International Journal for Parasitology 49 (2019) 225–233

Contents lists available at ScienceDirect

International Journal for Parasitology

journal homepage: www.elsevier.com/locate/ijpara

Local host-tick coextinction in neotropical forest fragments

Helen J. Esser [a,b,*], Edward Allen Herre [a], Roland Kays [a,c], Yorick Liefting [a,b], Patrick A. Jansen [a,b]

[a] Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Panama City, Panama
[b] Department of Environmental Sciences, Wageningen University & Research, P.O. Box 47, 6700 AA Wageningen, the Netherlands
[c] North Carolina Museum of Natural Sciences, and NC State University, 11 West Jones St. Raleigh, NC 27601, USA

ARTICLE INFO

Article history:
Received 26 March 2018
Received in revised form 27 July 2018
Accepted 2 August 2018
Available online 8 February 2019

Keywords:
Biodiversity loss
Host-parasite interactions
Forest fragmentation
Defaunation
Extinction cascade
Host specificity
Panama

ABSTRACT

Ticks are obligatory parasites with complex life cycles that often depend on larger bodied vertebrates as final hosts. These traits make them particularly sensitive to local coextinction with their host. Loss of wildlife abundance and diversity should thus lead to loss of tick abundance and diversity to the point where only generalist tick species remain. However, direct empirical tests of these hypotheses are lacking, despite their relevance to our understanding of tick-borne disease emergence in disturbed environments. Here, we compare vertebrate and tick communities across 12 forest islands and peninsulas in the Panama Canal that ranged 1000-fold in size (2.6–2811.3 ha). We used drag sampling and camera trapping to directly assess the abundance and diversity of communities of questing ticks and vertebrate hosts. We found that the abundance and species richness of ticks were positively related to those of wildlife. Specialist tick species were only present in fragments where their final hosts were found. Further, less diverse tick communities had a higher relative abundance of the generalist tick species *Amblyomma oblongoguttatum*, a potential vector of spotted fever group rickettsiosis. These findings support the host-parasite coextinction hypothesis, and indicate that loss of wildlife can indeed have cascading effects on tick communities. Our results also imply that opportunities for pathogen transmission via generalist ticks may be higher in habitats with degraded tick communities. If these patterns are general, then tick identities and abundances serve as useful bioindicators of ecosystem health, with low tick diversity reflecting low wildlife diversity and a potentially elevated risk of interspecific disease transmission via remaining host species and generalist ticks.

1. Introduction

Extinction cascades form one of the most insidious, but often ignored, drivers of biodiversity loss (Dunn et al., 2009). By eliminating organisms that are essential to the survival of others, the initial loss of a single keystone species can catalyse secondary extinctions throughout ecological communities (Colwell et al., 2012). Parasites are expected to be particularly prone to local coextinction because they need minimum thresholds of host abundance in order to maintain viable populations (Dobson et al., 2008). This is especially likely for parasites that show strong host specificity and/or have complex life cycles involving multiple host species (Koh et al., 2004; Lafferty, 2012). Thus, as host species are lost, parasite communities are expected to degrade to the point that only species with low host specificity remain (Dobson et al., 2008; Dunn et al., 2009; Lafferty, 2012).

The issue of host-parasite coextinction is highly relevant for disease risk, as parasites can negatively affect the health of their host either directly or indirectly as vectors of pathogens. Many of these pathogens – particularly those of medical and veterinary importance – are capable of infecting multiple host species (Woolhouse et al., 2001). While local extinction of certain host species (e.g., through habitat fragmentation or overexploitation) may cause the coextinction of specialist parasites and the pathogens that depend on them, generalist parasites and associated pathogens may be facilitated. First, generalist parasites are able to exploit multiple host species by definition, thereby promoting interspecific pathogen transmission (Ostfeld and Keesing, 2012). Second, in degraded wildlife communities, generalist parasites may feed proportionally more from host species that are competent reservoirs of pathogens, further increasing the potential for disease emergence (Allan et al., 2003; Keesing et al., 2010; Gottdenker et al., 2012). Therefore, understanding how host species loss affects the species composition and functional properties of communities of parasites, and hence the opportunities for pathogen transmission, is critically important.

* Corresponding author at: Laboratory of Entomology, Wageningen University, P. O. Box 16, 6700 AA Wageningen, the Netherlands.
E-mail address: helen.esser@wur.nl (H.J. Esser).

https://doi.org/10.1016/j.ijpara.2018.08.008
0020-7519/

One of the most important groups of parasites that vector pathogens are ticks. These obligatory ectoparasites of terrestrial vertebrates – mammals, birds, reptiles and sometimes amphibians – are known to transmit a wide variety of pathogenic microorganisms (Jongejan and Uilenberg, 2004). Their life cycle is characterized by multiple developmental stages and they are known to exhibit host specificity to varying degrees, especially as adults (Esser et al., 2016b). Due to their reliance on vertebrates and high mortality when they fail to find a host, ticks should be strongly affected by local loss of wildlife (Mihalca et al., 2011; Ostfeld and Keesing, 2012). Thus, larger and more diverse host communities should also harbour larger and more diverse tick communities.

Several past studies have already considered how the abundance of questing ticks varied between different sized forest fragments, using fragment size as a proxy for host abundance and diversity (Allan et al., 2003; Brownstein et al., 2005; Ogrzewalska et al., 2011). However, these studies used forest fragments situated in agricultural or suburban landscapes, where abundances of some host species may be elevated, or conversely, species loss may be exacerbated by increased hunting pressure, hence distorting expected biodiversity patterns based on island biogeography theory (Mendenhall et al., 2014). Other studies correlated the abundance of questing ticks with that of only one or a few focal host species (Rand et al., 2003; Ostfeld et al., 2006; Tagliapietra et al., 2011; Kilpatrick et al., 2014), but did not take into account that abundances and diversities of other, non-focal species in the host community may affect tick communities. Only rarely have studies directly assessed the abundance and species composition of broader host communities in relation to tick abundance (Szabó et al., 2009; Hofmeester et al., 2017a), and to our knowledge, no study has yet empirically tested how the species diversity of tick communities is affected by loss of host diversity.

In this study, we directly assessed the abundance and diversity of broader communities of both questing ticks and their hosts across 12 previously interconnected forest fragments of the Barro Colorado Nature Monument (BCNM) in the Panama Canal area. These fragments range 1000 fold in size, are largely surrounded by water, and are relatively well protected from poachers, providing an ideal opportunity for a natural experiment. We used drag sampling to survey questing ticks and camera trapping to survey terrestrial mammals. We predicted that fragments with larger and more diverse host communities supported larger and more diverse tick communities, and that less diverse tick communities were characterized by a higher relative abundance of generalist species.

2. Materials and methods

2.1. Study site

Fieldwork was carried out in the Barro Colorado Nature Monument (BCNM, 9°10′N, 79°51′W), a nature reserve that comprises 5400 ha of forested islands and peninsulas in the Gatun Lake section of the Panama Canal, Panama. The fragments were part of a more or less continuous forest until a century ago, when damming of the Chagres River produced forest islands and peninsulas. The islands are surrounded by Gatun Lake, the eastern peninsulas are separated from the nearby Soberania National Park by narrow land bridges and the clearings of the Panama Canal Railroad, and the western peninsulas are surrounded by pastureland and *Tectona grandis* teak plantations, inhospitable to forest wildlife. All sites support semi-deciduous tropical moist forests and are characterized by a seasonally moist tropical weather pattern (Leigh 1999).

