ORIGINAL ARTICLE

Parasite diversity declines with host evolutionary distinctiveness: A global analysis of carnivores

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Evolutionarily distinctive host lineages might harbor fewer parasite species because they have fewer opportunities for parasite sharing than hosts having extant close relatives, or because diverse parasite assemblages promote host diversification. We evaluate these hypotheses using data from 930 species of parasites reported to infect free-living carnivores. We applied nonparametric richness estimators to estimate parasite diversity among well-sampled carnivore species and assessed how well host evolutionary distinctiveness, relative to other biological and environmental factors, explained variation in estimated parasite diversity. Species richness estimates indicate that the current published literature captures less than 50% of the true parasite diversity for most carnivores. Parasite species richness declined with evolutionary distinctiveness of carnivore hosts (i.e., length of terminal ranches of the phylogeny) and increased with host species body mass and geographic range area. We found no support for the hypothesis that hosts from more diverse lineages support a higher number of generalist parasites, but we did find evidence that parasite assemblages might have driven host lineage diversification through mechanisms linked to sexual selection. Collectively, this work provides strong support for host evolutionary history being an essential predictor of parasite diversity, and offers a simple model for predicting parasite diversity in understudied carnivore species.

KEY WORDS: Body size, coevolution, diversity estimator, geographic range size, host diversification, sexual dimorphism.

Parasites, defined broadly to include viruses, bacteria, protozoa, and macroparasites, potentially account for greater than half of global species diversity (Poulin and Morand 2000; Dobson et al. 2008). The diversity of parasites is thought to be largely determined by the ecology of their hosts. For example, past work showed that the diversity of parasites harbored by a host species generally increases with host body mass, longevity, population density, and geographic range size (e.g., Poulin 1995; Ezenwa et al. 2006; Lindenfors et al. 2007). Environmental factors such as proximity to the equator and warmer temperatures also predict greater parasite diversity (e.g., Poulin and Morand 2000; Nunn et al. 2005). Less attention has been focused on the link between host evolutionary history and parasite diversity, which is surprising as host evolutionary history affects opportunities for parasites to colonize and evolve within and be lost from host lineages over evolutionary time. In turn, parasites play important roles in shaping key aspects of host evolutionary history, including speciation (reviewed in Poulin and Morand 2000; Page 2003). Identifying the evolutionary mechanisms that generate and maintain parasite diversity in natural ecosystems is important for advancing the field of macroecology in which one of the primary goals is to fully understand drivers of biodiversity as well as to predict the future of biodiversity (Smith et al. 2014). The goal of this study was to examine the importance of host evolutionary distinctiveness, relative to other biological and environmental factors, in explaining parasite diversity in wildlife hosts, and search for potential underlying mechanisms.

One hypothesis (H1) is that evolutionarily distinct host species will harbor fewer parasite species than hosts that diverged more recently (Nunn et al. 2004). This pattern could arise if
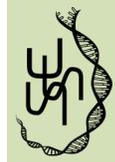
parasites exert strong selection pressure on their hosts to evolve defensive strategies, which might ultimately drive host diversification (Karvonen and Seehausen 2012; Marston et al. 2012). In many animals, sexually selected traits that signal heritable resistance to parasites have been shown to facilitate divergence among populations (Maan and Seehausen 2011). Pathogens can also drive allopatric divergence among host populations by selecting for antiparasite defenses linked to different suites of host traits in different populations (Buckling and Rainey 2002). Therefore, this "diversification hypothesis" (H1a) predicts that host species infected by a larger diversity of parasites experience stronger sexual selection. Furthermore, a negative correlation between host evolutionary distinctiveness and parasite diversity can be caused by the higher frequency of parasite sharing among closely related host species (e.g., Krasnov et al. 2010; Cooper et al. 2012; Huang et al. 2014). This could be due to closely related host species inheriting parasites from the same ancestral pool (Page 2003) and/or more opportunities for cross-species transmission and host shifts among closely related host species (Streicker et al. 2010). In comparison, divergent host species are likely to be distinct biologically, immunologically, and ecologically in ways that prevent maintenance of a common parasite community. This "differentiation hypothesis" (H1b) predicts that evolutionarily distinct hosts should harbor lower parasite diversity than closely related lineages owing to fewer shared parasites and fewer opportunities to acquire new parasites through cross-species transmission.

As an alternative hypothesis (H2), coevolutionary theories suggest that bursts of host diversification might follow from the evolution of effective antiparasite defenses within host lineages (Yoder and Nuismer 2010). Consequently, host species in clades that have experienced more diversification events might be better defended and thus have lower number of parasite species than more distinctive host species. Furthermore, because clade diversification is a net outcome of speciation and extinction, distinctive species might be survivors of those formerly large clades that have experienced low speciation rates and/or high extinction rates. Thus, clades might retain species from recent diversifications because lower parasite diversity in those clades allows a lower extinction rate. The "coevolution hypothesis" also holds that evolutionarily distinct species could represent stable environments for parasites over evolutionary time, allowing for the accumulation and retention of large numbers of parasite species (Buckling and Rainey 2002).

