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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 collected, and F_1 and F_2 are respectively the number of tick species observed only once (singletons) or twice (doubletons) on a host species. Values of $\widehat{S}_{Chao1}$ approach S_{obs} when the accumulation of tick species on a host has reached an asymptote.

We used the exponential of Shannon entropy (Shannon, 1948; MacArthur, 1965) to estimate the "true diversity" (rather than simply species richness) of the tick assemblage for each host species, following Jost (2006). Adapted to species-level analyses, Shannon entropy is based on both the number and relative abundance of tick species on each host species, thereby taking into account that some ticks are more common than others (Shannon, 1948). Exponential transformation linearizes the index and allows for diversity to be measured in units of "effective number of species", i.e. numbers of equivalent, equally abundant species. In contrast to Shannon entropy, true diversity obeys the "doubling principle", so that a host species with twice as many equally abundant tick species is twice as diverse (Jost, 2006). We calculated true diversity over contingency tables with I rows of host species and J columns of tick species, using the R package 'bipartite' (Dormann et al., 2008);

$$\exp\left(H_i'\right) = \exp\left(-\sum\nolimits_{j=1}^{S_{obs}} p_{ij} * \ln p_{ij}\right),$$

where H_i' is the Shannon entropy of the tick assemblage on host species i, and P_{ij} is the proportion

of tick species j on host species i. Values of true diversity are equal to S_{obs} for tick assemblages that are perfectly even, i.e., when all tick species are equally abundant.

We used Czekanowski's proportional similarity index (Schoener, 1968; Feinsinger et al., 1981) to quantify the proportion of the total tick population that is supported by each host species, again using the R package 'bipartite' (Dormann et al., 2008). When adapted to species-level analysis, this index measures the area of overlap between the frequency distribution of the tick assemblage on host species i with that of the total tick population across all hosts (Feinsinger et al., 1981);

$$PS_i = 1 - 0.5 \sum_j \left| p_{ij} q_j \right|,$$

where PS_i is the proportional similarity index for host species i, and q_j is the proportion of tick species j in the total tick population. Values of PS_i range from q_j for host species that harbor only one tick species j to 1 for host species that harbor tick assemblages in direct proportion to the tick population as a whole.

2.4. Statistical analysis

Because singletons (i.e. tick species observed only once) were relatively common among the host species in our dataset, we first explored whether the three indices used were truly independent of sampling effort (i.e., number of host individuals examined). To test for this we performed multiple regressions of the three indices on host body size and sampling effort. To meet underlying statistical assumptions (i.e., linearity of relationship, statistical independence of errors, homoscedasticity of errors, and normality of error distribution), we $\log_{10}$-transformed host body size, sampling effort, and $\widehat{S}_{Chao1}$ estimates prior to analyses. We used a logit-transformation for the PS_i index as these values represent proportions. For the adult tick fauna, estimated total species richness ($\widehat{S}_{Chao1}$) and true diversity ($e^{H_i'}$) were positively related to sample size, but proportional similarity (PS_i) was not. For the immature tick fauna, all three indices were positively related to sample size (Supplementary file 1, Table 1). To account for this bias, we substituted each index – with the exception of PS_i for adult ticks – by its residual deviation from a linear regression on sample size, following Poulin (1995) and others (Morand and Poulin, 1998; Nunn et al., 2003; Krasnov et al., 2004; Ezenwa et al., 2006). Since these residuals reflect the deviation of expected values under the regression model, they are independent of sample size and can be used as corrected estimates of the three indices (Poulin, 1995).

Another confounding factor in comparative analyses is that closely related host species may have similar parasite assemblages and/or may share host traits such as body size through phylogenetic inertia (Felsenstein, 1985). That is, host species are expected to co-vary in proportion to the amount of time they share in evolutionary history and have only been evolving independently since they diverged from their most recent common ancestor. Treating host species that share much of their phylogenetic history as statistically independent observations is therefore inappropriate, leading to pseudoreplication and higher Type I error rates (Felsenstein, 1985; Harvey and Pagel, 1991; Poulin, 1995). We tested whether phylogenetic correction was needed by estimating Pagel's λ statistic for host body size and each index of the tick assemblage structure using the R package 'phytools' (Pagel, 1999; Revell, 2012). Pagel's λ is a scaling parameter that expresses the similarity of the covariances among species relative to the covariances expected under a Brownian motion model of trait evolution. Values range from $\lambda = 0$ (no phylogenetic association of traits) to $\lambda = 1$ (strong phylogenetic dependence) (Münkemüller et al., 2012). We used log-likelihood ratio tests (LRT) based on Chi-Squared distributions with 1 degree of freedom to determine whether maximum likelihood estimates of λ values for each trait were significantly different from zero (Freckleton et al., 2002). The LRT indicated that more closely related host species tended to have similar body sizes and tick assemblage structures, indicating that phylogenetic correction was necessary (Supplementary file 1, Table 2).

We corrected for dependence of data points by using Felsenstein's comparative method of phylogenetically independent contrasts (Felsenstein, 1985, 2008; Pagel, 1992). Assuming a Brownian motion model of trait evolution, this method uses phylogenetic information to contrast the values of all pairs of sister host taxa. Original tip data (i.e., the mean values for a set of host species) are thereby transformed into values that are statistically independent and identically distributed. We computed contrasts using the R package 'ape' (Paradis et al., 2004). Specifically, we implemented

Table 1
Summary of the tick-host datasets: number of host orders and species that were sampled, number of observed tick species, and number of records (i.e., tick-host associations) per host group.

	Adult ticks dataset				Immature ticks dataset			
	# Host orders	# Host species	# Tick species	# records	# Host orders	# Host species	# Tick species	# Tick records
Birds	5	8	7	41	7	68	12	175
Mammals	10	51	38	5215	9	55	27	2252
Reptiles	2	13	2	182	1	5	3	45
Amphibians	1	1	1	56	1	2	3	4

Table 2
Unpublished tick-host associations used in this study.