The sampled fragments range widely in size as do the wildlife communities that they support (Asquith et al., 1997). The largest island, the 1560 ha Barro Colorado Island (BCI), supports a rich fauna with abundant populations of medium to large sized mammals such as the lowland paca *Cuniculus paca*, Central American agouti, *Dasyprocta punctata*, collared peccary *Pecari tajacu* and Central American red brocket, *Mazama temama* (Meyer et al., 2015). In contrast, the smallest islands do not have permanent populations of large mammals and some are too small to support even medium sized mammals (Asquith et al., 1997). Ticks are abundant in Panama, both in species and in numbers, and their natural host associations are relatively well-documented (Esser et al., 2016a, 2016b; Miller et al. 2016).

2.2. Sampling

We sampled 12 forest fragments that ranged in size from 2.6 to 2811 ha (Fig. 1) during January–March 2010. Fragment size was calculated in ESRI ArcGIS 9.3.1 from a Digital Elevation map with a resolution of 10 m (central Panama Geographic Information Systems coverage DVD, Version 2, 2007-04-25, Panama Canal Monitoring Project, United States Agency for International Development, the Smithsonian Tropical Research Institute and United States Geological Survey WEBB program). In each fragment, we established between one and six 1 ha sampling plots, depending on the size.

2.2.1. Wildlife surveys

We used arrays of camera traps (Kays, R., Tilak, S., Kranstauber, B., Jansen, P.A., Carbone, C., Rowcliffe, M.J., Fountain, T., Eggert, J., He, Z., 2010. Monitoring wild animal communities with arrays of motion sensitive camera traps. arXiv preprint arXiv:1009.5718) to estimate the relative abundance and diversity of wildlife species for each plot. Camera trapping is a reliable and non-invasive technique for the survey of medium to large sized terrestrial mammals and birds under all environmental conditions (Tobler et al., 2008; Kays et al., 2010 cited earlier). We used Reconyx RC55 (Reconyx Inc, Holmen, WI, USA) camera traps with a built-in infrared flash, a passive infrared motion sensor, and a 1/5th second trigger speed. Cameras were active 24 h per day every day and took sequences of 10 consecutive pictures per trigger, with no delay between triggers. We ran one camera trap for at least 8 days at each of 10 computer-generated random points per plot. Cameras were attached to tree stems 30 cm above ground level and were spaced at least 10 m apart, pointed in the direction with the most open understory. We used the walk test function of the cameras to measure the maximum detection distance for each camera as an estimate of the area surveyed. Detection distances ranged from 2.0-12.5 m (median: 5 m) among cameras, depending on vegetation density. All photographs were processed in a custom-made database (Kays et al., 2010 cited earlier). Pictures were grouped such that each sequence represented the passage of one individual animal or a group of social animals. Animal identifications were based on Reid (2009). Small birds, primates and reptiles were excluded from analyses as they are not reliably captured by camera traps. Further, wild primates are not naturally associated with any tick species in Panama, probably due to self-anointing behaviour (Verderane et al., 2007; Bermúdez et al., 2010).

Camera traps are analogous to questing ticks in that they detect and capture passing animals, where the rate at which animals pass a randomly placed camera trap is proportional to host availability (Hofmeester et al., 2017). The recurrence of the same host species passing a camera trap thus represents multiple host opportunity events for questing ticks, regardless of whether these passages were by the same individual animal. We followed the method described by Hofmeester et al. (2017) in that our camera traps were placed at the questing height of ticks and that photographic capture rates were adjusted for variation in detection distance

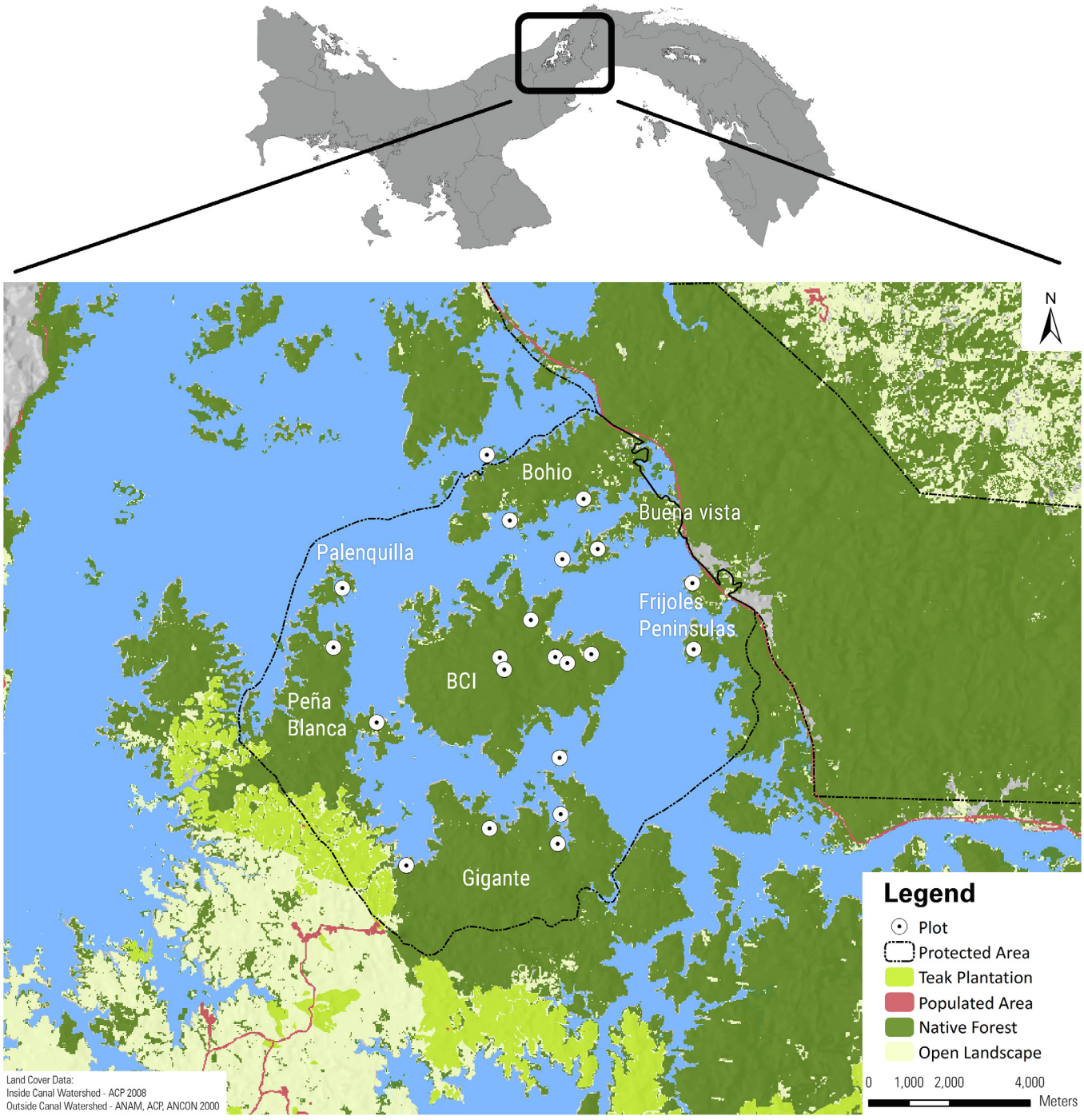

Fig. 1. Map of the study area. A total of 21 plots across 12 forest fragments were sampled for ticks and wildlife in the Barro Colorado Nature Monument, Gatun Lake, Panama. BCI = Barro Colorado Island.