In this study, we used data on parasites from free-living carnivore populations to directly examine the relationship between parasite biodiversity and host phylogenetic distinctiveness, relative to other ecological and environmental variables that could affect parasite diversity. Carnivores are one of the best-studied mammal groups and exhibit tremendous interspecific variation across a range of biological and ecological traits, and occupy geographic ranges from the tropics to the poles (Bininda-Emonds and Gittleman 2000; references in Huang et al. 2014). Carnivores have also been well studied for parasites, due in part to their close relationship to domesticated animals (De Castro and Bolker 2005; Lembo et al. 2008) and because infectious diseases have caused recent conservation concerns (e.g., Murray et al. 1999; references in Huang et al. 2014).

We combine multiple, global-scale datasets on carnivores and their parasites to test the prediction that host phylogenetic distinctiveness is an important predictor of parasite diversity. We compiled data on parasite occurrence from free-living carnivore populations based on primary studies published between 1986 and 2010, to which we applied several diversity estimators to predict the number of parasites species per host in the face of incomplete and uneven sampling effort. These diversity estimators extrapolate from reported richness to estimate the number of species that were likely to have been missed, using information on sampling intensity and the number of rare species (here, parasites only found in one or two studies). We then compared the relative importance of phylogenetic distinctiveness versus other ecological traits in explaining variation in the diversity of parasites infecting a carnivore species. Finally, we evaluated potential underlying mechanisms for the detected associations between parasite richness and host evolutionary distinctiveness, including possible links between parasites and sexual selection (as expected if parasites drive host diversification), and the sharing of generalist parasites with close relatives (as expected if host diversification supports greater parasite diversity through sharing and exchanging of parasites among host species).

Materials and Methods
GLOBAL CARNIVORE PARASITE DATABASE

We collated records of parasite occurrence in free-living terrestrial (fissiped) and marine (pinniped) carnivore populations from standardized searches of the primary literature between 2002 and 2010, and combined them with previously compiled datasets of carnivore parasites from publications spanning the years 1986–2002 (Lindenfors et al. 2007). The data collection procedure was similar to that of Lindenfors et al. (2007; also see procedure details in Huang et al. 2014 and Supporting Information). A total of 1157 references were included in our dataset, providing records of 930 parasite species found in wild populations of 159 carnivore species in 13 families. To estimate sampling effort (see below), another 67 parasite species and 7 host species were retained in our dataset even though the reported prevalence of the sampled parasite was zero (i.e., authors searched for the specific parasite in a given host but did not find evidence of infection, thus reported absence of the parasite). We corrected host species names that deviated from Wilson and Reeder's (Wilson and Reeder 2005) and

updated parasite species names using the most current taxonomic information available (see Supporting Information).

COMPARISONS OF PARASITE DIVERSITY ESTIMATORS

"Observed" parasite diversity for each carnivore species was defined as the number of parasite species reported (with prevalence > 0; hereafter, "reported parasite diversity") in at least one sampled population of a given host. Parasite species that were identified to genus but not to species were counted only when no other parasites from the same genus had been detected in that host species. Parasite species that were not identified to genus were excluded from this study. Carnivores not identified to the species level were also excluded from the analysis. We did not distinguish subspecies of carnivores or parasites.

Reported parasite diversity is expected to correlate strongly with the degree to which the host species has been sampled (thereafter, sampling effort; Poulin and Morand 2000; Nunn et al. 2003; Ezenwa et al. 2006; Lindenfors et al. 2007), but might stabilize for some well-sampled host species. Previous approaches that have included sampling effort as a covariate in statistical models and that assume log-linear relationships between reported parasite diversity and sampling effort (Nunn et al. 2003, 2005; Lindenfors et al. 2007) are not ideal for investigation at broad taxonomic scales because of heterogeneity in sampling strategies and sensitivity of detection techniques, as well as variation in sample sizes for different host populations and parasite species. For example, some wildlife hosts are studied repeatedly for the same parasite species because they are considered pathogen sources (reservoirs) for livestock infections (e.g., *Mycobacterium bovis* in European badgers, Murphy et al. 2010). Host species for which these studies take place might be assigned to a low residual measure of parasite diversity based on the high sampling effort, but this does not indicate that further searches for more parasite species will not result in a large addition to current records of parasite diversity. In contrast, the nonparametric diversity estimators that we used in this study significantly downweight such multiply reported parasites.

