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Tad Dallas
Louisiana State University

Lauren A. Holian
University of Florida

Grant Foster
University of Georgia

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What determines parasite species richness across host species?

Tad Dallas¹  | Lauren A. Holian² | Grant Foster³

¹Department of Biological Sciences,
Louisiana State University, Baton Rouge,
LA, USA

²Department of Biology, University of
Florida, Gainesville, FL, USA

³Odum School of Ecology, University of
Georgia, Athens, GA, USA

Correspondence

Tad Dallas
Email: tad.a.dallas@gmail.com

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Abstract

In Focus: Dáttilo, W., Barrozo-Chávez, N., Lira-Noriega, A., Guevara, R., Villalobos, F., Santiago-Alarcon, D., Neves, F. S., Izzo, T., & Ribeiro, S. P. (2020). Species-level drivers of mammalian ectoparasite faunas. *Journal of Animal Ecology*. <https://doi.org/10.1111/1365-2656.13216>. The question of what drives the number of parasite species able to infect a given host species is still a largely open question, despite decades of research. Dáttilo and colleagues examine the potential drivers of ectoparasite species across a large set of host species to explore the taxonomic and trait drivers of host-parasite interactions. Here, we contextualize their findings, explore what is known about parasite species richness, and identify some potential next steps towards answers.

KEYWORDS

ectoparasite, parasite diversity, parasite species richness, parasite specificity

What determines the number of species that can inhabit a given area? This question is fundamental to ecology, and has an analogue in parasitology as to what controls parasite species richness, the number of parasite species that infect a given host species (Kamiya, O'Dwyer, Nakagawa, & Poulin, 2014). While this is a longstanding question in the study of host-parasite interactions, universal drivers of parasite species richness have remained elusive (Canard et al., 2014; Morand, 2000; Poulin, 1997; Price &

Clancy, 1983; Stanko, Miklisová, De Bellocq, & Morand, 2002). A recent study by Dáttilo et al. (2020) contributes to our understanding of host-parasite associations by exploring parasite species richness across a wide taxonomic range of host species distributed broadly across the Nearctic and Neotropical regions of Mexico. In highlighting their findings, we address some of the fundamental constraints and important avenues in the study of host-parasite associations.

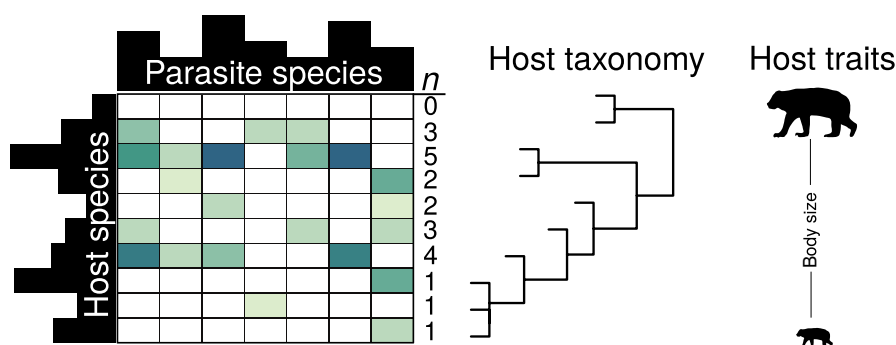


FIGURE 1 Host-parasite interactions, where the existence and frequency of interaction between host and parasite (darker blue colours indicating more frequent interactions) could be driven by the relative abundance of hosts and parasites (depicted as black marginal bar charts). The summed rows of this interaction matrix correspond to parasite species richness (the n column of the interaction matrix), which may be a factor of neutral dynamics, host taxonomy or host traits, among other possibilities

Parasite species are non-randomly distributed across different host species (Poulin, 2014; Poulin & Morand, 2000; Vázquez, Poulin, Krasnov, & Shenbrot, 2005). Parasite variation across hosts may be driven by a diversity of ecological and evolutionary factors (Figure 1). Even if we were to assume that host-parasite interactions are determined by neutral dynamics (Canard et al., 2014), parasite richness would vary between host species, as more abundant host and parasite species would interact more often, be detected more often and therefore have increased parasite richness. Understanding what drives variation in parasite species richness is both a long-standing and currently pressing need, as parasite diversity (a) is currently underestimated (Dallas, Huang, Nunn, Park, & Drake, 2017), (b) may be at risk due to extinctions (Carlson et al., 2017), and (c) is important to understand when identifying potential emerging infectious diseases (Geoghegan, Senior, Di Giallonardo, & Holmes, 2016). Dáttilo et al. (2020) evaluate whether taxonomic distance, trait variation (body mass and geographical range size) and geographic co-occurrence (diversity field) of hosts are associated with ectoparasite species richness.

Close relationships—taxonomic or phylogenetic—between host species may yield more similar parasite community composition (Wells, Gibson, & Clark, 2019) or parasite species richness (Nunn, Altizer, Jones, & Sechrest, 2003). Consistent with previous studies, Dáttilo et al. (2020) found a clear effect of host taxonomic distance on parasite species richness and parasite sharing patterns (fig. 4 in Dáttilo et al., 2020). Specifically, that the probability of ectoparasite sharing for two congeneric host species reached up to 90% and decreased precipitously as taxonomic distance increased. While this may be driven in part by parasites that are specific to certain host taxonomic levels (e.g. bat lice and the order Chiroptera), the decline in parasite sharing is sharp by the level of taxonomic Family (Dáttilo et al., 2020). The rapid decline associated with increasing taxonomic distance may reflect the co-evolutionary relationships between parasites and their hosts and the inherent temporal separation between lineages (e.g. bat flies tend to be quite specialized and species-rich). Alternatively, the importance of host phylogenetic or taxonomic distance to parasite sharing may be explained by more closely related hosts tending to have similar traits, which would affect the subsequent encounter and acquisition of parasite species.