between species. The resulting "passage rate" is then a standardized measure of the frequency at which questing ticks encounter vertebrate hosts (Hofmeester et al., 2017). Passage rates were calculated for each species by dividing the number of captures by the length of camera deployment (in days) and the effective detection distance (in m). The effective detection distance (d) depends on body mass (BM) as $d = 0.10\ BM + 2.84$ for the cameras and locations that we used (cf Rowcliffe et al., 2011). Thus, effective detection distances ranged from 2.8 m (for Robinson's mouse opossum *Marmosa robinsoni*) to 6.4 m (for white-tailed deer *Odocoileus virginianus*). If the maximum detection distance at a camera point was smaller than d due to vegetation blocking the view, we used the shorter distance. Passage rates were used to calculate a wildlife biomass rate (kg/m/day) for each plot by summing the product of passage rate and average body mass across all species. Wildlife biomass should explain differences in tick community composition better than wildlife abundance, as it weighs larger vertebrates more heavily (Esser et al., 2016a). Average body mass values for each species were taken from Reid (2009) and Rowcliffe et al. (2011).

We used the first order Jackknife (Jack1) index, an asymptotic estimator of species richness, to compute the number of species

that would be expected under exhaustive sampling using EstimateS version 9.1.0 (Colwell, 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Page User's Guide and application published at: http://purl.oclc.org/estimates). This index is considered more suitable for camera trapping data than the Chao indices (Tobler et al., 2008). Jack1 values were estimated by combining all camera trap data per fragment, with each camera trap representing a sampling unit. Outcomes were compared with the total number of species that were actually observed for each fragment to determine what fraction of the total wildlife species richness was captured by camera traps. Jack1 values that are equal to the observed species richness indicate that the accumulation of species has reached an asymptote (Colwell, 2013).

2.2.2. Tick surveys

We used drag sampling (Falco and Fish, 1992) to estimate the community composition of questing ticks in each plot. This standardized method involves pulling a white cotton cloth of 1 m width over the ground and through the vegetation along a line transect. We sampled four 50 m transects in each 1 ha plot, totalling 200 m^2. Transects ran in different directions to account for the heterogeneous distribution of ticks across the vegetation. Every 5 m, ticks were removed from the cloth with masking tape and stored in 97% ethanol. Fluctuations in abiotic conditions affect tick activity and hence sampling results. To minimize such effects, we collected ticks only on days without rain and sampled all of our sites in a short time frame, between 22nd January and 1st February 2010. Further, the sampling period coincided with Panama's dry season, which runs from late December to early May. Weather conditions are generally very stable during the dry season, with an average diurnal temperature of 26 °C and 80–85% humidity on the forest floor of BCI (Croat, 1978). We are thus confident that abiotic conditions between sites were comparable. The dry season is also the period of peak abundance of larvae, nymphs and adult ticks, thus maximizing the chances of collecting large numbers of ticks. Ticks were identified at the Gorgas Memorial Institute in Panama City, using an extensive reference collection and taxonomic keys provided by Fairchild et al. (1966) and Onofrio et al. (2006). Tick species richness was determined after combining all identified ticks per fragment.

2.3. Statistical analyses

All analyses were carried out in the R (version 3.5.1) programming language (R Core Team 2018. R foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org). We used linear mixed models (LMM) as implemented in the *nlme* package in R (Pinheiro et al., 2017. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-137) to evaluate the relationship of total wildlife species richness (Jack1) and biomass with forest fragment size, with fragment ID as random factor with varying intercept. Forest fragment size was $\log_{10}$-transformed prior to analyses. We used a LMM to test how the total number of tick species in each fragment was related to wildlife species richness and biomass, with fragment ID as a random factor with varying intercept and sample size (i.e., the number of adult ticks) as a weighting factor. We used generalized linear mixed models (GLMM) with a negative binomial distribution and log-link function as implemented in the R package *glmmADMB* (Skaug et al., 2016. Generalized Linear Mixed Models using 'AD Model Builder'. R package version 0.8.3.3.) to test how densities of adults, nymphs and larvae were related to wildlife species richness and biomass. Plot ID and fragment ID were used as random factors with varying intercept, with plots nested within fragments. Wildlife species richness and biomass were standardized prior to analyses by extracting the mean and dividing by two standard deviations (Gelman, 2008). We used a GLMM with a binomial distribution and logit link function to test how the proportional abundance of the only true generalist tick species in this study (*Amblyomma oblongoguttatum*) was related to tick species richness, with fragment ID as random factor with varying intercept. Because the proportional abundance of *A. oblongoguttatum* and tick species richness are not completely independent of each other, we compared the observed proportion with the expected proportion under the null hypothesis that each tick species is equally represented in the tick community. We calculated both marginal and conditional R^2 values for LMMs and GLMMs following Nakagawa et al. (2017), where marginal R^2 provides the variance explained by fixed factors and conditional R^2 provides the variance explained by both fixed and random factors. Finally, we used Mann-Whitney U tests to determine whether the abundance of specialist tick species (*Amblyomma naponense*, *Amblyomma tapirellum*, *Haemaphysalis juxtakochi*) was constrained to fragments where their final hosts (peccary and deer) were present. P values < 0.05 were considered statistically significant.

3. Results

The total camera trapping effort amounted to 1717 camera days. Camera traps captured 3391 animal passages in total, of which 3229 involved semi-terrestrial birds and mammals that were retained in the analysis. The total number of species recorded was 21, among which agouti, peccary and paca were the most common (Table 1). There were clear differences in wildlife communities among the fragments. Some species (e.g. the northern tamandua *Tamandua mexicana* and Central American red brocket deer) were recorded mostly on the largest islands, while others (e.g. white-tailed deer, brown four-eyed opossum *Metachirus nudicaudatus*, and forest rabbit *Sylvilagus brasiliensis*) were found exclusively on the mainland peninsulas (Supplementary Table S1). No large mammals (>10 kg) and no carnivores were recorded in the four smallest fragments, with the exception of tayra *Eira barbara* on one of these islands. On the smallest of the islands (2.6 ha), we recorded just two species: Tome's spiny rat *Proechimys semispinosus* and nine-banded armadillo *Dasypus novemcinctus* (Supplementary Table S1).

The estimated total species richness (Jack1) of wildlife ranged from two in the smallest fragment to 17.7 in the largest, and increased strongly with the log of fragment size (LMM: $\beta = 3.86$, $P < 0.001$, marginal $R^2 = 0.67$, conditional $R^2 = 0.96$, Fig. 2A). For most fragments, Jack1 estimates were equal or close to the actual observed number of species (Table 2), with cameras recording 73–100% of the estimated total number of species present in each fragment. This suggests that the sampling effort was sufficient. Wildlife biomass ranged more than 26-fold across fragments (0.3 to 7.9 kg d^{-1} m^{-1}) and increased strongly with the log of fragment size (LMM: $\beta = 1.81$, $P < 0.001$, marginal $R^2 = 0.74$, conditional $R^2 = 0.97$, Fig. 2B).