	Amblyomma auricularium	*Amblyomma dissimile*	*Amblyomma geayi*	*Amblyomma longirostre*	*Amblyomma mixtum*	*Amblyomma naponense*	*Amblyomma oblongoguttatum*	*Amblyomma ovale*	*Amblyomma pacae*
Host species (larvae)									
Artiodactyla									
Bos indicus	0	0	0	0	0	0	0	0	0
Carnivora									
Canis familiaris	0	0	0	0	0	0	0	0	0
Didelphimorphia									
Didelphis marsupialis	15	15	19	1	11	1	0	6	31
Marmosa robinsoni	0	0	1	0	0	0	0	0	0
Metachirus nudicaudatus	0	0	0	0	0	0	0	0	1
Philander opossum	4	0	0	0	0	0	0	0	1
Rodentia									
Hoplomys gymnurus	2	0	0	0	0	1	0	5	4
Proechimys semispinosus	7	16	8	0	0	2	0	15	1
Transandinomys talamancae	0	0	0	0	0	0	0	0	0
Squamata									
Ameiva sp.	0	0	0	0	0	0	0	0	0
Total	28	31	28	1	11	4	0	26	38
Hosts species (nymphs)									
Anura									
Rhinella alata	0	0	0	0	0	0	0	0	0
Rhinella marina	0	1	0	0	0	0	0	0	0
Artiodactyla									
Bos indicus	0	0	0	0	0	0	0	0	0
Pecari tajacu	0	0	0	0	0	2	2	0	0
Carnivora									
Canis familiaris	3	0	0	0	4	0	7	14	0
Nasua narica	0	0	0	0	0	0	0	0	0
Didelphimorphia									
Didelphis marsupialis	37	2	3	0	31	0	1	18	7
Metachirus nudicaudatus	0	0	0	0	0	0	0	0	0
Philander opossum	7	1	0	0	0	0	0	1	2
Perissodactyla									
Equus ferus caballus	0	0	0	0	34	0	3	0	0
Pilosa									
Tamandua mexicana	0	0	0	0	0	0	0	0	0
Primates									
Alouatta palliata	0	0	1	0	0	0	0	0	0
Homo sapiens	0	0	0	0	0	0	0	0	0
Rodentia									
Dasyprocta punctata	0	0	0	0	0	13	3	1	0
Hoplomys gymnurus	2	0	0	0	1	0	0	18	0
Hydrochoerus isthmius	0	0	0	0	1	0	0	0	0
Melanomys caliginosus	0	0	0	0	0	0	0	1	0
Proechimys semispinosus	9	0	0	0	1	1	0	54	0
Transandinomys bolivari	0	0	0	0	0	0	0	4	0
Transandinomys talamancae	0	0	0	0	0	0	0	8	0
Squamata									
Ameiva sp.	0	0	0	0	0	0	0	0	0
Basiliscus basiliscus	0	4	0	0	0	0	0	0	0
Boa constrictor	0	2	0	0	0	0	0	0	0
Iguana iguana	0	12	0	0	0	0	0	0	0
Leptophis depressirostris	0	0	0	0	0	0	0	0	0
Total	58	22	4	0	72	16	16	119	9

the recently extended version of Felsenstein's method, in which an orthonormal transformation is applied to compute contrasts with standardized coefficients (Felsenstein, 2008). Phylogenies of the vertebrate species in our data set follow the taxonomy of Wilson and Reeder (2005) with additional resolution derived from several sources (Supplementary file 1, Fig. 1). The resulting host phylogenies for the adult and immature tick datasets had respectively 19 and 22 taxonomic levels above species. Accurate branch length information were not available for the whole phylogenetic trees and we therefore set all branch lengths to unity. Because the method of independent contrasts requires a fully bifurcating tree, we randomly resolved polytomies into series of bifurcations with zero length branches, following Purvis and Garland (1993). Previous studies have shown that both Pagel's λ statistic and the independent contrasts method are robust to polytomies, missing branch length information, and evolutionary models different from Brownian motion (Diaz-Uriarte and Garland, 1998; Münkemüller et al., 2012). Relationships between contrasts of host body size and tick assemblage structure were tested using linear models forced through the origin, following Garland et al. (Garland et al., 1992). To evaluate the influence of phylogenetically controlled analyses, we also ran non-phylogenetic analyses using the actual species traits. All analyses were carried out with the R statistical software, version 3.2.4 (R Core Team, 2014).

3. Results

The final dataset for adult ticks included 5494 records,

Amblyomma parvum	*Amblyomma pecarium*	*Amblyomma sabanerae*	*Amblyomma tapirellum*	*Amblyomma varium*	*Haemaphysalis juxtakochi*	*Ixodes affinis*	*Ornithodoros puertoricensis*	*Rhipicephalus microplus*	*Rhipicephalus sanguineus s.l.*
Host species (larvae)									
Artiodactyla									
0	0	0	0	0	0	0	0	10	0
Carnivora									
0	0	0	0	0	0	0	0	0	9
Didelphimorphia									
0	0	81	0	4	71	0	0	0	0
0	0	3	0	0	0	1	0	0	0
0	0	19	0	0	0	0	0	0	0
0	0	24	0	0	0	0	0	0	0
Rodentia									
0	0	26	0	0	3	0	0	0	0
0	0	16	0	5	57	0	52	0	0
0	0	3	0	0	0	0	0	0	0
Squamata									
0	0	0	0	0	0	11	0	0	0
0	0	172	0	9	131	12	52	10	9
Hosts species (nymphs)									
Anura									
0	0	1	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
Artiodactyla									
0	0	0	0	0	0	0	0	18	3
0	6	0	6	0	4	0	0	0	0
Carnivora									
1	0	0	0	0	0	0	0	0	121
0	0	0	0	0	7	0	0	0	0
Didelphimorphia									
0	0	71	1	0	23	0	0	0	0
0	0	9	0	0	4	0	0	0	0
0	0	9	0	0	0	0	0	0	0
Perissodactyla									
0	0	0	0	0	0	0	0	0	0
Pilosa									
0	0	0	0	0	1	0	0	0	0
Primates									
0	0	0	0	0	0	0	0	0	0
0	1	0	20	1	10	0	0	0	0
Rodentia									
0	0	0	5	0	40	0	0	0	0
0	0	1	0	0	6	0	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	70	0	1	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	1	0	0	0
Squamata									
0	0	0	0	0	0	15	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	0
1	7	93	32	1	165	16	1	18	124

