RESEARCH ARTICLE

Species-level drivers of mammalian ectoparasite faunas

Wesley Dáttilo[1] | Nathalia Barrozo-Chávez[2] | Andrés Lira-Noriega[3] | Roger Guevara[4] | Fabricio Villalobos[4] | Diego Santiago-Alarcon[5] | Frederico Siqueira Neves[6] | Thiago Izzo[7] | Sérvio Pontes Ribeiro[8]

[1]Red de Ecoetología, Instituto de Ecología A.C., Xalapa, Mexico; [2]Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Federal de Mato Grosso, Cuiabá, Brazil; [3]Instituto de Ecología A.C., CONACyT, Xalapa, Mexico; [4]Red de Biología Evolutiva, Instituto de Ecología A.C., Xalapa, Mexico; [5]Red de Biología y Conservación de Vertebrados, Instituto de Ecología A.C., Xalapa, Mexico; [6]Departamento de Genética, Ecología e Evoluçã, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil; [7]Universidade Federal de Mato Grosso, Cuiabá, Brazil and [8]Laboratório de Ecohealth, Ecologia de Insetos de Dossel e Sucessão Natural, Universidade Federal de Ouro Preto, Ouro Preto, Brazil

Correspondence
Wesley Dáttilo
Email: wdattilo@hotmail.com; wesley.dattilo@inecol.mx

Handling Editor: Jenny Dunn

Abstract

1. Traditionally, most studies have described the organization of host–parasite interaction networks by considering only few host groups at limited geographical extents. However, host–parasite relationships are merged within different taxonomic groups and factors shaping these interactions likely differ between host and parasite groups, making group-level differences important to better understand the ecological and evolutionary dynamics of these interactive communities.

2. Here we used a dataset of 629 ectoparasite species and 251 species of terrestrial mammals, comprising 10 orders distributed across the Nearctic and Neotropical regions of Mexico to assess the species-level drivers of mammalian ectoparasite faunas. Specifically, we evaluated whether body weight, geographical range size and within-range mammal species richness (i.e. diversity field) predict mammal ectoparasite species richness (i.e. degree centrality) and their closeness centrality within the mammal–ectoparasite network. In addition, we also tested if the observed patterns differ among mammal orders and if taxonomic closely related host mammals could more likely share the same set of ectoparasites.

3. We found that ectoparasite species richness of small mammals (mainly rodents) with large proportional range sizes was high compared to large-bodied mammals, whereas the diversity field of mammals had no predictive value (except for bats). We also observed that taxonomic proximity was a main determinant of the probability to share ectoparasite species. Specifically, the probability to share ectoparasites in congeneric species reached up to 90% and decreased exponentially as the taxonomic distance increased.

4. Further, we also detected that some ectoparasites are generalists and capable to infect mammalian species across different orders and that rodents have a remarkable role in the network structure, being closely connected to many other taxa.

5. Hence, because many rodent species have synanthropic habits they could act as undesired reservoirs of disease agents for humans and urban animals. Considering the reported worldwide phenomenon of the proliferation of rodents accompanying

1 | INTRODUCTION

Mammals are one of the best-studied groups of terrestrial vertebrates (Jones & Safi, 2011). Because of homeothermy and their increased metabolism during periods of activity, mammalian bodies are excellent habitats for many different groups of parasites (Gregory, Keymer, & Harvey, 1996; Morand & Harvey, 2000). Nonetheless, a diverse array of factors and their interactions are determinants of successful ectoparasite–mammal relationships (Kamiya, O'Dwyer, Nakagawa, & Poulin, 2014; Owen, Waite, Holden, & Clayton, 2014). For instance, mammals have developed different mechanisms to avoid or reduce ectoparasite attacks and infections (e.g. host tolerance and immunological responses) that have shaped the evolution of host specificity (Combes, 2001; McAuliffe, 2016). In this host–parasite evolutionary arms race, ectoparasites have also evolved different strategies to maximize their encounters with their mammal hosts (e.g. straggling, phoresy, tolerance and surviving for a long time in extreme environmental conditions (DiBlasi et al., 2018; Whiteman, Santiago-Alarcon, Johnson, & Parker, 2004), turning parasites into a divergent selection force that ultimately can cause ecological speciation (Karvonen & Seehausen, 2012).

Concerning host traits, large-bodied mammals are expected to provide greater opportunities (i.e. surface area and complexity) for colonization by ectoparasites than small-bodied mammals (Esser et al., 2016; Krasnov, Shenbrot, Khokhlova, & Degen, 2004; Poulin, 2004, 2007; but see Poulin, Krasnov, Mouillot, & Thieltges, 2011). On the other hand, generally small-bodied animals are more abundant and live in denser populations than large-bodied animals, which facilities the horizontal transmission of parasites (Morand & Harvey, 2000; Morand, Krasnov, & Poulin, 2007; Nunn, Altizer, Jones, & Sechrest, 2003). However, it seems that host body mass and density may operate mainly at small spatial scales (i.e. local levels; Krasnov, Khokhlova, Shenbrot, & Poulin, 2008). Thus, when analyzed at the community level, the identified patterns tend to be highly contingent on the system under study, rendering no general patterns across parasite groups (Poulin, 2007).

Mammals have evolved at least since the late Cretaceous period, after which mammals underwent an adaptive radiation associated with phenotypic diversification, resulting in a wide variety of body shapes and sizes distributed worldwide (Bininda-Emonds et al., 2007; Raia et al., 2013). In this context, mammals with larger bodies are expected to offer more space and niches for ectoparasites, which will likely support higher parasite species richness (Ezenwa,

Price, Altizer, Vitone, & Cook, 2006). Furthermore, mammals with large geographical ranges may occupy many different habitats and tolerate a wide range of environmental conditions (Olalla-Tárraga, Torres-Romero, Amado, & Martínez, 2015; Slatyer, Hirst, & Sexton, 2013). Therefore, it is expected that these widely distributed mammals could be in contact with more parasite species, leading to an increase in their accumulated parasite richness per host species, regardless body size, as predicted by the niche breadth hypothesis (Bordes, Morand, Kelt, & Van Vuren, 2009; Krasnov et al., 2010; Krasnov, Poulin, Shenbrot, Mouillot, & Khokhlova, 2005; Lindenfors et al., 2007). At the same time, the accumulation of ectoparasites would be optimized if host mammal species occur in species-rich regions, where high co-occurrence of mammals could favor parasite transmission among different groups of species, resulting in a positive association between mammal co-occurrence and ectoparasite richness (Krasnov, Poulin, & Mouillot, 2011; Poulin, Guilhaumon, Randhawa, Luque, & Mouillot, 2011). Alternatively, mammals with large geographical ranges could also occur across parasite species-poor areas and consequently be associated with only few parasite species over ecological or evolutionary time. Therefore, processes operating at the large scale of species geographical distribution (e.g. allopatric and sympatric speciation, expansion and contraction) can also be important for explaining the association patterns between mammals and ectoparasites that we observe nowadays (Krasnov et al., 2011; Poulin, 2004), particularly when mammals and ectoparasites with different life history strategies are considered together (Krasnov et al., 2010).

In general, mammal–ectoparasite interactions present some evidence of specificity (Combes, 2001; Dick, 2007; Møller, Christe, & Garamszegi, 2005) as a result of different factors, from deterministic (e.g. niche-based assembly and environmental responses) to stochastic (e.g. neutral-based assembly, dispersal) and historical (e.g. geographical barriers, evolutionary diversification) processes that determine these interactions (Clayton, Bush, & Johnson, 2004; Harbison & Clayton, 2011; Thompson, 1994). Moreover, it is well known that co-evolutionary processes between parasites and hosts can promote the increase in similarity of parasitic faunas between taxonomically related hosts (Byers, Schmidt, Pappalardo, Haas, & Stephens, 2019; Hafner & Nadler, 1988; Owen et al., 2014; Poulin, 2010a). This is because phylogenetically closely related hosts tend to be more similar in their ecological, physiological, or immunological traits than phylogenetically distant host species (Krasnov et al., 2010; Poulin, 2010a; Woolhouse, Haydon, & Antia, 2005). Therefore, it is

expected that ectoparasites could best exploit closely related hosts in a similar way, despite similarities or differences of host ecological traits (e.g. population density, biogeographical distribution; Poulin, Krasnov, et al., 2011).

