



Contents lists available at ScienceDirect

International Journal for Parasitology

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

Forest edges affect ectoparasite infestation patterns of small mammalian hosts in fragmented forests in Madagascar[☆]

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ARTICLE INFO

Article history:

Received 14 November 2019

Received in revised form 15 January 2020

Accepted 16 January 2020

Available online xxxx

Keywords:

Habitat fragmentation

Lemurs

Rodents

Ticks

Mites

Lice

ABSTRACT

Habitat loss and fragmentation drive the worldwide depletion of biodiversity. Although it is known that anthropogenic disturbances severely affect host and ecosystem integrity, effects on parasites are largely understudied. This study aims to investigate if and how habitat fragmentation affects the composition of ectoparasite communities on small mammalian hosts in two networks of dry deciduous forest fragments in northwestern Madagascar. Forest sites differing in size, proportion of edge habitat and host density were studied in the Ankarafantsika National Park and in the Mariarano region. A total of 924 individuals of two mouse lemur species, *Microcebus murinus* ($n = 200$) and *Microcebus ravelobensis* ($n = 426$), and two rodent species, endemic *Eliurus myoxinus* ($n = 114$) and introduced *Rattus rattus* ($n = 184$), were captured to assess ectoparasite infestations. Ectoparasite prevalence and ectoparasite species richness were statistically related to nine ecological variables applying generalized linear mixed models. Hosts harbored ticks (*Haemaphysalis microcebi*), mites (*Schoutedenichia microcebi*, *Listrophoroides* spp., Laelaptidae gen. spp.) and sucking lice (*Lemurpediculus* spp., *Polyplax* sp., Hoplopleuridae gen. sp.). Parasite prevalence differed significantly between host species for all detected parasite taxa. Proximity to the forest edge led to a significant reduction in ectoparasites. Parasite-specific edge effects were observed up to a distance of 750 m from the forest edge. The obtained results imply that habitat fragmentation impacts ectoparasite communities, in particular by negatively affecting temporary parasite species. The results are best explained by an interplay of parasite life cycles, responses to changes in abiotic factors induced by edges and host-specific responses to habitat fragmentation. The negative responses of most studied ectoparasite taxa to forest edges and habitat fragmentation demonstrate their ecological vulnerability that may eventually threaten the integrity of ecosystems and potentially impact ectoparasite biodiversity worldwide.

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1. Introduction

With more than 7.5 billion individuals, the world's human population exerts an enormous pressure on our planet's ecosystems

[☆] Note: Nucleotide sequence data reported in this paper are available in GenBank under the accession numbers MN927203, MN935436, MN935445–MN935451, MN939409–MN939411, MN945158, MN945159, MN945217 and MN945218.

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(United Nations, 2017). As a consequence of ongoing population growth, human settlements, agriculture, mining, fishing and forestry require more and more space at the expense of natural ecosystems (Haddad et al., 2015). On the island of Madagascar, the human population is projected to increase from around 25 million people in 2017 to more than 50 million in 2050 (United Nations, 2017). Anthropogenic pressures are reflected in continued forest fragmentation and a massive loss of natural vegetation all over the island. According to Vieilledent et al. (2018), Madagascar has already lost 44% of its forest cover between 1953 and 2014, and 46% of the remaining forest is now located closer than 100 m from the forest edge. These changes impact the flora and fauna of the island that is well known for its outstanding biodiversity and high rates of endemism (Myers et al., 2000; Ganzhorn et al., 2001).

<https://doi.org/10.1016/j.ijpara.2020.01.008>

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Forest fragmentation primarily implies a loss of connectivity. It constrains dispersal and hence gene flow between habitats and leads to reduced genetic diversity in subpopulations (Sommer, 2003; Schlaepfer et al., 2018). Forest fragmentation also generates more habitat edges that alter the local environment and reach from the edge into the forest at varying depths. More specifically, abiotic edge-related changes (e.g. in temperature, humidity and ultraviolet radiation) can trigger biotic changes in the vegetation and in the local fauna (Malcolm, 1994; Kunin, 1998). Within fragments, restricted space and resources (Sweatman et al., 2017; Delciellos et al., 2018; Kamilar and Beaudrot, 2018) may lead to crowding effects, increased intra- and interspecific competition and thus to environmental stress (Farina et al., 2018). Stressed animals with lower genetic diversity may also suffer from reduced immune function and may therefore be more vulnerable to diseases and parasites (Khansari et al., 1990; Lafferty and Kuris, 1999; Belasen et al., 2019). Increased exposure to infective parasite stages in fragmented habitats (Chapman et al., 2005; Gillespie et al., 2005) and more frequent social contacts in crowded populations (Altizer et al., 2003; Gabriel et al., 2018) might further foster parasitism in fragments. Habitat fragmentation is also known to provide greater access for domestic and invasive animals to formerly remote areas, facilitating spillover events of new and potentially harmful parasites to wildlife. Studies on gastrointestinal parasites (Gillespie et al., 2005; Chapman et al., 2006; Gillespie, 2006; Trejo-Macías et al., 2007; Gillespie and Chapman, 2008; Froeschke et al., 2013; Klaus et al., 2018), blood parasites (Vaz et al., 2007; Fornberg, J., 2017. Host-Parasite Interactions: Insights From an Island Lizard. Master's thesis, University of Michigan, USA; Perez-Rodriguez et al., 2018) and ectoparasites (Ogrzewalska et al., 2011; Froeschke et al., 2013) documented higher levels of parasitism in vertebrates in fragmented than non-fragmented African, Asian, South and Central American habitats. Similarly, studies on Malagasy lemurs showed higher prevalences of parasites in populations inhabiting habitat fragments and disturbed ecosystems compared with those in continuous and undisturbed habitats (Raharivololona and Ganzhorn, 2009; Schwitzer et al., 2010; Junge et al., 2011). However, there is also evidence from some arthropod, reptilian and mammalian hosts for the opposite effect, i.e. lower parasite prevalence and parasite diversity in fragments (Merriam and Taylor, 1996; Vandergast and Roderick, 2003; Bush et al., 2013; Renwick and Lambin, 2013; Bolívar-Cimé et al., 2018; Martínez-Mota et al., 2018; Resasco et al., 2019). Such contradictory evidence suggests that our understanding of the consequences of habitat fragmentation and edge effects on host-parasite interactions and parasite communities is still very limited. Because host animals need to be closely examined to study ectoparasites in the wild, such studies are rather rare compared with those on gastrointestinal parasites, for which feces can be used and obtained non-invasively.

The present study aimed to evaluate the impact of fragmentation and habitat edges on ectoparasite infestation of four small mammal species inhabiting tropical deciduous dry forest in northwestern Madagascar: the two sympatric cheirogaleids, gray mouse lemur (*Microcebus murinus*, ~54 g) and golden-brown mouse lemur (*M. ravelobensis*, ~56 g) as well as two rodent species, the endemic western tuft-tailed rat (*Eliurus myoxinus*, ~66 g) and the invasive black rat (*Rattus rattus*, ~100 g). These four species are all nocturnal, arboreal or semi arboreal, utilize protected sleeping sites and occur in relatively high population densities.