We explored the reliability of different estimators for parasite diversity by comparing their performance on the six best-sampled host species: *Vulpes vulpes* (227 independent reports, i.e., references in our database), *Procyon lotor* (151 reports), *Meles meles* (84 reports), *Canis latrans* (80 reports), *C. lupus* (71 reports), and *Phoca vitulina* (63 reports). We used three nonparametric estimators that showed low bias and high accuracy in previous parasite diversity studies based on standardized field-collected data, including Chao 2, Jackknife, and Bootstrap (Poulin 1998; Walther and Morand 1998; Walther and Moore 2005). We also used the more recently developed abundance-based coverage estimator (ACE) with $\kappa = 2$ (Chao et al. 2006). Detailed methods for computing each estimate are provided in the Supporting Information. We treated each report as a sampling event, much like a random pool of samples from the species of interest. From the N published reports pertaining to a given host species, we randomly drew subpools of reports (without replacement) from 5 to N, 1000 draws of each subpool size; we counted the observed parasite diversity and estimated true diversity based on the subpools of reports. To compare the performance of estimators at low sample sizes, we searched for the minimum number of reports required to have >5% chance of covering the final estimate (based on all the included reports) for each method and each host species. We used this minimum number as the cut-off sampling effort for including host species in further analyses, described below.

HOST EVOLUTIONARY HISTORY AND ECOLOGICAL TRAITS

We quantified host phylogenetic distinctiveness as the terminal branch length, and two recently developed measures based on the equal-split (Redding and Mooers 2006) and fair-proportion (Isaac et al. 2007) algorithms, using the most recently published carnivore supertree (Nyakatura and Bininda-Emonds 2012). Terminal branch length accounts for the evolutionary distance of a species to all other species in the clade and ignores the effect of past evolutionary history before the most recent diversification event. In comparison, the other two measures incorporate the length of internal branches into the calculations of distinctiveness differently (see Supporting Information).

We obtained data for nine best-studied carnivore trait variables (Jones et al. 2009), including ecological traits that have been suggested or shown to correlate with parasite diversity: adult body mass (g), population density (number of individuals per km^2), geographic range area (km^2), and centroid latitude degree of the geographic range (absolute degree) (Nunn et al. 2005; Lindenfors et al. 2007). Host ecological trait data (except latitude) were log transformed. Additionally, we included four environmental variables: average temperature (°C), average precipitation (mm), average potential evapotranspiration (PET, mm) and average annual evapotranspiration (AET, mm) within each species' geographic range, which could be associated with the distribution and transmission dynamics of parasites (Guernier et al. 2004; Antonovics 2009; Fuller et al. 2012).

Because our initial analyses showed that parasite diversity declined with carnivore evolutionary distinctiveness (H1), we tested for relationships with covariates associated with two potential mechanisms that might cause this association. First, we examined whether diverse parasite assemblages might be promoting host diversification (H1a; Nunn et al. 2004) through more intense sexual selection in host lineages with greater parasite pressure by examining the effect of sexual dimorphism in host body mass. We used sex-specific body mass data (Bininda-Emonds and Gittleman 2000) to calculate the Lovich–Gibbons revised two-step ratio

(see Supporting Information for the formula; Gibbons and Lovich 1990; Lovich and Gibbons 1992), and ask whether host species harboring larger diversity of parasites display stronger host sexual dimorphism (Nunn et al. 2004). Thirty-five host species in our dataset displayed up to 230% larger body mass in male adults than in females, one species did not show dimorphism, and the rest showed up to 25% larger mass in females than in males.

Second, we asked whether generalist parasites (here, parasite species infecting >1 carnivore species) were more common, proportionally, in less distinctive hosts, which might have higher parasite diversity through parasite sharing (H1b; Huang et al. 2014). We calculated the proportion of generalist parasites using the reported (rather than estimated) parasite richness, as our analysis focused on a ratio rather than actual parasite numbers. We based assignments of species-specific versus generalist parasites on parasite records for all carnivore hosts sampled, irrespective of whether hosts were included in the final analyses.

STATISTICAL ANALYSIS

We first examined the influence of sampling effort on both reported and estimated (Chao 2, Jackknife, Bootstrap, ACE) parasite diversity using the Spearman rank-order correlation test to determine whether sampling effort should be included as a covariate in later analyses. Here, we followed previous studies to quantify sampling effort for a given host species using two measures: first, we counted the number of independent reports (references) included in the database, and second, we used the number of citations searchable in Web of Science (WOS) that were relevant to infectious disease (*host species binomial name* AND ["infectious disease" OR "infect*" OR "parasite*"]) (following Nunn et al. 2003; Lindenfors et al. 2007). Because our two measures of sampling efforts were highly correlated (Spearman's $\rho = 0.771$, $P < 0.001$) and analyses using the two measures showed qualitatively consistent results, in the main text we focus on results based on the number of reports included in our database.

We next investigated associations between parasite diversity with host evolutionary distinctiveness and other host traits. We first evaluated each host variable individually using a generalized linear model (GLM) to include sampling effort as a covariate when appropriate. We used random forest analyses (Breiman 2001) to compare the importance of evolutionary distinctiveness, host ecological traits, and environmental conditions within host geographic ranges. In this analysis, the importance of a variable is based on the decrease in residual sum of squares following variable inclusion. As an effort to provide a simple model for predicting parasite diversity in understudied host species, we searched for the best GLM of parasite diversity based on corrected Akaike information criterion (AICc), using the four most important variables identified in the random forest analyses. We

tested the residuals of the GLM for phylogenetic signals using Blomberg's K (Blomberg and Garland 2002), and when significant phylogenetic structure was detected ($P \leq 0.05$ for 1000 randomization), we repeated the analysis using phylogenetic generalized least squares models (PGLS).