Recently, host–parasite relationships have been investigated using an interaction network approach (Bellay et al., 2018; Poulin, 2010b). Traditionally, most studies have described the organization of parasite–host networks by considering only a few host groups (e.g. rodent–parasite, fish–parasite or bat–parasite networks) at small geographical extents (Canard et al., 2014; Fagundes, Antonini, & Aguiar, 2017; Lima Jr., Giacomini, Takemoto, Agostinho, & Bini, 2012; but see Dallas et al., 2019). This is probably due to the difficulty of sampling different taxonomic groups in the field, which translates into less data being available in the literature, further complicating data compilation and synthesis across taxa and regions (Dallas, Huang, Nunn, Park, & Drake, 2017). However, host–parasite interactions involve different taxonomic groups, and factors shaping these antagonistic relationships likely differ among host and parasite groups, making group-level differences relevant for the full network across different taxonomic groups (Pilosof, Morand, Krasnov, & Nunn, 2015). Thus, studying host–parasite relationships involving many taxonomic groups (i.e. multi-host networks) can help identifying those host species that could play an important role in the dispersal of parasites among host species (i.e. higher centrality in the network) in a more integrative way (Lafferty et al., 2008; Pilosof et al., 2015; Vázquez et al., 2007; Vázquez, Poulin, Krasnov, & Shenbrot, 2005).

Here, we evaluated whether body weight, geographical range size and within-range mammal species richness (i.e. diversity field) predict mammal ectoparasite species richness and their centrality within the mammal–ectoparasite network over a broad spatial scale, and also if observed patterns differ among mammalian orders. In addition, we also tested if taxonomically closely related host mammals are more likely share the 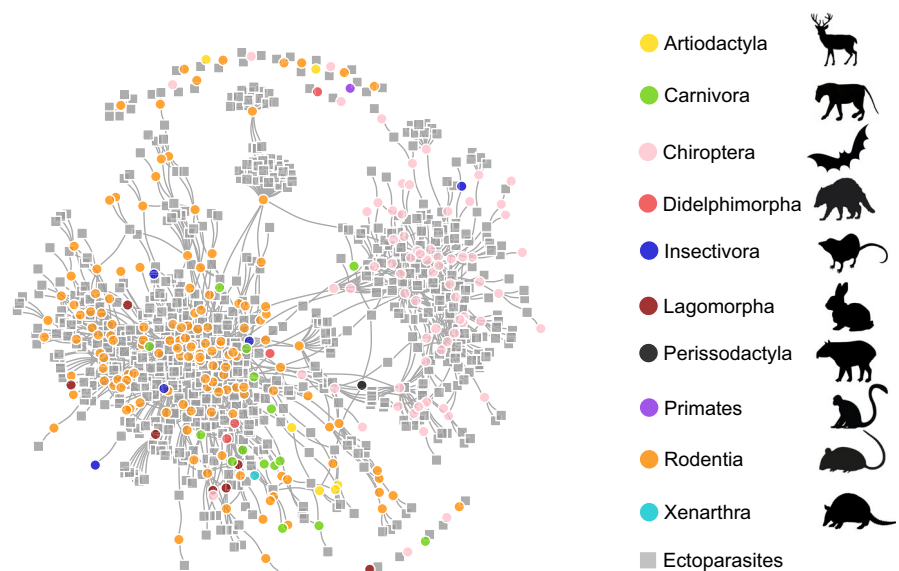same set of ectoparasites. For this, we used a dataset compiling 53 years (between 1950 and 2003) of information on 629 species of ectoparasites interacting with 251 species of terrestrial mammals, comprising 10 orders distributed across the Nearctic and Neotropical regions of Mexico. This study is a contribution towards understanding the determinants of ectoparasite species distributions on mammal species, combining a unique dataset to assess the patterns that emerge at a large spatial scale.

2 | MATERIALS AND METHODS

2.1 | Dataset

We used an extensive and robust dataset on the interactions between mammals of Mexico and their associated ectoparasites compiled between 1950 and 2003 by Whitaker Jr. and Morales-Malacara (2005), who corrected taxonomic mistakes, synonyms, and provided new taxonomic status following several studies. To standardize the pairs of interactions across all species, we used only those records identified at the species level for both mammals and ectoparasites, providing a total of 1,694 pairwise interactions between 251 mammal species and 629 ectoparasite species. The mammals included 10 orders: Artiodactyla (n = 6 species), Carnivora (n = 15 species), Chiroptera (n = 71 species), Didelphimorphia (n = 4 species), Insectivora (n = 5 species), Lagomorpha (n = 7 species), Perissodactyla (n = 1 species), Primates (n = 1 species), Rodentia (n = 139 species) and Xenarthra (n = 2 species), representing 44.3% of all mammals occurring in Mexico (~542 spp., according to Álvarez-Castañeda, Alvarez, & González-Ruiz, 2017). Ectoparasites belonged to seven superorders and orders: Acariformes (n = 18 mite species, n = 277 chiggers species), Coleoptera (n = 6 species), Diptera (n = 47 species), Hemiptera (n = 2 species), Ixodida (n = 37 species), Phthiraptera (n = 81 chewing lice species, n = 37 sucking lice species) and Siphonaptera (n = 124 species; Figure 1). Additionally, we also

FIGURE 1 A multi-interaction network involving 1,694 interactions between 251 mammal species and 629 ectoparasite species compiled from 1950 to 2003 in Mexico. Each node represents either a mammal species (indicated in colors at the order level) or an ectoparasite species (grey squares), and lines represent mammal–ectoparasite interactions

Legend:
- Artiodactyla
- Carnivora
- Chiroptera
- Didelphimorpha
- Insectivora
- Lagomorpha
- Perissodactyla
- Primates
- Rodentia
- Xenarthra
- Ectoparasites

compiled from the literature the mean body mass (kg) of each mammal species according to Ceballos and Oliva (2005).

2.2 | Geographical range size and co-occurrence of mammal species

For each mammal species, we described its range size within Mexico and the degree of co-occurrence with other mammal species by means of its diversity field (Arita, Christen, Rodríguez, & Soberón, 2008; Villalobos & Arita, 2010). We first obtained the distributional ranges (extents of occurrence maps within Mexico) of all mammals from CONABIO (Mexican National Commission for Knowledge and Use of Biodiversity; http://www.conabio.gob.mx/informacion/gis/). Then, we overlaid a grid of 0.5° × 0.5° cells into these maps to build a presence–absence matrix of mammals within the country. The range size of each mammal species was defined as its proportional range size, calculated as the fraction of occupied cells relative to the total within the Mexican territory. Later, we described the species-level co-occurrence patterns among mammals by calculating the diversity field of each species (Arita et al., 2008; Villalobos & Arita, 2010) as the mean number of other mammal species that co-occur within its range (i.e. occupied cells; Villalobos, Rangel, & Diniz-Filho, 2013). A species' diversity field characterizes the assemblages occupied throughout its range, thus reflecting its tendency to occur in species-rich or species-poor regions (Villalobos et al., 2013). Due to the lack of available information on the distribution of 29 species, proportional range sizes and diversity fields were only calculated for 222 species (over 88% of the 251 species in our matrix).

2.3 | Centrality in the mammal–ectoparasite interaction network

We built a 251 (*i*, mammals) by 629 (*j*, ectoparasites) binary interaction matrix (***A***), where A_{ij} = 1 represents an extant interaction between the *i* mammal species and the *j* ectoparasite species. Non-existing interactions were coded as zero. We then drew the network as an energy two-mode graph (Kamada–Kawai free method) obtained using the IGRAPH package in R. This layout method was set to optimize the position of each node separately, displaying the species according to their number of links and how they interact with other components in the network.

For each mammal species, we also calculated the closeness centrality (CC) to measure species importance in the network. CC scores range from 0 to 1, and a mammal species is central in the network when it has a high CC value. We calculated CC using the BIPARTITE package in R (Dormann, Fründ, Blüthgen, & Gruber, 2009). Note that ectoparasite species richness is also a centrality estimate (i.e. degree centrality), defined as the number of links incident upon a host species (i.e. the number of ties that a host species has). In some cases, CC and degree centrality (ectoparasite species richness)

are typically collinear, and consequently are dependent upon each other. However, we did not find collinearity between degree centrality and CC since the variance inflation factor (VIF) value was low (VIF = 1.41), indicating that both measures are complementary in our study. This is because while degree centrality is a simple count of the total number of connections linked to a given mammal species, CC measures how closely a mammal species is connected to other mammal species in the network based on the shortest paths of the ectoparasite species shared between them. Importantly, although there was a low connectance in our network due to the high number of species with a single interaction, these species have a low impact on the overall network structure because after their exclusion the network descriptors did not change strongly. Connectance: total network = 0.0107, without singletons: 0.0188; linkage density: total network = 10.81, without singletons: 10.59; links per species: total network = 1.92, without singletons: 2.52.