Both mouse lemur species forage solitarily during the night on a mixed and seasonally variable diet of insects, insect secretions, fruit, gum and nectar in various compositions (Thorén et al., 2011, 2016). During the day, the animals sleep mainly in groups in sheltered sleeping sites. The distribution of *M. murinus* is large and stretches along the west coast of Madagascar up to the Sofia

river (Mittermeier, 2010). The gray mouse lemur prefers wooden tree holes as sleeping sites (Radespiel et al., 2003), shows female dominance and can be considered a dietary generalist (reviewed in Radespiel, 2016). The endangered golden-brown mouse lemur occurs only between the Betsiboka and Mahajamba rivers (Olivieri et al., 2007; Rakotondravony and Radespiel, 2009). *Microcebus ravelobensis* shows no clear female dominance and forms mixed-sex sleeping groups in various types of sleeping sites (Radespiel et al., 2003; Thorén et al., 2010; Eichmueller et al., 2013). There is only one study available investigating the influence of habitat disturbance and fragmentation on ectoparasites in mouse lemurs; however, no habitat-related effects on infestation patterns in the southwestern *M. griseorufus* were found (Ehlers et al., 2019). Regarding gastrointestinal parasites, Rakotoniaina et al. (2016) found no effects of habitat degradation in *M. murinus*, whereas Raharivololona and Ganzhorn (2009) showed different effects of fragment size and the level of degradation depending on the gastrointestinal parasite species.

The western tuft-tailed rat (*E. myoxinus*, Nesomyidae) is endemic to the spiny and dry deciduous forests along the west coast of Madagascar. This herbivorous solitary forager is promiscuous and sleeps solitarily in tree holes (Carleton, 1994; Ramanamanjato and Ganzhorn, 2001; Sommer et al., 2002; Randrianjafy et al., 2008; Goodman, 2016. *Eliurus myoxinus* IUCN Red List Threatened Species. <https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T7623A22238673.en> (accessed 21 March 2019)). Black rats (*R. rattus*, Muridae) were introduced to Madagascar approximately 3000–10,000 years ago during the course of human colonization of the island (Tollenaere et al., 2010). They are now widely distributed all over the island (Goodman, 1995). Black rats live solitarily or in social groups of up to 50 individuals (Münster, M., 2003. Molekulargenetische Untersuchungen zur Populationsdifferenzierung von *Rattus rattus* L. auf Madagaskar. Diploma thesis, University of Hamburg, Germany). The omnivorous rats feed on seeds, fruit and invertebrates (Clark, 1982; Shiels et al., 2014). Self-built nests, consisting of various different materials, exposed or in already available cavities, serve as shelters in times of inactivity (Münster, M., 2003. Diploma thesis, cited earlier). Although studies on other populations worldwide show a simultaneous presence of many different endo- and ectoparasites at high prevalences (Mafiana et al., 1997; Claveria et al., 2005; Singla et al., 2008; Siti Shafiyah et al., 2012; Pakdel et al., 2013), the recently arrived and expanded *R. rattus* subpopulation on Madagascar might have a reduced ectoparasite parasite species richness (EPSR) in comparison to native species as this is known for invasive species in general (Torchin et al., 2003; Colautti et al., 2004). It is suspected that *R. rattus*, as an invasive species, may also contribute to the spread of non-endemic parasites to native animals (Smith and Carpenter, 2006).

To elucidate the impact of fragmentation and habitat edges on ectoparasite infestation, we investigated to what extent host-related (e.g. species, body mass, sex, population density) as well as habitat-related factors (e.g. forest size, proportion of edge habitat, distance to the forest edge) influence the composition of ectoparasite communities and prevalences in the four host species in two dry deciduous forest landscapes in northwestern Madagascar. Due to potentially reduced defensive ability and greater exposure to parasites of host animals in fragmented and degraded habitats, we expect higher ectoparasite prevalences and a higher EPSR in hosts colonizing fragments. Decreasing fragment size and increasing edge effects are assumed to increase environmental stress of the hosts and hence their susceptibility to ectoparasite infestations. Hosts living close to the forest edge are therefore expected to show higher infestation rates and harbor more ectoparasite species than animals dwelling in the forest interior. Moreover, hosts from fragments with a high proportion of edge

habitat are expected to be infested at higher rates and with more ectoparasite species than animals from fragments with a low proportion of edge habitat. In addition, certain host-related factors such as species differences, sex, body mass and host population density will be taken into account.

2. Material and methods

2.1. Study regions

Two networks of dry deciduous forest fragments, one in the Ankarafantsika National Park (ANK) and one in the Mariarano Region (MAR), Madagascar, were studied in the dry seasons (May to October) of the years 2017 and 2018 (Fig. 1). In each region, several continuous forest sites and forest fragments were chosen for the study. In ANK the sites were situated in the western part of the park (16°18'S, 46°42'E, 75 km southeast of Mahajanga) and located on a plateau (ca. 180 m above sea level) without any open water body in close proximity. The landscape in between the patches of forest is characterized by a dry savannah-like grass vegetation (mostly *Aristida barbicollis*) (Steffens and Lehman, 2016), lacking larger numbers of bushes or trees. Periodic bushfires and sporadically grazing cattle maintain the uniform character of the matrix. The dry forest of MAR, managed by the local municipality Mariarano, is located close to the coast (15°24'S, 46°44'E, 50 km northeast of Mahajanga) at an altitude of 20–90 m above sea level. Rice fields and savannah interspersed with palm trees (*Bismarckia nobilis*) in varying densities separate forest patches. The river Mariarano crosses the area in a north-south direction; channels for rice field irrigation, streams and ponds are omnipresent and provide humidity throughout the year. Riverine vegetation maintains a potential connection between forest patches in the central part of this study region. The seasonal climate in both study landscapes is characterized by a hot and humid rainy season (November to April) and a cooler dry season (May to October). Forest edges were defined according to Steffens (Steffens, T., 2017. Biogeographic patterns of lemur species richness and occurrence in a fragmented landscape. PhD thesis, University of Toronto, Canada). Global Positioning System (GPS) data was collected by walking along edges and transects. Data was then processed applying the software QGIS (QGIS Development Team, 2018. QGIS Geographic Information System, version 2.18.9, Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>) to determine distances to the edge, 50 m edge zone, and forest size. Continuous forest patches were measured using polygons based on satellite footage from Google Earth Pro (Google, 2018. Google Earth Pro, version 7.3.2., <http://www.earth.google.com> (accessed in December, 2018)), processed in QGIS.

2.2. Host capture and ectoparasite sampling

In ANK, 31 transects were installed in 27 forest fragments and four transects in the continuous forest (Fig. 1A). In MAR, 18 transects were installed in 13 forest fragments and eight transects across three patches of continuous forest (Fig. 1B). All transects pointed perpendicularly from the forest edge to the interior of the forest. Transects ranged in length from 40 m to 490 m in forest fragments to reach the center, and from 150 m to 1000 m in the continuous forest to reach core forest areas. Sherman live traps (Sherman Traps, Inc., Tallahassee, FL, USA), baited with banana pieces, were installed in pairs every 10 m along the transects and were placed on branches varying in height between 0.5 and 2.5 m. Trapping took place three times per transect at intervals of 3 days. Traps were set up in the late afternoon and checked in the early morning of the following day. The host population den-

sity was approximated by the number of animals of a species captured per 100 installed traps. Examinations of the captured animals were conducted during the morning, and animals were released at their individual capture sites in the evening of the same day. Rodents were anesthetized prior to examination with ketamine ("Ketamin 10%", Medistar, Germany) and xylazine ("Xylazin 20 mg/ml", Serumwerk Bernburg AG, Germany) (80 mg/kg of ketamine and 16 mg/kg of xylazine for *R. rattus*, 70 mg/kg of ketamine and 12 mg/kg of xylazine for *E. myoxinus*) injected intramuscularly into the gluteus maximus muscle of the hind limb. Captured animals were marked with coded ear clippings, weighed and sexed. Body measurements according to Hafen et al. (1998) were taken. The ears as well as the coat of the head, back, abdomen, tail and limbs were systematically scanned by eye for ectoparasites. Ectoparasites were stored in ethanol (90–96%) or in RNAlater® (Qiagen, the Netherlands). In order to enable comparison of the body mass of host specimens from different species, values for body mass were standardized. For each host species, the lightest animal was assigned a value of 0 and the heaviest animal a value of 100, while all other individuals were assigned a proportional value between these two extremes.

