

Parasite sharing in wild ungulates and their predators: Effects of phylogeny, range overlap, and trophic links

Patrick R. Stephens¹  | Sonia Altizer¹ | Vanessa O. Ezenwa^{1,2} | John L. Gittleman¹ | Emili Moan³ | Barbara Han⁴ | Shan Huang⁵ | Paula Pappalardo¹

¹Odum School of Ecology, University of Georgia, Athens, Georgia

²Department of Infectious Diseases, College of Veterinary Medicine, University of Georgia, Athens, Georgia

³Department of Statistics, North Carolina State University, Raleigh, North Carolina

⁴Cary Institute of Ecosystem Studies, Millbrook, New York

⁵Senckenberg Biodiversity and Climate Research Centre (BiK-F), Frankfurt (Main), Germany

Correspondence

Patrick R. Stephens
Email: prsteph@uga.edu

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Abstract

1. Understanding factors that facilitate interspecific pathogen transmission is a central issue for conservation, agriculture, and human health. Past work showed that host phylogenetic relatedness and geographical proximity can increase cross-species transmission, but further work is needed to examine the importance of host traits, and species interactions such as predation, in determining the degree to which parasites are shared between hosts.
2. Here we consider the factors that predict patterns of parasite sharing across a diverse assemblage of 116 wild ungulates (i.e., hoofed mammals in the Artiodactyla and Perissodactyla) and nearly 900 species of micro- and macroparasites, controlling for differences in total parasite richness and host sampling effort. We also consider the effects of trophic links on parasite sharing between ungulates and carnivores.
3. We tested for the relative influence of range overlap, phylogenetic distance, body mass, and ecological dissimilarity (i.e., the distance separating species in a Euclidean distance matrix based on standardized traits) on parasite sharing. We also tested for the effects of variation in study effort as a potential source of bias in our data, and tested whether carnivores reported to feed on ungulates have more ungulate parasites than those that use other resources.
4. As in other groups, geographical range overlap and phylogenetic similarity predicted greater parasite community similarity in ungulates. Ecological dissimilarity showed a weak negative relationship with parasite sharing. Counter to our expectations, differences, not similarity, in host body mass predicted greater parasite sharing between pairs of ungulate hosts. Pairs of well-studied host species showed higher overlap than poorly studied species, although including sampling effort did not reduce the importance of biological traits in our models. Finally, carnivores that feed on ungulates harboured a greater richness of ungulate helminths.
5. Overall, we show that the factors that predict parasite sharing in wild ungulates are similar to those known for other mammal groups, and demonstrate the importance of controlling for heterogeneity in host sampling effort in future analyses of parasite sharing. We also show that ecological interactions, in this case trophic

links via predation, can allow sharing of some parasite species among distantly related host species.

KEYWORDS

Artiodactyla, Carnivora, cross-species transmission, helminth, host range, pathogen, Perissodactyla, predation

1 | INTRODUCTION

Emerging infectious diseases that threaten humans, domesticated animals and wildlife are disproportionately represented by pathogens that cross host species boundaries (Cleaveland, Laurenson, & Taylor, 2001; Daszak, Cunningham, & Hyatt, 2000; Woolhouse, 2002). Predicting the risk of novel disease emergence events requires, in part, identifying factors that allow parasites, defined here as any disease causing organism from viruses, bacteria, and protozoa to helminths and arthropods, to transmit between multiple host species (Fenton & Pedersen, 2005; Streicker et al., 2010). One way of exploring this question is to determine what factors are associated with sharing of parasites among different host species (Pedersen & Davies, 2009). Two factors known to predict parasite sharing are the geographical proximity and phylogenetic relatedness among host species (e.g., Gilbert & Webb, 2007; Huang, Bininda-Emonds, Stephens, Gittleman, & Altizer, 2014; Pedersen & Davies, 2009; Streicker et al., 2010). In particular, host species with overlapping geographical ranges might encounter similar parasite species through interspecific contact or via environmental exposure (e.g., Streicker et al., 2010). Moreover, closely related host species have been shown to share a higher proportion of parasite taxa (e.g., Davies & Pedersen, 2008; Gilbert & Webb, 2007; Huang et al., 2014), either due to common descent of parasites in diversifying host lineages (Ricklefs & Fallon, 2002), or because genetically similar host species share molecular and immunological factors that facilitate the establishment of similar parasites (Longdon, Hadfield, Webster, Obbard, & Jiggins, 2011). Closely related hosts might also share similar physical, life history and ecological traits (e.g., body mass, lifespan, latitude, geographical range size, diet) that result in the transmission and maintenance of similar parasites (Cooper, Griffin, Franz, Omotayo, & Nunn, 2012; Huang et al., 2014). For example, Huang et al. (2014) found that host phylogenetic affinity and trait similarity were the two strongest predictors of parasite sharing among wild carnivores.

Ecological interactions such as competition, mutualism, and predation can also create opportunities for parasite sharing. Interactions between predators and prey are among the best characterized direct ecological interactions, and can provide important pathways for parasites to invade new host species, such as through direct contact with fur, skin, and bodily fluids, as well as through ingestion of parasites themselves. Some of the best studied predator–prey interactions occurring among mammals are between carnivores (order: Carnivora) and ungulates. Large carnivores such as wolves, lions, and cheetahs, for example, prey almost exclusively on ungulates (Sheldon, 1992;

Sunquist & Sunquist, 2002). As a consequence, the parasites found in some carnivore species may have been passed on by their ungulate prey. Indeed, several case studies demonstrate or speculate that, particularly when stressed by circumstances such as drought or food shortages, predators can be exposed to potentially fatal infections harboured by infected prey (Leendertz et al., 2017). Although past studies have quantified trophic transmission of complex life cycle parasites in predator–prey communities (Lafferty, Dobson, & Kuris, 2006; Thielgtes et al., 2013), further work is needed to characterize overlap in predator–prey parasite communities more broadly, and to extend this work beyond (strictly) trophically transmitted parasites.