2.4 | Mammal taxonomic distance and probability of sharing ectoparasites

We calculated the probability of sharing ectoparasites between mammal species based on their taxonomic distance following Gilbert Magarey Suiter and Webb (2012). We used taxonomic distances instead of phylogenetic distances between mammals mainly because no robust phylogeny including all Mexican mammals is yet available and the most comprehensive species-level phylogeny of the whole class (Bininda-Emonds et al., 2007) has low resolution particularly for rodents, the largest group in our dataset. Mammal taxonomic distance was estimated by first assigning all mammal species into hierarchically organized taxonomic nodes using the Integrated Taxonomic Information System (http://www.itis.gov; a partnership of U.S., Canadian, and Mexican agencies and taxonomic specialists). We considered nine taxonomic levels: kingdom, subkingdom, phylum, class, subclass, order, family, genus and species, which provide enough resolution to compare between pairs of species (Bellay, Lima, Takemoto, & Luque, 2011; Cagnolo, Salvo, & Valladares, 2011; Naisbit, Rohr, Rossberg, Kehrli, & Bersier, 2012; Poulin & Mouillot, 2003).

Within our mammal–ectoparasite interaction network we dropped ectoparasite species with a single interaction from analyses because of a high uncertainty of prediction for nodes with too low incidences. Thus, matrix ***A*** included 251 mammal species and 199 ectoparasite species. Based on this matrix ***A***, each mammal species (*i*, row in ***A***) was considered as the source of the j_s parasites connected to it and the source for a random sample of the other hosts to calculate the coefficients of the logistic regression using the taxonomic distance (number of taxonomic levels that that separates them) between hosts as the predictor variable, and those coefficients were then used to calculate the probability of a host getting infected by the ectoparasites. This analysis was performed using the package GEOTAX for R (Robles-Fernández & Lira-Noriega, 2017).

2.5 | Data analysis

We used GLMs to test if (a) the ectoparasite species richness and (b) CC (dependent variables) differed between mammal orders (independent variable). For both models, model assumptions were tested through residual analysis. When significant differences were observed, we performed contrast analyses to determine differences between pairs of mammal orders (Crawley, 2013). For residual and contrast analyses we used the RT4BIO package in R (Reis Jr., Oliveira, & Borges, 2015). Note that these analyses included those orders with at least five species (replicates), thus Primates, Perissodactyla and Xenarthra were excluded.

Then, we fitted generalized additive mixed models (GAMMs) including smoothing functions to explore the relationships between ectoparasite richness as a function of body weight, proportional range size (at the scale of Mexico), and the diversity field. We used the MGCV package in R (Wood, 2015) to fit all GAMM models. Mammal species within each order were added as a random factor. To fit the model, we transformed the three predictor variables as follow: the body weight was transformed with the natural logarithm, and the proportional range size and the diversity field, whose values range between asymptotic limits were transformed with the natural logarithm of their reciprocal values. We also fitted generalized additive models (GAMs) only to Rodentia and Chiroptera (together and separately) due to their disproportionately higher number of species in our dataset. It is

important to note that we performed centrality calculation for all 251 species in our dataset but the models were only estimated for those 222 species for which proportional range size and diversity field estimates were available. In the case of ectoparasite richness, the model was fitted following a negative binomial distribution with the logarithmic link function and theta (defined initially as the overall mean of ectoparasite richness, and iteratively updated with the function *gamm*) considering the high number of species with few interactions and potential overdispersion in the data. For CC, we used gamma distribution with squared root as link function due its flexibility with regards to not normally distributed data (i.e. its density can assume a wide variety of shapes). In addition, one of the main characteristics of the gamma probabilistic distribution is that the variance increases with the mean, which closely suits the fact that the higher the centrality of a given species, the higher is the variation of the impact of that species over the estimates of the metric all over the network. High centrality values are expected to be associated to high variability on the estimates of the metric over the whole network if links were randomly dropped to estimate standard errors (see Figure 2d). Note that, we checked if there was collinearity among our predictor variables using the VIF and found that VIF values were low (<1.5); therefore, collinearity was not a problem in our study (Appendix S1). The R codes used for data analysis are available to the reader on Zenodo (see Data Accessibility Statement for more information).
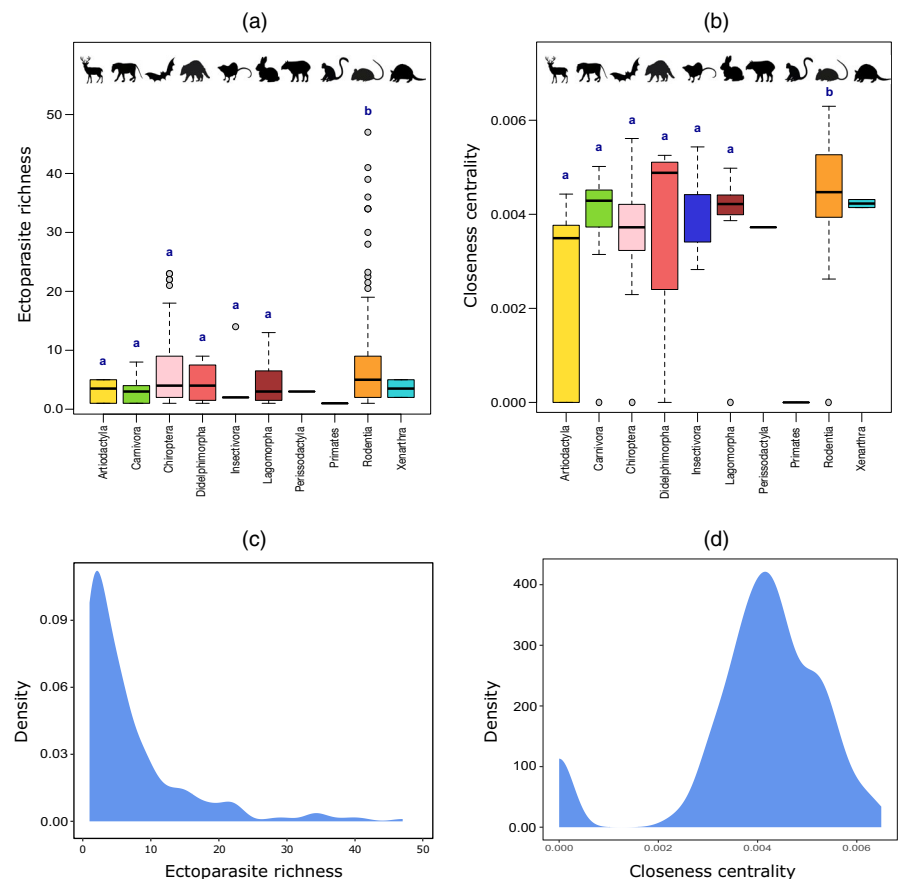

FIGURE 2 Values of (a) richness of ectoparasites associated and (b) closeness centrality (CC) observed between different mammal orders in Mexico. Boxplots sharing the same case letters are not significantly different according to contrast analysis. The distribution density of (c) ectoparasite richness and (d) CC values is shown in the letters

3 | RESULTS

We found that the associated ectoparasite species richness (Figure 2a) and CC (Figure 2b) differed between mammal orders (richness: χ^2 = 19.15, df = 240, p < 0.001; centrality: F = 3.86, df = 240, p < 0.001). Rodentia showed the highest associated ectoparasite species richness (M ± SD: 8.02 ± 9.16; range: 1–47 species; χ^2 = 11.69, df = 245, p < 0.001) and CC (M ± SD: 0.003 ± 0.001; range: 0–0.006; F = 17.89, df = 245, p < 0.001). All other mammal orders did not differ either in ectoparasite richness and CC (all p > 0.05). Of the 10 species with the highest ectoparasite richness, nine were Rodentia and one Chiroptera. For CC, the first 10 species with the highest values were represented exclusively by Rodentia.