2.3. Ectoparasite identification

The collected ectoparasites were grouped morphologically by applying incident light and transmitted light microscopy. Classification was based on determination keys and taxonomic literature published by Hoogstraal et al. (1965), Walker et al. (2003) and Klein et al. (2018) on ticks, Stekolnikov and Fain (2004) and Stekolnikov (2018, Stekolnikov et al., 2019) on mites of the family Trombiculidae, Fain (1977, 1981) and Bochkov and Fain (2003) on mites of the family Atopomelidae, Tipton (1957) and Domrow and Taufflieb (1963) on mites of the family Laelaptidae and Ward (1951), Voss (1966), Kim and Emerson (1974) and Durden et al. (2010, 2018) on sucking lice.

Eight ticks, eight chigger mites (Trombiculidae), six predatory mites (Laelaptidae), five fur mites (Atopomelidae) and 23 sucking lice from different host species and sampling sites were chosen for Sanger sequencing to evaluate the morphological species assignments. A part of the cytochrome *c* oxidase subunit 1 (*cox1*) gene was amplified using primers Cox1F and Cox1R (Chitimia et al., 2010) for tick and primers L6625 and H7005 (Hafner et al., 1994) for sucking louse specimens, while a part of the 18S rRNA gene was amplified from mite specimens using primers 18Sfw and rev960 (Dabert et al., 2010). Genomic DNA isolation and PCRs were conducted as described by Klein et al. (2018). PCR products were custom Sanger-sequenced (SeqLab Sequence Laboratories Göttingen, Germany). Resulting nucleotide sequences were aligned using the software Geneious 10.2.3 (<https://www.geneious.com>) and compared with sequences available in NCBI GenBank by BLAST sequence comparison. Nucleotide sequence orders not yet available in GenBank were deposited under accession nos. MN927203, MN935436, MN935445-MN935451, MN939409-MN939411, MN945158, MN945159, MN945217 and MN945218. The tool "MrBayes" (Bayesian inference in phylogeny) of the software Geneious 10.2.3 was employed for phylogenetic analyses performed with 1,100,000 bootstraps.

2.4. Data analyses

Presence-absence data of each ectoparasite taxon and the number of simultaneously present ectoparasite taxa (EPSR) on individual hosts were used as dependent variables in generalized linear mixed models (GLMMs) using the "lme4" package in the software R (R Foundation for Statistical Computing, Vienna, Austria, <https://www.R-project.org>) and RStudio (Integrated Development for R.

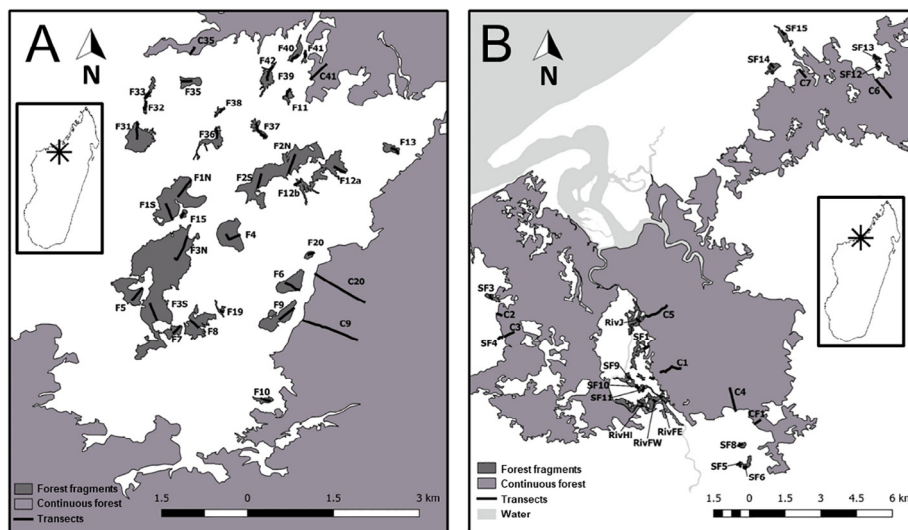


Fig. 1. Maps of two studied networks of fragmented dry deciduous forest in Madagascar, one in the western part of the Ankarafantsika National Park (A) and one in the Mariarano region (B). Transects are marked with individual identifiers (eg. F20, C4). Modified after [Andriatsitohaina et al., 2020](#).

RStudio, Inc., Boston, USA, <http://www.rstudio.com>). The results of 1279 ectoparasite examinations (including a second examination of individuals when recaptured) were merged to single data points of ectoparasite statuses of 924 individual hosts. No ectoparasite examination was conducted when the animal was captured a third time. Analyses were performed on two sets of data. The full dataset contained all observed host individuals ($n = 924$), while a smaller dataset included hosts trapped in forest fragments only ($n = 479$). One individual had to be excluded from both datasets for modelling the occurrence of mites of the family Trombiculidae and two individuals had to be excluded for modelling the occurrence of Atopomelidae. These animals escaped during the examination before status ascertainment of Trombiculidae and Atopomelidae was completed.

Four different global models (models A–D; [Table 1](#)) were generated for each parasite taxon, with binomial assumption and logit-link for the presence/absence of ticks, mites and sucking lice and with Poisson assumption and log-link for EPSR on each individual host. Separate models were fitted for the full and for the smaller dataset, since fragment-specific parameters (percent edge area) could not be calculated for data from continuous forest transects ([Table 1](#)). To prevent the inclusion of correlated factors within a model, two global models were calculated for each dataset – models A and B for the full dataset and model C and D for the smaller dataset from forest fragments (cf. [Table 1](#) for model composition). Fixed factors (predictor variables) included the host species (*M. murinus*, *M. ravelobensis*, *E. myoxinus*, *R. rattus*), host sex (male, female), host population density (number of captured hosts per 100 installed traps), standardized host body mass (cf. section 2.2), distance of capture place from the forest edge (m), forest type (continuous forest, forest fragment), forest size (log ha) and percent edge habitat of a fragment (surface in close proximity (≤ 50 m) to the forest edge compared with the total fragment size). Values for forest size were log-transformed to achieve normal distribution. Since [McGoogan \(2011\)](#). Edge effects on the behaviour and ecology of *Propithecus coquereli* in Northwest Madagascar. Doctoral thesis, University of Toronto, Canada) showed a significant change in abiotic factors at 50 m distance from forest edges in ANK and a higher threshold value would lead to a loss of variance in our dataset, a 50 m edge strip was chosen to characterize differences in shape and relative representation of the edge between forest fragments. Random factors included sampling

Table 1

Composition of four different global generalized linear mixed models, fitted for each ectoparasite taxon and the ectoparasite species richness as dependent variables separately.