comprising 211 unique tick-host combinations among 41 tick species from 8 genera and 71 host species from 18 orders. The final dataset for immature ticks included 2476 records, comprising 246 unique tick-host combinations among 30 tick species from 8 genera and 130 host species from 18 orders. Both datasets contained tick species from the same genera, (i.e., Amblyomma, Antricola, Argas, Dermacentor, Haemaphysalis, Ixodes, Ornithodoros, and Rhipicephalus) as well as representatives from a diverse range of vertebrate host taxa (i.e., birds, mammals, reptiles, and amphibians), and are available as supplementary file 2. In the adult tick dataset, mammals were the best represented group in terms of taxonomic diversity of both host and tick species, as well as in having the largest number of records (Table 1). In the immature tick dataset, birds were the taxonomically most diverse host group, but mammals had the highest diversity of tick species and the largest number of records (Table 1).

More than half (54%) of the records for immature ticks (562 larvae and 776 nymphs) consisted of unpublished data, including a considerable number of tick-host associations that have never been recorded in the literature (Table 2). This is mostly due to the fact that the larvae and nymphs of several tick species in our dataset (e.g., *Amblyomma pecarium*, *A. sabanerae*, *A. tapirellum*) remain as of yet undescribed morphologically, while many others have been described only recently (see Guglielmone et al., 2014). The use of DNA sequencing allowed us to identify the immature stages of these tick species and their respective host associations. New host records include Didelphidae (Didelphimorphia) for larvae of *A. geayi*, *A. longirostre*, *A. naponense*, *A. pacae*, *A. sabanerae*, and for

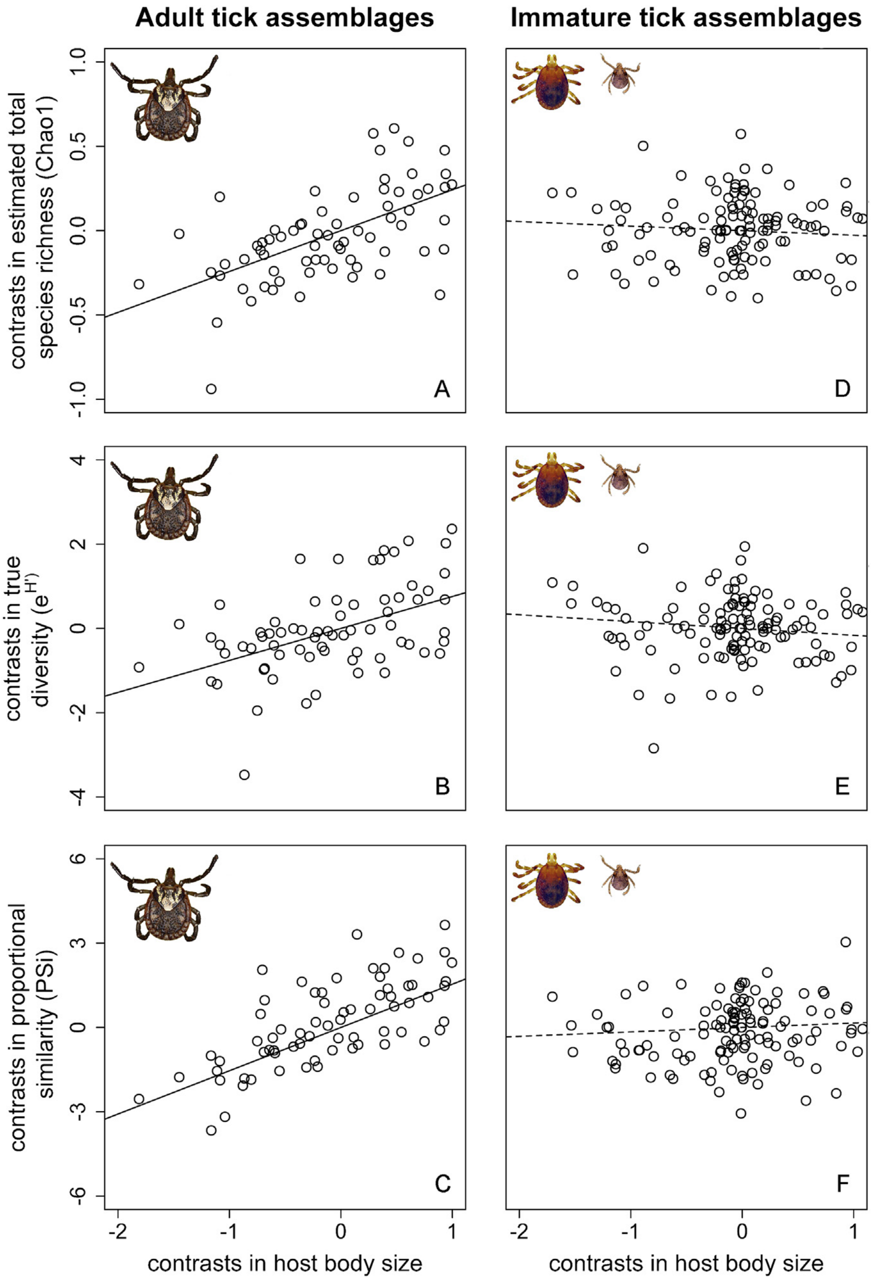

Fig. 1. Relationship between host body size and the structure of adult and immature tick assemblages. Estimated total species richness (a), true diversity (b), and proportional similarity (c) of adult tick assemblages were significantly related to host body size, but no such relationships were found for immature tick assemblages (d–f). Plotted values are phylogenetically independent contrasts. Regressions were run through the origin and corrected for sampling effort.