In this study, we examined patterns of parasite sharing in wild terrestrial ungulates from the orders Artiodactyla (even-toed ungulates) and Perissodactyla (odd-toed ungulates). Terrestrial ungulates are distributed across almost every ecoregion—from tropical forest to Arctic tundra. The parasites of wild ungulates are also well-characterized (Ezenwa, Price, Altizer, Vitone, & Cook, 2006; Stephens et al., 2017), in part owing to the importance of many ungulate species as natural resources for humans (Apollonio, Andersen, & Putman, 2010). Crucially, infectious diseases represent an escalating problem for wild ungulate management (Gortázar, Acevedo, Ruiz-Fons, & Vicente, 2006), as exemplified by the recent devastating outbreak of *Pasteurella multocida* that killed over 200,000 endangered Saiga (*Saiga tatarica*) in Kazakhstan (Kock et al., 2018). As such, understanding the factors that predict patterns of parasite sharing in this host group has direct conservation implications. Further, as close phylogenetic relatives of many economically important domestic species (e.g., cattle, sheep, goats, horses), wild ungulates can serve as conduits of emerging diseases to domestic animals and humans (Jolles & Ezenwa, 2015; Taylor, Latham, & Mark, 2001). In recent years, outbreaks of disease such as anthrax (Blackburn, McNyset, Curtis, & Hugh-Jones, 2007) and blue tongue (Wilson & Mellor, 2009) have been increasing in frequency and severity in both wild and domestic ungulates. Thus, a clearer picture of determinants of parasite sharing in wild ungulates could help identify risk factors for parasite spillover to domestic species.

Using a comparative dataset of nearly 900 parasite species reported from 116 host species, we first investigate whether the factors previously shown to be important determinants of parasite sharing in other mammal groups (Cooper et al., 2012; Davies & Pedersen, 2008; Huang et al., 2014), namely geographical range overlap and phylogenetic similarity, predict greater parasite sharing in wild ungulates. Our multivariate models also included metrics of ecological and morphological similarity, with the prediction that host

species with similar biological traits would be more likely to share parasite species in common. We also explicitly test the degree to which sampling effort affects estimates of parasite sharing among species (i.e., do pairs of well-studied host species tend to show greater overlap in our data than poorly studied species?). Finally, we consider the potential for trophic links between predators and prey to drive parasite sharing among distantly related host species by testing whether mammalian carnivores that feed on ungulates harbour more ungulate parasites relative to carnivores that predominantly feed on other host groups.

2 | MATERIALS AND METHODS

2.1 | Data sources and predictor variables

Data on host-parasite associations came from the Global Mammal Parasite Database v. 2.0 (GMPD, Stephens et al., 2017). Only host and parasite species records resolved to the species level were included in the analyses. The ungulate data in the GMPD include records for 116 host species from 12 families in the Artio- and Perissodactyla; and 886 parasite species, including prions, viruses, bacteria, protozoa, helminths, and arthropods (see metadata of Stephens et al., 2017 for additional details on literature sources, sampling methods, taxonomic references, and additional background information on these data).

Host-phylogenetic relationships were based on a previously published supertree of all mammals (Fritz, Bininda-Emonds, & Purvis, 2009). The phylogenetic distance that separates pairs of host species was characterized using two measures: (a) divergence time separating species in millions of years (myr) and (b) the number of divergence (i.e., speciation) events that separate species in the tree.

Geographical range overlap among hosts was characterized using range shapefiles downloaded from the International Union for the Conservation of Nature (<https://www.iucnredlist.org/resources/spatial-data-download>). Range overlap was quantified using three measures: (a) scoring pairs of host species either "0" for no overlap and "1" for pairs with at least some overlap, (b) area of overlap in km², and (c) percentage range overlap (i.e., range area of species with smaller range/area of overlap).

Ecological similarity of species was characterized primarily based on trait data from PanTHERIA (Jones et al., 2009), with some additional data from Ultimate Ungulates (<http://www.ultimateungulate.com/>), a website containing data on ungulate morphological, life history and ecological traits derived from the primary literature. This approach allowed for maximum coverage of as many traits as possible at the species level. Traits used to construct distance matrices were described in full in Jones et al. (2009), and included: body mass (g), geographical range area (km²), median gestation length (days), litter size, dietary breadth, maximum longevity (months), trophic level, neonatal mass (g), and age at sexual maturity (days). Because data for different traits have various ranges and distributions, all trait data were standardized into the same distribution with the same mean and variance using the R library cluster v. 2.0.5 (Maechler

et al., 2015) before distance matrices were constructed. Two measures of ecological similarity between host species based on these traits were considered: (a) difference in the median adult body mass in grams (after log-transformation) and (b) the distance that separates host species in a Euclidian distance matrix constructed from all nine traits. Body mass is highly correlated with many ecological and morphological traits across species in general (Calder, 1984; Peters, 1983), and in ungulates is strongly associated with variation in the types of plant resources species forage on (Illius & Gordon, 1992). Distance among species in multivariate trait space is another widely used measure of ecological disparity (Laliberté & Legendre, 2010) that has been used in previous studies of parasite sharing (Huang et al., 2014; Streicker et al., 2010). Euclidian distances between species were identical to Gower's distances (Podani, 1999) for the same set of traits calculated using the FD package in R (Laliberté, Legendre, & Shipley, 2014).

