater phylogenetic distance are expected to be less similar genetically and biologically (Harvey & Pagel 1991; Harvey 1996; Freckleton, Harvey & Pagel 2002), resulting in molecular, immunological, and ecological barriers to cross-species transmission and establishment in new hosts (Pfennig 2000; De Vienne, Hood & Giraud 2009; Longdon *et al.* 2011). Previous work on major vertebrate groups (Poulin 1995), particularly mammals (Nunn *et al.* 2003; Ezenwa *et al.* 2006; Lindenfors *et al.* 2007), showed that host biological and ecological traits (e.g. body mass, life history, latitude, geographic range area, and population density) explain variation in parasite species richness, and these same traits could limit parasite sharing owing to the challenges parasites face in adapting to hosts with differing biological traits.

Despite a number of clear hypotheses about key determinants of host range, most studies of limits to host range to date focused on very narrow scales of host–parasite associations (e.g. Ricklefs & Fallon 2002; Streicker *et al.* 2010). We are aware of only a handful of studies that synthesized natural parasite sharing patterns across large numbers of host and parasite taxa in a comparative framework (e.g. Krasnov *et al.* 2010 on extoparasites in rodents; Poulin 2010 on parasites in five families of fish), with only two studies of mammal hosts (Davies & Pedersen 2008; Cooper *et al.* 2012) both focusing on primates as a model host group. Both Davies & Pedersen (2008) and Cooper *et al.* (2012) agree that host phylogenetic relatedness is a highly useful predictor of parasite sharing between primate species; Cooper *et al.* (2012) further examined the importance of host biological trait similarity. Testing whether these same patterns hold for broad-scale host–parasite associations in other host taxa could help predict factors that increase the likelihood of parasite host-switching, and may uncover general rules to identify problematic parasites before they emerge in humans or at-risk hosts in domestic or natural populations.

In this study, we focus on predictors of parasite sharing in the mammalian order of Carnivora, a well-studied clade with a highly resolved phylogeny. Carnivore species capture tremendous variation in body size, geographic range, and latitude (Purvis, Mace & Gittleman 2001). Importantly, carnivores play key roles in ecosystems (Purvis, Mace & Gittleman 2001) and a high fraction of this group (27%) is threatened with global extinction (Schipper *et al.* 2008). In part owing to their close association with domesticated lineages, a large volume of data have accumulated on carnivore parasites and infectious diseases (Lindenfors *et al.* 2007). Infectious diseases caused by generalist pathogens such as rabies and canine distemper viruses have negatively impacted wild carnivore populations such as African wild dogs (Alexander & Appel 1994; Kat *et al.* 1995), Ethiopian wolves (Laurenson *et al.* 1998; Randall *et al.* 2004), black-footed ferrets (Thorne & Williams 1988) and Caspian seals (Kennedy *et al.* 2000). Thus, understanding the mechanisms underlying parasites sharing among carnivore species has crucial implications for management and conservation of this group.

Here, we examine the relative importance of host phylogenetic relatedness, geographic range overlap and biological trait similarity in predicting parasite assemblage similarity among free-living carnivore species. We define parasites broadly to include both macroparasites (helminths, arthropods) and microbial infectious agents (viruses, bacteria and protozoa). Our prediction is that overall similarity in parasite assemblages will increase with host phylogenetic relatedness, geographic range overlap and biological and ecological trait similarity. We also test whether the relative importance of host factors differs among parasite groups. In particular, overlap in virus communities might depend more strongly on host geography than host phylogeny, given that past work has suggested that viruses can evolve rapidly and thus readily adapt to new hosts (Woolhouse, Taylor & Haydon 2001; Parrish *et al.* 2008; Elena & Froissart 2010), and given that a high proportion of viruses have been described as multi-host generalists (Cleaveland, Laurenson & Taylor 2001; Pedersen *et al.* 2005). By comparison, larger and longer lived parasites such as helminths and arthropods might show a stronger association between community similarity and host phylogeny. Finally, we examine host evolutionary relatedness across the full assemblage of carnivore species infected by each parasite to ask whether, irrespective of the number of host species infected, parasites show more restricted host ranges than expected by chance (i.e. are clustered on the host phylogeny).