Because host evolutionary distinctiveness was negatively correlated with parasite diversity, we conducted a final set of analyses to investigate potential underlying mechanisms. We used PGLS to examine how parasite diversity was associated with host sexual dimorphism in body mass, and used Spearman rank-order tests to compare host evolutionary distinctiveness to the proportion of generalist parasites.

Because different analyses have various requirements for data completeness, we reported the specific sample size for each analysis in the results. All analyses were conducted in R (R Development Core Team 2012) using the packages ape (Paradis et al. 2004), CAIC (Orme et al. 2009), caper (Orme 2012), and picante (Kembel et al. 2010) for phylogenetic analyses; randomForest (Liaw and Wiener 2002) for the random forest analyses; and MASS (Venables and Ripley 2002), AICcmodavg (Mazerolle and Mazerolle 2012), and arm (Gelman and Hill 2007) for other multivariate analyses.

Results
REPORTED AND ESTIMATED PARASITE SPECIES RICHNESS

For the six best-sampled carnivore species, accumulation curves of reported parasite diversity showed only limited sign of saturation (Fig. S1), indicating that the published literature reflects only a fraction of the total parasite biodiversity in wild carnivore hosts. Comparisons of diversity estimators based on simulated sampling showed that Chao 2 and ACE consistently required fewer reports to cover the final estimates of parasite diversity than the Jackknife and Bootstrap estimators (Table S2; Fig. S1). Therefore, we only report results of parasite diversity tests using Chao 2 and ACE estimates below.

Parasite diversity was estimated for 45 host species (Table S1) with at least nine published studies of parasitism, based on our estimated minimum number of reports required (see Materials and Methods). Although Chao 2 and ACE estimates were positively correlated with sampling effort (Fig. S2; Chao 2: $R^2 = 0.232$ with $P < 0.001$; ACE: $R^2 = 0.244$ with $P < 0.001$), these correlations were much weaker than the correlation between reported parasite diversity and sampling effort ($R^2 = 0.730$; $P < 0.001$). Sampling effort was retained as a covariate in all further analyses. Total parasite diversity across the 159 carnivore hosts included in our original dataset was estimated to range from 1722 (Chao 2 estimate) to 2251 (ACE estimate), relative to 930 reported parasite species.

PARASITE DIVERSITY, HOST EVOLUTIONARY DISTINCTIVENESS, AND ECOLOGICAL TRAITS

Among the 45 host species with estimated parasite richness, a total of 30 carnivore species were included in our analyses of parasite diversity in relation to host evolutionary distinctiveness and ecology (with complete data for all traits as a requirement). All three measures of evolutionary distinctiveness (terminal branch length, equal-split, and fair-proportion) were highly correlated with each other (Fig. S3). Only terminal branch length was significantly associated with estimated parasite diversity (host species on longer terminal branches harbored lower estimated parasite diversity for both ACE and Chao 2; Table S3). No measures of evolutionary distinctiveness were significantly associated with reported parasite diversity (Table S3).

Random forest analyses also showed strikingly different variable rankings for reported and estimated parasite diversity, but similar results for the two nonparametric parasite diversity estimates (Fig. 1, Chao 2 and ACE; see Fig. S4 for results from analyses using sampling effort based on WOS citations for each host species). Adult body mass, terminal branch length, and geographic range area were the most important predictors of estimated species richness (Fig. 1). Partial dependence analyses showed that estimated parasite diversity was negatively associated with host terminal branch length and positively associated with host body mass and geographic range area (Fig. 2; final pseudo-$R^2 = 0.178$ for both Chao 2 and ACE estimates, and see Fig. S5). In comparison, for reported parasite diversity, sampling effort was the most important predictor, but other host variables show much lower importance. Among host variables, the four most important variables were centroid point latitude degree, average AET, population density, and the average precipitation in the host geographic range. We found similar results when we repeated the analysis for reported parasite diversity to include all host species with complete data for relevant traits regardless the number of reports for parasitism ($n = 63$ carnivore species, Fig S6), or calculated the residual reported parasite diversity from a linear model based on sampling effort to be the response variable (Figs S7, S8).