2.2 | Characterizing parasite sharing

Overlap in the parasite species that infect pairs of hosts was quantified using two measures of assemblage similarity: (a) the Jaccard index and (b) the Corrected Jaccard index (Huang et al., 2014). Jaccard's index is a common measure of β diversity based on presence/absence data (Koleff, Gaston, & Lennon, 2003) and has been used in several past studies of parasite sharing among hosts (Davies & Pedersen, 2008; Huang et al., 2014; Pedersen & Davies, 2009). It is defined as $j = a/(a + b + c)$ where a is the number of species shared between host species, b is the number of species found in the first host but not the second, and c is the number of species found in the second host but not the first. However, the maximum value of j is constrained by the disparity in the number of parasites that occur in the hosts species considered. For example, if a host species with one parasite reported is compared to a species with ten, the maximum value of the Jaccard index is $1/(1 + 9 + 0) = 0.1$. We therefore repeated analyses using the corrected Jaccard index, $jc = j/mj$, where j is the observed value of the Jaccard index and mj is the maximum possible value of the Jaccard index given the number of parasites in the host species being compared (Huang et al., 2014). We also conducted a simple simulation to illustrate this problem with the Jaccard index, and show that the Corrected Jaccard index is not influenced by the disparity in the number of species in assemblages being compared (Figure S1).

2.3 | Quantifying biases in study effort

A key factor to consider in studies of parasite diversity in wild hosts is uneven sampling effort among host species, with better studied host species (i.e., more individuals sampled, more papers published) having higher reported numbers of parasite species (Ezenwa et al., 2006; Huang, Drake, Gittleman, & Altizer, 2015; Nunn, Altizer, Jones, & Sechrest, 2003). Even though better studied host species pairs should have higher reported numbers of shared parasites, surprisingly few studies of parasite sharing have

investigated whether that leads to a higher *proportion* of shared parasites (i.e., higher jaccard's scores) and thus necessitates correction for sampling bias (but see Walker, Plein, Morgan, & Vesik, 2017). Methods commonly used to account for uneven sampling effort in studies of parasite species richness, such as analysis of residuals of parasite richness fitted to sampling effort (Lindenfors et al., 2007; Nunn et al., 2003) or the use of nonparametric estimators of richness such as Chao2 (Huang et al., 2015), are not straightforward to apply to measures of parasite sharing. Thus, whether well-studied pairs of host species show greater measures of parasite overlap, and how best to control for this bias, when present, remain empirical and statistical challenges. To address this issue, sampling effort for each host species was characterized based on the number of previously published references that appeared for species name (Latin binomials and common synonyms) in a Web of Science (WOS) search of TOPIC or TITLE. Searches were conducted through the University of Georgia web portal to WOS on August 24, 2015. Values for host species pairs were summed during analyses to produce a measure of the total study effort applied to both host species, and this was used either as a covariate or as a weighting factor during statistical analyses (see below).

2.4 | Predictors of parasite sharing among ungulate hosts

All data processing and statistical analyses were conducted using R v. 3.3.2 (R Core Development Team, 2008). We first conducted a bivariate analysis using Spearman's rank to determine which predictor variables should be included in multivariate analyses (see Table S1). In the case of host phylogenetic distance and geographical range overlap, the different measures that we considered showed nearly identical correlations, with values of Spearman's ρ that varied by <0.01 (Table S1). We therefore chose divergence time in myr as our measure of host phylogenetic distance as it is a more commonly used measure than number of divergence events (e.g., Davies & Pedersen, 2008). We used percentage overlap as our measure of geographical range overlap as it varies continuously, like the other predictors we included in multivariate models, and is not constrained to be small when one of the host species being compared has a small

geographical range (i.e., it is potentially less affected by this host species identity effect). Initial bivariate tests showed that the two measures of ecological similarity differed in their directional associations with parasite sharing: ecological distance showed a weak negative correlation with parasite sharing, and body mass differences showed a weak positive correlation. Therefore, we included both in further analyses and discussion.

Model selection for multivariate analyses was initially conducted by comparing the AIC scores of generalized additive models (GAMs), estimated using the R package "mgcv" v. 1.8-17 (Wood, 2001). Analyses of the combined data were performed using both Jaccard and Corrected Jaccard values for pairs of host species as the response variables (i.e., as measures of parasite community similarity), and all models included range overlap, WOS citations, and phylogenetic distance as predictors. Models that included both ecological distance and body mass differences were compared to models that included only one or the other or that excluded both, since these two predictors showed weak but contrasting correlations in bivariate analyses. For both measures of parasite sharing, the AIC scores of the model that included all predictor variables was essentially tied (i.e., delta AIC <2) with the model that excluded ecological distance but included mass differences (Table S2). Here we present results using the former model in full (Table 1), since it includes information on an additional variable. Results using raw and Corrected Jaccard's measures of overlap were qualitatively identical (see Results).

To investigate how predictors of parasite sharing depended on the parasite group considered (i.e., viruses, bacteria, protozoa, helminths or arthropods; there were too few records of fungi or prions for separate analyses), we repeated GAM analyses using all five predictors in models of Corrected Jaccard's index values calculated from datasets pruned to only include parasites in one of each of the five groups. WOS citations also showed a strong correlation with measures of parasite sharing. We dealt with this bias in two ways. In analyses using generalized additive models, logged WOS citations was included as a covariate, similarly to some past studies of parasite richness in primates (Altizer, Nunn, & Lindenfors, 2007; Nunn, Altizer, Sechrest, & Cunningham, 2005). In boosted regression tree analyses (below), logged WOS citations was used as a weighting factor, such that better studied pairs of species had a greater influence

Predictor	Response variable			
	Jaccard		Corrected Jaccard	
	F	p-Value	F	p-Value
Percent range overlap (Smaller range/Area of overlap)	118.65	<0.0001	79.38	<0.0001
log(Divergence time, Myr)	37.09	<0.0001	43.77	<0.0001
log(Total WOS citations)	6.39	<0.0001	6.86	<0.0001
log(Mass difference, g)	3.73	0.054	1.73	0.092
log(Ecological dissimilarity)	0.51	0.609	0.51	0.283

TABLE 1 Results of GAM analyses of parasite sharing in wild ungulates. Table S2 shows the fit of all six GAM models considered. Predictor variables and Jaccard indices (with and without correcting for uneven parasite richness between host species pairs) are as described in Materials and Methods text

on the outcome of analyses, but data from all species pairs were still included in the analysis.