Materials and methods

HOST–PARASITE DATA

We compiled global data on parasite occurrence in free-ranging carnivore populations from studies published between 1986 and 2010. Briefly, we conducted systematic searches of the online data base Web of Science (http://thomsonreuters.com/web-of-science) using carnivore species Latin binomials and common taxonomic variants. We included only primary references of a particular infectious agent and followed a recently updated mammal taxonomy (Wilson & Reeder 2005) consistent with the most recently published carnivore phylogeny (Nyakatura & Bininda-Emonds 2012). For each host–parasite combination, we recorded parasite type (helminth, protozoan, virus, arthropod, bacteria and fungus), sampling locality, dates of sampling and information on the number of animals sampled and prevalence. Our initial data set included 1156 references providing records of 995 parasite species detected in free-living populations of 158 carnivore species, for a total of 3369 unique host–parasite species combinations. Using

these data, we quantified the similarity between parasite assemblages in pairwise combinations of host species that both had a minimum of five reported parasite species (to avoid using hosts that were poorly sampled for parasites), which reduced the data set to 64 host species. Note that the number of reports on parasite infectious for a host species does not show phylogenetic bias in our data set (Blomberg's $K = 0{\cdot}118$, $P = 0{\cdot}425$).

We used two measures of parasite community similarity in our analyses: (i) the Jaccard index (J) and (ii) a modified version of Jaccard index that accounted for uneven parasite numbers between host pairs (i.e. corrected Jaccard index). The Jaccard index is commonly used to quantify differences between two (or more) assemblages (Koleff, Gaston & Lennon 2003) as follows:

$$J = \frac{|A \cap B|}{|A \cup B|}.$$

In our case, A and B represent the two parasite assemblages in two different host species, $A \cap B$ represents those parasite shared between the two species and A U B refers to all parasites infecting at least one of the two host species.

When the two parasite assemblages differ in size, J is limited by the size of the smaller assemblage (i.e. potential maximum J is equal to A divided by B, if A is a subset of B). In some cases, dissimilarity indicated by a low J is largely due to the difference in size, instead of the composition of the parasite assemblages in the two host species. We acknowledge that the difference in assemblage size can indicate differences in host species' capacities to support parasite diversity, and thus has valuable implications for wildlife disease management. However, the number of parasite species associated with a host species based on the published literature depends heavily on the effort that has been put on sampling the host species for parasites (Nunn *et al.* 2003; Lindenfors *et al.* 2007). To limit the contribution of uneven parasite numbers on estimates of parasite community similarity, we developed a corrected Jaccard index (CJ) by dividing J by the potential maximum J:

$$\text{Corrected } J = \frac{|A \cap B|}{|A \cup B|} \Big/ \frac{\min(|A|, |B|)}{\max(|A|, |B|)}.$$

To investigate predictors of parasite community similarity, we calculated J and CJ using all parasite data combined, and we also calculated these measures separately using parasite data for the following five groups: helminths, arthropods, viruses, bacteria and protozoa.

HOST PHYLOGENETIC DISTANCE, GEOGRAPHIC RANGE OVERLAP AND TRAIT DISSIMILARITY

We quantified host phylogenetic distance for each carnivore species pair using three measures to capture different aspects of evolutionary history. First, we extracted time since divergence between species pairs from a dated species level phylogenetic supertree (chronogram) of existing carnivore species (Nyakatura & Bininda-Emonds 2012). Secondly, we extracted the genetic distance between host species from a molecular phylogenetic supertree reconstructed using the same multi-gene data set used by Nyakatura & Bininda-Emonds (2012). Using RAxML v 7.2.8 (Stamatakis 2006b), these data were fitted to the topology of the carnivore supertree under a ML framework using a GTR + CAT (Stamatakis 2006a) model, with model parameters fitted to each gene individually. Thirdly, to assess the effect of host divergence events on parasite assemblage similarity (Poulin & Morand 2000), we counted the number of existing divergence events between pairs of host species included in our analyses using the carnivore supertree. We acknowledge that this underestimates the actual number of divergence events in the evolutionary history by missing events associated with extinct species. All three phylogenetic variables were positively correlated: divergence events with time since divergence: $N = 2016$, $R^2 = 0{\cdot}458$, $P < 0{\cdot}001$; divergence events with genetic distance: $N = 2016$, $R^2 = 0{\cdot}484$, $P < 0{\cdot}001$; and genetic distance and time since divergence: $N = 2016$, $R^2 = 0{\cdot}822$, $P < 0{\cdot}001$ (Fig. S1, Supporting information).