	Data set	Fixed factors	Random factors
Model A	All host individuals	host sex + host density + host body mass + host species + distance to edge + host species * cont. vs. frag. + cont. vs. frag.	sampling site + sampling year + month
Model B	All host individuals	host sex + host density + host body mass + host species + distance to edge + host species * forest size + forest size	sampling site + sampling year + month
Model C	All hosts from forest fragments	host sex + host density + host body mass + host species + distance to edge + percentage edge + distance to the cont. forest	sampling site + sampling year + month
Model D	All hosts from forest fragments	host sex + host density + host body mass + host species + distance to edge + forest size + distance to the cont. forest	sampling site + sampling year + month

cont., continuous sites; frag., fragmented sites.

region (ANK, MAR), sampling year (2017, 2018) and month (May, June, July, August, September, October). Because different host species showed different habitat preferences and tolerance of habitat fragmentation and degradation ([Andriatsitohaina et al., 2020](#)), the interaction term host species * forest type (continuous versus fragmented) was added to model A and host species * forest size was added to model B (cf. [Table 1](#) for details). The selection of models for interpretation was carried out for each global model (A–D) by using the automated model selection function (“dredge”) of the R-package “MuMIn” ([Barton, 2018](#). Mu-MIn: Multi-model inference. R Package Version 0.12.2/r18. <http://R-Forge.R-project.org/projects/mumin/>) based on the Akaike Information Criterion (AIC) method described by [Burnham and Anderson \(2002\)](#). When using this algorithm, the corrected AIC (AICc) values of models with all possible predictor variable combinations were compared. All best models ($\Delta AICc < 2$) were identified and listed, and full details of the models A–D with the lowest to highest AICc weights

(ω) were computed (Akaike, 1979; Wagenmakers and Farrell, 2004; Nakagawa et al., 2017). Host species were compared whenever the species parameter was significant in the best model, and comparisons were based on post-hoc comparisons (Tukey test) performed with the R-package “multcomp” (Hothorn et al., 2008).

3. Results

A total of 200 *M. murinus*, 426 *M. ravelobensis*, 184 *R. rattus* and 114 *E. myoxinus* were trapped and examined for ectoparasites throughout the study (Table 2). While individuals of *M. ravelobensis* were captured primarily in continuous forests, individuals from other host species were mainly found in forest fragments as already published by Andriatsitohaina et al., 2020. Five types of ectoparasites (ticks, Trombiculidae mites, Laelaptidae mites, Atopomelidae mites and sucking lice) were observed during the present study (Fig. 2). Between zero and five ectoparasite taxa were harbored by individual hosts with a mean EPSR of 1.94 across host species. The overall ectoparasite prevalence of all examined host individuals was 39% (360/924) for ticks, 53% (488/923) for Trombiculidae, 17% (159/924) for Laelaptidae, 27% (253/924) for Atopomelidae and 57% (528/924) for sucking lice. Table 3 provides an overview on the results of the best models with lowest AICc. All modelling results are based on the interpretation of all models with (Δ AICc < 2). Detailed information on these models is provided in the Supplementary Tables S1–S6.

3.1. Ticks

While the two mouse lemur species had rather high tick prevalences (25% (49/200) on *M. murinus* and 71% (303/426) on *M. ravelobensis*), the prevalence in rodents was rather low (3% (3/114) on *E. myoxinus* and 3% (5/184) on *R. rattus*). All ticks were morphologically assigned to the genus *Haemaphysalis* (Fig. 2).

Comparison of the obtained partial *cox1* gene sequences of eight analyzed ticks (two from *M. murinus*, four from *M. ravelobensis*, one each from *R. rattus* and *E. myoxinus*) showed 97–99% nucleotide identity among them. According to BLAST results, sequence identity was 97–99% with the recently described species *Haemaphysalis microcebi* (GenBank accession no. MG132089; query cover 96–100%), followed by 86–87% identity with *Haemaphysalis hystricis* (JX573137; query cover 98–100%) and *Haemaphysalis concinna* (KY364906; query cover 98–100%). Thus, the results suggest that the ticks obtained from all four host species belonged to *H. microcebi*.

GLMMs (overview in Table 3, details in Supplementary Table S1) showed no influence of host sex, host body mass and host-habitat-interaction on tick infestation, while significant effects of the factors of host population density, host species, distance from the forest edge, edge percentage, forest type (continuous versus fragmented) and forest size were detected. Host population density was positively associated with the presence of ticks in the best models A and D (Fig. 3). The two mouse lemur species were significantly more often infested than both rodent species. Tick prevalence was higher in the continuous forest than in forest fragments (Fig. 4) and increased significantly with increasing distance from the forest edge (Fig. 5). Increasing forest patch size had a positive effect on tick infestations in the full dataset (model B), but not in the fragment dataset (model D). Additionally, the percentage of edge habitat of a fragment was negatively associated with tick prevalence (model C).

3.2. Trombiculidae mites

Chigger mite larvae were found around the eyes and along the ears and snouts of 29% of *M. murinus* (57/199), 80% of *M. ravelobensis* (342/426), 16% of *R. rattus* (29/184) and 53% of *E. myoxinus* (60/114). Trombiculidae specimen sampled from different host

Table 2
Number of ectoparasite hosts captured in continuous dry forests versus dry forest fragments of northwestern Madagascar.

	<i>Microcebus murinus</i>	<i>Microcebus ravelobensis</i>	<i>Rattus rattus</i>	<i>Eliurus myoxinus</i>	Total
Continuous forest	42 (21%)	337 (79%)	34 (19%)	32 (28%)	445 (48%)
Fragmented forest	158 (79%)	89 (21%)	150 (81%)	82 (72%)	479 (52%)

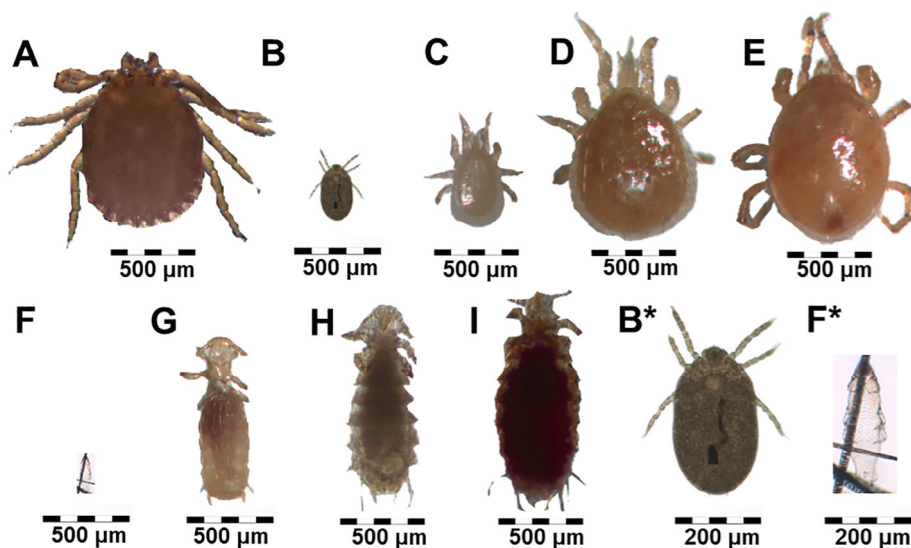


Fig. 2. Ectoparasite morphotypes and species in this study. (A) *Haemaphysalis microcebi*, (B) Trombiculidae mite (scaled up (B*)), (C) *Aetholaelaps trilyssa* (Laelaptidae) infesting both mouse lemur species, (D) Laelaptidae mite infesting *Rattus rattus*, (E) Laelaptidae mite infesting *Eliurus myoxinus*, (F) *Listrophoroides* sp. (Atopomelidae, scaled up (F*)), (G) *Lemurpediculus* sp. infesting mouse lemurs, (H) *Polyplax* sp. infesting *R. rattus*, (I) *Hoplopleura* sp. infesting *R. rattus* and *E. myoxinus*.

species did not obviously differ in morphology (Fig. 2) and could be assigned to the recently described species *Schoutedenia microbei* found infesting *M. murinus* in ANK (Stekolnikov et al., 2019). However, gene sequences of this species are not yet available. Sequencing and aligning the partial 18S rRNA gene of eight analyzed mites (two from *M. murinus*, four from *M. ravelobensis*, one from *R. rattus*, one from *E. myoxinus*) showed 99–100% identity among the specimens and a BLAST comparison resulted in 99–100% identity to Trombiculidae sp. (MG132094; query cover 81–98%) followed by 97–99% identity to *Eutrombicula splendens* (KY922159; query cover 97–100%).