The four most important variables identified by each random forest of regression trees for the estimated parasite diversity were also those with the best data availability. Therefore, we expanded our analysis to include 44 host species, with complete data for the four variables, to identify the best GLM models for predicting estimated parasite diversity. Both Chao 2- and ACE-estimated parasite diversities were best predicted by terminal branch length, together with sampling effort (Table 1). Because significant phylogenetic structure was detected in the residual ACE parasite diversity estimator (but not Chao 2) from GLM models including geographic range area ($K = 0.224$, $P = 0.049$; Table S4), we repeated analyses using PGLS and found the same overall result (Table S5).
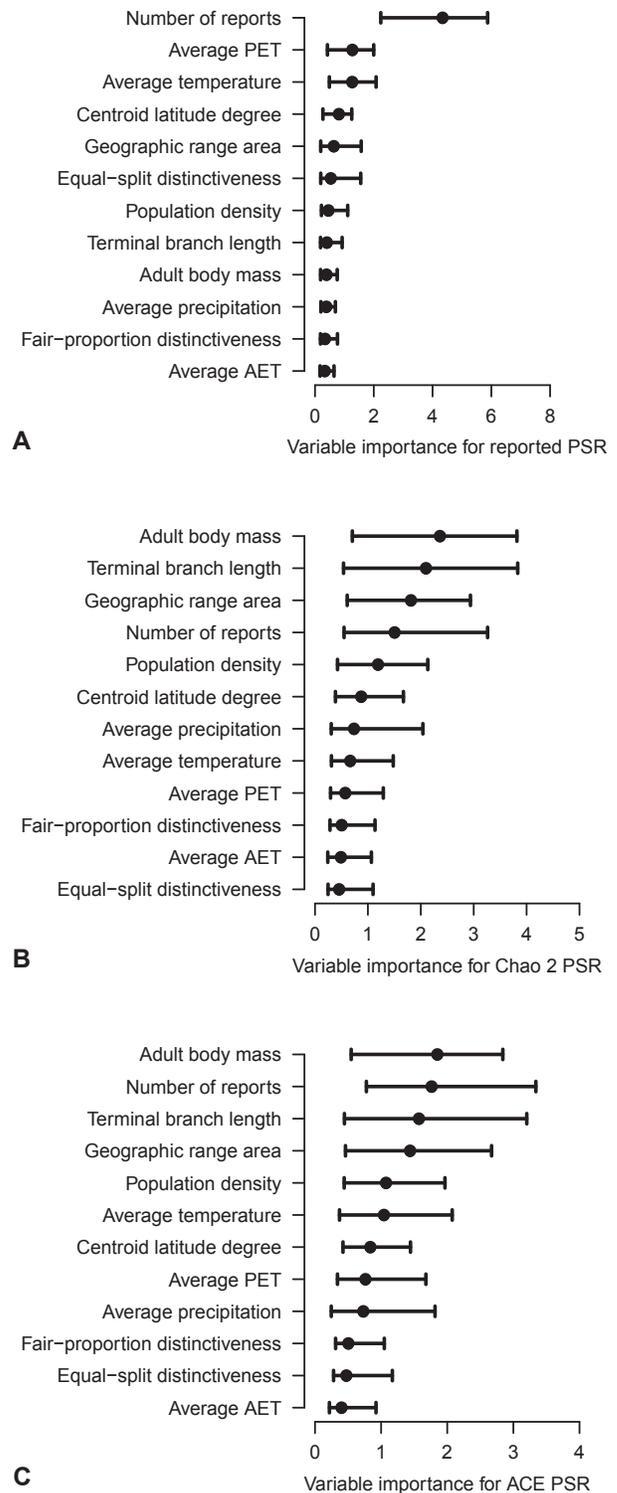

Figure 1. Variable importance determined by the random forest analysis for reported parasite species richness (PSR) (A) and PSR estimated using Chao 2 (B) and ACE (C) methods. Variables are ordered from most important (top) to least important. The importance of each variable is quantified as the increase of node impurity (residual sum of squares) if the variable is excluded, where a high increase indicates high importance of the variable. The 90% confidence intervals (indicated by error bars) are generated from 1000 bootstrapped data (5% and 95% quantiles).
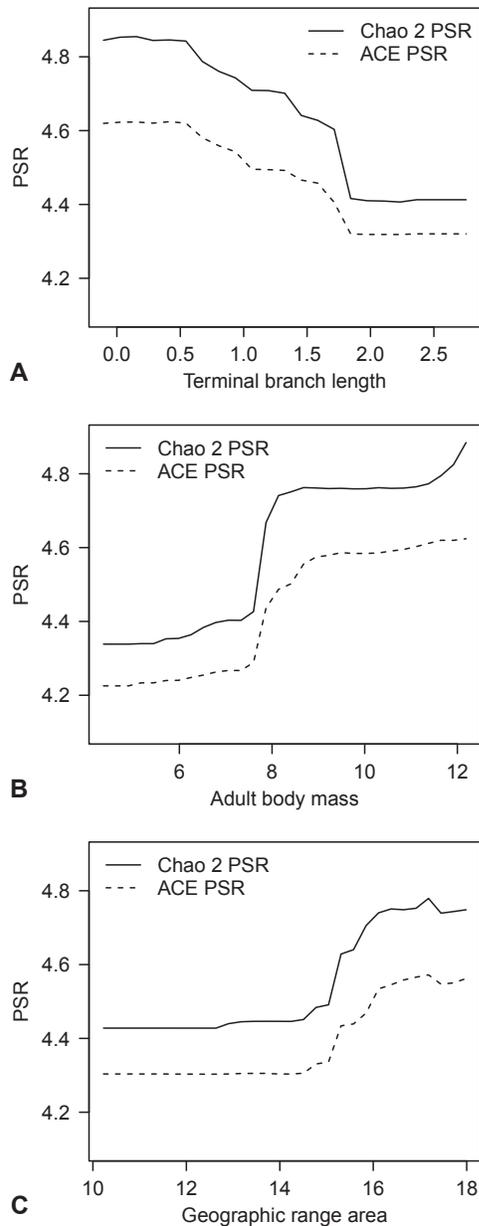
Figure 2. Partial dependency of Chao 2 (solid) and ACE (dashed) estimated parasite diversity (PSR) on the three most important variables from random forest analyses: **(A)** host terminal branch length, **(B)** adult body mass, and **(C)** geographic range area. In each of the three cases, for each value of the variable on the horizontal axes, average PSR estimates were calculated based on the data of all the other variables not included using the random forest model for Chao 2 and ACE estimates of parasite diversity. All axes were natural log transformed.