We quantified trait similarity (or dissimilarity) between host species pairs in two ways. First, we focused on body mass, as this measure correlates with a wide range of other ecological and physiological traits in plants and animals (Western 1979; Brown 1995); body mass also correlates positively with parasite richness in primates and carnivores (Nunn *et al.* 2003; Lindenfors *et al.* 2007). Further, body mass is one of the best-studied traits in mammals with excellent data availability (available for over 87% of carnivores, and all species included in this study except one for which we used the genus-wide average). Using adult body mass (average for males and females, in grams) from the species-level mammalian trait data base PanTHERIA (Jones *et al.* 2009), we calculated the absolute difference in log adult body mass for host pairs as a surrogate of their overall biological trait dissimilarity. Secondly, we used a composite measure that included adult body mass and eight additional biological traits that have been quantified for at least 90% of our host species from the PanTHERIA data base (Jones *et al.* 2009). Additional traits included adult head body length (mm), gestation length (days), inter birth interval (days), litter size (number of offspring), maximum longevity (months), sexual maturity age (days), trophic level (1 = herbivore, 2 = omnivore, and 3 = carnivore) and weaning age (days). For any trait of a species with missing data, we used the genus-wide average. We used the resulting log-transformed data to construct a pairwise Euclidean distance matrix (a matrix of pairwise distances in a nine-dimension trait space, see details in Lele 1991; Lele & Richtsmeier 1991). The body mass difference and overall trait dissimilarity of carnivore host species pairs were significantly positively correlated ($N = 2016$, $R^2 = 0{\cdot}906$, $P < 0{\cdot}001$; Fig. S2, Supporting information). Although carnivore body mass and other life-history traits tend to show phylogenetic structure (Bininda-Emonds & Gittleman 2000), the actual evolutionary processes are complex (Losos 2008; Cooper & Purvis 2010). We found that the time since divergence (phylogenetic distance on a dated tree as used in previous work) explains little variation in either body mass difference ($R^2 = 0{\cdot}035$, $P < 0{\cdot}001$) or overall biological similarity ($R^2 = 0{\cdot}041$, $P < 0{\cdot}001$), despite significant slopes. Further the AIC scores of models including both trait data and phylogenetic distance were lower than those of models that included only one or the other.

Finally, we obtained geographic range maps for all 64 host species from the IUCN Global Mammal Assessment (Schipper *et al.* 2008), and matched these to our standardized host taxonomy (Wilson & Reeder 2005) to calculate host geographic overlap in two ways. First, we calculated the absolute areas of all pairwise range intersections. Secondly, we calculated the ratio of the intersection area to the area of the union of the two ranges, and then we divided the ratio by the maximum expected value (the ratio of the small range to the large range) to generate a proportional

range overlap variable. All geographic data were processed in ArcGIS™ 10 (Esri, New York, NY, USA). The two measures of geographic range overlap examined here are highly correlated for host pairs with overlapping geographic ranges ($N = 621$, $R^2 = 0{\cdot}967$, $P < 0{\cdot}001$; Fig. S3, Supporting information). Finally, to be consistent with prior work (e.g. Davies & Pedersen 2008), we distinguished host pairs with any extent of geographic range overlap from host pairs whose ranges do not overlap (overlap area = 0 km^2) and evaluated whether parasite assemblage similarity is more predictable for the former. Again, little variation in geographic overlap area is explained by time since divergence ($R^2 = 0{\cdot}030$, $P < 0{\cdot}001$).

STATISTICAL ANALYSES

We first explored associations between parasite assemblage similarity (*J* and *CJ*) and each of the seven host variables (three measures of phylogenetic relatedness, two measures of geographic range overlap, and two measures of trait similarity) using the relatively conservative Spearman's rank-order test (for detecting monotonic relationships) without assuming any linear relationship (Legendre & Fortin 2010). Next, we constructed a generalized linear model (GLM) to predict parasite assemblage similarity focusing on host variables significant in pair-wise correlation tests. Our full model included main effects that were significant in pair-wise tests. We selected the final model by following Crawley (2005) and retained terms that resulted in substantially higher AIC scores (>4) when omitted. Adding interaction terms among variables in the final model did not improve the model substantially (i.e. did not reduce AIC), so we focused on main effects. To further explore the importance of range overlap for parasite community similarity, we re-analysed the data using only host pairs that had some degree of geographic ranges (excluding any zeros). For all analyses, we examined the predictors of parasite assemblage similarity using data for all parasites combined, and repeated tests of similarity for each of the five major parasite groups (i.e. arthropods, bacteria, helminths, protozoa and viruses).