No significant effects of the factors of host sex, host population density and host weight on Trombiculidae infestations were shown by GLMMs (overview in Table 3, details in Supplementary Table S2). Infestation probability was significantly higher in mouse lemurs and *E. myoxinus* than in *R. rattus*. Model A showed a higher infestation risk for *M. ravelobensis* than for *M. murinus* and model B showed *E. myoxinus* having a higher infestation risk than all other host species. By referring to host individuals from forest fragments only, the significant difference between *M. murinus*, *M. ravelobensis* and *E. myoxinus* disappeared, but the infestation risk of *R. rattus* remained the lowest (model C and D). Interactions between forest type and host species (model A) as well as forest size and host species (model B) were significant. Except for *R. rattus*, Trombiculidae infestations were found significantly more likely in individuals captured in continuous forests than in forest fragments (Supplementary Fig. S1). Further, increasing distance from the forest edge was associated with significantly higher infestations in models A to C (Fig. 5). Similarly, increasing forest size had a positive effect on the Trombiculidae infestation risk in continuous forests and forest fragments (model B and D; Fig. 4), and in the latter a higher percentage of edge habitat had a negative effect (model C).

3.3. Laelaptidae mites

The prevalence of Laelaptidae mites (17%) was the lowest of all ectoparasite types observed, with infestation rates of 42% (83/200) on *M. murinus*, 2% (9/426) on *M. ravelobensis*, 33% (61/184) on *R. rattus* and 5% (6/114) on *E. myoxinus*. Laelaptidae mites found on the different host species differed in morphology and were thus grouped into three different morphotypes (Fig. 2). The two mouse lemur species shared one morphotype, which was morphologically identified as *Aetholaelaps trilyssa* (Domrow and Taufflieb, 1963), while the rodents *R. rattus* and *E. myoxinus* were infested with different morphotypes, which could not be identified.

Sequence alignments of the partial 18S rRNA gene derived from six mites (two from *M. murinus*, one from *M. ravelobensis*, two from *R. rattus* and one from *E. myoxinus*) confirmed the morphological classification. Sequences from mites infesting mouse lemurs showed 99–100% identity among them. Sequences from mites found on *R. rattus* were also 99–100% identical. Identities of only 97% were found between different morphotypes. BLAST comparisons showed highest similarities to mites belonging to the family Laelaptidae. Mites found on mouse lemurs showed highest identity to *Stratiolaelaps* sp. (KY922102; 98–99% identity, query cover 97–100%) and *Laelaspis* sp. (FJ911848; 97–98% identity, query cover 88–100%), while a sequence comparison with the morphologically assigned species *A. trilyssa* was not possible because no sequences are available yet. Mites found on *E. myoxinus* showed highest identity to *Stratiolaelaps* sp. (KY922102; 99% identity, query cover 100%) and those on *R. rattus* to *Ondatraelaelaps multispinosus* (FJ911843; 98–99% identity, query cover 100%).

GLMMs (overview in Table 3, details in Supplementary Table S3) revealed no significant effects of the factors of host sex, host density and host–habitat–interaction on Laelaptidae prevalence. However, host body mass was positively associated with

Laelaptidae infestations in the full dataset (model A and B). *Microcebus murinus* and *R. rattus* had a significantly higher infestation risk than *M. ravelobensis* and *E. myoxinus* (all models). An increasing distance from the forest edge was positively associated with Laelaptidae prevalence in the full dataset (model A and B), however, Laelaptidae were found significantly more often in forest fragments than in continuous forests (model A; Fig. 4), and increasing forest size had a decreasing effect on infestations (model B). Concordant with these results, hosts from forest fragments with a higher percentage of edge habitat showed higher infestation rates with Laelaptidae mites (model C).

3.4. Atopomelidae mites

Fur mites of the family Atopomelidae were found on 46% (92/200) of *M. murinus*, 24% (102/426) of *M. ravelobensis* and 52% (59/114) of *E. myoxinus*, but were not found on *R. rattus*. Sampled mite specimens (Fig. 2F) appeared morphologically similar between the three infested host species and were categorized as genus *Listrophoroides*.

Phylogenetic analyses of the sequenced partial 18S rRNA gene from five mites (three from *M. murinus*, each one from *M. ravelobensis* and *E. myoxinus*) showed the distinction of two groups, one infesting both mouse lemur species, exhibiting a sequence identity of 98–99%, and the other infesting *E. myoxinus*. When comparing mite sequences from mouse lemurs with those from *E. myoxinus*, identity ranged only from 92–94%. By applying BLAST comparisons, mites infesting both mouse lemur species showed highest identity with *Listrophoroides lemniscornis* (EU152587; 99% identity, query cover 94%) and *Listrophoroides africanus praomys* (EU152588; 98–99% identity, query cover 94%), whereas mites infesting *E. myoxinus* showed highest similarities to *Listrophoroides aethiopicus* (EU152586; 93% identity, query cover 100%) and *Listrophoroides africanus praomys* (EU152588; 92% identity, query cover 100%).

GLMMs (overview in Table 3, details in Supplementary Table S4) revealed no significant effects of host sex, host population density, distance of the hosts capture place from the forest edge, forest type, forest size and percentage of edge habitat on Atopomelidae infestations. However, increasing host body mass was positively associated with Atopomelidae prevalence (models A and B). Host species differences were evident, as *R. rattus* did not have fur mites. Besides, *E. myoxinus* and *M. murinus* were significantly more often infested than *M. ravelobensis*. In the full dataset, *E. myoxinus* showed similar infestation rates as *M. murinus* (model A and B), but higher rates in forest fragments (model C and D).

3.5. Sucking lice

Sucking lice were frequently detected on *M. murinus* (49%, 98/200), *M. ravelobensis* (78%, 334/426) and *R. rattus* (51%, 94/184), but rarely found on *E. myoxinus* (2%, 2/114). Three different morphotypes were observed. The first was found on both mouse lemur species (Fig. 2G), the second was infesting *R. rattus* (Fig. 2H) and the third morphotype was present on *R. rattus* and in two cases as a single specimen each on *E. myoxinus* (Fig. 2I). Based on morphological criteria, the first morphotype was assigned to the genus *Lemurpediculus*, the second to the genus *Polyplax* and the third to the genus *Hoptopleura*.

Sequences of partial *cox1* genes were obtained from 23 sucking louse specimen (six from *M. murinus*, 10 from *M. ravelobensis*, six from *R. rattus* and one from *E. myoxinus*). Sucking lice found on *M. murinus* showed 97–99% identity among them, while identity among louse specimens on *M. ravelobensis* ranged between 95% and 100%. When comparing sucking louse sequences from

Table 3

Results of general linear mixed models with lowest corrected Akaike information criterion (i.e. best models) for predictor variables. Factors not tested in the models are marked in dark grey; factors excluded from the best model are marked in light grey.