A total of 21,262 ticks were collected from the 12 fragments, including 18,336 larvae, 2596 nymphs and 330 adults (Table 3). Immature stages of *Haemaphysalis* and *Amblyomma* formed the majority of all ticks captured (60% and 38%, respectively). The total number of tick species ranged from two to seven per fragment (Table 2) and increased with wildlife species richness and biomass (LMM: wildlife richness $\beta = 2.13$, $P < 0.05$, wildlife biomass $\beta = 2.64$, $P < 0.01$, marginal $R^2 = 0.59$, conditional $R^2 = 1.00$, Fig. 3A, B). Abundances of adult ticks increased with wildlife species richness, but not with wildlife biomass (GLMM: wildlife richness $\beta = 2.73$, $P < 0.01$, wildlife biomass $\beta = 0.09$, $P > 0.05$, marginal $R^2 = 0.59$, conditional $R^2 = 0.94$, Fig. 3C, D). Abundances of nymphs increased with both wildlife species richness and biomass (GLMM: wildlife

Table 1
Wildlife recorded by arrays of non-baited camera traps across 12 forest fragments in the Barro Colorado Nature Monument, Panama.

Latin species name[a]	Common name[a]	No. of captures	% of all captures	No. of fragments	Smallest fragment (ha)
Dasyprocta punctata	Central American agouti	1495	46.3	11	3.4
Pecari tajacu	Collared peccary	649	20.1	8	65.5
Cuniculus paca	Lowland paca	337	10.4	11	3.4
Nasua narica	White-nosed coati	203	6.3	8	65.5
Mazama temama	Central American red brocket	110	3.4	3	69.6
Proechimys semispinosus	Tome's spiny rat	97	3.0	11	2.6
Odocoileus virginianus	White-tailed deer	97	3.0	6	65.5
Dasypus novemcinctus	Nine-banded armadillo	51	1.6	10	2.6
Didelphis marsupialis	Common opossum	39	1.2	9	7.2
Leopardus pardalis	Ocelot	34	1.1	5	65.5
Tinamus major	Great tinamou	31	1.0	5	7.6
Sciurus granatensis	Red-tailed squirrel	25	0.8	5	53.6
unknown mouse sp.	Unknown mouse sp.	15	0.5	2	753.1
Tamandua mexicana	Northern tamandua	13	0.4	2	5.9
Metachirus nudicaudatus	Brown four-eyed opossum	12	0.4	2	69.6
Eira barbara	Tayra	9	0.3	4	3.4
Conepatus semistriatus	Striped hog-nosed skunk	4	0.1	1	956.0
Cabassous centralis	Northern naked-tailed armadillo	3	<0.1	2	69.6
Marmosa robinsoni	Robinson's mouse opossum	2	<0.1	1	1567.3
Sylvilagus brasiliensis	Tapeti	2	<0.1	1	65.5
Puma yagouaroundi	Jaguarundi	1	<0.1	1	65.5

[a] Nomenclature follows Wilson and Reeder (2005).

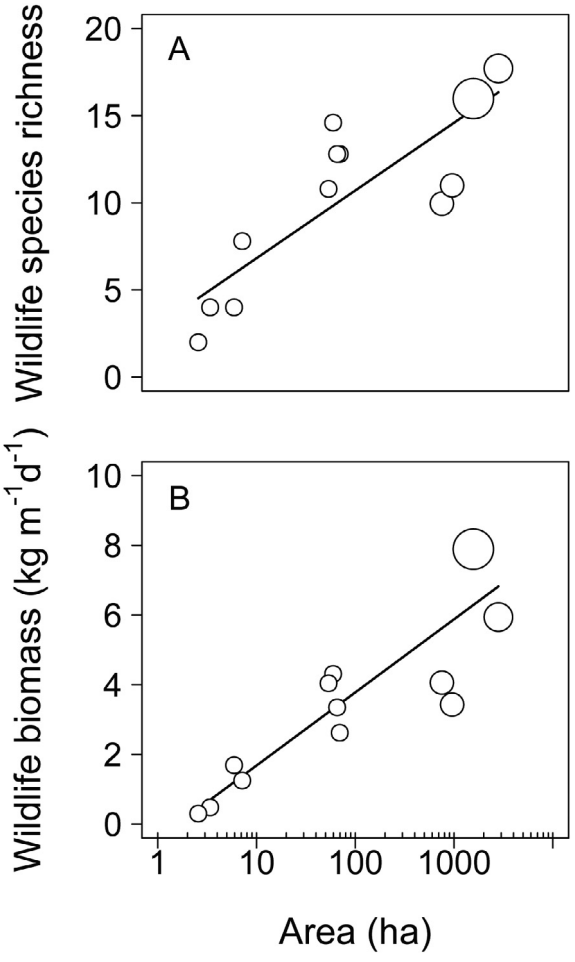

Fig. 2. Species richness and biomass of wildlife communities across 12 different sized forest fragments in the Barro Colorado Nature Monument, Panama. Wildlife (A) total species richness and (B) biomass increased significantly with forest fragment size. Dot size is proportional to sampling intensity (i.e., number of plots).

richness $\beta = 2.89$, $P < 0.001$, wildlife biomass $\beta = 0.90$, $P < 0.001$, marginal $R^2 = 0.48$, conditional $R^2 = 0.75$, Fig. 3C, D). Larval abundance increased with wildlife species richness, but not with wildlife biomass (GLMM: wildlife richness $\beta = 1.91$, $P < 0.05$, wildlife biomass $\beta = 0.75$, $P > 0.05$, marginal $R^2 = 0.39$, conditional $R^2 = 0.87$, Fig. 3C, D).

Seven tick species from three genera were identified to the species level (Table 3). Of these, six showed host specificity for large mammals during the adult stage: adult *A. naponense* and *Amblyomma pecarium* feed almost exclusively on peccary, adult *Amblyomma ovale* feed predominantly on carnivorous species, adult *A. tapirellum* have been collected from various large mammals but mostly from tapir, adult *H. juxtakochi* chiefly parasitize ungulates, particularly deer, and adult *Ixodes affinis* are mainly associated with deer and big cats (Guglielmone et al., 2014; Esser et al., 2016b). Three of these tick species, *A. ovale*, *A. pecarium* and *I. affinis*, were found in only one or two large fragments. The other three host-specific species, which occurred in at least five different fragments, were found only where their final host species were present (one-tailed Mann-Whitney U test: *H. juxtakochi*: $U = 2$, $P < 0.01$; *A. naponense*: $U = 6$, $P < 0.05$; *A. tapirellum*: $U = 6$, $P < 0.05$; Fig. 5).

Only one of the collected tick species, *A. oblongoguttatum,* is a true generalist; it has been collected from at least 27 host species of nine different vertebrate orders in Panama alone (Esser et al., 2016b). This species occurred even in one of the smallest fragments, where no other adult ticks were found. The observed proportion of *A. oblongoguttatum* decreased in a concave downward curve with tick species richness (GLMM: odds ratio = 0.59, $P < 0.05$, marginal $R^2 = 0.11$, conditional $R^2 = 0.23$, Fig. 4), whereas under the null hypothesis the curvature was expected to be negative, but concave upward (Fig. 4). Thus, with loss of tick species, the observed proportion of *A. oblongoguttatum* in the tick community increased faster than expected by chance.

4. Discussion

Host extirpation should lead to coextinction of specialist ticks, with generalist ticks becoming increasingly prevalent in species-poor communities. Our direct measures of the relative abundance and diversity of both wildlife and questing tick communities across 12 forest fragments in Panama allowed us to perform the first empirical tests for these relationships. We found that larger forest fragments had larger and more diverse wildlife communities, which in turn supported larger and more diverse tick communities.