Finally, because initial results showed that phylogenetic relatedness was an important predictor of parasite sharing, we used a different approach to further explore the phylogenetic constraints on host range. Specifically, we examined the distribution of all host species infected by each individual parasite species across the host phylogenetic tree, and calculated a measure of phylogenetic species variability (PSV; Helmus *et al.* 2007a,b) for each assemblage of host species infected by a given parasite species. PSV is an inverse measure of the overall phylogenetic similarity of host species in an assemblage, and is independent from the number of host species (Helmus *et al.* 2007a). Based on the same phylogenetic tree, host species in an assemblage with a low PSV are more closely related to each other than species with a high PSV, regardless the number of species in the assemblage. To test whether the host range of a parasite is constrained by host phylogenetic relatedness, we focused our analysis on parasites reported to infect five or more hosts. We simulated random associations (using the same total number of reported hosts for each parasite) and estimated the lower 5% PSV quantile for this random distribution. We considered parasites with PSV values below the 5% quantile of simulated host range PSV to be highly constrained by host phylogeny, and compared the proportions of parasites showing phylogenetically constrained host ranges in our five parasite groups.

All analyses were conducted in R 2.12.2 (R Development Core Team 2012) with packages *ape* (Paradis, Claude & Strimmer 2004) and *picante* (Kembel *et al.* 2010) for phylogenetic analyses, and *MASS* (Venables & Ripley 2002) for other statistical analyses. Variable effect sizes were calculated using package *effects* (Fox 2003).

Results

The 64 carnivore species included in this study gave rise to 2016 pairwise host combinations, for which 1522 host pairs shared at least one parasite in common. The Jaccard index (*J*) and corrected Jaccard index (*CJ*) calculated from pairwise host combination were correlated (Spearman's $\rho = 0{\cdot}530$, $P < 0{\cdot}001$), but their values differed from each other for most (74·6%) host pairs (Fig. S4, Supporting information). Because analyses of *J* and *CJ* showed generally congruent results, we present results for *CJ* only in the main text, as this variable was more independent of sampling effort for records of parasitism across host species. Among carnivore species pairs, *CJ* ranged from 0 to 1, with a mean of 0·148 (±0·169 SD) and median of 0·093.

Measures of total parasite *CJ* were significantly correlated with all host variables tested in our bivariate analyses, and were explained particularly well by a few variables (separately) considering Spearman's rank-order test is relatively conservative. Total parasite *CJ*'s strongest association is with the number of divergence events ($\rho = -0{\cdot}347$, $P < 0{\cdot}001$), and the second strongest association is with overall trait dissimilarity ($\rho = -0{\cdot}312$, $P < 0{\cdot}001$; Table S1, Supporting information), with evolutionarily closely related and biologically similar host species sharing more parasite species. Similarly, tests for major parasite subgroups showed the strongest correlations between helminth *CJ* and the number of divergence events ($\rho = -0{\cdot}441$, $P < 0{\cdot}001$) as well as time since divergence ($\rho = -0{\cdot}322$, $P < 0{\cdot}001$; Table S2, Supporting information). Strong correlations also existed between virus *CJ* and host trait dissimilarity ($\rho = -0{\cdot}326$, $P < 0{\cdot}001$), as well as time since divergence ($\rho = -0{\cdot}292$, $P < 0{\cdot}001$). Other significant but weaker correlations are summarized in Table S2 (Supporting information).

We included all significant correlates in the full GLM models and conducted model simplification based on AIC to identify the best predictors for *CJ* between host species. The number of divergence events, trait dissimilarity and geographic overlap area were retained in our final model of total parasite *CJ*, and the predictive power, based on pseudo-R^2, was stronger when only hosts with overlapped geographic ranges were considered (Figs 1 and 2, Table 1). When we repeated the analyses for different parasite subgroups, different factors were important in the final models (Fig. 1, Table S3, Supporting information). In particular, models for helminth and virus assemblage similarity resulted in higher predictive powers than models over any other parasite groups (helminth: pseudo-$R^2 = 0{\cdot}186$; virus:

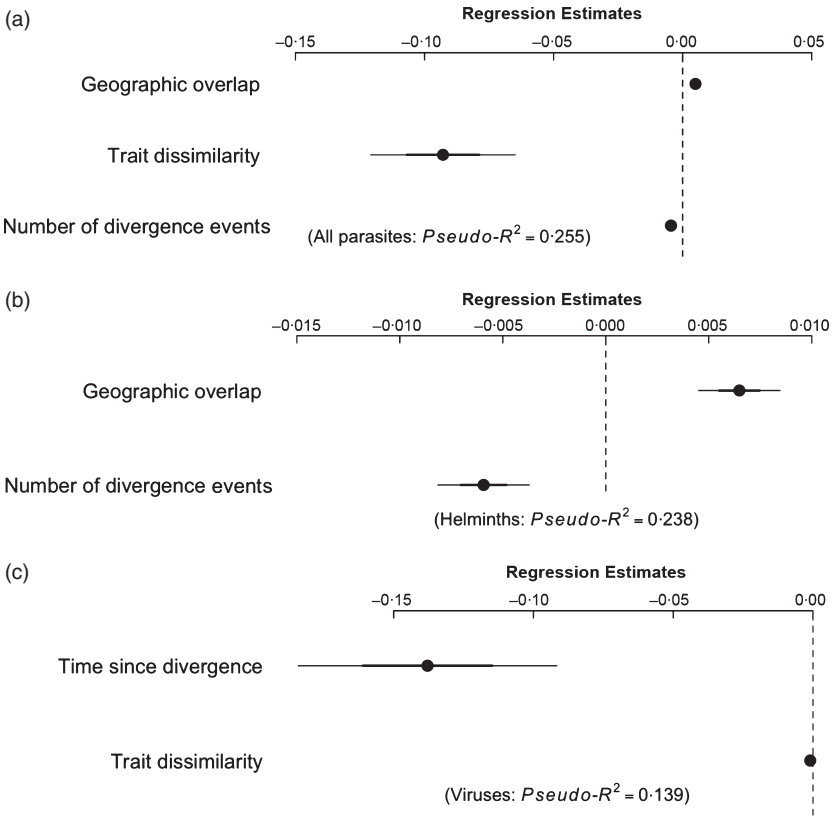

Fig. 1. Estimated coefficients of variables retained in final models for predicting overall parasite assemblage similarity (a), as well as helminth (b) and virus (c) assemblage similarities in host pairs with overlapping geographic ranges. Black lines indicate standard errors and grey lines indicate the 95% confident interval (lack of lines for some variables indicate that the confident intervals are smaller than the size of the dots). See statistics in Tables 1 and S3 (Supporting information).

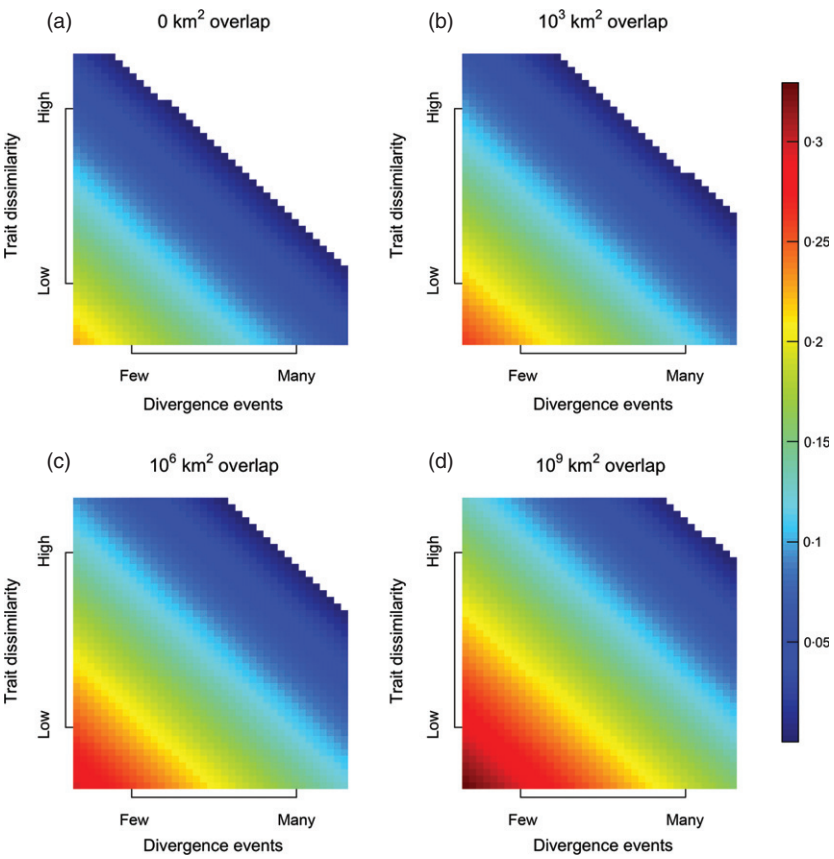

Fig. 2. Total parasite assemblage similarity (*CJ*, from low in light grey to high in black) predicted by the final GLM model for pairs of host species with (a) no overlap in geographic distribution, (b) 10^3 km^2 of geographic overlap, (c) 10^6 km^2 of geographic overlap and (d) 10^9 km^2 of geographic overlap (see Table 1 for specific parameters). White colour indicates that *CJ* is predicted to be 0. A colour version of this figure is presented in supporting online materials. GLM, generalized linear model. (A colour version of this figure is available online.)