nymphs of *A. oblongoguttatum, A. tapirellum*, *A. sabanerae*; Echimyidae (Rodentia) for larvae of *A. geayi*, *A. pacae*, *A. naponense, A. sabanerae*, *A. varium*, and for nymphs of *A. naponense, A. sabanerae*, *A. varium;* Dasyproctidae (Rodentia) for nymphs of *A. naponense*, *A. oblongoguttatum*, *A. tapirellum*; Tayassuidae (Artiodactyla) for nymphs of *A. pecarium*, *A. tapirellum*; Atelidae (Primates) for nymphs of *A. geayi*; Equidae (Perissodactyla) for nymphs of *A. oblongoguttatum*; Colubridae (Squamata) and Cricetidae (Rodentia) for larvae and nymphs of *A. sabanerae*; and Teiidae (Squamata) for larvae and nymphs of *Ixodes affinis*. We also report, for the first time, human infestation with nymphs of *A. geayi* and *A. varium* (Table 2).

Estimates of total species richness ($\widehat{S}_{Chao1}$), true diversity ($e^{H_i'}$), proportional similarity (PS_i), and host body size were positively-skewed and shared similar ranges for both adult and immature ticks faunas. However, the medians were significantly different (Table 3). For adults, for example, the 21% ‘richest host species’ (for which $\widehat{S}_{Chao1} \geq 5$) together harbored 71% of all adult tick species. Likewise, for immature ticks, the 18% ‘richest host species’ (for which $\widehat{S}_{Chao1} \geq 3$) together harbored 80% of all immature tick species. Thus, a small proportion of the host species sustained a large proportion of the tick species.

Host body size was positively related to the estimated total species richness (Fig. 1a), true diversity (Fig. 1b), and proportional similarity (Fig. 1c) of adult tick assemblages after controlling for the effects of sampling effort and host phylogeny. No such relationship was found for immature tick assemblages (Fig. 1d–f, Table 4). Similar results with only marginal differences were obtained when

Table 3
Summary statistics for the assemblage structure of adult and immature tick fauna and host body size.

Variables	Adult ticks			Immature ticks			Mann-whitney test[a]	
	range	Median	Skewness	range	Median	Skewness	*U*	*P*-value
Tick assemblage structure								
Estimated total species richness	1–16.99	2	2.28	1–18.99	1	4.46	5614.5	0.005
True diversity	1–8.09	1.30	2.29	1–6.85	1	2.46	5375	0.034
Proportional similarity	~0.00–0.46	0.06	1.18	~0.00–0.54	0.04	2.10	5239	0.113
Host body size	4–7917.86	208.01	4.26	2.52–7917.86	13.12	7.36	7666.5	<0.001

[a] The Mann-Whitney U tests are for differences in the medians between adult and immature tick faunas.

Table 4
Results of linear regression between host body size and tick assemblage structure. Results are separated for non-phylogenetic (species values) and phylogenetically controlled (independent contrasts) analyses. Both analyses were controlled for sampling effort.

Tick assemblage structure	Species values				Independent contrasts			
	F ratio (df)	β	*P*	R^2_{adj}	*F* ratio (df)	β	*P*	R^2_{adj}
Adult tick fauna	(1, 69)				(1, 69)			
Estimated total species richness	37.43	0.24	<0.001	0.34	36.88	0.24	<0.001	0.34
True diversity	21.62	0.75	<0.001	0.23	21.97	0.76	<0.001	0.23
Proportional similarity	77.31	1.77	<0.001	0.52	59.91	1.54	<0.001	0.46
Immature tick fauna	(1, 128)				(1, 128)			
Estimated total species richness	2.89	−0.04	0.092	0.01	0.34	−0.01	0.559	−0.01
True diversity	3.33	−0.19	0.070	0.02	1.59	−0.12	0.210	<0.01
Proportional similarity	0.08	0.04	0.782	−0.01	2.08	0.19	0.152	0.01

we did not control for host phylogeny (Table 4). When we repeated the analyses with only those host species for which at least 10 individuals were examined, the positive relationships for adult ticks became even stronger, whereas any relationship between host body size and tick assemblage structure was still lacking for immature ticks (Supplementary file 1, Table 3).

4. Discussion

Our study provides the first empirical evidence for an increase of species richness and diversity of adult tick assemblages with host body size across a wide range of vertebrate host taxa. The proportional similarity of adult tick assemblages also increased with host body size, indicating that larger host species sustained a larger portion of the total adult tick fauna than smaller host species. In contrast, no such relationships were found for immature ticks, indicating that their assemblage structure is independent of host body size. Correcting for host phylogeny did not alter these relationships. These findings suggest that the adult ticks in this highly diverse system preferentially parasitize larger-bodied host species, whereas the immature ticks may potentially have a more opportunistic feeding strategy.

The contrasting results for adult and immature ticks stresses the importance of analyzing their respective host associations independently. Lumping different transmission stages for parasites with complex life cycles may cloud any stage-specific relationship of parasite richness with host body size, particularly if those species are indirectly transmitted (Arneberg, 2002). This is clearly demonstrated by our study, in which we found strong relationships of host body size with tick assemblage structure for adult ticks, but not for immature ticks. When host associations for adult and immature ticks were combined, all relationships became non-significant (results not shown). Such lumping could also explain the discrepancies among comparative studies of other parasite groups across a range of birds, mammals, reptiles, amphibians, and fish. While the host body size – parasite species richness relationship was positive in some studies (Gregory et al., 1996; Arneberg, 2002; Ezenwa et al., 2006; Huang et al., 2014), it was less consistent (Poulin, 1995; Hughes and Page, 2007; Kiffner et al., 2014) or even absent in others (Feliu et al., 1997; Morand and Poulin, 1998; Clayton and Walther, 2001; Stanko et al., 2002; Nunn et al., 2003; Krasnov et al., 2004) after host phylogeny was controlled for. Future comparative studies should therefore account for potential variation among different transmission stages by analyzing their host associations separately.