Ectoparasite/ EPSR	Host data	Model	AICc	Host-related factors					Habitat-related factors			
				Model B/D	All models				All models	Model A	Model B/D	Model C
				Host/habitat interaction term	Species	Density	Sex	Body mass	Distance from edge	Forest type (cont. vs. frag.)	Forest size (log ha)	Percent edge area
<i>Temporary ectoparasites</i>												
<i>H. microcebi</i>	all	A	584.8		Mm, Mr > Em, Rr	+			+	x (cont. ↑)		
	all	B	604.8		Mm, Mr > Em, Rr	ns			+		+	
	frag.	C	229.8		Mm, Mr > Em, Rr	ns					–	
	frag.	D	237.2		Mm, Mr > Em, Rr	+			+			
Trombiculidae	all	A	782.1	x (interaction)	Mr > Em, Mm > Rr				+	x (cont. ↑)		
	all	B	816.8	x (interaction)	Em > Mr, Mm, Rr				+		+	
	frag.	C	417.2		Em, Mr, Mm > Rr				+		+	
	frag.	D	408.5		Em, Mr, Mm > Rr			ns			+	
Laelaptidae	all	A	545.5		Mm > Rr > Em, Mr			+	+	x (frag. ↑)		
	all	B	539.7		Mm > Rr > Em, Mr			+	+		–	
	frag.	C	431.0		Mm > Rr > Em, Mr			ns			+	
	frag.	D	428.0		Mm > Rr > Em, Mr			ns			–	
<i>Stationary ectoparasites</i>												
Atopomelidae	all	A	789.1		Em, Mm > Mr > Rr		ns	+				
	all	B	789.1		Em > Mm > Mr > Rr		ns	+				
	frag.	C	332.8		Em > Mm > Mr > Rr							
	frag.	D	332.8		Mr > Mm, Rr > Em							
Sucking lice	all	A	955.7		Mr > Mm, Rr > Em	+	ns	–	+			
	all	B	955.7		Mr > Mm, Rr > Em	+	ns	–	+			
	frag.	C	534.6		Mr > Mm, Rr > Em	+	X				–	
	frag.	D	537.3		Mr, Mm > Em, Rr	+	X	(♂ > ♀)				
EPSR	all	A	2636.7	ns	Mr, Mm > Em, Rr	ns			+	ns		
	all	B	2652.5		Mr, Mm > Em, Rr	+			+		+	
	frag.	C	1251.6		Mr, Mm > Em, Rr						–	
	frag.	D	1254.9		Mm, Mr > Em, Rr	ns			+			

EPSR, ectoparasite species richness; AICc, corrected Akaike information criterion; cont., continuous; frag., fragmented; x, significant effect; +, significant positive effect; –, significant negative effect; ns, not significant; Mm, *Microcebus murinus*; Mr, *Microcebus ravelobensis*; Em, *Eliurus myoxinus*; Rr, *Rattus rattus*.

M. murinus with those of *M. ravelobensis*, identities ranged only between 83% and 88%, suggesting the presence of two different louse species on the lemurs. Sequences from sucking lice infesting *R. rattus* showed a division into two groups concordant with the morphological classification. These groups of *Polyplax* and *Hoplopleura* sucking lice showed an identity of only 73–74% in comparison. Identities within groups ranged from 98–99%. BLAST results largely confirmed the morphological genus assignment. Sucking louse specimens from *M. murinus* exhibited high identities to *Lemurpediculus* sp. 1 (MG983748; 99–100% identity, query cover 92–97%), while specimens from *M. ravelobensis* revealed highest identity to *Lemurpediculus* sp. 2 (MG983747; 97–100% identity, query cover 68–82%). *Lemurpediculus verruculosus* (HM171447) showed only 82–84% identity (query cover 91–100%) to sucking louse sequences from both mouse lemur species. A new sucking louse species, *Lemurpediculus madagascariensis*, found on *M. murinus* in ANK has been recently described based on morphological characteristics (Durden et al., 2018). Although *L. madagascariensis* sequences are not yet available, morphological criteria provide evidence that the sucking lice found on *M. murinus* belong to this species. According to the genetic results, sucking lice from *M. ravelobensis* likely represent an undescribed species of the genus *Lemurpediculus*.

Sequences of sucking lice found on *R. rattus* only showed highest identities to *Polyplax spinulosa* (EU162140, HQ542196 and HQ542195; 98–99% identity, query cover 98–99%), confirming the morphological assignment at least to the genus *Polyplax*. Sucking lice from the third morphotype present on *R. rattus* and two

E. myoxinus revealed highest identities to *Hoplopleura quadridentata* (EU375771; 78–79% identity, query cover 91%) and *Hoplopleura kitti* (KJ648943; 77% identity, query cover 98–99%), suggesting assignment to the family Hoplopleuridae.

Modeling (overview in Table 3, details in Supplementary Table S5) did not show significant effects of forest type, forest size and host-habitat-interaction on the infestation rates with sucking lice. However, males were more often infested than females in the fragments, but not in the full dataset. Higher host population densities were associated with higher prevalences (all models; Fig. 3). In the full dataset, sucking louse infestation rates were positively associated with low host body mass. Furthermore, increasing distance from the forest edge had a positive effect on infestation rates (model A and B; Fig. 5). Similarly, high percentages of edge habitat in forest fragments were negatively associated with the occurrence of sucking lice (model C).

3.6. Ectoparasite species richness (EPSR)

On average, *M. murinus* was infested with 1.90, *M. ravelobensis* with 2.56, *E. myoxinus* with 1.14 and *R. rattus* with 1.03 different ectoparasite taxa. GLMMs (overview in Table 3, details in Supplementary Table S6) did not show significant effects of host sex, host body mass and host-habitat-interaction on EPSR. EPSR was found to be significantly higher in host populations with higher densities in two out of five models generated with the full dataset (model A and B; Fig. 3; Supplementary Table S6). The two mouse lemur species exhibited a significantly higher EPSR than the two rodent

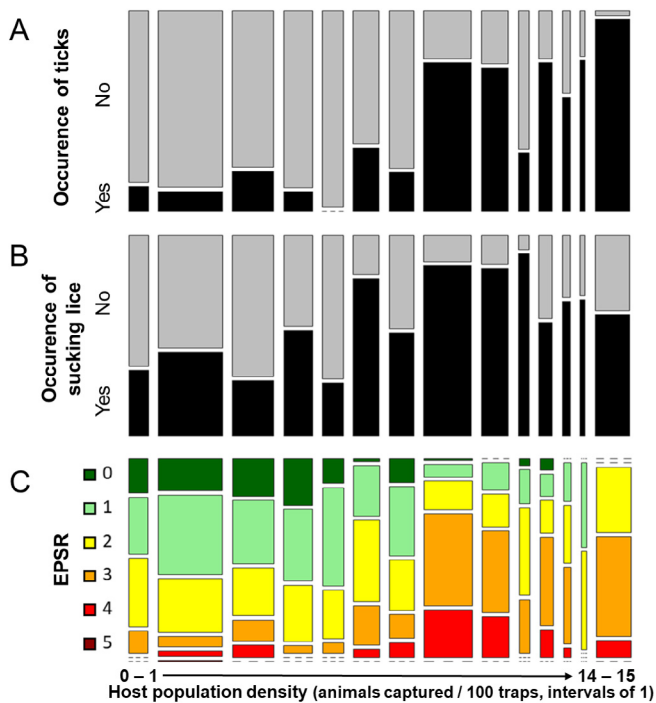


Fig. 3. Occurrence of ectoparasites in this study significantly affected by host population density. (A) Ticks, (B) sucking lice and (C) ectoparasite species richness related to host population density. The widths of the columns correspond to the number of sampled host individuals.

species (all models). Increasing distance from the forest edge was positively associated with EPSR in three models (model A, B and D; Fig. 5). Moreover, a significantly higher EPSR in hosts from continuous forests than in hosts from forest fragments was found in two out of five generated models (model A; Fig. 4; Supplementary Table S6). In the full dataset, increasing forest size was shown to be

linked to a higher EPSR (model B). Similarly, an increasing percentage of edge habitat in the forest fragment dataset was associated with lower EPSR (model C).