To further investigate how the results vary depending upon the parasite group considered, we used boosted regression trees implemented in the R package “gbm” v. 2.1.1 (Ridgeway, 2006). Boosted regression trees is an ensemble machine learning method that summarizes the structure of a large number of regression trees for a response variable and a set of predictors (Elith, Leathwick, & Hastie, 2008). The implementation of the method in the package “gbm” was useful for our analyses because it returns “relative importance” scores that always sum to 100, making for a relatively straightforward interpretation of differences in the importance of biological predictors among parasite groups. Models used a learning rate of 0.01, 10,000 trees, an interaction depth of 2, and fivefold cross-validation. The same parameters were used across all models to ensure that the relative importance scores were roughly comparable, though model fits and the qualitative results proved robust to the choice of model parameters during preliminary analyses. The direction and shape of correlations between predictor and response variables were assessed using marginal effects plots, where all but one predictor variable was integrated out of the model to generate low dimensional projections (Friedman, 2001).

2.5 | Analysis of parasite sharing among carnivores and ungulates

To explore how trophic links between mammalian carnivores and ungulates could affect parasite sharing, we mined the literature on carnivore biology (see Appendix S1) and scored carnivore species found in the GMPD based on their dietary preference: “0” for species not known to prey on ungulates, “1” for species reported to feed on ungulates on rare occasions, or “2” for species including ungulates as a consistent element of the diet. For example, *Felis sylvestris* has been reported to occasionally take young antelope, but was scored a “1” because its primary prey are rodents and lagomorphs throughout its range. The majority of species scored “2” feed largely or exclusively on ungulates. A few species such as *Ursus arctos* for which ungulates are a predominant prey item but only in some parts of the range or during some parts of the year were also scored a “2”.

We conducted analyses to quantify if parasite sharing between carnivores and ungulates is related to the trophic links among them. Analyses were conducted using ANOVA both with 0, 1, 2 scoring of carnivore hosts, and combining the latter two categories (i.e., comparing species with no records of ungulate predation (0's) to those with at least some reports, 1's and 2's,) as predictor variables. Analyses using three category scoring were also repeated using Spearman's rank to reflect the fact that the difference in the diet of species scored 0 versus 2 is arguably larger than that between a species scored 0 and 1, but the results of these analyses were qualitatively identical those using ANOVA and we do not report them. To quantify parasite sharing among carnivores and ungulates, the list of carnivore parasites in the GMPD was pruned down to those that also occur in at least one ungulate host species, and this list was used to

calculate the parasite species richness of each carnivore species in the GMPD (i.e., richness of parasites known to occur in ungulates). Data used for this analysis included 118 carnivore hosts and 643 carnivore parasite species. We did not subset the data to link particular ungulates to specific carnivore species reported to feed on them as this would have greatly reduced our sample sizes, but we consider our results an informative starting point for estimating the effects of trophic links on parasite sharing between the two groups.

Study effort for each carnivore host species was characterized using the same method used for ungulates (WOS citations, described earlier in Materials and Methods). One set of analyses was conducted comparing differences in raw parasite richness between host groups. Another set of analyses was conducted comparing residuals to a GAM where observed parasite richness (parasites common to carnivores and ungulates) was fitted to WOS citations. Analyses were repeated based on all parasite species and parasites of particular groups (e.g., helminths, viruses). The analysis of the full dataset and the one parasite group that showed significant correlations in analyses of raw data and residuals were repeated using a Phylogenetic ANOVA (Garland, Dickerman, Janis, & Jones, 1993) implemented using the R package “geiger” v. 2.0.6 (Pennell et al., 2014). This implementation does not allow the model to be adjusted for the amount of phylogenetic signal observed in model residuals (see discussion in Revell, 2010). We therefore directly measured the amount of phylogenetic signal found in model residuals using Pagel's λ (Pagel, 1999), and in turn used this value of λ to transform the internal branches of our phylogenetic tree prior to conducting our final Phylogenetic ANOVA analysis. As a result, the amount of phylogenetic “correction” applied to the model accurately reflected the amount of phylogenetic signal in the model residuals.

3 | RESULTS

We found the strongest support for geographical range overlap, sampling effort, and phylogenetic similarity as important predictors of greater parasite sharing among ungulates based on corrected Jaccard indices (Figures 1 and 2). Multivariate analyses using GAMs (Table 1) showed similar results to bivariate analyses (Table S1). Models that included both body mass differences and ecological dissimilarity were tied with models that included mass only (i.e., $\Delta AIC < 2$, Table S2). These two sets of models showed the lowest overall AIC scores despite that fact that neither mass differences nor ecological dissimilarity showed significant p -values (Table 1). Analyses using boosted regression trees (with WOS citations as a weighting factor) confirmed the results of bivariate and GAM analyses with respect to the relative influence of predictor variables when all parasites are considered (although ecological dissimilarity had greater relative importance scores than mass difference).