Table 1. Generalized linear models for predicting parasite assemblage *CJ* (log-transformed) between all carnivore host pairs (*L*) and pairs with overlapped geographic ranges (*R*). Pseudo-R^2 is calculated as 1-(residual deviance/null deviance). To avoid zeros in the data, we added 1 to each variable containing zeros before log transformation; excluding zeros in the *CJ* (a total of 494 host pairs; 109 with overlapped geographic ranges) did not change the final models but increased the pseudo-R^2, as indicated in parentheses. In each case, our full model contained all seven variables: three phylogenetic relatedness variables, two biological trait dissimilarities indices and two geographic overlap measures. Only variables retained in each final model are shown in the table

	All hosts (N = 2016)		Overlapped hosts (N = 621)	
Variables	Coefficient (P)	Pseudo-R^2	Coefficient (P)	Pseudo-R^2
Number of divergence events	−0·004 ± 0·0004 (P < 0·001)	0·195 (0·211)	−0·005 ± 0·001 (P < 0·001)	0·255 (0·297)
Log trait dissimilarity	−0·095 ± 0·007 (P < 0·001)		−0·093 ± 0·014 (P < 0·001)	
Log geographic overlap	0·003 ± 0·0003 (P < 0·001)		0·005 ± 0·001 (P < 0·001)	

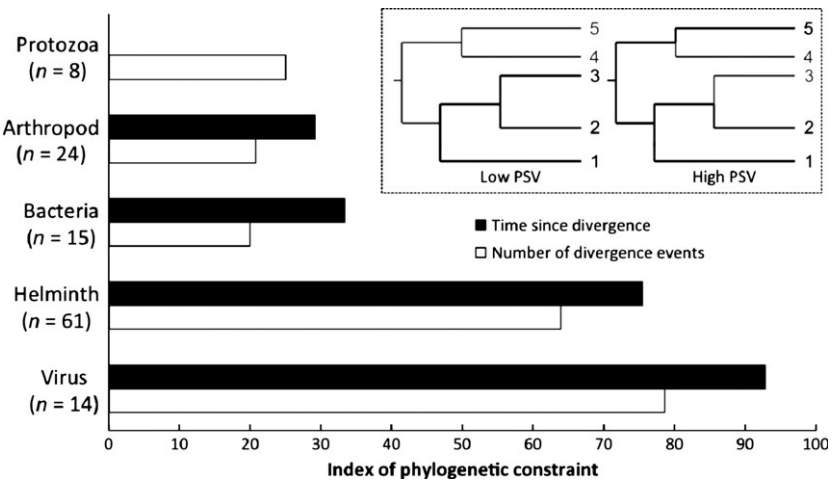

Fig. 3. Degree to which parasites are constrained by host phylogeny, expressed as the percentage of parasite species in each major group that have observed host phylogenetic species variability (PSV) equal to or below the bottom 5% quantile of the null PSV values calculated from randomly selected host species. As illustrated in the conceptual graph in the upper right corner, parasites infecting hosts with a low PSV are more constrained by phylogeny than those infecting host species with a high PSV. Results for PSV based on the chronogram (i.e. time since divergence) are shown in solid black bars, and the cladogram (i.e. number of divergent events) in open bars. Protozoa showed the lowest degree of phylogenetic constraint, whereas viruses and helminths were most strongly restricted to related host species.

pseudo-R^2 = 0·172). For helminths, the number of divergence events between hosts and area of host geographic range overlap were important factors, while for viruses, the final model included time since host divergence, genetic distance between hosts, and host trait similarity. The number of divergence events between hosts was also important for arthropod and bacteria assemblage similarity. As with total parasite *CJ*, models for bacteria and helminths explained higher proportions of the variation in *CJ* when restricted to host species pairs with overlapping geographic ranges (e.g. helminth: pseudo-R^2 = 0·238, further results in Table S3, Supporting information).