What might explain the discrepancy between the host body size – tick diversity patterns between adult and immature ticks? A plausible explanation is higher host specificity in adult ticks for species with a multi-host life cycle. Most of the tick species in our dataset follow a three-host life cycle, in which larvae, nymphs and adults feed from different host individuals that may belong to distinct species (Guglielmone et al., 2014). While immature ticks use these hosts only for feeding, the adults of many tick species also use hosts for finding a mating partner. This difference might drive selection for more host-specific feeding, apparently for larger-bodied species, in adult ticks and more opportunistic feeding in immature ticks (Espinaze et al., 2015).

In addition, several morphological and physiological characteristics of adult ticks may facilitate specificity for larger-bodied host species. Adult ticks have larger surface area to volume ratios and are therefore less sensitive to water stress, a major cause of mortality, than the smaller immature ticks (Randolph and Storey, 1999). This difference in desiccation risk is reflected by the vertical position at which adult and immature ticks quest for a host: immature ticks tend to stay closer to the more moist conditions at the base of the vegetation, thereby having access to host species of all body sizes, whereas adult ticks quest in higher vegetation layers, where they may miss the smaller host species (Randolph and Storey, 1999). Adult ticks also have higher fat reserves and a slower metabolic rate than immature ticks, allowing them to quest and survive for longer periods of time, which in turn increases their chances of encountering large-bodied host species that typically have lower population densities (Randolph, 2004).

A meta-analysis on host specificity in Neotropical hard ticks indeed showed that immature ticks tend to be less host-specific than their adult counterparts (Nava and Guglielmone, 2013). One hypothesis put forward by the authors is that larvae and nymphs may have greater adaptive plasticity than adult ticks (Nava and

Guglielmone, 2013). However, a recent experimental test showed that while immature ticks were less discriminating in their host choice than adults, their engorgement success and survival rates dropped drastically when feeding on atypical host species (Dietrich et al., 2014). Thus, there should be at least some selection for host use during the immature life stages as well, so that one would expect a relationship, albeit weak, between the assemblage structure of immature ticks and host traits such as body size. Variation in the quality of our dataset could partially account for the lack of such relationship. Over half of our immature tick data originate from published sources that had different objectives and therefore different sampling protocols. Further, while adult ticks are easily spotted and identified morphologically, immature ticks are more easily missed and, in our study region, notoriously difficult to identify based on morphology. As a result, most published studies typically report only a small number of identified immature ticks. Future studies that aim to identify much larger samples of the immature tick fauna on a given host species are much needed if we are to elucidate which host traits determine the assemblage structure of immature ticks.

Alternatively, the assemblage structure of immature ticks may be related to specific host traits that vary *among* individuals of a host species rather than *across* host species. For example, physiological and/or behavioral differences between male and female hosts may explain why some studies found sex-biased parasitism, usually towards male hosts, in both Ixodid and Argasid immature ticks (Krasnov et al., 2012). Tick assemblage structure may also show temporal and/or spatial variability, but few studies have examined these variations in the tropics (Lareschi and Krasnov, 2010). Future comparative studies in tropical regions should target specific host species for which detailed information can be collected through space and time, including individual host traits (e.g. sex, age, reproductive status) and environmental conditions (e.g. relative humidity, ambient temperature, season). Such studies are then able to test for the independent effects of both intrinsic (host-related) and extrinsic (environmental) factors on the structure of tick assemblages.

Finally, our findings provide additional confirmation that tick-host interactions follow the Pareto principle (Woolhouse et al., 1997), i.e., that a minority of host species harbor a majority of tick species. The highly skewed distribution in which parasites and pathogens are dispersed over their hosts has previously been demonstrated for tick burdens (Kiffner et al., 2011b; Marsot et al., 2012) and tick-borne disease transmission (Perkins et al., 2003). Our results indicate that the same principle also applies to tick species richness, with approximately 20% of the host species harboring 80% of all tick species, a pattern also known as the ‘20/80’ rule (Woolhouse et al., 1997).

The findings of our study are relevant for human and veterinary health as well as biodiversity conservation. We show that adult ticks preferentially feed from larger-bodied host species, which suggests that humans and livestock have an increased risk of acquiring tick bites from a wide range of species. On the other hand, large species of wildlife tend to be disproportionally affected by anthropogenic disturbances such as habitat loss and fragmentation (Cardillo et al., 2005). Loss of these species is therefore likely to result in host-tick coextinction events, even if immature stages feed opportunistically (Lafferty, 2012). As parasites play critical roles in ecological and evolutionary processes, such losses may profoundly affect ecosystem functioning as well as the long-term persistence of vertebrate hosts by indirectly favoring generalist parasites and pathogens (Gómez and Nichols, 2013).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ijppaw.2016.10.001.

References

Altizer, S., Nunn, C.L., Thrall, P.H., Gittleman, J.L., Antonovics, J., Cunningham, A.A., Cunnningham, A.A., Dobson, A.P., Ezenwa, V., Jones, K.E., Pedersen, A.B., Poss, M., Pulliam, J.R.C., 2003. Social organization and parasite risk in mammals: integrating theory and empirical studies. Ann. Rev. Ecol. Evol. S 34, 517–547.

Anderson, K., Ezenwa, V.O., Jolles, A.E., 2013. Tick infestation patterns in free ranging African buffalo (Syncercus caffer): effects of host innate immunity and niche segregation among tick species. Int. J. Parasitol. Parasites Wildl. 2, 1–9.

Anderson, R.M., May, R.M., 1978. Regulation and stability of host-parasite population interactions: I. Regulatory processes. J. Anim. Ecol. 219–247.

Apanaskevich, D.A., Bermúdez, S.E., 2013. Description of a new *Dermacentor* (Acari: Ixodidae) species, a parasite of wild mammals in Central America. J. Med. Entomol. 50, 1190–1201.