4. Discussion

This study aimed to evaluate the effects of forest fragmentation and forest edges on ectoparasite infestation risk and species richness in four different host species. The modeling approach allowed us to differentiate between the effects of various host-related (species, population density, sex, body mass) and habitat-related (forest type, distance to the edge, forest size, percentage of edge habitat) factors, while controlling for certain spatio-temporal effects (year, month, region). The five ascertained ectoparasite groups (ticks, Trombiculidae, Laelaptidae, Atopomelidae and sucking lice) and the EPSR were differently affected by this suite of host-related factors and by fragmentation and edge effects, which will be discussed below.

4.1. Ectoparasite infestation risk of different host species

In general, the four different host species investigated in this study resemble each other in their body size, nocturnal activity pattern, an overlapping diet and a more or less pronounced arboreality. Nevertheless, this study revealed substantial differences in the composition of their ectoparasite communities. Possible reasons for these differences could be ectoparasite host specificity but also variable host exposure due to differences in social organization and habitat use.

If a parasite species shows high host specificity, it should not be found infesting different host species or genera, and native hosts should show a higher EPSR than introduced hosts. Ectoparasites with high host specificity were sucking lice, Laelaptidae mites and Atopomelidae mites. Sucking lice are known for their high level of host specificity (Morand and Krasnov, 2007; Durden et al., 2018). In accordance with this expectation, a total of four

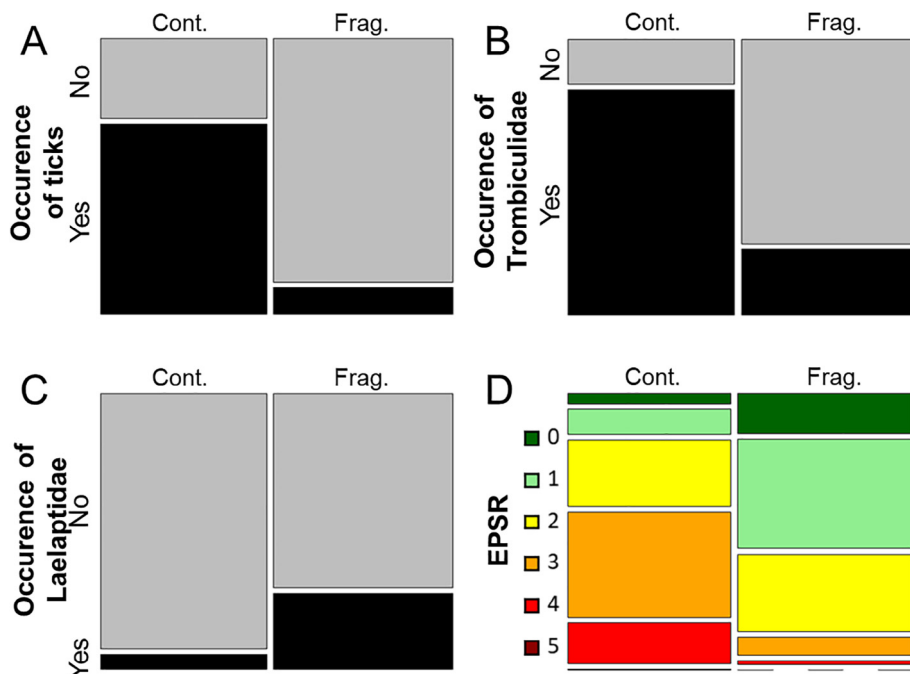


Fig. 4. Occurrence of temporary ectoparasites and ectoparasite species richness in continuous (Cont.) and fragmented (Frag.) dry forest sites in northwestern Madagascar. (A) Ticks, (B) the family Trombiculidae, (C) the family Laelaptidae, (D) ectoparasite species richness. The widths of the columns correspond to the number of sampled host individuals.

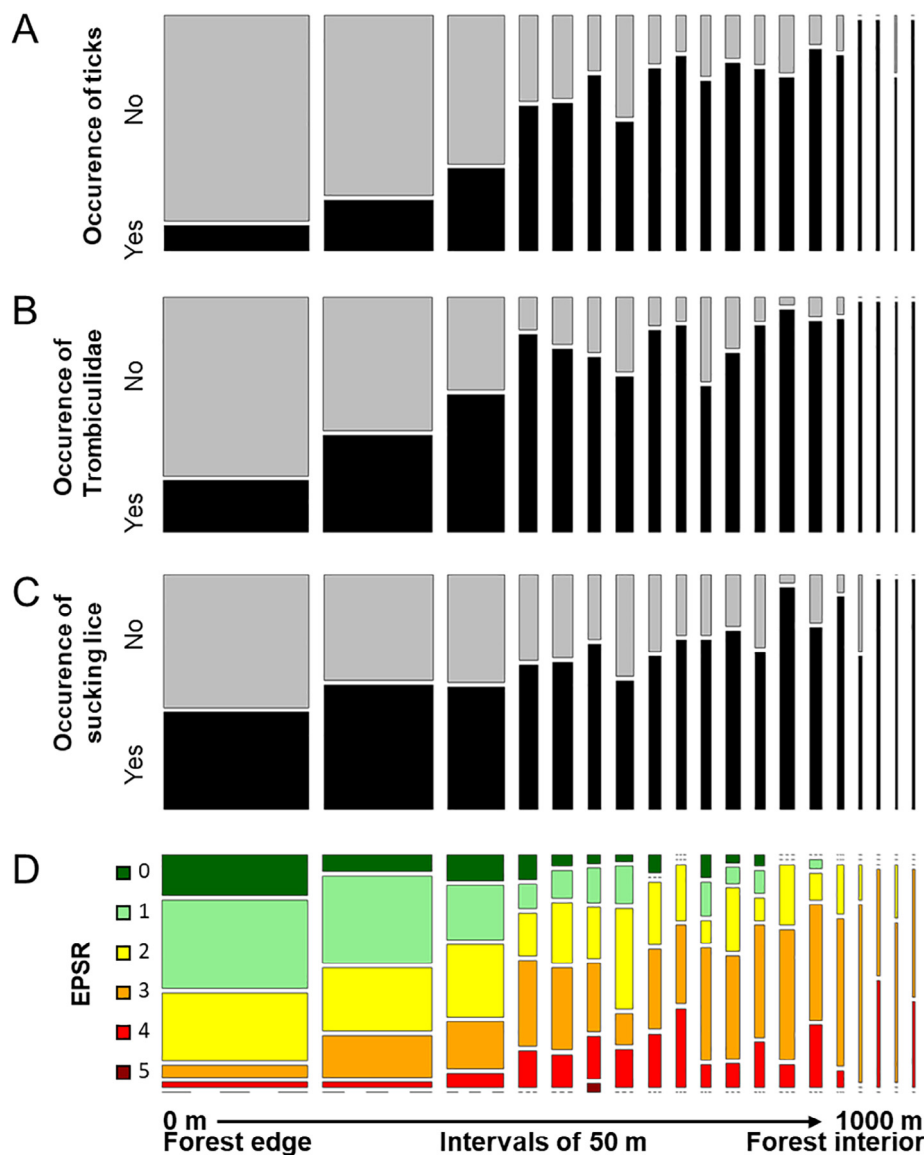


Fig. 5. Occurrence of significantly affected ectoparasites in full dataset modelling. (A) Ticks, (B) the family Trombiculidae, (C) sucking lice and (D) ectoparasite species richness along a distance gradient from the forest edge (0 m) to the forest interior (1000 m) of dry forest sites in northwestern Madagascar. The widths of the columns correspond to the number of sampled host individuals.

host-specific sucking lice taxa were found in this study. Two *Lemurpediculus* taxa were found on the two mouse lemur species, whereas *R. rattus* even had two lice taxa, *Polyplax* sp. and *Hoplopleuridae* gen. species. Remarkably, *E. myoxinus* probably does not host sucking lice at all, since the two single cases of *Hoplopleuridae* gen. sp. on *E. myoxinus* were most likely the result of an accidental infestation.