Finally, because host phylogenetic distance was the strongest predictor for total parasite assemblage similarity and for assemblage similarity of four out of the five parasite subgroups, we calculated a measure of host phylogenetic divergence (host PSV) for each parasite species that was reported to infect five or more carnivore hosts (N = 122 parasites, including 24 arthropods, 15 bacteria, 61 helminths, eight protozoa and 14 viruses). We found no relationship between the number of host species affected and host PSV (Fig. S5, Supporting information). Our null estimates for PSV values (based on randomly selected species from the host phylogeny) significantly exceeded the actual PSV values for approximately half of all parasites examined here (Fig. 3). Specifically, between 59·2% (based on chronogram PSV) and 49·6% (based on cladogram PSV; Fig. S5, Supporting information) of all parasites (mostly helminths) infected host species with PSV values equal to or below the 5% quantile of the PSV calculated from randomly selected hosts. Among the five parasite subgroups, helminths and viruses were more clustered on the host phylogeny (i.e. were more restricted to closely related hosts) relative to parasites in other groups (Figs 3 and S6, Supporting information).

Discussion

Host phylogenetic distance was the strongest predictor of parasite community similarity in wild carnivore hosts:

closely related carnivores shared a higher proportion of parasite species in common relative to distantly related hosts. Among the three measures of phylogenetic distance that we considered, the number of divergence events that separated two host species was the strongest correlate of overall parasite assemblage similarity (as indicated by results from both bivariate and multivariate analyses), consistent with the 'missing the boat' hypothesis (Page 2003). Our final model for predicting total parasite community similarity also included overall host trait dissimilarity, consistent with the idea that carnivores with similar diets, social behaviour and life-history traits might encounter or support infections by similar parasite species. Host geographic range overlap also predicted parasite assemblage similarity, likely due to increased opportunities for cross-species transmission arising from hosts overlapping in habitat use or by physical encounters (Streicker *et al.* 2010).

The positive association among parasite sharing, host phylogenetic relatedness (i.e. −1*phylogenetic distance) and geographic range overlap observed here for carnivores is congruent with recent findings in two other mammal groups. Across primates, host phylogenetic relatedness and geographic range overlap were key predictors of parasite community similarity based on both analyses of broad parasite assemblages (Davies & Pedersen 2008; Cooper *et al.* 2012) and also in more focused tests of lentivirus host switching (Charleston & Robertson 2002). Across 23 North American bat species, Streicker *et al.* (2010) found that both their phylogenetic distance and geographic proximity predicted the frequency of cross-species transmission of rabies. The strength of associations between parasite community overlap and host phylogenetic relatedness observed here for carnivores were weaker than those found in primates (Davies & Pedersen 2008; Cooper *et al.* 2012), possibly due to broader geographic distribution and greater ecological variation in carnivores (Sunquist 2002; Schipper *et al.* 2008). Thus, parasite occurrence in carnivores might depend more strongly on heterogeneous environmental conditions and biological traits. Given results observed for mammals examined to date, it is likely that similar processes control parasite distributions in other host groups, though the weighting of these processes may differ across taxa. In support of this idea, geographic distance has also been suggested a strong positive predictor for parasite assemblage similarity in fish (Poulin 2003; Timi, Luque & Poulin 2010) and marine invertebrates (Thieltges *et al.* 2009). Associations between host trait similarity and parasite community similarity have yet to be studied for most host–parasite systems, and further work is needed to identify the particular host traits that determine overlap in parasite communities, and how these might differ across host and parasite groups.

Results here showed differences in key predictors of parasite community overlap among parasite groups. In particular, helminth and virus assemblage similarities depended most strongly on host phylogenetic relatedness, while similarities in other parasite groups are less predictable by the factors we analysed. When we analysed parasite host range in a different way – by measuring host relatedness across the carnivore species affected (based on published reports of wild populations, not on experimental infections) – we found that for helminths and viruses, their host species were more clustered on phylogeny relative to other parasite types (regardless the number of host species they infect). The finding that helminth distribution across carnivores was associated with host phylogeny is consistent with previous findings that many helminth species tend to have taxonomically restricted host ranges (Poulin & Mouillot 2003; Pedersen *et al.* 2005; Rosas-Valdez & de León 2010; Cooper *et al.* 2012). This is possibly because helminths interact with hosts through complex processes that are often associated with specific host behavioural and physiological traits (Anderson & May 1992; Poulin 1994; Vickery & Poulin 2002), and distantly related carnivore species tend to be dissimilar in behaviours and physiology (Gittleman 1985, 2001; Bininda-Emonds & Gittleman 2000). Therefore, expanding the phylogenetic range of hosts might require dramatic changes in strategies for parasite transmission and within-host persistence, and such changes might be more challenging for helminths to overcome because of their long generation times relative to many microparasites.