Arneberg, P., 2002. Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. Ecography 25, 88–94.

Arner, A.J., 2012. The Curious Case of the Cane Toad (Rhinella Marina): an Assessment of Exploratory Behavior and Foraging Success of an Invasive Vertebrate in a Novel Environment. Master thesis. Texas Tech University.

Bermúdez, S.E., Torres, S., Aguirre, Y., Domínguez, L., Bernal, J., 2015a. A review of *Ixodes* (Acari: Ixodidae) parasitizing wild birds in Panama, with the first records of *Ixodes auritulus* and *Ixodes bequaerti*. Syst. Appl. Acarol. 20, 847–853.

Bermúdez, S.E., Esser, H.J., Miranda, R., Moreno, R., 2015b. Wild carnivores (Mammalia) as hosts for ticks (Ixodida) in Panama. Syst. Appl. Acarol. 20, 13–19.

Bermúdez, S.E., Miranda, R., Kadoch, N., 2013. Reporte de larvas de *Ornithodoros puertoricensis* Fox 1947 (Ixodida: Argasidae) parasitando a *Rhinella marina* (L. 1758) (Anura: Bufonidae) en David, Chiriquí, Panamá. Puente Biológico 5, 81–85.

Bermúdez, S.E., Eremeeva, M.E., Karpathy, S.E., Samudio, F., Zambrano, M.L., Zaldivar, Y., Motta, J.A., Dasch, G.A., 2009. Detection and identification of Rickettsial agents in ticks from domestic mammals in eastern Panama. J. Med. Entomol. 46, 856–861.

Bermúdez, S.E., Miranda, R.J., Smith, D., 2010. Tick species (Ixodida) in the summit municipal park and adjacent areas, Panama City, Panama. Exp. Appl. Acarol. 52, 439–448.

Bermúdez, S.E., Zaldivar, Y., Spolidorio, M.G., Moraes-Filho, J., Miranda, R.J., Caballero, C.M., Mendoza, Y., Labruna, M.B., 2011. Rickettsial infection in domestic mammals and their ectoparasites in El Valle de Antón; Colcé; Panamá. Vet. Parasitol. 177, 134–138.

Blackburn, T.M., Brown, V.K., Doube, B.M., Greenwood, J.J., Lawton, J.H., Stork, N.E., 1993. The relationship between abundance and body size in natural animal assemblages. J. Anim. Ecol. 519–528.

Brunner, J.L., Ostfeld, R.S., 2008. Multiple causes of variable tick burdens on small-mammal hosts. Ecology 89, 2259–2272.

Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R., Sechrest, W., Orme, C.D.L., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species. Science 309, 1239–1241.

Chao, A., 1984. Nonparametric estimation of the number of classes in a population. Scand. J. Stat. 11, 265–270.

Clayton, D., Walther, B.A., 2001. Influence of host ecology and morphology on the diversity of Neotropical bird lice. Oikos 94, 455–467.

Colwell, R.K., 2013. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. Version 9. User's Guide and application published at. http://purl.oclc.org/estimates (accessed 16.06.16.).

De Magalhães, J., Costa, J., 2009. A database of vertebrate longevity records and their relation to other life-history traits. J. Evol. Biol. 22, 1770–1774.

Diaz-Uriarte, R., Garland, T., 1998. Effects of branch length errors on the performance of phylogenetically independent contrasts. Syst. Biol. 47, 654–672.

Dietrich, M., Lobato, E., Boulinier, T., McCoy, K., 2014. An experimental test of host specialisation in a ubiquitous polar ectoparasite: a role for adaptation? J. Anim. Ecol. 83, 576–587.

Dormann, C.F., Gruber, B., Fründ, J., 2008. Introducing the bipartite package: analysing ecological networks. R. News 8, 8–11.

Dunn, L.H., 1923. The ticks of Panama, their hosts, and the diseases they transmit. Am. J. Trop. Med. 3, 91–104.

Dunning, J.B.J., 2007. CRC Handbook of Avian Body Masses, second ed. CRC Press, Boca Raton, Florida.

Eisenberg, J.F., 1989. Mammals of the Neotropics. In: The Northern Neotropics: Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana, vol. 1. The University of Chicago Press, Chicago.

Espinaze, M.P., Hellard, E., Horak, I.G., Cumming, G.S., 2015. Analysis of large new South African dataset using two host-specificity indices shows generalism in both adult and larval ticks of mammals. Parasitology 1–8.

Esser, H.J., Herre, E.A., Blüthgen, N., Loaiza, J.R., Bermúdez, S.E., Jansen, P.A., 2016. Host specificity in a diverse Neotropical tick community: an assessment using quantitative network analysis and host phylogeny. Parasite. Vector 9 (pp).

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.

Fairchild, G.B., Kohls, G.M., Tipton, V.J., 1966. The ticks of Panama (Acarina: Ixodidea). In: Wenzel, R.L., Tipton, V.J. (Eds.), Ectoparasites of Panama. Field Museum of Natural History, Chicago, pp. 167–219.

Feinsinger, P., Spears, E.E., Poole, R.W., 1981. A simple measure of niche breadth. Ecology 62, 27–32.

Feldman, A., Meiri, S., 2013. Length–mass allometry in snakes. Biol. J. Linn. Soc. 108, 161–172.

Feliu, C., Renaud, F., Catzeflis, F., Hugot, J.-P., Durand, P., Morand, S., 1997. A comparative analysis of parasite species richness of Iberian rodents. Parasitology 115, 453–466.

Felsenstein, J., 1985. Phylogenies and the comparative method. Am. Nat. 125, 1–15.

Felsenstein, J., 2008. Comparative methods with sampling error and within-species variation: contrasts revisited and revised. Am. Nat. 171, 713–725.

Freckleton, R.P., Harvey, P.H., Pagel, M., 2002. Phylogenetic analysis and comparative data: a test and review of evidence. Am. Nat. 160, 712–726.