Results both of GAM and boosted regression analyses showed that the relative importance of predictors depended on the parasite group considered (Figure 1, Table S3). Plots of marginal effects showed that the correlations were in the same direction as bivariate

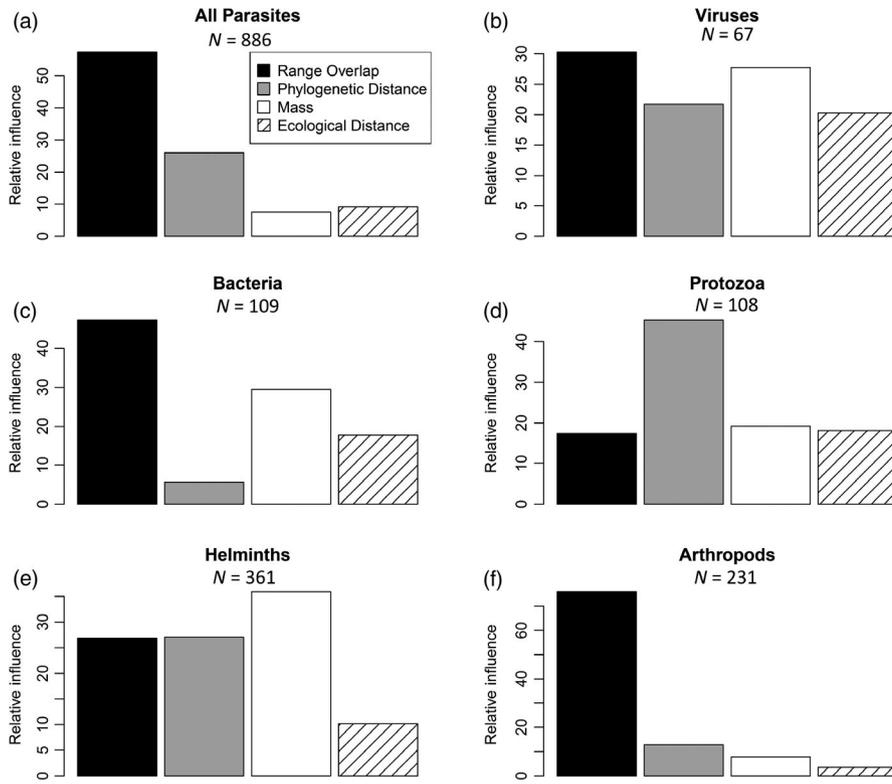


FIGURE 1 Relative importance of biological predictors of Corrected Jaccard measures of parasite sharing for pairs of ungulate species when weighted by logged total WOS citation count in boosted regression tree analyses, using all parasites combined (a) and different sub-groups of parasites (b–f). “N” indicates the number of parasite species of each group in data used for analyses. WOS: Web of Science

analyses (Table S1, Figure S4) and in the same direction across parasite groups, with the exception of ecological dissimilarity, which varied among groups (when significant, see Tables S3 and S4, Figure S5). For example, in analyses including all parasites ecological dissimilarity was negatively correlated with parasite sharing, but in protozoa the opposite was true.

Spline plots of the fitted GAM models of all data showed evidence of nonlinear relationships between parasite sharing and both range area and phylogenetic distance (Figure 2). In particular, parasite sharing increased initially with small amounts of range area overlap, and then plateaued, such that species with moderate to large overlap were equally likely to share parasites (Figure 2a). Greater phylogenetic distance had little impact on parasite sharing in close relatives, but parasite sharing decreased with distance for host pairs separated by 25 million years or more divergence time (Figure 2b). Results using raw Jaccard scores were qualitatively identical to those based on corrected scores with respect to rank order relative influence of variables in each model. For model fits and reports of the optimal number of boosting iterations (i.e., the number of trees used to compute the relative influence of model variables) in each model see Table S4.

We accounted for differences in sampling effort using citation count as a covariate in GAM analyses and as a weighting factor in boosted regression tree analyses. The relative importance scores of the biological predictors of parasite sharing were similar across these different approaches for taking into account uneven sampling effort (Table S1, Table 1, and Figure 1a). In GAM analyses, sampling effort was also a much weaker correlate of overlap than the best

biological predictors both overall (Table 1) and in individual host groups (Table S3)

When carnivore species were categorized based whether or not they have been reported to feed on ungulates in the wild, the richness of known ungulate parasites that infected each carnivore host was generally similar after correcting for variation in sampling effort, with the exception of analyses focused on helminths. Carnivores reported to feed on ungulates had significantly more ungulate helminth parasites (e.g., Figure 3) in analyses of both raw parasite richness data, and residual parasite richness correcting for study effort, and in both phylogenetically informed (p -value of phylogenetic ANOVA using 10,000 simulations 0.0364) and uninformed (Table 2, Table S5) analyses. Our results were qualitatively identical regardless of whether we used binary or three category coding of levels of ungulate carnivory (Table 1, Table S5).

4 | DISCUSSION

Our study provided support for both phylogenetic similarity and geographical range overlap as predictors of greater parasite sharing in wild ungulates, in line with findings from several other host groups (Davies & Pedersen, 2008; Huang et al., 2014; Streicker et al., 2010). At the same time, ecological differences between species were less important to patterns of parasite sharing in ungulates (Table 1, Figure 1a) than in primates (Cooper et al., 2012) and carnivores (Huang et al., 2014). Our investigation of the potential for predator–prey interactions to drive parasite sharing between distantly related