Table 2
Data on wildlife and tick communities across 12 forest fragments in the Barro Colorado Nature Monument, Panama.

Fragment	No. plots	Area (ha)	Wildlife			Questing ticks			
			No. observed species	No. estimated species (Jack1)	Biomass (kg m^{-1} d^{-1})	Adult density (200 m^{-2})	Nymphal density (200 m^{-2})	Larval density (200 m^{-2})	No. tick species
Gigante	3	2811.3	14	17.71	5.94[a]	13.7[a]	301.3[a]	1072.3[a]	4
Barro Colorado Island	6	1567.3	15	15.98	7.89	12[a]	93.3[a]	601.5[a]	7
Peña blanca	2	956.0	11	11.00	3.43[a]	31.5[a]	247[a]	1615[a]	5
Bohio	2	753.1	10	11.9	4.06[a]	26.5[a]	61.5[a]	405.5[a]	5
Frijoles point	1	69.6	11	12.80	2.62	51	148	3275	4
Frijoles island	1	65.5	11	12.80	3.35	5	51	1000	4
Palenquilla	1	59.6	11	14.60	4.31	17	303	2361	2
Buena vista	1	53.6	9	10.80	4.04	27	0	23	5
Palm island	1	7.2	6	7.80	1.25	0	3	113	2
Mona grita	1	5.9	4	4.00	1.69	0	3	5	2
Trap island	1	3.4	4	4.00	0.48	1	6	665	2
Refuge island	1	2.6	2	2.00	0.30	0	1	27	2

[a] Average across plots.

Table 3
Ticks captured with standardized drag sampling across 12 forest fragments in the Barro Colorado Nature Monument, Panama.

Species	Larvae	Nymphs	Adults (male)	Adults (female)	% of all captures	No. fragments
Amblyomma	7450	612	–	–	37.9	12
A. naponense	–	–	14	14	0.1	6
A. oblongoguttatum	–	–	117	106	1.0	9
A. ovale	–	3	–	–	<0.1	1
A. pecarium	–	–	–	2	<0.01	2
A. tapirellum	–	–	31	26	0.3	5
Haemaphysalis						12
H. juxtakochi	10,849	1981	11	8	60.4	12
Ixodes	37	–	–	–	0.2	1
I. affinis	–	–	1	–	<0.01	1
Total	18,336	2596	174	156	100	12

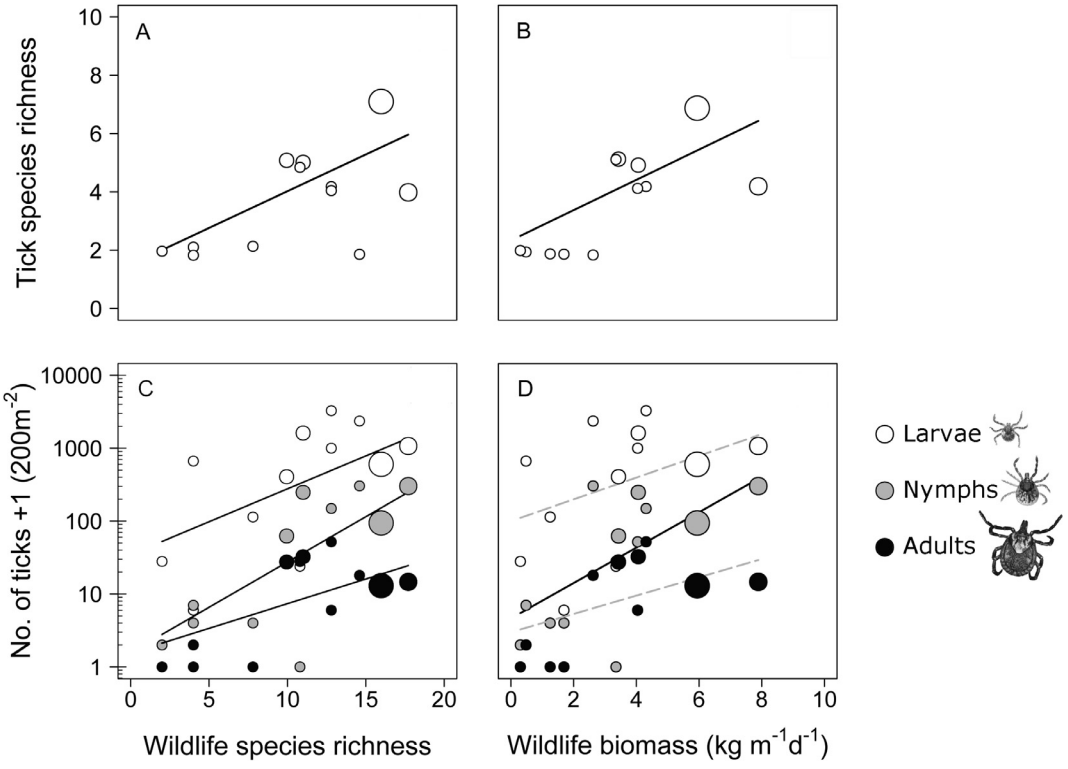

Fig. 3. Relationships between species richness and abundance of tick and vertebrate host communities across 12 different sized forest fragments in the Barro Colorado Nature Monument, Panama. Tick species richness increased significantly with (A) wildlife species richness and (B) wildlife biomass. Abundances of questing adults (black), nymphs (grey) and larvae (white) of ticks also increased with (C) wildlife species richness and (D) wildlife biomass, although the latter relationship was only significant for nymphs. Dashed lines represent non-significant relationships. Dot size is proportional to sampling intensity (i.e., number of plots).

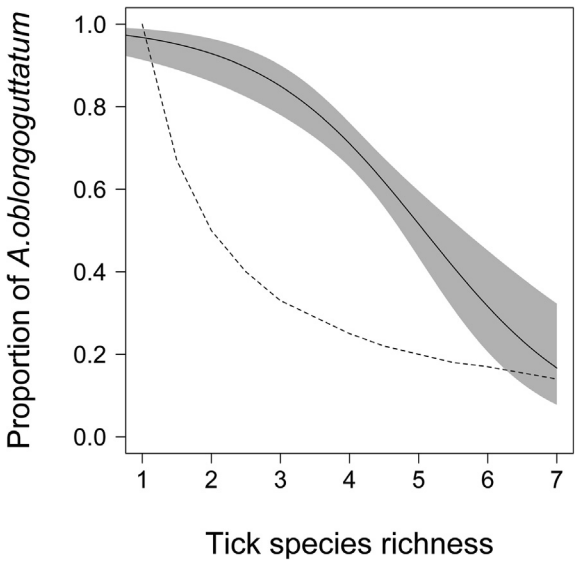

Fig. 4. Relationship between the proportional abundance of *Amblyomma oblongoguttatum*, the only true generalist tick species in this study, and tick species richness across 12 different sized forest fragments in the Barro Colorado Nature Monument, Panama. Black line represents the binomial regression fit for the observed proportion with upper and lower confidence intervals (grey area). Dashed line represents the expected proportion under the null hypothesis that all tick species are equally abundant in the population. The proportion of *A. oblongoguttatum* increased more strongly with loss of tick species than expected under the null hypothesis.