For species richness of ectoparasites the GAMM accounted for 40% of the total deviance with significant smoothing terms for body weight (F = 7.14, p < 0.001), including all mammal orders and also Chiroptera and Rodentia together (41% of the total deviance: F = 5.42, p < 0.001; Figure 3a,c). The same was true for the proportional range size for all mammal orders (F = 10.61, p < 0.001) and also for Chiroptera and Rodentia together (F = 14.81, p < 0.001), whereas for the diversity field the smoothing term was not significant in any case (F = 0.17, p = 0.14 and F = 0.01, p = 0.53). When we separated these two mammal orders, we found that body weight (F = 11.43, p < 0.001) and proportional range size (F = 18.91, p < 0.001) remained significant predictors of Rodentia ectoparasite richness (deviance explained: 53%). In the case of Chiroptera, only a higher proportional range size explained higher ectoparasite richness (deviance explained: 27%; F = 4.13, p < 0.001). In general, we observed that the ectoparasite richness increased with the proportional range size for small mammals as a whole and for Rodentia in particular. This was most evident for mammals between 30 and 200 g in which the number of species of ectoparasites increased sharply with proportional range size (Figure 3a). For CC the model accounted for 27% of the total deviance with significant smoothing terms for body weight including all mammal orders (F = 10.41, p < 0.001) and for Chiroptera and Rodentia together (40% of the total deviance: F = 12.06, p < 0.001; Figure 3b,d). For the proportional range size the same pattern was observed for all mammal orders (F = 13.45, p < 0.001) and for Chiroptera and Rodentia together (F = 19.16, p < 0.001). For diversity field, the smoothing term was not significant either for all mammal orders (F = 0.11, p = 0.73) or for Chiroptera and Rodentia together (F = 0.01, p = 0.96). When we separated these two dominant mammal orders, we found that body weight (F = 19.04, p < 0.001) and proportional range size (F = 18.11, p < 0.001) remained significant predictors of Rodentia
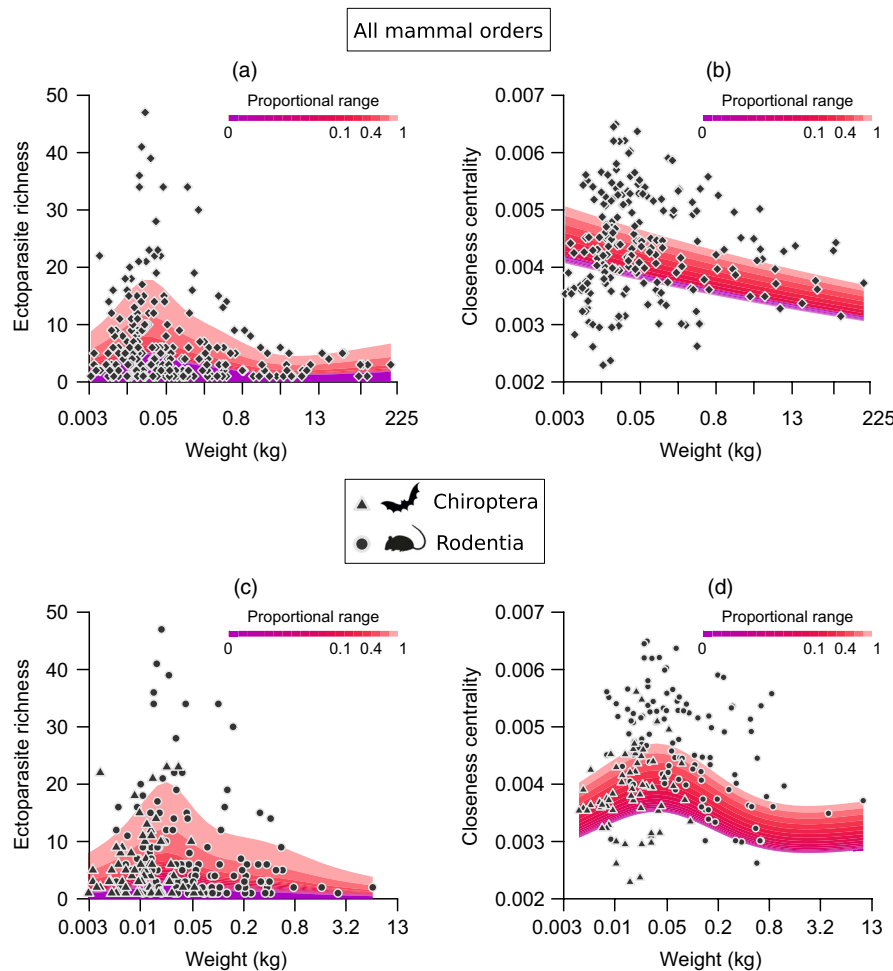

FIGURE 3 Generalized additive mixed model including smoothing function exploring the relationships between ectoparasite species richness and closeness centrality with the natural log of body weight and proportional geographical range. We fitted the models including all mammal orders (a, b) separately only to Rodentia and Chiroptera (c, d)

CC (deviance explained: 30%). For Chiroptera CC, we observed significant and positive effects of body weight ($F = 4.31$, $p = 0.04$), proportional range size ($F = 10.29$, $p < 0.001$) and diversity field ($F = 4.44$, $p = 0.03$; deviance explained: 13%).

Hence, the models described an increase of CC for mammal species with low body weight and large proportional range size (Figure 3b), also observed for ectoparasite richness (except for Chiroptera). We also explored these same relationships between ectoparasite species richness and CC with body weight and proportional range size without the outlier species of Chiroptera and Rodendia (based on the Cook's distance) and found the same results.

3.1 | Mammal taxonomic distance and probability of sharing ectoparasites

We observed that large taxonomic distances between pairs of species decreases sharply the probability of sharing ectoparasites between mammal species (Figure 4). In all cases (i.e. each ectoparasite species) the logistic regression coefficient was negative, also for the overall regression done with the random subsets (whole matrix analysis). More specifically, mammals of the same genus have 90% probability of sharing ectoparasites between them, whereas mammals of the same family have 43% probability, decreasing exponentially as taxonomic distance increases.
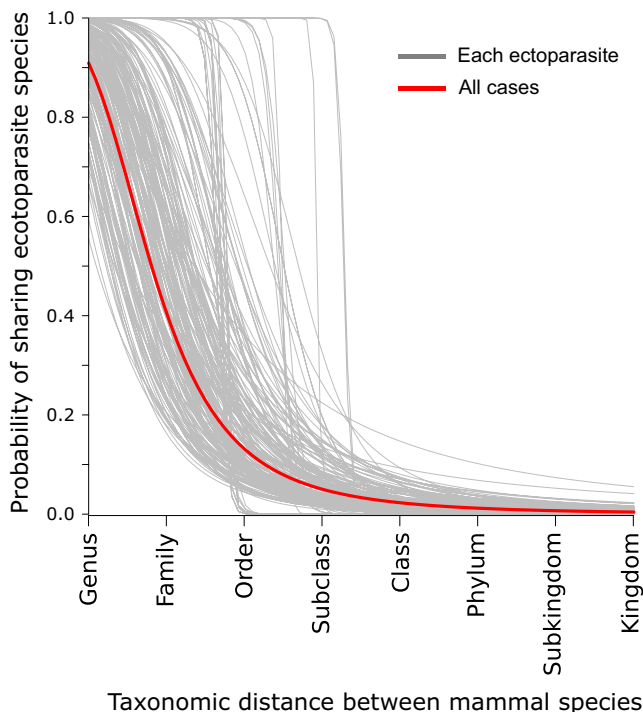

FIGURE 4 Relationship between the taxonomic distance between mammal species and their probability of sharing ectoparasite species. Lines are predicted from logistic regressions for each ectoparasite–mammal interaction (grey thin lines) and the best fit for all interactions together (red thick line)

4 | DISCUSSION

In this study we show that that body weight and proportional range size of terrestrial mammals throughout Mexico were good predictors of both ectoparasite species richness and host CC within the interaction network. More specifically, we found that mammals distributed over a large portion of the country had greater ectoparasite richness and exhibited higher interaction centrality within the mammal–ectoparasite network. Also, our results add further evidence to previous findings supporting taxonomic similarity as a major driver of the probability of sharing ectoparasites among pairs of mammal species. In our case, taxonomically close mammal species (in the same genus) were more likely to share ectoparasite species and the probability of sharing ectoparasites declined rapidly (two orders of magnitude) at the order level. Thus, our findings support host body weight and geographical range size as two general predictors of their parasite richness (Kamiya et al., 2014; Morand, 2015).