Generally, host traits that enhance the probability of encountering a parasite species (e.g. large geographic range), or acquiring a parasite (e.g. low immune investment) are associated with higher parasite species richness. Dáttilo et al. (2020) find that host species with larger geographic ranges tended to have more parasite species, consistent with previous meta-analytical findings (Kamiya et al., 2014) and findings in other host-parasite systems (Nunn et al., 2003; Poulin, 1997). However, Dáttilo et al. (2020) also find that small-bodied species tended to have higher parasite species richness, which is at odds with other studies (e.g. Bordes, Morand, & Ricardo, 2008; Kamiya et al., 2014; Poulin, 2004). This may be due to differential sampling effort, as extremely well-studied host species also tend to be small-bodied (e.g. rodents and bats).

Species associations—including both antagonistic and mutualistic associations—may change across spatial or environmental gradients (Pellissier et al., 2018), as determined in part by species geographic range overlap, environmental conditions, density-dependence and the context of the local community (Travis, Brooker, Clark, & Dytham, 2006; Tylisanakis & Morris, 2017). As a result, the scope of the study may determine the patterns observed. Dáttilo et al. (2020) found that body mass and proportional range size were good predictors of ectoparasite richness, and that taxonomic similarity was a major driver of the probability of sharing ectoparasites for mammals distributed across Mexico. However, these factors may differentially influence parasite richness across spatial scales and even at various levels of taxonomic groupings.

The influence of geographic scale is important, as parasite species richness may be estimated for a specific location (Hughes & Page, 2007; Morand et al., 2000), an entire region (De Bellocq, Morand, & Feliu, 2002), or at global scale (Dallas et al., 2018). Ideally, estimates of parasite species richness for a given host species would include information on the entire geographic distribution of the host species, as findings based on a subset of the host range may lead to distinct results, though this may be logistically challenging. Often, it is assumed that parasite species richness is conserved spatially, such that a host species infected by five parasite species in one area will likely be infected by five parasite species in another. Dáttilo et al. (2020) and colleagues present an analysis of parasite species richness which encompasses a large geographic area (Nearctic and Neotropical regions of Mexico) and a diverse set of mammal species. Given the geographic study area, Dáttilo et al. (2020) found that members of the genus *Peromyscus* tended to have relatively high parasite species richness. This genus has an extensive geographic range, is well-sampled and is among one of the more parasitized groups in other parts of their ranges as well (Morand & Poulin, 1998; Poulin, 1995).

The genus *Peromyscus* not only highlights the potential issue of geographic scale, but also the influence of sampling and detection biases of host-parasite associations (Carlson et al., 2020; Dallas, Huang, et al., 2017). Dominant species in a community should be more easily sampled, increasing the probability of detecting a host-parasite association. However, the reason that these host species are easily sampled is because they are common and have dense populations, facilitating horizontal transmission of parasites. Disentangling the roles of sampling and detection bias from ecologically relevant factors that may predispose host species to have higher parasite species richness is an important consideration. For the case of *Peromyscus*, Dáttilo et al. (2020) highlight this point in their discussion, stating that variation in 'sampling effort can be a strong predictor of host-parasite relationships'. Additionally, Chiroptera highlight how taxon-specific characteristics may influence patterns in host-parasite associations. Amongst the studied mammalian hosts, Chiroptera were the only group to exhibit a positive relationship between geographic co-occurrence (diversity field) and closeness centrality (Dáttilo et al., 2020). Whether this pattern is driven by geographic distribution or life-history traits, understanding potential exceptions and differing roles within

multi-host-parasite networks presents an important avenue for future research.

Dáttilo et al. (2020) recommend the implementation of regional or global standardized host sampling schemes as a means to detect potentially zoonotic parasites. While we agree that identifying potential parasite spillover is a worthy goal, the preferential sampling of already well-sampled species (e.g. many *Peromyscus* species) may simply enhance the sampling and detection bias already present. However, using predictive models to examine parasite sharing with humans or closely related species could be a way to estimate zoonotic potential (Farrell, Berrang-Ford, & Davies, 2013), or by network-based approaches which explicitly consider host and pathogen species associations (Dallas, Park, & Drake, 2017; Evans, Dallas, Han, Murdock, & Drake, 2017). Further, standardized global sampling will promote our understanding of the spatial distribution of parasite species, and how this may be affected by climate change (Carlson et al., 2020). While standardizing global sampling may be logistically infeasible, leveraging existing data from museum records, published data and governmental surveys may provide some insight into large-scale patterns of parasite diversity and host-parasite associations. Lastly, considering the entire complex structure of host and parasite community associations is an important frontier (Dormann, Fründ, & Schaefer, 2017; Pellissier et al., 2018; Tylianakis & Morris, 2017), as this formulation allows for a body of theory and tools to be applied to estimate (Carlson, Zipfel, Garnier, & Bansal, 2019; Jordano, 2016), understand (Poulin, 2010) and predict (Dallas, Park, et al., 2017) host-parasite associations.

AUTHORS' CONTRIBUTIONS

All authors contributed to the writing of this manuscript.

DATA AVAILABILITY STATEMENT

There are no associated data with this manuscript.

ORCID

Tad Dallas  <https://orcid.org/0000-0003-3328-9958>

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