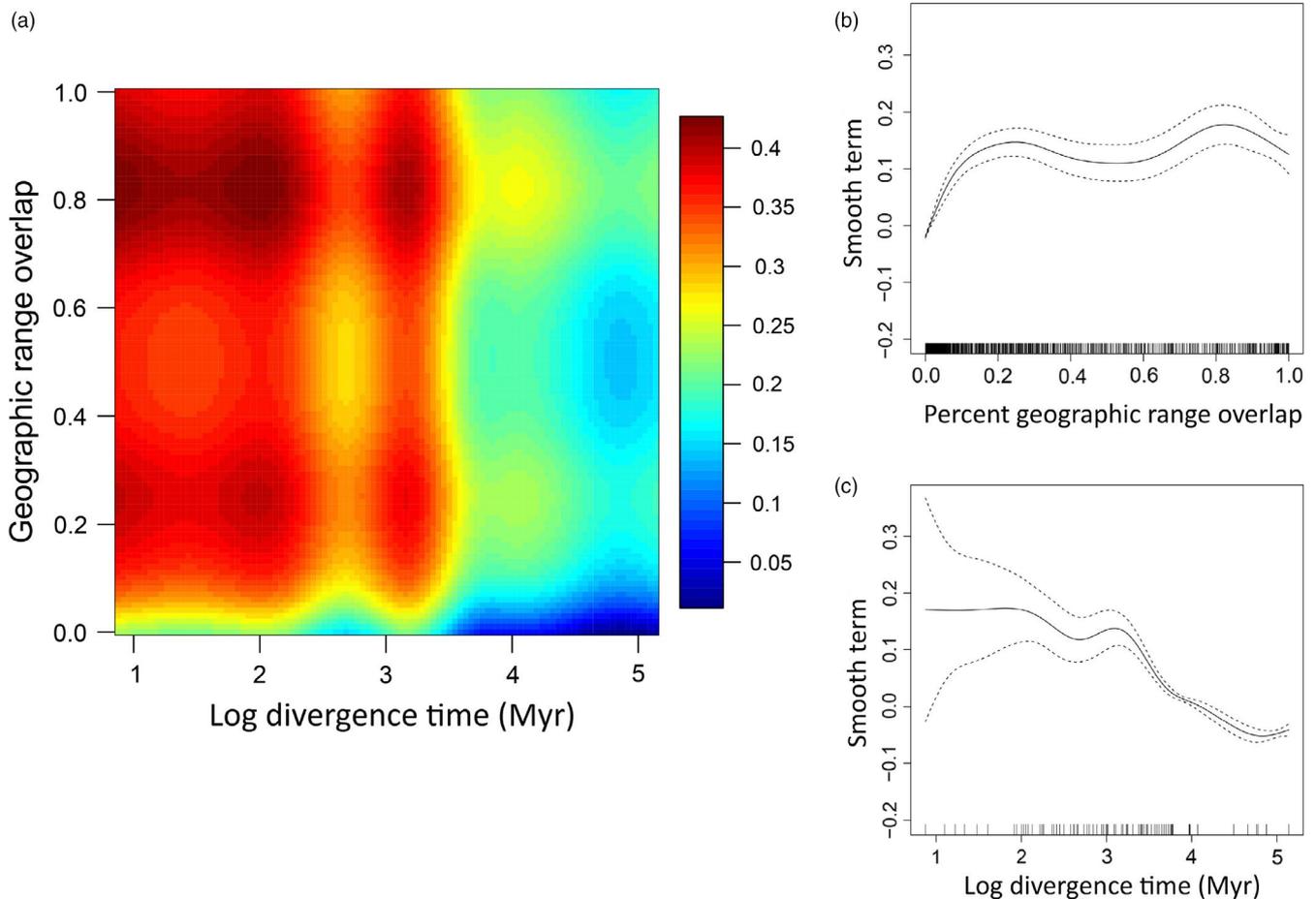


FIGURE 2 GAM model of the effects of phylogenetic distance and range overlap on corrected Jaccard's measure of parasite sharing. (a) Prediction of corrected Jaccard values, indicated by the color gradient, were generated based on a simple GAM including time since divergence (log transformed, in million years) and (proportional) geographical range overlap, both of which were sampled 100 times with equal intervals within the data ranges of the full dataset. Data were plotted using the R package “fields” (Furrer, Nychka, & Sain, 2009). (b) Component smooth functions for GAM model plotted on the scale of percentage of geographical range overlap. (c) Component smooth functions for GAM model plotted on the scale of phylogenetic distance separating pairs of host species. GAM: generalized additive model

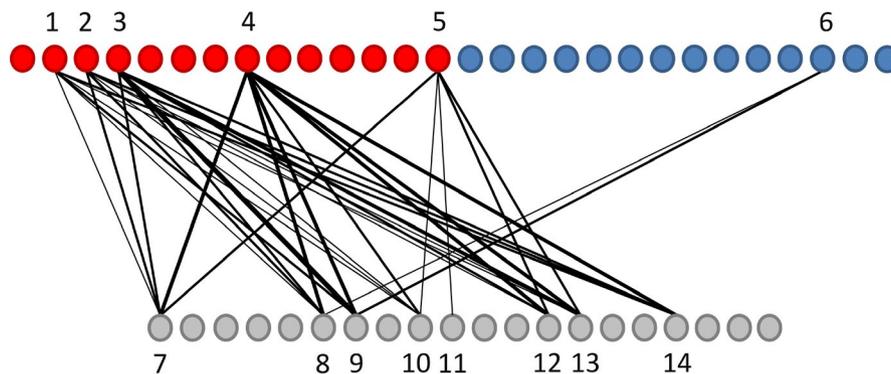


FIGURE 3 Helminth sharing between carnivores and ungulates. Shown here are data from the representative carnivore family Canidae and the ungulate family Cervidae (sensu lato). Black lines link cervid-canid pairs that share at least one helminth species, and numbers indicate the identity of species involved in these links: 1. *Canis aureus*, 2. *Canis latrans*, 3. *Canis lupus*, 4. *Lycalopex culpaeus*, 5. *Vulpes vulpes*, 6. *Vulpes lagopus*, 7. *Alces alces*, 8. *Capreolus capreolus*, 9. *Cervus elpahus*, 10. *Cervus nippon*, 11. *Dama dama*, 12. *Odocoileus virginianus*, 13. *Odocoileus hemionus*, 14. *Rangifer tarandus*. The thickness of the lines represents the number of helminth species shared in common, which varies from one to four. Red circles indicate canids that have been reported to prey on ungulates in at least some parts of their range, blue circles indicate species that have not been reported to prey on ungulates, and grey circles indicate cervids