Many studies have shown that host population density and body mass influence the diversity of parasites at small spatial scales (Arneberg, Skorping, Grenfell, & Read, 1998; Esser et al., 2016; Morand & Poulin, 1998). Indeed, the probability of taking up a parasite in the population increases exponentially with the density of individuals and it can spread horizontally in the population through frequent contact among individuals (Stanko, Miklisová, de Bellocq, & Morand, 2002; see Medeiros, Ricklefs, Brawn, & Hamer, 2015 for an example on vector-borne parasites). Moreover, large animals with long life spans are exposed to parasite sources for longer periods of time and offer more micro-habitats for the parasites to live in than smaller hosts with high individual turnover (Bell & Burt, 1991; Poulin, 2007; Santiago-Alarcon, MacGregor-Fors, Kühnert, Segelbacher, & Schaefer, 2016). However, the association between parasite species richness and body weight can vary according to the host–parasite system under study (Poulin, Krasnov, et al., 2011). Here, we showed that mammals with small body weight and large range size across Mexico had higher ectoparasite richness and centrality within the complete mammal–ectoparasite interaction network. This could happen because small mammals tend to exhibit higher population densities, facilitating the dispersal of ectoparasites among them, particularly those with direct transmission life cycles (Poulin & Morand, 2004). Such negative effect of body size on ectoparasite richness was evident for mammals as a whole and separately for Rodentia, the most speciose group in our data. However, we did not observe the same effect for Chiroptera, the second most speciose group. In the case of Chiroptera, this could be related to the smaller range of bat body sizes compared to those of rodents and mammals within Mexico and specifically across the Neotropics (Arita, 1993).

Complementarily, large geographical ranges can increase the diversity of parasites that may be encountered by mammals and transmitted horizontally across their populations and throughout evolutionary time, thus influencing parasite richness and centrality in the host–parasite network (Bagge, Poulin, & Valtonen, 2004; Bordes et al., 2009; Poulin, Krasnov, et al., 2011). Indeed, proportional range size was positively related with both ectoparasite

richness and centrality of Mexican mammals, as well as for Rodentia and Chiroptera separately. Such a result may respond to the high diversity across the Mexican Transition Zone for a wide variety of taxonomic groups (e.g. beetles: Halffter, 1976; ants: Dáttilo et al., 2020; mammals: Ortega & Arita, 1998), which is a large region of Mexico forming wide ecotones and transition areas between the Nearctic and Neotropical bioregions (Morrone, 2010). Note that the overall findings for mammals may be influenced by the Rodentia, since they not only represent the richest group in our dataset and richest order of mammals as a whole, but they could also be more easily/often sampled in the compiled studies, which could lead to conflation in terms of richness. Therefore, the important role of rodents in the network needs to be interpreted with caution in order to avoid biased inferences, since variation in sampling effort can be a strong predictor of host–parasite relationships (Byers et al., 2019; Poulin, 1997).

Additionally, it is expected that host species with large geographical ranges will have greater probability of acquiring new ectoparasite species because of both larger niche breadth and horizontal transmission among host species with overlapping geographical distributions (Bordes et al., 2009). Such geographical co-occurrence potentially facilitates the transmission among species (Krasnov et al., 2004; Poulin & Morand, 2004), driving the central position of widely distributed host taxa in the mammal–ectoparasite interaction network. Indeed, we observed that the diversity field of Chiroptera was positively related to their centrality in the network but not for their ectoparasite richness, which may be due to the fact that bats is the only group of flying mammals and their life history traits (e.g. roosting in caves) separates them from directly interacting with other mammal groups, thus reducing the number of shared ectoparasite species. Furthermore, this could be related to the higher proportional range and co-occurrence of bats with other mammals, compared to mammals as a whole and rodents only (as shown in this study: Supporting Information). We did not find evidence that co-occurrence among mammals as a whole and for Rodentia alone could be a predictor of their ectoparasite richness (as for Chiroptera) or their centrality within the studied mammal–ectoparasite interaction network. Indeed, mammals and rodents with the highest diversity field did not show the highest ectoparasite richness, which may be explained by life history traits leading different mammal species to not interact even when using the same local environment. Alternatively, a poor association between host species richness and parasite species discovery could explain this. Also, this lack of influence of co-occurrence on mammal ectoparasite richness and centrality could be related to our use of species range maps and spatial resolution of our study. Range maps (i.e. extents of occurrence) may overestimate (or underestimate) species distributions and thus any derived pattern of species co-occurrence and richness. As such, a species' diversity field can certainly be high (i.e. many species co-occurring within its range) but its overlap with some species can be minimal in certain regions of its range (e.g. overlapping in only a few cells across its range). Moreover, there can be few (or none) ectoparasite species in such regions, thus obscuring a potential relationship between diversity field and parasite richness. In addition, the spatial resolution of our analyses can only describe species co-occurrence at large spatial scales without directly addressing local scale species coexistence. At each spatial scale, there may be different spatial processes in action, from geographical speciation and range dynamics at the large scale to individual aggregation and population dynamics at the local scale (McGill, 2010). As such, some potential relationships may be obscured by commission/omission errors derived from our use of range maps and a grid cell system.

More precisely, the lack of an effect of the mammalian diversity field on ectoparasite richness (for mammals as a whole and separately for rodents and bats) and host network centrality (for mammals as a whole and rodents alone) is concordant with our findings of ectoparasite sharing probabilities. We showed that the probability of sharing ectoparasite species among mammal hosts decreases rapidly as the taxonomic distance increases between any pair of mammals, implying potential phylogenetic constraint on host breadth (Park et al., 2018; Pilosof et al., 2015). Alternative, non-mutually exclusive hypotheses could explain this pattern. First, the operation of evolutionary filters that would decrease the probability for any given host species to co-occur with other closely related species from which ectoparasites are readily transmitted (Thompson, 1994). Indeed, the decay in the probability of sharing ectoparasites among taxonomically distant mammals suggests a high level of specialization driven by the host's evolutionary history (e.g. physical, physiological, immunological responses; Park et al., 2018; Poulin, 2010a; Schulenburg, Kurtz, Moret, & Siva-Jothy, 2009). Second, taxonomic distance could also capture trait dissimilarity among species, as taxonomic closely related species usually tend to be more similar than distantly related ones. Likewise, taxonomic distance also inform about geographical distribution, since taxonomically close mammals tend to overlap their spatial extents as a result of spatial and evolutionary processes (e.g. speciation and climatic niche conservatism; Riddle, Hafner, & Alexander, 2000; Villalobos et al., 2013). Accordingly, evolutionary filters, trait dissimilarity and spatial processes may be acting to explain why taxonomically close mammal species have higher probability of sharing their ectoparasites.

Although distant taxa are unlikely to share ectoparasites among themselves (as shown here), there are many serious and generalist pathogens that can be readily transmitted by one extremely generalist ectoparasite (e.g. Diptera) and spread between mammals of different orders, even subclasses as shown here (Figure 4; Graham, Hassan, Burkett-Cadena, Guyer, & Unnasch, 2009; Sotomayor-Bonilla et al., 2019). Beyond biodiversity conservation issues, rodents and bats are reservoirs of many human diseases, and many exhibit synanthropic habits (Stenseth et al., 2003) posing serious health threats on top of environmental changes (Estrada-Peña, Ostfeld, Peterson, Poulin, & de la Fuente, 2014). Moreover, Rodentia's ectoparasites are known to be vectors of bacteria, viruses, cestodes, nematodes, and other micro-organisms already causing human zoonotic diseases (Asiry & Fetoh, 2014; Rafique, Rana, Khan, & Sohail, 2009). Here we found that four of

the six most central rodent species in the mammal–ectopatasite interaction network belong to the genus *Peromyscus* (*P. difficilis*, *P. boylii*, *P. maniculatus* and *P. melanotis*), which are well sampled and recorded rodents across Mexico and potential reservoirs of rodent-borne diseases such as Lyme disease (Rand et al., 1993), hantaviruses (Salazar-Bravo et al., 2004) and arenaviruses (Fulhorst et al., 2002). Finally, several species of Chiroptera (the other most important mammal order in our study) are also known to act as reservoirs of generalist Diptera-borne flaviviruses that can cause serious human diseases (e.g. dengue virus, Japanese encephalitis virus, West Nile virus; Sotomayor-Bonilla et al., 2019). In this sense, our results and conclusions can subsidize the construction of an early warning system on how ecological community changes may affect human–animal health risks. One must define continental or global data sampling protocols involving different taxonomic groups, and ecological interactions that can surrogate the present less precise, subjective, alerts on natural human health threats.