Gallivan, G., Horak, I., 1997. Body size and habitat as determinants of tick infestations of wild ungulates in South Africa. S. Afr. J. Wildl. Res. 27, 63–70.

García, G.G., Castro, A., Rodriguez, I., Bermúdez, S.E., 2014. Ixodid ticks of *Hydrochaeris isthmius* goldman 1912 (Rodentia: Caviidae) in Panama. Syst. Appl. Acarol. 19, 404–408.

Garland, T., Harvey, P.H., Ives, A.R., 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst. Biol. 41, 18–32.

Gómez, A., Nichols, E., 2013. Neglected wild life: parasitic biodiversity as a conservation target. Int. J. Parasitol. Parasites Wildl. 2, 222–227.

Greer, K.A., Canterberry, S.C., Murphy, K.E., 2007. Statistical analysis regarding the effects of height and weight on life span of the domestic dog. Res. Vet. Sci. 82, 208–214.

Gregory, R.D., Keymer, A.E., Harvey, P.H., 1996. Helminth parasite richness among vertebrates. Biodivers. Conserv. 5, 985–997.

Guglielmone, A.A., Robbins, R.G., Apanaskevich, D.A., Petney, T.N., Estrada-Peña, A., Horak, I., 2014. The Hard Ticks of the World. Springer, Dordrecht.

Harrison, A., Scantlebury, M., Montgomery, W.I., 2010. Body mass and sex-biased parasitism in wood mice *Apodemus sylvaticus*. Oikos 119, 1099–1104.

Harvey, P.H., Pagel, M.D., 1991. The Comparative Method in Evolutionary Biology. Oxford university press, Oxford.

Heylen, D., Adriaensen, F., Van Dongen, S., Sprong, H., Matthysen, E., 2013. Ecological factors that determine *Ixodes ricinus* tick burdens in the great tit (*Parus major*), an avian reservoir of *Borrelia burgdorferi s.l.* Int. J. Parasitol. 43, 603–611.

Hofmeester, T.R., Coipan, E.C., van Wieren, S.E., Prins, H.H.T., Takken, W., Sprong, H., 2016. Few vertebrate species dominate the *Borrelia burgdorferi* s.l. life cycle. Environ. Res. Lett. 11 (043001).

Huang, S., Bininda-Emonds, O.R., Stephens, P.R., Gittleman, J.L., Altizer, S., 2014. Phylogenetically related and ecologically similar carnivores harbour similar parasite assemblages. J. Anim. Ecol. 83, 671–680.

Hughes, J., Page, R.D., 2007. Comparative tests of ectoparasite species richness in seabirds. BMC Evol. Biol. 7, 1.

Hughes, V.L., Randolph, S.E., 2001. Testosterone depresses innate and acquired resistance to ticks in natural rodent hosts: a force for aggregated distributions of parasites. J. Parasitol. 87, 49–54.

Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375.

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. Biol. Rev. 89, 123–134.

Kiffner, C., LÖDige, C., Alings, M., Vor, T., Rühe, F., 2011a. Body-mass or sex-biased tick parasitism in roe deer (*Capreolus capreolus*)? A GAMLSS approach. Med. Vet. Entomol. 25, 39–45.

Kiffner, C., Stanko, M., Morand, S., Khokhlova, I.S., Shenbrot, G.I., Laudisoit, A., Leirs, H., Hawlena, H., Krasnov, B.R., 2014. Variable effects of host characteristics on species richness of flea infracommunities in rodents from three continents. Parasitol. Res. 113, 2777–2788.

Kiffner, C., Vor, T., Hagedorn, P., Niedrig, M., Rühe, F., 2011b. Factors affecting patterns of tick parasitism on forest rodents in tick-borne encephalitis risk areas. Ger. Parasitol. Res. 108, 323–335.

Krasnov, B.R., Bordes, F., Khokhlova, I.S., Morand, S., 2012. Gender-biased parasitism in small mammals: patterns, mechanisms, consequences. Mammalia 76, 1–13.

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'. J. Anim. Ecol. 73, 1121–1128.

Kuris, A.M., Blaustein, A.R., Alio, J.J., 1980. Hosts as islands. Am. Nat. 116, 570–586.

Lafferty, K.D., 2012. Biodiversity loss decreases parasite diversity: theory and patterns. Philos. T. Roy. Soc. B 367, 2814–2827.

Lareschi, M., Krasnov, B.R., 2010. Determinants of ectoparasite assemblage structure on rodent hosts from South American marshlands: the effect of host species, locality and season. Med. Vet. Entomol. 24, 284–292.

Lee, K.A., 2006. Linking immune defenses and life history at the levels of the individual and the species. Integr. Comp. Biol. 46, 1000–1015.

MacArthur, R.H., 1965. Patterns of species diversity. Biol. Rev. 40, 510–533.

Marsot, M., Henry, P.-Y., Vourc'h, G., Gasqui, P., Ferquel, E., Laignel, J., Grysan, M., Chapuis, J.-L., 2012. Which forest bird species are the main hosts of the tick, *Ixodes ricinus*, the vector of *Borrelia burgdorferi* sensu lato, during the breeding season? Int. J. Parasitol. 42, 781–788.

Martins, T.F., Onofrio, V.C., Barros-Battesti, D.M., Labruna, M.B., 2010. Nymphs of the genus *Amblyomma* (Acari: Ixodidae) of Brazil: descriptions, redescriptions, and identification key. Ticks Tick. Borne Dis. 1, 75–99.

Meiri, S., 2010. Length–weight allometries in lizards. J. Zoology 281, 218–226.

Miller, M.J., Esser, H.J., Loaiza, J.R., Herre, E.A., Aguilar, C., Quintero, D., Alvarez, E., Bermingham, E., 2016. Molecular ecological insights into Neotropical bird–tick Interactions. PLoS ONE 11, e0155989.

Morand, S., Poulin, R., 1998. Density, body mass and parasite species richness of terrestrial mammals. Evol. Ecol. 12, 717–727.