Group	Raw data			Residuals to WOS citations		
	Mean 0	Mean 1	p-Value	Mean 0	Mean 1	p-Value
All parasites	3.59	8.85	0.004	-0.338	0.802	0.269
Viruses	1.39	1.81	0.152	-0.052	0.082	0.617
Bacteria	2.96	3.19	0.803	0.246	-0.269	0.390
Protozoa	1.34	1.46	0.630	0.070	-0.101	0.382
Helminths	1.00	2.93	0.005	-0.299	0.481	0.035
Arthropods	1.45	3.24	0.047	-0.161	0.361	0.425

GAM: generalized additive model; WOS: Web of Science.

Bold values indicates statistical significance at $\alpha = 0.05$.

host groups (ungulates and carnivores) showed that, for helminth parasites, trophic links do seem to be important in explaining the composition of parasite communities (Table 2). This study further investigated the effects of sampling bias on the ability to detect predictors of parasite sharing between species. Although sampling effort appears to influence parasite sharing measures, accounting for sampling effort did not qualitatively change support for biological factors drive patterns of sharing.

Both host geographical range overlap and phylogenetic similarity showed evidence for nonlinear relationships with parasite sharing (Figure 2B,C, Figures S2 and S3), and their relative importance differed among parasite sub-groups (Figure 1). Ungulates with any range overlap at all are much more likely to share parasites than those that do not overlap in range, but further range overlap does not lead to further increases in parasite sharing. One possibility is that parasites often occur throughout most of the range of hosts they infect. If most parasites only inhabited a limited subset of the range of their hosts we would expect greater range overlap to provide more transmission opportunities, and this does not appear to be the case. This would also explain why all three measures of geographical range overlap exhibited similar correlations with parasite sharing, a result consistent with past work on parasite sharing in primates (Davies & Pedersen, 2008). Similarly, parasite sharing decreased nonlinearly with host phylogenetic distances; this effect was less important for closely related hosts, and became more important beyond a threshold of relatedness both overall (Figure 2) and in most parasite groups (Figure S3). This could indicate that key biological traits not examined here (e.g., immunological, cellular, molecular) might be similar for closely related hosts, scale with phylogenetic distance, and strongly influence the ability of parasites to successfully infect more distantly host species.

Our analyses also considered the influence of host biological and ecological similarity on parasite sharing, which we quantified both as differences in adult body mass between species and distances in multivariate trait space. Past work showed that host ecological similarity predicted greater parasite sharing in both primates (Cooper et al., 2012) and carnivores (Huang et al., 2014). In ungulates, trait dissimilarity showed a similar directional relationship, but it was much weaker than reported for primates or carnivores. Two possible explanations for this difference might be that ungulates show less divergence in biological traits than

TABLE 2 ANOVA analysis for the number of ungulate parasites infecting carnivore species that have been reported (1) and have not been reported (0) to feed on ungulates. "Residuals" refers residuals of a GAM of parasite richness versus host WOS citation counts used to account for variation in study effort (see Materials and Methods)

other mammal groups, or that variation in other factors not considered here (such as environmental temperature or rainfall regimes) are more important predictors of ungulate parasite sharing. Somewhat surprisingly, parasite sharing was greater for host species that were more dissimilar in body mass (Table S3, Figure S4), though this effect was relatively weak in analyses of combined data (Table 1, Table S1). This pattern might be due to ungulates with differing body masses showing a greater tendency to coexist locally due to feeding on different resources. We investigated this post hoc hypothesis by testing whether species with differing body masses were more likely to show range overlap than species with similar masses. Body mass difference was regressed against geographical range overlap using Spearman's rank. As predicted, species of different body sizes tended to have greater range overlap than those of similar sizes ($\rho = 0.069$, p -value < 0.0001), and the strength of the correlation was similar to that observed between mass difference and parasite sharing (Table S1).

The relative influence of different predictors also varied widely among parasite groups. For example, range overlap was by far the strongest predictor of arthropod sharing, nearly to the exclusion of other factors in the case of BRT analyses (Figure 1). This may be related to the fact that many of the arthropods included in our data are environmentally transmitted ectoparasites such as ticks. However the factors driving this and other differences observed among parasite groups clearly warrant further investigation. The diversity of parasites included in our data also varied considerably among parasite groups, ranging from 67 species of viruses to 361 species of helminths, but this does not seem to have unduly influenced the outcome of our analyses. For example, if the high number of helminth species was a strong source of bias, we would have expected the results from pooled analyses that included all parasites to resemble those in helminths. Yet, in helminths, differences in host body mass had the strongest influence on patterns of overlap, whereas for all parasites combined, body mass had the least influence. Moreover, even in the sub-group with the smallest number of parasite species (viruses), boosted regression tree analyses were based on comparison of 1,880 host-species pairs. Taken together, these observations suggest that biologically meaningful differences in the ecology and transmission dynamics of various parasite groups influence parasite sharing among hosts, a prediction that could be explored in future work.

Like most previous studies of parasite sharing (e.g., Cooper et al., 2012; Davies & Pedersen, 2008; Huang et al., 2014), to maximize data included in analyses, we did not distinguish between parasites detected using different methods (e.g., presence based on visual observation or microscopy, PCR detection of parasite genetic material, or inference of host exposure based on antibody presence). Although we acknowledge that some detection methods are more or less sensitive, offer differential ability for parasite taxonomic resolution, and provide different information on active infection versus prior exposure, we assume that all methods provide evidence that a given parasite does infect a given host species at least occasionally. Because not all detected parasites are capable of reproducing in a given host species, we acknowledge that a subset of the hosts-parasite associations included in our study might represent dead ends for transmission.