AUTHORS' CONTRIBUTIONS

W.D. and N.B.-C. conceived the ideas and designed the methodology; W.D., A.L.-N., R.G. and F.S.N. analysed the data. All authors contributed to the interpretation of the results, provided critical feedback on the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Raw data were sourced (Whitaker Jr. & Morales-Malacara, 2005). Response and predictor variables that support the findings were deposited in Figshare: http://doi.org/10.6084/m9.figshare.10216631 (Dáttilo, 2019). The R codes used for data analysis are available to the reader on Zenodo: https://doi.org/10.5281/zenodo.3706353 (Dáttilo, 2020).

ORCID

Wesley Dáttilo https://orcid.org/0000-0002-4758-4379
Roger Guevara https://orcid.org/0000-0003-0768-3580
Fabricio Villalobos https://orcid.org/0000-0002-5230-2217
Diego Santiago-Alarcon https://orcid.org/0000-0002-4914-5580
Frederico Siqueira Neves https://orcid.org/0000-0002-2691-3743
Thiago Izzo https://orcid.org/0000-0002-4613-3787

REFERENCES

Álvarez-Castañeda, S. T., Alvarez, T., & González-Ruiz, N. (2017). *Keys for identifying Mexican mammals*. Baltimore, MD: The Johns Hopkins University Press.

Arita, H. T. (1993). Rarity in Neotropical bats: Correlations with phylogeny, diet, and body mass. *Ecological Applications*, 3, 506–517. https://doi.org/10.2307/1941919

Arita, H. T., Christen, J. A., Rodríguez, P., & Soberón, J. (2008). Species diversity and distribution in presence-absence matrices: Mathematical relationships and biological implications. *The American Naturalist*, 172, 519–532. https://doi.org/10.1086/590954

Arneberg, P., Skorping, A., Grenfell, B., & Read, A. F. (1998). Host densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society B: Biological Sciences*, 265, 1283–1289. https://doi.org/10.1098/rspb.1998.0431

Asiry, K. A., & Fetoh, B. E. S. A. (2014). Occurrence of ectoparasitic arthropods associated with rodents in Hail region northern Saudi Arabia. *Environmental Science and Pollution Research*, 21, 10120–10128. https://doi.org/10.1007/s11356-014-3016-3

Bagge, A. M., Poulin, R., & Valtonen, E. T. (2004). Fish population size, and not density, as the determining factor of parasite infection: A case study. *Parasitology*, 128, 305–313. https://doi.org/10.1017/S0031182003004566

Bell, G., & Burt, A. (1991). The comparative biology of parasite species diversity: Internal helminths of freshwater fish. *Journal of Animal Ecology*, 60, 1047–1063. https://doi.org/10.2307/5430

Bellay, S., Lima, D. P., Takemoto, R. M., & Luque, J. L. (2011). A host-endoparasite network of Neotropical marine fish: Are there organizational patterns? *Parasitology*, 138, 1945–1952. https://doi.org/10.1017/S0031182011001314

Bellay, S., Oda, F. H., Campião, K. M., Yamada, F. H., Takemoto, R. M., & de Oliveira, E. F. (2018). Host-parasite networks: An integrative overview with tropical examples. In W. Dáttilo & V. Rico-Gray (Eds.), *Ecological networks in the tropics* (pp. 127–140). Cham, Switzerland: Springer.

Bininda-Emonds, O. R., Cardillo, M., Jones, K. E., MacPhee, R. D., Beck, R. M., Grenyer, R., … Purvis, A. (2007). The delayed rise of present-day mammals. *Nature*, 446, 507–512. https://doi.org/10.1038/nature05634

Bordes, F., Morand, S., Kelt, D. A., & Van Vuren, D. H. (2009). Home range and parasite diversity in mammals. *The American Naturalist*, 173, 467–474. https://doi.org/10.1086/597227

Byers, J. E., Schmidt, J. P., Pappalardo, P., Haas, S. E., & Stephens, P. R. (2019). What factors explain the geographical range of mammalian parasites? *Proceedings of the Royal Society B: Biological Sciences*, 286, 20190673. https://doi.org/10.1098/rspb.2019.0673

Cagnolo, L., Salvo, A., & Valladares, G. (2011). Network topology: Patterns and mechanisms in plant-herbivore and host-parasitoid food webs. *Journal of Animal Ecology*, 80, 342–351. https://doi.org/10.1111/j.1365-2656.2010.01778.x

Canard, E. F., Mouquet, N., Mouillot, D., Stanko, M., Miklisova, D., & Gravel, D. (2014). Empirical evaluation of neutral interactions in host-parasite networks. *The American Naturalist*, 183, 468–479. https://doi.org/10.1086/675363

Ceballos, G., & Oliva, G. (2005). *Los mamíferos silvestres de México*. México: Fondo de Cultura Económica.

Clayton, D. H., Bush, S. E., & Johnson, K. P. (2004). Ecology of congruence: Past meets present. *Systematic Biology*, 53, 165–173. https://doi.org/10.1080/10635150490265102

Combes, C. (2001). *Parasitism: The ecology and evolution of intimate interactions*. Chicago, IL: University of Chicago Press.

Crawley, M. J. (2013). *The R book* (2nd. ed.). Hoboken, NJ: Wiley.

Dallas, T. A., Han, B. A., Nunn, C. L., Park, A. W., Stephens, P. R., & Drake, J. M. (2019). Host traits associated with species roles in parasite sharing networks. *Oikos*, 128, 23–32. https://doi.org/10.1111/oik.05602

Dallas, T., Huang, S., Nunn, C., Park, A. W., & Drake, J. M. (2017). Estimating parasite host range. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20171250.

Dáttilo, W. (2019). Response and predictor variables used to study the species-level drivers of mammalian ectoparasite faunas. *Figshare*, https://doi.org/10.6084/m9.figshare.10216631

Dáttilo, W. (2020). wdattilo/Ectoparasites: Mammalian ectoparasites project (Version 1.0). *Zenodo*, https://doi.org/10.5281/zenodo.3706353

Dáttilo, W., Vásquez-Bolaños, M., Ahuatzin, D. A., Antoniazzi, R., Chávez-González, E., Corro, E., … MacGregor-Fors, I. (2020). Mexico ants: Incidence and abundance along the Nearctic–Neotropical interface. *Ecology*, https://doi.org/10.1002/ecy.2944

DiBlasi, E., Johnson, K. P., Stringham, S. A., Hansen, A. N., Beach, A. B., Clayton, D. H., & Bush, S. E. (2018). Phoretic dispersal influences parasite population genetic structure. *Molecular Ecology*, 27, 2770–2779. https://doi.org/10.1111/mec.14719

Dick, C. W. (2007). High host specificity of obligate ectoparasites. *Ecological Entomology*, 32, 446–450. https://doi.org/10.1111/j.1365-2311.2007.00836.x

Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). Indices, graphs and null models: Analyzing bipartite ecological networks. *The Open Ecology Journal*, 2, 7–24. https://doi.org/10.2174/1874213000902010007

Esser, H. J., Foley, J. E., Bongers, F., Herre, E. A., Miller, M. J., Prins, H. H., & Jansen, P. A. (2016). Host body size and the diversity of tick assemblages on Neotropical vertebrates. *International Journal for Parasitology: Parasites and Wildlife*, 5, 295–304. https://doi.org/10.1016/j.ijppaw.2016.10.001

Estrada-Peña, A., Ostfeld, R. S., Peterson, A. T., Poulin, R., & de la Fuente, J. (2014). Effects of environmental change on zoonotic disease risk: An ecological primer. *Trends in Parasitology*, 30, 205–214. https://doi.org/10.1016/j.pt.2014.02.003

Ezenwa, V. O., Price, S. A., Altizer, S., Vitone, N. D., & Cook, K. C. (2006). Host traits and parasite species richness in even and odd-toed hoofed mammals, Artiodactyla and Perissodactyla. *Oikos*, 115, 526–536. https://doi.org/10.1111/j.2006.0030-1299.15186.x

Fagundes, R., Antonini, Y., & Aguiar, L. (2017). Overlap in cave usage and period of activity as factors structuring the interactions between bats and *Ectoparasites*. *Zoological Studies*, 56, 1–11.