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., Thuiller, W., 2012. How to measure and test phylogenetic signal. Methods Ecol. Evol. 3, 743–756.

Murgas, I.L., Castro, A.M., Bermúdez, S.E., 2013. Current status of *Amblyomma ovale* (Acari: Ixodidae) in Panama. Ticks Tick. Borne Dis. 4, 164–166.

Nava, S., Guglielmone, A.A., 2013. A meta-analysis of host specificity in Neotropical hard ticks (Acari: Ixodidae). Bull. Entomol. Res. 103, 216–224.

Nava, S., Beati, L., Labruna, M.B., Cáceres, A.G., Mangold, A.J., Guglielmone, A.A., 2014. Reassessment of the taxonomic status of *Amblyomma cajennense* (Fabricius, 1787) with the description of three new species, *Amblyomma tonelliae* n. sp., *Amblyomma interandinum* n. sp. and *Amblyomma patinoi* n. sp., and reinstatement of *Amblyomma mixtum* Koch, 1844, and *Amblyomma sculptum* Berlese, 1888 (Ixodida: Ixodidae). Ticks Tick. Borne Dis. 5, 252–276.

Nunn, Charles L., Altizer, S., Jones, K.E., Sechrest, W., 2003. Comparative tests of parasite species richness in primates. Am. Nat. 162, 597–614.

Pagel, M., 1999. Inferring the historical patterns of biological evolution. Nature 401, 877–884.

Pagel, M.D., 1992. A method for the analysis of comparative data. J. Theor. Biol. 156, 431–442.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20, 289–290.

Patterson, B.D., Costa, L.P., 2012. Introduction to the history and geography of Neotropical mammals. In: Patterson, B.D., Costa, L.P. (Eds.), Bones, Clones, and Biomes: the History and Geography of Recent Neotropical Mammals. The University of Chicago Press, Chicago, pp. 1–4.

Perkins, S.E., Cattadori, I.M., Tagliapietra, V., Rizzoli, A.P., Hudson, P.J., 2003. Empirical evidence for key hosts in persistence of a tick-borne disease. Int. J. Parasitol. 33, 909–917.

Pollock, N.B., Vredevoe, L.K., Taylor, E.N., 2012. How do host sex and reproductive state affect host preference and feeding duration of ticks? Parasitol. Res. 111, 897–907.

Poulin, R., 1995. Phylogeny, ecology, and the richness of parasite communities in vertebrates. Ecol. Monogr. 65, 283–302.

Poulin, R., 2004. Macroecological patterns of species richness in parasite assemblages. Basic Appl. Ecol. 5, 423–434.

Purvis, A., Garland, T., 1993. Polytomies in comparative analyses of continuous characters. Syst. Biol. 42, 569–575.

R Core Team, 2014. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Randolph, S.E., 2004. Tick ecology: processes and patterns behind the epidemiological risk posed by ixodid ticks as vectors. Parasitology 129, S37–S65.

Randolph, S.E., Storey, K., 1999. Impact of microclimate on immature tick-rodent host interactions (Acari: Ixodidae): implications for parasite transmission. J. Med. Entomol. 36, 741–748.

Reid, F., 2009. A Field Guide to the Mammals of Central America and Southeast Mexico. Oxford University Press, New York.

Revell, L.J., 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3, 217–223.

Ridgely, R.S., Gwynne, J.A., 1989. A Guide to the Birds of Panama: with Costa Rica, Nicaragua, and Honduras, second ed. Princeton University Press, Princeton.

Schoener, T.W., 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49, 704–726.

Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27, 379–423.

Smith, F.A., Lyons, S.K., Ernest, S.M., Jones, K.E., Kaufman, D.M., Dayan, T., Marquet, P.A., Brown, J.H., Haskell, J.P., 2003. Body mass of late quaternary mammals: ecological archives E084-094. Ecology 84, 3403.

Sonenshine, D.E., 1991. Biology of Ticks. Oxford University Press, New York.

Stanko, M., Miklisová, D., Goüy de Bellocq, J., Morand, S., 2002. Mammal density and patterns of ectoparasite species richness and abundance. Oecologia 131, 289–295.

Tälleklint, L., Jaenson, T.G.T., 1997. Infestation of mammals by *Ixodes ricinus* ticks (Acari: Ixodidae) in south-central Sweden. Exp. Appl. Acarol. 21, 755–771.

Venzal, J.M., Estrada-Peña, A., Mangold, A.J., González-Acuña, D., Guglielmone, A.A., 2008. The *Ornithodoros (Alectorobius) talaje* species group (Acari: Ixodida: Argasidae): description of *Ornithodoros (Alectorobius) rioplatensis* n. sp. from southern South America. J. Med. Entomol. 45, 832–840.

Vor, T., Kiffner, C., Hagedorn, P., Niedrig, M., Rühe, F., 2010. Tick burden on European roe deer (*Capreolus capreolus*). Exp. Appl. Acarol. 51, 405–417.

West, G.B., Brown, J.H., Enquist, B.J., 1999. The fourth dimension of life: fractal geometry and allometric scaling of organisms. Science 284, 1677–1679.

Wilson, K., Bjørnstad, O., Dobson, A., Merler, S., Poglayen, G., Randolph, S., Read, A., Skorping, A., 2002. Heterogeneities in macroparasite infections: patterns and processes. In: Hudson, P.J., Rizzoli, A., Grenfell, B.T., Heesterbeek, H., Dobson, A.P. (Eds.), The Ecology of Wildlife Diseases. Oxford University Press, pp. 6–44.

Wilson, D.E., Reeder, D.M., 2005. Mammal Species of the World: a Taxonomic and Geographic Reference. John Hopkins University Press, Baltimore.

Woolhouse, M.E., Dye, C., Etard, J.-F., Smith, T., Charlwood, J., Garnett, G., Hagan, P., Hii, J., Ndhlovu, P., Quinnell, R., 1997. Heterogeneities in the transmission of infectious agents: implications for the design of control programs. P. Natl. Acad. Sci-Biol. 94, 338–342.