MECHANISMS UNDERLYING THE EVOLUTIONARY DISTINCTIVENESS–PARASITE DIVERSITY RELATIONSHIP

Because evolutionarily distinct host species tend to have lower parasite diversity than species with living close relatives, we

Table 1. Generalized linear models (GLM) of estimated parasite diversity.

Models	Chao 2 estimator		ACE estimator	
	AICc	ΔAICc	AICc	ΔAICc
Terminal branch length (TBL)	74.86	0	77.36	0
Adult body mass (ABM)	88.16	13.30	84.86	7.50
Geographic range area (GRA)	89.47	14.61	84.41	7.05
TBL + ABM	75.37	0.51	78.58	1.22
TBL + GRA	76.48	1.62	79.05	1.69
ABM + GRA	90.08	15.22	86.44	9.08
All	76.67	1.81	80.73	3.37

Sampling effort measured as the number of reports was included as a co-variate in all models. Note that complete data were available for 44 host species to be included in these models. ΔAICc for each model was calculated as the difference from the lowest AICc (i.e., model AICc – lowest AICc).

further investigated two potential mechanisms: (H1a) whether sexual selection might underlie the association between parasite diversity and host evolutionary history and (H1b) whether evolutionary distinctive hosts harbor lower proportions of generalist parasite species. In 41 host species with sufficient data, male-biased sexual dimorphism was significantly correlated with estimated parasite diversity (Table S6; Fig. 3). Stronger male bias is also associated with shorter terminal branches (based on phylogenetic independent contrast, Spearman's $\rho = 0.327$, $P = 0.040$). However, we found no association between the proportion of generalist parasites and the host terminal branch length (Spearman's $\rho = 0.048$, $P = 0.754$). We did not detect a significant phylogenetic signal in the residual proportion of generalist parasites from a linear model based on host terminal branch length ($K = 0.160$, $P = 0.276$). We constrained this analysis to relatively well-studied host species (sampled in at least nine reports, $n = 45$), and all host species harbor above 50% generalist parasite species. We obtained qualitatively consistent results when we defined generalist as parasites infecting more than three or five host species.

Discussion

Parasites are an essential component of biodiversity and can contribute to the generation and maintenance of diversity in other species (Nunn et al. 2004; Johnson et al. 2013). Identifying factors associated with high parasite diversity in well-studied host groups such as carnivores is important for understanding the ecological and evolutionary principles that govern parasite diversity. Additionally, because most host species on Earth have not been well sampled for parasites, understanding key determinants of
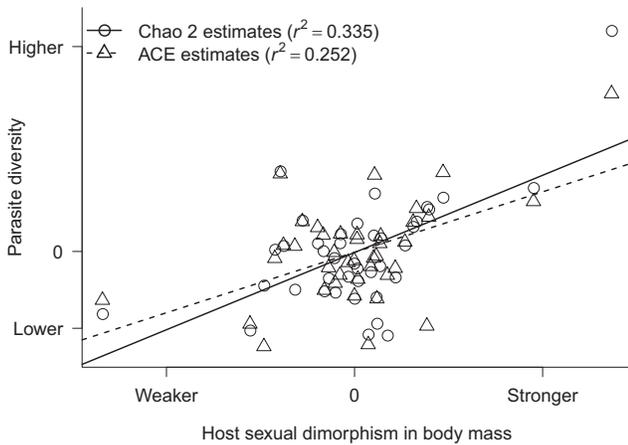
Figure 3. The relationship between parasite diversity and host sexual dimorphism in body mass based on phylogenetic independent contrasts. Parasite diversity was based on the residual estimated parasite diversity (Chao 2 and ACE estimators) from linear regressions with the number of reports. The illustrated trend lines were based on the parameters from bivariate linear models. All variables have been transformed into phylogenetic independent contrasts. Both linear models show significant correlations ($P <$ 0.001), and the correlations remain significant or marginally significant after removing the two extreme on both ends (Chao 2: $P = 0.043$; ACE: $P = 0.064$).

parasite diversity can help predict parasite diversity in hosts for which biological trait data are available in the absence of parasite sampling. Our analysis of carnivores showed that overall parasite diversity declined with host evolutionary distinctiveness (measured in terminal branch length), which was the most consistent and robust predictor of parasite diversity of the variables examined here. This finding is consistent with a previous study of primates that showed greater parasite diversity in host species from more rapidly diversifying clades (Nunn et al. 2004) and suggests a strong association between parasite diversity and host diversification through sexual selection.