Also, tick species known to exhibit high host specificity as adults were absent in fragments in which their final hosts were not recorded so that species-poor communities were increasingly comprised of a generalist tick species. These results support the predictions and imply that loss of wildlife has cascading effects on tick communities through local host-parasite coextinction.

Our finding that species richness and biomass of wildlife increased with forest fragment size is consistent with previous studies and island biogeography theory (Andrén, 1994; Turner, 1996; Chiarello, 1999; Fahrig, 2003; Kinnaird et al., 2003). That species richness of ticks, in turn, increased linearly with wildlife species richness and biomass is also in agreement with theoretical predictions (Lafferty, 2012). The presence of multiple life stages, strong host specificity, and higher extinction risk for hosts than non-hosts should all increase the risk of host-parasite coextinction (Lafferty, 2012). The tick species in our study region have three life stages, show high host specificity in the adult stage (Esser et al., 2016b), and tend to use large mammals as final hosts (Esser et al., 2016a), which need sufficiently large habitats to maintain viable population sizes and are thus the first to disappear from small and isolated fragments (Cardillo et al., 2005; Meyer et al., 2015). Our finding that specialist ticks were absent from fragments where their final hosts were lacking shows that ticks could become locally coextinct, as has previously been suggested (Durden and Keirans, 1996; Mihalca et al., 2011). Similar patterns were found in a study that focussed on birds and their lice across forest fragments in southern China (Bush et al., 2013). Clearly, the continuous presence of final hosts is indispensable for sustaining parasite populations.

As ticks depend on hosts for their development and survival, tick abundance is widely believed to increase with host abundance (Ostfeld and Keesing, 2012). We found that tick abundance increased with both wildlife species richness and biomass, although the latter relationship was significant only for nymphs. Richer host communities provide more feeding opportunities for ticks (Schmidt and Ostfeld, 2001), possibly from higher quality

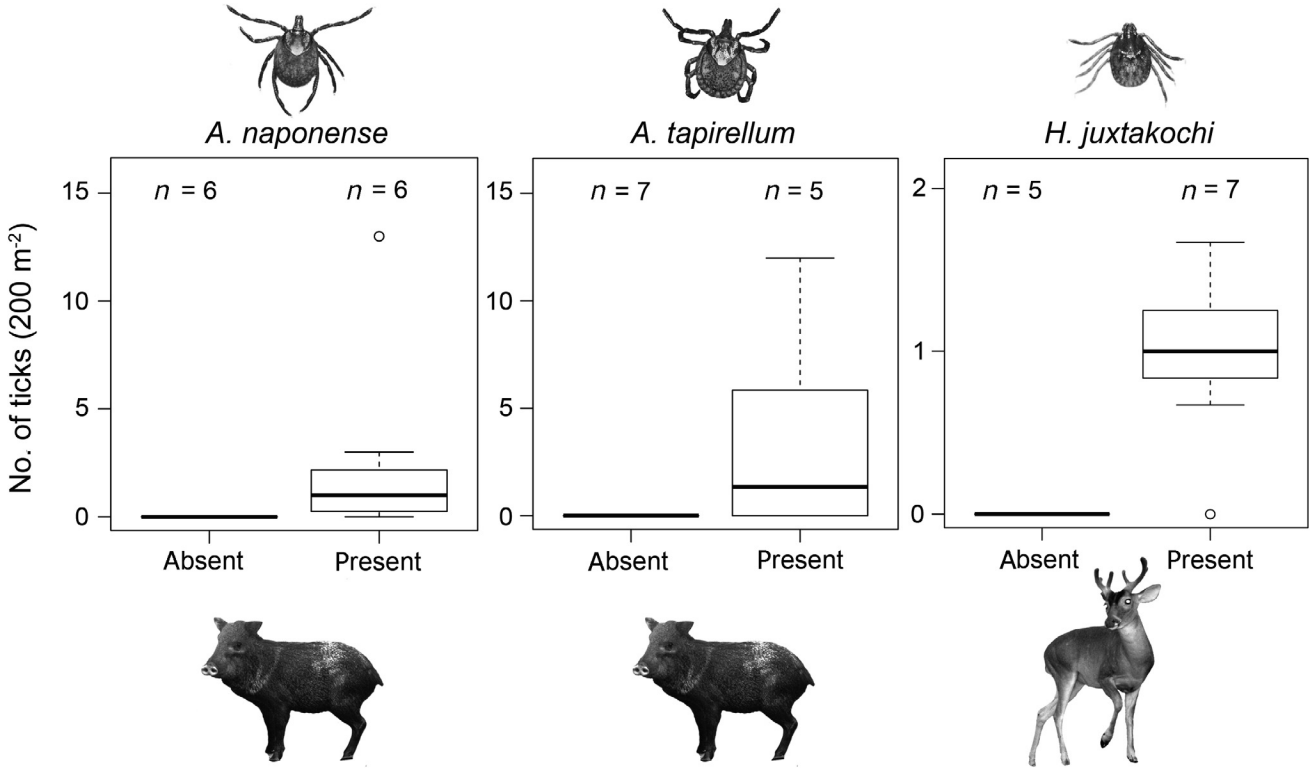

Fig. 5. Median abundances of specialist tick species in forest fragments with and without their specific host species across 12 different sized forest fragments in the Barro Colorado Nature Monument, Panama. Specialist tick species were only present where their final host species was present. Deer include both Central American red brocket and white-tailed deer.

hosts (Keesing et al., 2009), and can thus support more diverse, and hence larger, tick communities. Our results are consistent with those of Ogrzewalska et al. (2011), who found that abundances of questing ticks increased with fragment size across 12 Brazilian forest fragments. Although final hosts were reported to be absent from the smallest fragments in that study, it had no quantitative data on host communities to test for relationships between the community composition of ticks and that of their hosts across the fragments, which – in addition – were isolated by agricultural land instead of water (Ogrzewalska et al., 2011). Our results agree with and extend those previous findings by providing direct abundance and diversity estimates of hosts and ticks.

Our finding that less diverse tick communities were characterized by a higher proportion of generalists may have implications for tick-borne pathogen transmission, as generalist vectors are more likely to transmit pathogens among different host species (Ostfeld and Keesing, 2012). Specifically, we found that the relative abundance of *A. oblongoguttatum* increased as the tick community became more depauperate, and this relationship was stronger than expected by chance. This tick species was the only true host generalist in this study. It has been recorded from at least 27 species within nine different orders including humans, livestock, pets and wild animals in Panama alone (Esser et al., 2016b). Flexibility in host selection apparently allows this species to persist in even the most degraded environments, where specialist ticks disappear. Recently, spotted fever group (SFG) *Rickettsia* were isolated from *A. oblongoguttatum* ticks in Panama and Brazil, suggesting a potential role for this tick as vector for these pathogens (Bermúdez et al., 2009; Aguirre et al., 2018). Further, several of its wild host species are synanthropic mammals that have been implicated as amplifying hosts for SFG *Rickettsia*, including small rodents, opossums, forest rabbits, capybaras and coyotes (Labruna, 2009; Dantas-Torres et al., 2012; Bermúdez et al., 2017). Given that generalist vectors may feed proportionally more from disease reservoir hosts in degraded habitats, where these host species proliferate, opportunities for pathogen transmission may be higher in sites with high relative abundances of generalist ticks (Allan et al., 2003; Keesing et al., 2010; Gottdenker et al., 2012).