Our analysis is one of the first to test whether trophic links might be important in allowing parasites beyond those with known trophic transmission to be shared among relatively distantly related species. Trophically-transmitted parasites that use phylogenetically distant animals as intermediate versus definitive hosts are well known to have crucial importance in food web connectance and for host population and community ecology (Lafferty et al., 2006; Thielges et al., 2013). Some foodborne illnesses transmitted through the consumption of animal tissue could also be considered a form of trophic transmission, and have been well studied in humans and other species (Scallan et al., 2011; Tauxe, 1997). More generally, trophic links might cause a wide spectrum of parasites, beyond these traditionally recognized groups, to be shared across distantly related hosts.

Results here showed that some carnivores that feed on wild ungulates did have more known ungulate parasites based on analyses of raw parasite richness, although most of these patterns disappeared when accounting for uneven sampling effort. The differences seen in the raw data likely reflect the fact that carnivores that feed on ungulates are often better studied than other species, and so more parasites are known in those species overall. Supporting this explanation is the fact that overall parasite richness in carnivores found in the GMPD is highly correlated with ungulate parasite richness (spearman's $\rho = 0.877$, $p < 0.0001$). The one exception was helminths, which showed significant correlations when controlling for uneven sampling effort. Our results were also qualitatively identical regardless of whether we used binary coding or three category coding of carnivores (i.e., distinguishing between species that prey upon ungulates only rarely and those for which ungulates are a consistent prey item, Table S5), perhaps indicating that the intensity of predation has little impact on the potential for trophic transmission. It is possible that predation infrequent with respect to the behaviour of most individuals might represent a relatively stable connection in terms of community dynamics, but this and other possible explanations require further investigation. Helminth links between carnivore and ungulate hosts appear to be driven by a subset of host species (e.g., Figure 3), and might also have been driven by parasites such as cestodes and trematodes with complex life cycles and trophic transmission, although we did not isolate parasites by

transmission mode in this study. We also did not attempt to group host species by region or to link individual ungulate species prey to particular carnivore species predators. The importance of parasite transmission mode and distinct predator-prey linkages are important questions for future studies, and potentially of crucial importance as the range of helminths of wildlife, domestic animals, and humans are expanding rapidly in response to climate change and globalization (e.g., Davidson, Romig, Jenkins, Tryland, & Robertson, 2012; Jenkins, Schurer, & Gesy, 2011; Jenkins et al., 2013). Results here suggest that further work is needed to examine how trophic links and other direct ecological interactions between hosts could serve as an avenue for parasite transmission among distantly related species, particularly using more geographically and ecologically explicit analyses.

Many past studies of parasite richness showed that better studied host species have more parasite species reported to infect them (e.g., Ezenwa et al., 2006; Huang et al., 2015; Nunn et al., 2003), and in our analyses of carnivores, we used a similar protocol to that of previous studies to account for variation in sampling effort. However, our results also showed, for the first time, that uneven sampling effort also affects measures of parasite overlap among hosts, with better studied host species pairs having greater estimated parasite sharing. We utilized two very different strategies for dealing with this issue. In some analyses, we used study effort as a covariate together with biological predictors, and in others as a weighting factor. The first method treats sampling effort as a source of bias that we account for in much the same way that some studies of the relationship between continuous traits account for variation in body mass among species or individuals (e.g., Christians, 1999; Clarke & Johnston, 1999). The latter method acknowledges that better studied species are likely more accurately characterized, and tests whether the apparent importance of various biological factors changes when we down-weight data from pairs of poorly-studied species compared to well-studied species. Similar findings for these two different approaches (Table S1, Table 1, and Figure 1a) suggest that our results with respect to biological predictors are robust, and that past studies of parasite sharing which did not explicitly consider sampling effort may not have been unduly biased. However, we also suggest that future studies of parasite sharing should take into account variation in study effort among host species pairs owing to the high heterogeneity in study effort among wild hosts.

Our results have implications for ungulate conservation and management. According to the IUCN, nearly 50% of wild ungulate species are vulnerable or endangered (Schipper et al., 2008), and parasites are a source of threat to a larger proportion of ungulates relative to other mammalian groups (Pedersen, Jones, Nunn, & Altizer, 2007). Given the wide global distribution of domestic ungulates, it seems likely that most wild ungulate species have at least some contact or spatial proximity to domestic species such as pigs, cattle, and sheep. Our results suggest that for species of conservation concern, those that are also close relatives of domestic species, such as the critically endangered pygmy hog (*Porcula salvania*) and Saola (*Pseudoryx nghetinhensis*), could be more susceptible to

disease emergence from such contacts. Conversely, wild ungulates are an important source of livestock pathogens (Cleaveland et al., 2001; Martin, Pastoret, Brochier, Humblet, & Saegerman, 2011; VanderWaal, Atwill, Isbell, & McCowan, 2014). Overall, in our analyses, geographical range overlap exceeds any other biological consideration in explaining patterns of parasite sharing among ungulates (Table 1). Our results indicate that regardless of their phylogenetic relationships or ecological characteristics, widespread species, such as white-tailed deer (*Odocoileus virginianus*) or red deer (*Cervus elaphus*), should be a particular focus of disease surveillance efforts.

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AUTHORS' CONTRIBUTIONS

P.R.S. designed the study and wrote first drafts of the manuscript. P.R.S., E.M., B.H., S.H., and P.P. collected data and performed statistical analyses. All authors contributed to manuscript preparation and editing, and gave final approval for submission.

DATA ACCESSIBILITY

Data used in this study are available from Stephens et al. (2017).

ORCID

Patrick R. Stephens  <https://orcid.org/0000-0003-1995-5715>

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