Two other host ecological traits, body mass and geographic range area, were positively associated with parasite diversity in carnivores, a finding that is consistent with previous comparative analyses of parasite diversity in primates (Nunn et al. 2003) and ungulates (Ezenwa et al. 2006). These characteristics might provide a wide variety of ecological niches for parasites and thus allow maximized parasite diversity (Poulin and Morand 2000). In our dataset, host species with both large body mass and extensive geographic ranges included brown bears (*Ursus arctos*), leopards (*Panthera pardus*), lions (*P. leo*), and gray wolves (*C. lupus*). Nevertheless, only terminal branch length was included in our final GLM models as an essential factor for predicting parasite diversity. Surprisingly, when we examined two other evolutionary distinctiveness measures that incorporate deeper

evolutionary history shared by related species, we found no significant associations with parasite diversity. It is possible that the more recent evolutionary history captured by the terminal branch length is more important for contemporary host–parasite associations than other measures of host distinctiveness.

Our analyses further suggested that the negative association between parasite diversity and host evolutionary distinctiveness is due to parasites driving host diversification through host sexual selection (supporting H1a, the "diversification hypothesis"). Specifically, we found that stronger male-biased sexual dimorphism was displayed by host species harboring large parasite diversity (a similar pattern was tested for in primates but not found; Nunn et al. 2004). This relationship could reflect the possibility that hosts with greater parasite diversity might experience more intense sexual selection on traits that signal parasite resistance or tolerance to prospective mates (Hamilton and Zuk 1982; Moore and Wilson 2002). At the same time, sexual selection has been identified as a key driver of speciation, such that species with more intense sexual selection might also be from clades that recently diversified (Maan and Seehausen 2011). As expected by this link between sexual selection and lineage diversification, we also found a significant correlation between terminal branch length and sexual dimorphism in carnivore hosts. We note that the terminal branch length data might not represent the real evolutionary age of the species, as extinct species and lineages are not included in the phylogenetic tree (Nyakatura and Bininda-Emonds 2012). Therefore, further data (e.g., robust fossil record) that can provide direct window to past diversification dynamics would be very helpful for understanding the underlying mechanisms. Surprisingly, neither reported ($K = 0.163$, $P = 0.227$) nor estimated parasite richness (Chao 2: $K = 0.177$, $P = 0.171$; ACE: $K = 0.192$, $P = 0.109$) showed evidence of phylogenetic structure under the assumption of a Brownian motion model of evolution. Future work focused on examining host–parasite associations should evaluate how different evolutionary scenarios would shape the associations between parasitism and sexual dimorphism.

Although it has been shown in multiple systems that closely related host species have higher frequencies of parasite sharing (Krasnov et al. 2010; Cooper et al. 2012; Huang et al. 2014), we think it unlikely that this serves as a causative mechanism generating the observed association between parasite diversity and host distinctiveness (rejecting H1b, the "differentiation hypothesis"). Our results suggest the proportion of generalist parasites does not vary according to the terminal branch length of the host species, similar to the observation in primates (Nunn et al. 2004). Thus, the lower frequency with which evolutionarily distinctive hosts share parasites with other host species might cause host species on longer terminal branches to have fewer numbers of generalist parasites, but not out of proportion with the total number of parasite species. Recent development in network analyses

provides a framework for investigating complex parasite sharing dynamics, and future investigation using this approach will might identify mechanistic links between parasite diversity in carnivores and network-based features such as host centrality (Anderson and Sukhdeo 2011; Gómez et al. 2013).

According to our interpretation of estimated parasite diversity, current records of parasite diversity in wild carnivores are far from complete. Despite the effort invested in this well-studied group for which parasites have received much attention, at least half the parasites from wild carnivores remain to be discovered, based on studies published through 2010. Even in the best-studied carnivore species, the reported parasite diversities do not asymptote, and the estimated parasite diversities greatly exceed the reported diversity. Our results can help guide further research on parasite diversity in several ways. In particular, our statistical model can identify host species that are currently not well sampled for parasites but for which we might expect parasite diversity to be relatively high. These might include species such as tigers (*P. tigris*), jaguars (*P. onca*), and side-striped jackals (*C. adustus*), which are large-bodied, widely distributed, and from more rapidly diversifying clades; these species are not currently well represented in the parasite literature.