Owing to their high mutation rates, short generation times, and potential for rapid within-host evolution, viruses were previously thought to be less constrained by host phylogeny than other parasite types and also have been characterized as more likely to emerge in novel host species that are not necessarily closely related to established hosts (Morse 1995; Cleaveland, Laurenson & Taylor 2001; Pedersen *et al.* 2005). Importantly, several viruses in our data base infect a wide range of carnivore species, such as canine distemper virus (53 host species) and rabies virus (34 host species), yet even these two viruses and most other viruses in our data base had host ranges that were significantly more clustered on host phylogeny than expected by chance. This pattern might arise if cross-species transmission occurs more commonly between ecologically similar hosts, or if successful infection is more likely for hosts that are similar at cellular and molecular levels. Importantly, our finding that virus occurrence was substantially constrained by host phylogeny is consistent with a recent analysis of rabies virus lineages across North American bats (Streicker *et al.* 2010) and together these studies indicate that host species barriers might not be as readily overcome by rapid viral evolution as previously thought.

Conclusions and implications

The severe impacts of recent emerging infectious diseases on humans, domesticated animals and wildlife have raised the critical issue of predicting novel pathogen introductions

for effective disease prevention or management of at-risk populations (Cleaveland, Laurenson & Taylor 2001; Cleaveland *et al*. 2002; Jones *et al*. 2008; Fuller *et al*. 2012). Carnivores in particular have been severely impacted by pathogen outbreaks, including those shared with domesticated animals such as canine distemper virus (Alexander & Appel 1994; Laurenson *et al*. 1998), rabies (Kat *et al*. 1995; Randall *et al*. 2004), parvavirus (Laurenson *et al*. 1998) and heartworms (Pappas & Lunzman 1985). Global data bases of host phylogeny, ecology and geographic distribution could be powerful tools for identifying future pathogen emergence by inferring a candidate pool of parasites based on the phylogenetic distance, trait similarity and geographic overlap between current and potential hosts (Davies & Pedersen 2008; Pedersen & Davies 2009; Cooper *et al*. 2012). For example, the simplest prediction we might make is that carnivores that are closely related and biologically similar to domesticated dogs should be vulnerable to pathogen spillover from dog populations in the same region.

Parasite occurrence patterns remain poorly quantified for the majority of wildlife species, particularly those that are in hard-to-access locations, show cryptic behaviours or are of low public health concern (Hopkins & Nunn 2007). To our knowledge, about 44% of all carnivore species have not been sampled for parasitism as reflected in the published literature through 2010, and similarly high fractions of primates and hoofed mammals remain poorly sampled for parasites and pathogens (Nunn *et al*. 2003; Ezenwa *et al*. 2006). Our analysis suggests that knowledge of mammal phylogeny, ecology and geographic distribution could be used for predicting which parasites might be present in these understudied hosts. In particular, it is likely that understudied species share parasites with their close relatives, and biological similarity as well as geographic overlap further increases this likelihood; thus, this information could be used to predict the probability of particular parasite species in a given host.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Relationships between the three measures of pair-wise host phylogenetic distances.

Figure S2. The relationship between adult body mass (g) difference (after log transformation) and overall trait dissimilarity for carnivore host species pairs.

Figure S3. The relationships between our two measures of pair-wise host geographic range overlaps.

Figure S4. Relationships between the Jaccard index (*J*) and corrected Jacchard index (*CJ*) of parasite assemblages between pairs of carnivore host species, in comparison with a one-to-one line (red).

Figure S5. Relationships between host species number and host PSV calculated based on three different host phylogenetic trees.

Figure S6. Mean host PSV in different groups of parasites.

Table S1. The Spearman's rank correlations between parasite assemblage similarity and different measures of host evolutionary distance, geographic overlap and ecological similarity.

Table S2. The Spearman's rank correlations between parasite assemblage dissimilarity of different taxonomic groups and different measures of host evolutionary distance, geographic overlap and ecological similarity.

Table S3. Generalized linear models for predicting parasite assemblage corrected Jaccard index (*CJ*) of different parasite taxonomic groups between carnivore host pairs.