Fulhorst, C. F., Bennett, S. G., Milazzo, M. L., Murray Jr., H. L., Webb Jr., J. P., Cajimat, M. N., & Bradley, R. D. (2002). Bear Canyon virus: An arenavirus naturally associated with the California mouse (*Peromyscus californicus*). *Emerging Infectious Diseases*, 8, 717–721. https://doi.org/10.3201/eid0807.010281

Gilbert, G. S., Magarey, R., Suiter, K., & Webb, C. O. (2012). Evolutionary tools for phytosanitary risk analysis: Phylogenetic signal as a predictor of host range of plant pests and pathogens. *Evolutionary Applications*, 5, 869–878. https://doi.org/10.1111/j.1752-4571.2012.00265.x

Graham, S. P., Hassan, H. K., Burkett-Cadena, N. D., Guyer, C., & Unnasch, T. R. (2009). Nestedness of ectoparasite-vertebrate host networks. *PLoS ONE*, 4, e7873. https://doi.org/10.1371/journal.pone.0007873

Gregory, R. D., Keymer, A. E., & Harvey, P. H. (1996). Helminth parasite richness among vertebrates. *Biodiversity & Conservation*, 5, 985–997. https://doi.org/10.1007/BF00054416

Hafner, M. S., & Nadler, S. A. (1988). Phylogenetic trees support the co-evolution of parasites and their hosts. *Nature*, 332, 258. https://doi.org/10.1038/332258a0

Halffter, G. (1976). Distribución de los insectos en la zona de transición Mexicana. Relaciones con la entomofauna de Norteamérica. *Folia Entomológica Mexicana*, 35, 1–64.

Harbison, C. W., & Clayton, D. H. (2011). Community interactions govern host-switching with implications for host–parasite coevolutionary history. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 9525–9529. https://doi.org/10.1073/pnas.1102129108

Jones, K. E., & Safi, K. (2011). Ecology and evolution of mammalian biodiversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 2451–2461. https://doi.org/10.1098/rstb.2011.0090

Kamiya, T., O'Dwyer, K., Nakagawa, S., & Poulin, R. (2014). What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biological Reviews*, 89, 123–134. https://doi.org/10.1111/brv.12046

Karvonen, A., & Seehausen, O. (2012). The role of parasitism in adaptive radiations—when might parasites promote and when might they constrain ecological speciation? *International Journal of Ecology*, 2012, id280169. https://doi.org/10.1155/2012/280169

Krasnov, B. R., Khokhlova, I. S., Shenbrot, G. I., & Poulin, R. (2008). How are the host spectra of hematophagous parasites shaped over evolutionary time? Random choice vs selection of a phylogenetic lineage. *Parasitology Research*, 102, 1157–1164. https://doi.org/10.1007/s00436-008-0884-9

Krasnov, B. R., Mouillot, D., Shenbrot, G. I., Khokhlova, I. S., Vinarski, M. V., Korallo-Vinarskaya, N. P., & Poulin, R. (2010). Similarity in ecto-parasite faunas of Palaearctic rodents as a function of host phylogenetic, geographic or environmental distances: Which matters the most? *International Journal for Parasitology*, 40, 807–817. https://doi.org/10.1016/j.ijpara.2009.12.002

Krasnov, B. R., Poulin, R., & Mouillot, D. (2011). Scale-dependence of phylogenetic signal in ecological traits of ectoparasites. *Ecography*, 34, 114–122. https://doi.org/10.1111/j.1600-0587.2010.06502.x

Krasnov, B. R., Poulin, R., Shenbrot, G. I., Mouillot, D., & Khokhlova, I. S. (2005). Host specificity and geographic range in haematophagous ectoparasites. *Oikos*, 108, 449–456. https://doi.org/10.1111/j.0030-1299.2005.13551.x

Krasnov, B. R., Shenbrot, G. I., Khokhlova, I. S., & Degen, A. A. (2004). Flea species richness and parameters of host body, host geography and host 'milieu'. *Journal of Animal Ecology*, 73, 1121–1128. https://doi.org/10.1111/j.0021-8790.2004.00883.x

Lafferty, K. D., Allesina, S., Arim, M., Briggs, C. J., De Leo, G., Dobson, A. P., … Thieltges, D. W. (2008). Parasites in food webs: The ultimate missing links. *Ecology Letters*, 11, 533–546. https://doi.org/10.1111/j.1461-0248.2008.01174.x

Lima Jr., D. P., Giacomini, H. C., Takemoto, R. M., Agostinho, A. A., & Bini, L. M. (2012). Patterns of interactions of a large fish–parasite network in a tropical floodplain. *Journal of Animal Ecology*, 81, 905–913. https://doi.org/10.1111/j.1365-2656.2012.01967.x

Lindenfors, P., Nunn, C. L., Jones, K. E., Cunningham, A. A., Sechrest, W., & Gittleman, J. L. (2007). Parasite species richness in carnivores: Effects of host body mass, latitude, geographical range and population density. *Global Ecology and Biogeography*, 16, 496–509. https://doi.org/10.1111/j.1466-8238.2006.00301.x

McAuliffe, K. (2016). *This is your brain on parasites: How tiny creatures manipulate our behavior and shape society*. New York, NY: Mariner Books.

McGill, B. J. (2010). Matters of scale. *Science*, 328, 575–576. https://doi.org/10.1126/science.1188528

Medeiros, M. C., Ricklefs, R. E., Brawn, J. D., & Hamer, G. L. (2015). Plasmodium prevalence across avian host species is positively associated with exposure to mosquito vectors. *Parasitology*, 142, 1612–1620. https://doi.org/10.1017/s0031182015001183

Møller, A. P., Christe, P., & Garamszegi, L. Z. (2005). Coevolutionary arms races: Increased host immune defense promotes specialization by avian fleas. *Journal of Evolutionary Biology*, 18, 46–59. https://doi.org/10.1111/j.1420-9101.2004.00774.x

Morand, S. (2015). (macro-) Evolutionary ecology of parasite diversity: From determinants of parasite species richness to host diversification. *International Journal for Parasitology: Parasites and Wildlife*, 4, 80–87.

Morand, S., & Harvey, P. H. (2000). Mammalian metabolism, longevity and parasite species richness. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267, 1999–2003. https://doi.org/10.1098/rspb.2000.1241

Morand, S., Krasnov, B. R., & Poulin, R. (2007). *Micromammals and macroparasites: From evolutionary ecology to management*. Tokyo, Japan: Springer Science & Business Media.

Morand, S., & Poulin, R. (1998). Density, body mass and parasite species richness of terrestrial mammals. *Evolutionary Ecology*, 12, 717–727. https://doi.org/10.1023/A:1006537600093

Morrone, J. J. (2010). Fundamental biogeographic patterns across the Mexican transition zone: An evolutionary approach. *Ecography*, *33*, 355–361. https://doi.org/10.1111/j.1600-0587.2010.06266.x

Naisbit, R. E., Rohr, R. P., Rossberg, A. G., Kehrli, P., & Bersier, L. F. (2012). Phylogeny versus body size as determinants of food web structure. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 3291–3297. https://doi.org/10.1098/rspb.2012.0327

Nunn, C. L., Altizer, S., Jones, K. E., & Sechrest, W. (2003). Comparative tests of parasite species richness in primates. *The American Naturalist*, *162*, 597–614. https://doi.org/10.1086/378721

Olalla-Tárraga, M. Á., Torres-Romero, E. J., Amado, T. F., & Martínez, P. A. (2015). Phylogenetic path analysis reveals the importance of niche-related biological traits on geographic range size in mammals. *Global Change Biology*, *21*, 3194–3196. https://doi.org/10.1111/gcb.12971

Ortega, J., & Arita, H. T. (1998). Neotropical-Antarctic limits in the Middle America as determined by bat distributions. *Journal of Mammalogy*, *79*, 772–783.