We demonstrate here the utility of diversity estimators for global-scale parasite datasets from heterogeneous sources to which these estimators are rarely applied. Because true parasite diversity is not known for wild carnivore species, we cannot test the accuracy of the estimators used in our study (but see assessment using controlled samples and simulations in Poulin 1998; Walther and Moore 2005). However, our further analyses showed stronger correlations between estimated richness and host evolutionary distinctiveness and ecological factors than with sampling effort, suggesting the estimated parasite diversity is biologically meaningful. Our results on the association of parasite diversity with host body size and geographic range size are also consistent with patterns found in other systems (Nunn et al. 2003; Ezenwa et al. 2006), and thus warrant generalization to a broad taxonomic scale. In conclusion, therefore, our analyses provide support for the further use of diversity estimators in future broad-scale studies of parasite diversity, for which parasite diversity is almost always undersampled. The primary drawback to our use of the nonparametric estimators in this study is the loss of host species from the analysis for which sampling did not meet our minimum threshold of nine published studies, thus reducing the dataset from 159 carnivore hosts with parasite data to just 45 species with sufficient records to estimate parasite diversity. We acknowledge that the effort of studying carnivore species, or any taxonomic group, has not been evenly made across the whole clade, and the species represented in our dataset is not necessarily a random subset with respect to all biological aspects. As in many wildlife systems, the carnivore species that suffer data deficiency for parasite infection,

as well as for other biological traits, tend to be small-bodied and exhibit relatively restricted ranges of distribution (e.g., Brodie 2009; see a more general discussion on taxonomic bias from conservation perspectives in Clark and May 2002). However, the spans of our data for the three key variables: evolutionary distinctiveness, body mass, and geographic range area in the 45 host species, respectively, cover the traits in 98.6%, 99.6%, and 93.4% of all carnivore species with data available for each variable. Our study thus provides realistic insights on broad-scale patterns of parasite diversity in wildlife. It is also worth pointing out that the difficulty of expanding data coverage should not hinder investigation, as careful examination of incomplete data, like our study, can provide valuable guidelines for further sampling.

Carnivores are one of several mammalian orders that have high percentages of globally threatened species, with 26.7% species at risk of extinction or already extinct in the wild (according to the IUCN Red List of Threatened Species[TM]; http://www.iucnredlist.org/, last accessed on May 23, 2012). Importantly, as carnivore hosts face extinction, so might their parasites, especially those specific to a given host species or genus. The topic of co-extinctions of hosts and parasites has received some attention in recent years, but most current estimates of biodiversity loss fail to consider parasitic taxa (Koh et al. 2004; Dobson et al. 2008; Dunn et al. 2009). Although it is still impossible to achieve a complete record of parasite species infecting wild carnivore populations, evolutionary distinctiveness, body mass, and geographic range area can be used as predictors of parasite diversity based on a simple model we developed. Our study highlights the importance of host phylogenetic information in explaining parasite diversity, and suggests that parasite diversity might contribute to driving host diversification and promoting host diversity. Parasites have often been considered a threat to biodiversity because of their negative impact on host population persistence (Murray et al. 1999; De Castro and Bolker 2005). But, considered from an evolutionary perspective, parasites might actually play important roles in maintaining and promoting biodiversity, and might themselves be worthy of conservation attention (Johnson et al. 2013).

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Associate Editor: A.-L. Laine
Handling Editor: R. Shaw

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. PSR estimated based on randomly subsampled reports using four different methods in comparison with the accumulated PSR observed in the reports.

Figure S2. Relationships between the number of parasite reports (in dataset or in WOS) on each host species and PSR reported (a and b) or estimated using the Chao 2 (c and d) and ACE (e and f) methods. All observations have been log transformed.

Figure S3. Relationships between the three measures of evolutionary distinctiveness (ED) included in our analyses.

Figure S4. Variable importance determined by the random forest analysis for observed and estimated parasite species richness (PSR), using the number of parasite-related citations in Web of Science (WOS) as a measure of sampling effort.

Figure S5. Psudo-R^2 of the random forests for estimated PSR.

Figure S6. Variable importance determined by the random forest analysis for observed parasite species richness (PSR) in all 63 host species that have been reported in at least one study and have complete data for host traits.

Figure S7. Variable importance determined by the random forest analysis for residual observed parasite species richness (PSR) from a regular linear model based on the number of reports included in the dataset.

Figure S8. Variable importance determined by the random forest analysis for residual observed parasite species richness (PSR) from a regular linear model based on the number of reports included in the dataset.

Table S1. Forty-five host species that have been sampled in at least nine reports for parasites.

Table S2. Minimum sampling effort (MinSE) to cover (with 95% quantiles) the final estimates of PSR using different methods.

Table S3. Summary statistics of GLM models showing the relationship between parasite diversity (observed and estimated) and individual variables.

Table S4. Phylogenetic signal (Blomberg's K) in residual parasite diversity from generalized linear models (GLM).

Table S5. Phylogenetic generalized least square models (PGLS) of estimated parasite diversity.

Table S6. Model parameters for estimated parasite diversity and host sexual dimorphism, using generalized linear models and phylogenetic generalized least square models.