On the other hand, inference of disease risk is complicated by the fact that the higher proportion of generalist ticks was accompanied by low tick abundance, which reduces the rate at which individual hosts encounter ticks. Since disease risk is the product of the likelihood of tick encounter and the likelihood of tick infection (Randolph and Dobson, 2012), the relative strength of each of the two responses (i.e., higher proportions of generalists versus lower tick abundance) will ultimately determine whether loss of wildlife either increases or decreases the risk to which individuals are exposed when crossing these fragments.

The combination of tick drag sampling and camera trapping provides a new and informative community-wide approach for the study of tick-host relationships (Hofmeester et al., 2017b). However, it is important to also recognize the limitations of our methods. First, our sampling focused on terrestrial mammals, while other groups of vertebrates such as wild birds are also known hosts for immature stages of neotropical ticks (Miller et al., 2016). Birds may help recolonize diminishing tick populations on small islands and fragments by dispersing ticks from adjacent mainland sites. On the other hand, the survival of ticks is ultimately limited by the availability of final hosts for the adult stage, which are typically larger bodied host species (Esser et al., 2016a), which we did properly sample. Second, our survey of ticks was incomplete. Many species of ticks known to be common on the host species that we recorded with cameras were not present among the identified ticks, possibly because the drag sampling method is not as effective for collecting those tick species. The use of CO_2 traps is a well-established alternative tool for collecting ticks (Cançado et al., 2008). However, a pilot study with CO_2 traps in the same study site yielded only *A. tapirellum*, *A. naponense*, *A. oblongoguttatum*, and *H. juxtakochi*, all of which were also captured by drag sampling in the current study. More complete tick-host associations can be established by directly collecting ticks from individual host animals. Future studies should therefore ideally use a combination of drag sampling and live trapping to collect ticks from both the free environment and directly from hosts across a disturbance gradient.

We provide evidence for a positive relationship between wildlife and tick abundance and diversity in this tropical forest ecosystem. Further, we show local coextinction of specialist ticks with specific large-bodied vertebrates, which serve as their final hosts, following forest fragmentation. Finally, we show that a higher relative abundance of generalists characterizes species-poor tick communities that coincide with depleted vertebrate host populations. Given that generalist ticks may feed proportionally more from disease reservoir hosts in degraded environments (Allan et al., 2003; Keesing et al., 2010; Gottdenker et al., 2012), our findings collectively imply greater opportunities for pathogen transmission in habitats with impoverished tick communities. If these patterns are general, then tick identities and abundances serve as useful bioindicators of ecosystem health, with low tick diversity reflecting low wildlife diversity (Ogrzewalska et al., 2011; Lafferty, 2012; Bush et al., 2013) and a potentially elevated risk of interspecific disease transmission via remaining host species and generalist ticks.

Acknowledgements

We thank the Smithsonian Tropical Research Institute (Panama) and the Gorgas Memorial Institute (Panama) for facilities and logistical support; Sergio Bermúdez for species identifications and comments; Frans Bongers, Walter Carson, Tim Hofmeester, Madelon Lohbeck, Frank Sterck, and Mark Torchin for comments. This study was funded by the Smithsonian Institution, USA (47BIODIVERSITY) Grand Challenges Award (to PAJ and EAH), the graduate school of Production Ecology and Resource Conservation of Wageningen University, the Netherlands (PE&RC A30) (to PAJ and HJE), the National Science Foundation, USA (DEB 0717071 to RK) and the Netherlands Foundation of Scientific Research (NWO-ALW 863-07-008 to PAJ). This work was also supported by a grant from the Simons Foundation, USA (429440,WTW).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpara.2018.08.008.

References

Aguirre, A.A.R., Garcia, M.V., da Costa, I.N., Csordas, B.G., da Silva Rodrigues, V., Medeiros, J.F., Andreotti, R., 2018. New records of tick-associated spotted fever group *Rickettsia* in an Amazon-Savannah ecotone, Brazil. Ticks Tick. Borne Dis. 9, 1038–1044.

Allan, B.F., Keesing, F., Ostfeld, R.S., 2003. Effect of forest fragmentation on Lyme disease risk. Conserv. Biol. 17, 267–272.

Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71, 355–366.

Asquith, N.M., Wright, S.J., Clauss, M.J., 1997. Does mammal community composition control recruitment in Neotropical forests? Evidence from Panama. Ecology 78, 941–946.

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., Gottdenker, N., Krishnvajhala, A., Fox, A., Wilder, H.K., González, K., Smith, D., López, M., Perea, M., Rigg, C., Montilla, S., Calzada, J.E., Saldaña, A., Caballero, C.M., Lopez, J.E., 2017. Synanthropic mammals as potential hosts of tick-borne pathogens in Panama. PLoS ONE 12, e0169047.

Brownstein, J., Skelly, D., Holford, T., Fish, D., 2005. Forest fragmentation predicts local scale heterogeneity of Lyme disease risk. Oecologia 146, 469–475.

Bush, S., Reed, M., Maher, S., 2013. Impact of forest size on parasite biodiversity: implications for conservation of hosts and parasites. Biodivers. Conserv. 22, 1391–1404.

Cançado, P.H.D., Piranda, E.M., Mourão, G.M., Faccini, J.L.J., 2008. Spatial distribution and impact of cattle-raising on ticks in the Pantanal region of Brazil by using the CO_2 tick trap. Parasitol. Res. 103, 371.

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.

Chiarello, A.G., 1999. Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. Biol. Conserv. 89, 71–82.

Colwell, R.K., Dunn, R.R., Harris, N.C., 2012. Coextinction and persistence of dependent species in a changing world. Annu. Rev. Ecol. Evol. Syst. 43, 183–203.

Croat, T.B., 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford.

Dantas-Torres, F., Aléssio, F.M., Siqueira, D.B., Mauffrey, J.-F., Marvulo, M.F.V., Martins, T.F., Moraes-Filho, J., Camargo, M.C.G.O., D'auria, S.R.N., Labruna, M.B., Ramos Silva, J.C., 2012. Exposure of small mammals to ticks and rickettsiae in Atlantic Forest patches in the metropolitan area of Recife, North-eastern Brazil. Parasitology 139, 83–91.

Dobson, A., Lafferty, K.D., Kuris, A.M., Hechinger, R.F., Jetz, W., 2008. Homage to Linnaeus: how many parasites? How many hosts? Proc. Natl. Acad. Sci. U.S.A. 105, 11482–11489.

Dunn, R.R., Harris, N.C., Colwell, R.K., Koh, L.P., Sodhi, N.S., 2009. The sixth mass coextinction: are most endangered species parasites and mutualists? Proc. Biol. Sci. 276, 3037–3045.

Durden, L.A., Keirans, J.E., 1996. Host-parasite coextinction and the plight of tick conservation. Am. Entomol. 42, 87–91.

Esser, H.J., Foley, J.E., Bongers, F., Herre, E.A., Miller, M.J., Prins, H.H., Jansen, P.A., 2016a. Host body size and the diversity of tick assemblages on Neotropical vertebrates. Int. J. Parasitol. Parasites Wildl. 5, 295–304.

Esser, H.J., Herre, E.A., Blüthgen, N., Loaiza, J.R., Bermúdez, S.E., Jansen, P.A., 2016b. Host specificity in a diverse Neotropical tick community: an assessment using quantitative network analysis and host phylogeny. Parasit. Vect. 9, 372.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515.

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, USA, pp. 167–219.