Owen, J. P., Waite, J. L., Holden, K. Z., & Clayton, D. H. (2014). Does antibody binding to diverse antigens predict future infection? *Parasite Immunology*, *36*, 573–584. https://doi.org/10.1111/pim.12141

Park, A. W., Farrell, M. J., Schmidt, J. P., Huang, S., Dallas, T. A., Pappalardo, P., & Davies, T. J. (2018). Characterizing the phylogenetic specialism–generalism spectrum of mammal parasites. *Proceedings of the Royal Society B: Biological Sciences*, *285*, 20172613. https://doi.org/10.1098/rspb.2017.2613

Pilosof, S., Morand, S., Krasnov, B. R., & Nunn, C. L. (2015). Potential parasite transmission in multi-host networks based on parasite sharing. *PLoS ONE*, *10*, e0117909. https://doi.org/10.1371/journal.pone.0117909

Poulin, R. (1997). Species richness of parasite assemblages: Evolution and patterns. *Annual Review of Ecology and Systematics*, *28*, 341–358. https://doi.org/10.1146/annurev.ecolsys.28.1.341

Poulin, R. (2004). Macroecological patterns of species richness in parasite assemblages. *Basic and Applied Ecology*, *5*, 423–434. https://doi.org/10.1016/j.baae.2004.08.003

Poulin, R. (2007). Are there general laws in parasite ecology? *Parasitology*, *134*, 763–776. https://doi.org/10.1017/S0031182006002150

Poulin, R. (2010a). Decay of similarity with host phylogenetic distance in parasite faunas. *Parasitology*, *137*, 733–741.

Poulin, R. (2010b). Network analysis shining light on parasite ecology and diversity. *Trends in Parasitology*, *26*, 492–498. https://doi.org/10.1016/j.pt.2010.05.008

Poulin, R., Guilhaumon, F., Randhawa, H. S., Luque, J. L., & Mouillot, D. (2011). Identifying hotspots of parasite diversity from species–area relationships: Host phylogeny versus host ecology. *Oikos*, *120*, 740–747. https://doi.org/10.1111/j.1600-0706.2010.19036.x

Poulin, R., Krasnov, B. R., Mouillot, D., & Thieltges, D. W. (2011). The comparative ecology and biogeography of parasites. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *366*, 2379–2390. https://doi.org/10.1098/rstb.2011.0048

Poulin, R., & Morand, S. (2004). *Parasite biodiversity*. Washington, DC: Smithsonian Institution Press.

Poulin, R., & Mouillot, D. (2003). Parasite specialization from a phylogenetic perspective: A new index of host specificity. *Parasitology*, *126*, 473–480. https://doi.org/10.1017/S0031182003002993

Rafique, A., Rana, S. A., Khan, H. A., & Sohail, A. (2009). Prevalence of some helminths in rodents captured from different city structures including poultry farms and human population of Faisalabad, Pakistan. *Veterinary Journal*, *29*, 141–144.

Raia, P., Carotenuto, F., Passaro, F., Piras, P., Fulgione, D., Werdelin, L., & Fortelius, M. (2013). Rapid action in the Palaeogene, the relationship between phenotypic and taxonomic diversification in Coenozoic mammals. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20122244. https://doi.org/10.1098/rspb.2012.2244

Rand, P. W., Lacombe, E. H., Smith Jr., R. P., Rich, S. M., Kilpatrick, W. C., Dragoni, C. A., & Caporale, D. (1993). Competence of *Peromyscus maniculatus* (Rodentia: Cricetidae) as a reservoir host for *Borrelia burgdorferi* (Spirochaetares: Spirochaetaceae) in the wild. *Journal of Medical Entomology*, *30*, 614–618. https://doi.org/10.1093/jmedent/30.3.614

Reis Jr., R., Oliveira, M. L., & Borges, G. R. A. (2015). *RT4Bio: R tools for biologists (RT4Bio)*. R package version 1.0.

Riddle, B. R., Hafner, D. J., & Alexander, L. F. (2000). Phylogeography and systematics of the *Peromyscus eremicus* species group and the historical biogeography of North American warm regional deserts. *Molecular Phylogenetics and Evolution*, *17*, 145–160. https://doi.org/10.1006/mpev.2000.0841

Robles-Fernández, Á. L., & Lira-Noriega, A. (2017). Combining phylogenetic and occurrence information for risk assessment of pest and pathogen interactions with host plants. *Frontiers in Applied Mathematics and Statistics*, *3*. https://doi.org/10.3389/fams.2017.00017

Salazar-Bravo, J., Armién, B., Suzán, G., Armién, A., Ruedas, L. A., Avila, M., … Yates, T. L. (2004). Serosurvey of wild rodents for hantaviruses in Panama, 2000–2002. *Journal of Wildlife Diseases*, *40*, 103–109. https://doi.org/10.7589/0090-3558-40.1.103

Santiago-Alarcon, D., MacGregor-Fors, I., Kühnert, K., Segelbacher, G., & Schaefer, H. M. (2016). Avian haemosporidian parasites in an urban forest and their relationship to bird size and abundance. *Urban Ecosystems*, *19*, 331–346. https://doi.org/10.1007/s11252-015-0494-0

Schulenburg, H., Kurtz, J., Moret, Y., & Siva-Jothy, M. T. (2009). Introduction. Ecological immunology. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, *364*, 3–14. https://doi.org/10.1098/rstb.2008.0249

Slatyer, R. A., Hirst, M., & Sexton, J. P. (2013). Niche breadth predicts geographical range size: A general ecological pattern. *Ecology Letters*, *16*, 1104–1114. https://doi.org/10.1111/ele.12140

Sotomayor-Bonilla, J., Tolsá-García, M. J., García-Peña, G. E., Santiago-Alarcon, D., Mendoza, H., Alvarez-Mendizabal, P., … Suzán, G. (2019). Insights into the host specificity of mosquito-borne flaviviruses infecting wild mammals. *EcoHealth*, *16*, 726–733. https://doi.org/10.1007/s10393-019-01442-2

Stanko, M., Miklisová, D., de Bellocq, J. G., & Morand, S. (2002). Mammal density and patterns of ectoparasite species richness and abundance. *Oecologia*, *131*, 289–295. https://doi.org/10.1007/s00442-002-0889-5

Stenseth, N. C., Leirs, H., Skonhoft, A., Davis, S. A., Pech, R. P., Andreassen, H. P., … Wan, X. (2003). Mice, rats, and people: The bio-economics of agricultural rodent pests. *Frontiers in Ecology and the Environment*, *1*, 367–375. https://doi.org/10.1890/1540-9295(2003)001[0367:MRAPTB]2.0.CO;2

Thompson, J. N. (1994). *The coevolutionary process*. Chicago, IL: University of Chicago Press.

Vázquez, D. P., Melián, C. J., Williams, N. M., Blüthgen, N., Krasnov, B. R., & Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, *116*, 1120–1127. https://doi.org/10.1111/j.2007.0030-1299.15828.x

Vázquez, D. P., Poulin, R., Krasnov, B. R., & Shenbrot, G. I. (2005). Species abundance and the distribution of specialization in host–parasite interaction networks. *Journal of Animal Ecology*, *74*, 946–955. https://doi.org/10.1111/j.1365-2656.2005.00992.x

Villalobos, F., & Arita, H. T. (2010). The diversity field of New World leaf-nosed bats (Phyllostomidae). *Global Ecology and Biogeography*, *19*, 200–211. https://doi.org/10.1111/j.1466-8238.2009.00503.x

Villalobos, F., Rangel, T. F., & Diniz-Filho, J. A. F. (2013). Phylogenetic fields of species: Cross-species patterns of phylogenetic structure and geographical coexistence. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20122570.

Whitaker Jr., J. O., & Morales-Malacara, J. B. (2005). Ectoparasites and other associates (Ectodytes) of mammals of Mexico. In V. Sánchez-Cordero & R. Medellín (Eds.), *Contribuciones mastozoológicas en homenaje a Bernardo Villa* (pp. 535–665). Mexico City, Mexico: Instituto de

Biología, Universidad Nacional Autónoma de México, Comisión Nacional para el Uso y Conocimiento de la Biodiversidad.

Whiteman, N. K., Santiago-Alarcon, D., Johnson, K. P., & Parker, P. G. (2004). Differences in straggling rates between two genera of dove lice (Insecta: Phthiraptera) reinforce population genetic and cophylogenetic patterns. *International Journal for Parasitology*, *34*, 1113–1119. https://doi.org/10.1016/j.ijpara.2004.06.003

Wood, S. (2015). *mgcv: Mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation*. Bristol, UK: R-project.

Woolhouse, M. E., Haydon, D. T., & Antia, R. (2005). Emerging pathogens: The epidemiology and evolution of species jumps. *Trends in Ecology & Evolution*, *20*, 238–244. https://doi.org/10.1016/j.tree.2005.02.009

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Dáttilo W, Barrozo-Chávez N, Lira-Noriega A, et al. Species-level drivers of mammalian ectoparasite faunas. *J Anim Ecol*. 2020;00:1–12. https://doi.org/10.1111/1365-2656.13216