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Host body size and the diversity of tick assemblages on Neotropical vertebrates

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ABSTRACT

Identifying the factors that influence the species diversity and distribution of ticks (Acari: Ixodida) across vertebrate host taxa is of fundamental ecological and medical importance. Host body size is considered one of the most important determinants of tick abundance, with larger hosts having higher tick burdens. The species diversity of tick assemblages should also be greater on larger-bodied host species, but empirical studies testing this hypothesis are lacking. Here, we evaluate this relationship using a comparative dataset of feeding associations from Panama between 45 tick species and 171 host species that range in body size by three orders of magnitude. We found that tick species diversity increased with host body size for adult ticks but not for immature ticks. We also found that closely related host species tended to have similar tick species diversity, but correcting for host phylogeny did not alter the relationships between host body size and tick species diversity. The distribution of tick species was highly aggregated, with approximately 20% of the host species harboring 80% of all tick species, following the Pareto principle or 20/80 Rule. Thus, the aggregated pattern commonly observed for tick burdens and disease transmission also holds for patterns of tick species richness. Our finding that the adult ticks in this system preferentially parasitize large-bodied host species suggests that the ongoing anthropogenic loss of large-bodied vertebrates is likely to result in host-tick coextinction events, even when immature stages feed opportunistically. As parasites play critical roles in ecological and evolutionary processes, such losses may profoundly affect ecosystem functioning and services.

1. Introduction

Parasites are an important component of natural communities, in which host species are habitat to a wide range of microparasites (e.g., bacteria and protozoa) and macroparasites (e.g., helminths and arthropods) (Nunn et al., 2003). Parasite species richness and abundance varies both among and within host taxa, suggesting that some host species are more likely to be parasitized than others (Wilson et al., 2002). As parasites are able to profoundly affect host survival, fecundity and population dynamics, identifying which host traits explain the non-random pattern in which parasites are distributed across host lineages is highly relevant for human and veterinary medicine, as well as wildlife conservation (Morand and Poulin, 1998; Altizer et al., 2003; Nunn et al., 2003; Ezenwa et al., 2006; Huang et al., 2014). Knowing which host traits increase the likelihood of parasite host-switching to livestock, humans, or re-introduced wildlife, and predicting which parasites are present in understudied host species, will allow assessing which host species are at greatest risk from infectious diseases by identifying 'problematic' parasites such as host generalists before they emerge (Huang et al., 2014).

Body size is the host trait most often invoked to explain the structure of parasite assemblages (Poulin, 2004). Larger hosts have larger external surface areas and thus represent larger "habitats" that provide more space and resources for parasites to exploit

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(Kuris et al., 1980; Poulin, 1995). Larger hosts also have larger home ranges, travel longer distances, and may visit more diverse habitats than smaller species, all of which increases their likelihood of acquiring a diverse parasite fauna (Nunn et al., 2003; Krasnov et al., 2004). On the other hand, body size is negatively correlated with population density (Blackburn et al., 1993; Arneberg, 2002). Less abundant hosts have lower probabilities of contacting parasites and should therefore accumulate fewer species and individuals of parasites than hosts living at higher densities (Anderson and May 1978; Morand and Poulin, 1998). Large-bodied hosts also tend to have slower life-history strategies, which is considered a trade-off for higher immunocompetence (Lee, 2006), so that larger hosts may be more resistant to tick parasitism. Yet a recent meta-analysis identified host body size as a key universal determinant of parasite species richness across host and parasite taxa (Kamiya et al., 2014). However, one group of parasitic organisms that have rarely been considered in these studies, but which are of considerable medical and veterinary concern, are ticks.

Ticks (Acari: Ixodida) are excellent models for studies on the ecology and evolution of host-parasite associations as they are obligatory blood-feeding arthropods that parasitize every class of terrestrial vertebrates around the world (Sonenshine, 1991). Like other parasites, ticks are found on only a subset of all apparently suitable hosts (Randolph, 2004), and which host characteristics drive ecological patterns in tick parasitism remains poorly resolved. While some studies have found clear relationships between intraspecific host traits and tick burdens (Tälleklint and Jaenson, 1997; Hughes and Randolph, 2001; Harrison et al., 2010; Vor et al., 2010; Kiffner et al., 2011a, 2011b; Anderson et al., 2013; Heylen et al., 2013), others have not (Brunner and Ostfeld, 2008; Pollock et al., 2012). These earlier studies, however, largely focused on a single tick species, mostly from the *Ixodes ricinus* species complex, and its distribution across one or two host species. In contrast, only few studies have examined host determinants of tick parasitism for a broader range of host taxa (Gallivan and Horak, 1997; Marsot et al., 2012; Hofmeester et al., 2016; Miller et al., 2016) and the question of how the species diversity of tick assemblages (i.e., the “tick fauna” of a host species, *sensu* Poulin (2004)) covaries with interspecific host traits such as body size remains unresolved.