Falco, R.C., Fish, D., 1992. A comparison of methods for sampling the deer tick, I*xodes dammini*, in a Lyme disease endemic area. Exp. Appl. Acarol. 14, 165–173.

Gelman, A., 2008. Scaling regression inputs by dividing by two standard deviations. Stat. Med. 27, 2865–2873.

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

Gottdenker, N.L., Chaves, L.F., Calzada, J.E., Saldaña, A., Carroll, C.R., 2012. Host life history strategy, species diversity, and habitat influence *Trypanosoma cruzi* vector infection in changing landscapes. PLoS Negl. Trop. Dis. 6, e1884.

Hofmeester, T.R., Jansen, P.A., Wijnen, H.J., Coipan, E.C., Fonville, M., Prins, H.H., Sprong, H., van Wieren, S.E., 2017a. Cascading effects of predator activity on tick-borne disease risk. Proc. Biol. Sci. 284, 20170453.

Hofmeester, T.R., Rowcliffe, J.M., Jansen, P.A., 2017b. Quantifying the availability of vertebrate hosts to ticks: a camera-trapping approach. Front. Vet. Sci. 4, 115.

Jongejan, F., Uilenberg, G., 2004. The global importance of ticks. Parasitology 129, S3–S14.

Keesing, F., Belden, L.K., Daszak, P., Dobson, A., Harvell, C.D., Holt, R.D., Hudson, P., Jolles, A., Jones, K.E., Mitchell, C.E., Myers, S.S., Bogich, T., Ostfeld, R.S., 2010. Impacts of biodiversity on the emergence and transmission of infectious diseases. Nature 468, 647–652.

Keesing, F., Brunner, J., Duerr, S., Killilea, M., LoGiudice, K., Schmidt, K., Vuong, H., Ostfeld, R.S., 2009. Hosts as ecological traps for the vector of Lyme disease. Proc. Biol. Sci. 276, 3911–3919.

Kilpatrick, H.J., Labonte, A.M., Stafford III, K.C., 2014. The relationship between deer density, tick abundance, and human cases of Lyme disease in a residential community. J. Med. Entomol. 51, 777–784.

Kinnaird, M.F., Sanderson, E.W., O'Brian, T.G., Wibisono, H.T., Woolmer, G., 2003. Deforestation trends in a tropical landscape and implications for endangered large mammals. Conserv. Biol. 17, 245–257.

Koh, L.P., Dunn, R.R., Sodhi, N.S., Colwell, R.K., Proctor, H.C., Smith, V.S., 2004. Species coextinctions and the biodiversity crisis. Science 305, 1632–1634.

Labruna, M., 2009. Ecology of *Rickettsia* in South America. Ann. N. Y. Acad. Sci. 1166, 156–166.

Lafferty, K.D., 2012. Biodiversity loss decreases parasite diversity: theory and patterns. Philos. Trans. R. Soc. Long B: Biol. Sci. 367, 2814–2827.

Leigh, E.G., 1999. Tropical Forest Ecology: A view from Barro Colorado Island. Oxford University Press, New York.

Mendenhall, C.D., Karp, D.S., Meyer, C.F., Hadly, E.A., Daily, G.C., 2014. Predicting biodiversity change and averting collapse in agricultural landscapes. Nature 509, 213–217.

Meyer, N., Esser, H.J., Moreno, R., van Langevelde, F., Liefting, Y., Oller, D.R., Vogels, C. B.F., Carver, A.D., Nielsen, C.K., Jansen, P.A., 2015. An assessment of the terrestrial mammal communities in forests of Central Panama, using camera-trap surveys. J. Nat. Conserv. 26, 28–35.

Mihalca, A., Gherman, C., Cozma, V., 2011. Coendangered hard-ticks: threatened or threatening? Parasit Vectors 4, 1–7.

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.

Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J. R. Soc. Interface 14, 20170213.

Ogrzewalska, M., Uezu, A., Jenkins, C.N., Labruna, M.B., 2011. Effect of forest fragmentation on tick infestations of birds and tick infection rates by *Rickettsia* in the Atlantic forest of Brazil. EcoHealth 8, 320–331.

Onofrio, V., Labruna, M.B., Pinter, A., Giacomin, F., Barros-Battesti, D.M., 2006. Comentários e chaves as espécies do gênero *Amblyomma*. In: Barros-Battesti, D., Arzua, M., Bechara, G. (Eds.), Carrapatos de importância médico-veterinária da regiao Neotropical. Instituto Butantan, Brasil, pp. 53–82.

Ostfeld, R.S., Canham, C.D., Oggenfuss, K., Winchcombe, R.J., Keesing, F., 2006. Climate, deer, rodents, and acorns as determinants of variation in Lyme-disease risk. PLoS Biol. 4, e145.

Ostfeld, R.S., Keesing, F., 2012. Effects of host diversity on infectious disease. Annu. Rev. Ecol. Evol. Syst. 43, 157–182.

Rand, P.W., Lubelczyk, C., Lavigne, G.R., Elias, S., Holman, M.S., Lacombe, E.H., Smith Jr., R.P., 2003. Deer density and the abundance of *Ixodes scapularis* (Acari: Ixodidae). J. Med. Entomol. 40, 179–184.

Randolph, S.E., Dobson, A., 2012. Pangloss revisited: a critique of the dilution effect and the biodiversity-buffers-disease paradigm. Parasitology 139, 847–863.

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

Rowcliffe, J.M., Carbone, C., Jansen, P.A., Kays, R., Kranstauber, B., 2011. Quantifying the sensitivity of camera traps: an adapted distance sampling approach. Methods Ecol. Evol. 2, 464–476.

Schmidt, K.A., Ostfeld, R.S., 2001. Biodiversity and the dilution effect in disease ecology. Ecology 82, 609–619.

Szabó, M.P.J., Labruna, M.B., Garcia, M.V., Pinter, A., Castagnolli, K.C., Pacheco, R.C., Castro, M.B., Veronez, V.A., Magalhães, G.M., Vogliotti, A., Duarte, J.M.B., 2009. Ecological aspects of the free-living ticks (Acari: Ixodidae) on animal trails within Atlantic rainforest in south-eastern Brazil. Ann. Trop. Med. Parasitol. 103, 57–72.

Tagliapietra, V., Rosà, R., Arnoldi, D., Cagnacci, F., Capelli, G., Montarsi, F., Hauffe, H., Rizzoli, A., 2011. Saturation deficit and deer density affect questing activity and local abundance of *Ixodes ricinus* (Acari, Ixodidae) in Italy. Vet. Parasitol. 183, 114–124.

Tobler, M.W., Carrillo-Percastegui, S.E., Leite Pitman, R., Mares, R., Powell, G., 2008. An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. Anim. Conserv. 11, 169–178.

Turner, I.M., 1996. Species loss in fragments of tropical rain forest: a review of the evidence. J. Appl. Ecol. 33, 200–209.

Verderane, M.P., Falótico, T., Resende, B.D., Labruna, M.B., Izar, P., Ottoni, E.B., 2007. Anting in a semifree-ranging group of *Cebus apella*. Int. J. Primatol. 28, 47.

Wilson, D.E., Reeder, D.M. (Eds.), 2005. Mammal species of the world: a taxonomic and geographic reference, vol. 1. Johns Hopkins University Press, Baltimore.

Woolhouse, M.E.J., Taylor, L.H., Haydon, D.T., 2001. Population biology of multihost pathogens. Science 292, 1109–1112.