Species-rich communities of ticks and hosts, such as those found in the New World tropics, provide a great opportunity to tackle this question. Here, we used comparative analyses to assess whether and how tick species richness, diversity, and proportional similarity (henceforward tick assemblage structure) were related to host body size across a wide range of vertebrate host groups in Panama. We show that the results are dependent on tick life stage, with positive relationships of tick assemblage structure with host body size for adult ticks, but a lack of any relationship for immature ticks. We provide possible explanations for this difference and discuss the implications of our findings.

2. Methods

2.1. Study area

We compiled data on tick-host associations from Panama, a country that supports a large diversity of vertebrates, many of which are endemic to the Neotropics (Patterson and Costa, 2012). Panama is also rich in ticks, both in species and in numbers (Fairchild et al., 1966). Over forty species of ticks from seven genera and two families have been reported so far, and new species continue to be described (Fairchild et al., 1966; Apanaskevich and Bermúdez, 2013; Nava et al., 2014; Bermúdez et al., 2015a). Tick-host associations in Panama have been recorded from a wide variety of environmental conditions and habitats, ranging from mangrove swamps to tropical forests and from savannahs to high-altitude cloud forests (Fairchild et al., 1966). Panama has tropical moist weather with an average diurnal temperature of 27 °C. Average temperature and humidity are high throughout most of the country, but considerably milder at elevations >600 m. Elevation ranges from ca. 0–3500 m. Rainfall varies both regionally (ca. 1750–4000 mm) and temporally, with a pronounced dry season in the lowlands from January to April (Ridgely and Gwynne, 1989).

2.2. Data compilation

We used data from Dunn (1923), Fairchild et al. (1966), Bermúdez et al. (2009,2010,2011,2013,2015a,b), Apanaskevich and Bermúdez (2013), Murgas et al. (2013), García et al. (2014), Esser et al. (2016), and Miller et al. (2016). In addition, we collected larvae and nymphs from vertebrate hosts between 2008 and 2014, including humans, domestic animals, and wildlife (mammals, amphibians, and reptiles), the latter of which were either found as road kills or sampled during live-capture studies. We searched the entire body of hosts, but only collected ticks found firmly attached, and preserved these in 95% ethanol. Larvae and nymphs of the genus *Rhipicephalus* (*Boophilus*) and nymphs of *Haemaphysalis* were identified using the taxonomic keys provided by Fairchild et al. (1966). Nymphs of *Amblyomma ovale* were identified using the taxonomic keys of Martins et al. (2010). *Ornithodoros puertoricensis* larvae were identified by morphological descriptions in Venzal et al. (2008) and later confirmed by 16S rDNA sequencing. Larvae and/or nymphs of *Amblyomma*, *Haemaphysalis,* and *Ixodes* ticks that could not be identified based on morphology were sequenced using 16S rDNA, or using the mtDNA COI barcoding fragment, following Miller et al. (2016).

Given the ectoparasitic nature of ticks, host body size is best reflected by the skin surface area of each host species. Since such data is not readily available, we used the allometric scaling relationship between body mass M and skin surface area A as a measure of host body size, where $A \propto M^{2/3}$ (West et al., 1999). Data on host body mass (average for males and females, in grams) for each species were obtained from various sources (Eisenberg, 1989; Smith et al., 2003; Dunning, 2007; Greer et al., 2007; De Magalhães and Costa, 2009; Reid, 2009; Meiri, 2010; Arner, 2012; Feldman and Meiri, 2013) and hence raised to a 2/3 power prior to analyses.

2.3. Characterization of tick assemblage structure

We used non-parametric methods that consider differences in species abundance (i.e. the number of ticks collected per host species) to compute three indices that have been widely used in ecology: estimated total species richness, true diversity, and proportional similarity. Each of these indices characterizes a different aspect of the tick assemblage structure across vertebrate host species. We used the Chao1 index (Chao, 1984), an asymptotic estimator of species richness, to compute the number of tick species per host species that would be expected under exhaustive sampling, using the EstimateS software package version 9.1.0 (Colwell, 2013). Estimation of Chao1 is based on the concept that the number of species that remain undetected in a sample can be estimated from the number of rare species observed within that sample;

$$\widehat{S}_{Chao1} = S_{obs} + \left(\frac{n-1}{n}\right)\left(\frac{F_1(F_1-1)}{2(F_2+1)}\right),$$

where $\widehat{S}_{Chao1}$ is the estimated total tick species richness, S_{obs} is the observed tick species richness, n is the number of individual ticks