Host specificity of Laelaptidae mites has previously been described by [Gettinger \(1992\)](#), who found most species of the genus *Laelaps* to be monoxenous on small rodent hosts in Brazil. In our study, mites from the family Laelaptidae also showed host specificity, as *Microcebus* spp., *E. myoxinus* and *R. rattus* were infested by different species. In accordance with our results, fur mites of the genus *Listrophoroides* (family Atopomelidae) were previously categorized as mono- or oligoxenous ([Bochkov et al., 2005](#)). Genetic analyses in this study suggest a moderate host specificity with the presence of two species, one infesting the two mouse lemur species and one infesting *E. myoxinus*. Although atopomelid mites of the genus *Listrophoroides* were previously described to

infest rodents of the genus *Rattus* ([Bochkov et al., 2004](#)), we did not find any *R. rattus* with Atopomelidae mites. This result suggests that the spill-over of native Atopomelidae mites to *R. rattus* as an invasive host species might not yet have happened.

The two other parasite groups, ticks and Trombiculidae mites, did not show a distinct host specificity in our study, i.e. the same parasite taxon was found on mouse lemurs and rodents. However, rodent infestations with *Haemaphysalis microcebi* ticks were rare (3× on *E. myoxinus*, 5× on *R. rattus*), indicating a certain host preference for the mouse lemur species or the presence of factors limiting infestations of rodent hosts, e.g. ecological factors limiting tick exposure or behavioral factors such as more efficient grooming leading to enhanced removal of ticks. In general, host specificity in ticks is highly variable between species, even within genera ([Hoogstraal and Aeschlimann, 1982](#); [Gray et al., 2014](#)), and data on host range is not available for *H. microcebi*. It could be expected that rodents, despite being partly arboreal, spend more time on the ground, where most hard ticks seek for their hosts, and therefore should have higher prevalences. Further hard ticks of the genera

Haemaphysalis, *Ixodes* and *Amblyomma* were previously described to occur in Malagasy small mammal communities (Hoogstraal and Theiler, 1959; Hoogstraal et al., 1966; Uilenberg et al., 1979; Takahata et al., 1998; Walker et al., 2003), but were not found in this study. Inactivity during our period of sampling and the preference of other hosts than our four investigated host species are possible reasons.

As expected, the EPSR of the native taxa (*Microcebus* spp. and *E. myoxinus*) was higher (1.90 on *M. murinus*, 2.56 on *M. ravelobensis*, 1.14 on *E. myoxinus*) than that of the introduced *R. rattus* (1.03). However, significant differences were only found between the two mouse lemur species and *R. rattus*, which might have lost a range of ectoparasites during the process of colonization (Torchin et al., 2003; Colautti et al., 2004; Strona and Fattorini, 2014).

Differences in host biology and exposure may explain different prevalences of Trombiculidae mites, but also Laelaptidae mites and sucking lice. Prevalences of Trombiculidae mites were significantly higher in mouse lemurs and *E. myoxinus* than in *R. rattus*, which might be related to different rates of exposure or different habitat preferences of the different host species. More specifically, *R. rattus* occurred in high numbers in fragments which seem to offer rather unfavorable habitats for Trombiculidae mites. Laelaptidae mites showed low prevalences in *M. ravelobensis* and *E. myoxinus*, and significantly higher prevalences in *M. murinus* and *R. rattus*. In contrast to *M. ravelobensis*, sleeping groups of *M. murinus* are often found in wooden tree holes during the day (Radespiel et al., 1998, 2003; Thorén et al., 2010). These protected shelters are regarded as the basis for infestations with Laelaptidae mites as nest-associated parasites (Morand and Krasnov, 2007). In the case of the rodents, the rather solitary lifestyle of *E. myoxinus* (Poor, 2005. ADW: Nesomyidae “Nesomyidae” (On-line), Animal Diversity Web. <https://animaldiversity.org/accounts/Nesomyidae/#39f95f0feb72e1f0a27191488d7d4752> (accessed 18 April 2019)) might explain the lower prevalences of laelaptid mites compared with *R. rattus*, which are highly social and form large groups that also share nesting sites (Münster, M., 2003. Diploma thesis, cited earlier). Finally, *M. ravelobensis* had a significantly higher infestation risk with sucking lice than the closely related *M. murinus* which may be due to differences in social grouping patterns (= composition of sleeping groups, Radespiel et al., 2003) or different habitat preferences (Andriatsitohaina et al., 2020) which may lead to different louse exposure and transmission risks. Differences in sucking louse prevalences between *M. ravelobensis* and *R. rattus* might be explained by differences in grooming efficiency or again by different habitat preferences for continuous forest (*M. ravelobensis*) versus fragments (*R. rattus*).

4.2. Effects of host sex and body mass on ectoparasites

In general, no effect of host sex on ectoparasite prevalences and the EPSR was found. Only higher prevalences of sucking lice on male hosts could be shown in some models. A male bias in parasite load is reported in many studies and usually explained by either immune suppression due to higher levels of testosterone in males or sometimes by a predominant role of male hosts in parasite transmission, e.g. via sex differences in ranging behavior and/or sociality (Soliman et al., 2001; Klein, 2004; Schalk and Forbes, 2006; Kraus et al., 2008; Zohdy et al., 2012; Godfrey, 2013). For ectoparasites in lemurs, a higher male infestation is described for sucking lice on brown mouse lemurs (*M. rufus*) by Zohdy et al. (2012). However, studies on sucking lice on golden-brown and gray mouse lemurs (*M. ravelobensis* and *M. murinus*) by Klein et al. (2018) and gray-brown mouse lemurs (*M. griseorufus*) by Ehlers et al. (2019), on ticks on ring-tailed lemurs (*Lemur catta*) by Takahata et al. (1998), and on ticks as well as Laelaptidae mites

on Milne-Edward's sportive lemurs (*Lepilemur edwardsi*) by Hokan et al. (2017) found no effects of host sex on parasite prevalences.

Although using body mass as an approximation for fitness is a controversial metric, high values in adult animals are often attributed to good health (Gaillard et al., 2000). In the present study, a significant negative correlation between the infestation risk and body mass was detected for sucking lice only. This result may be either explained by a higher susceptibility of weakened animals or by age. Immunity against sucking lice might be reduced in debilitated animals and should also be, as it develops over time, less efficient at a young age (Wikel, 1982). Adult hosts with low body mass and young hosts might thus both show higher prevalences and infestation intensities of sucking lice. However, a study by Klein et al. (2018) could not show effects of host age or body mass on sucking louse infestations in mouse lemurs in a nearby forest in ANK.

A positive link between increasing body mass and increasing parasite prevalence was found for Laelaptidae and Atopomelidae in our study. According to the “well-fed host hypothesis”, hosts with higher body mass should be more attractive and profitable for parasites (Arneberg, 2002; Christe et al., 2003; Hawlena et al., 2005). An underlying age effect can be relevant as hosts with higher body mass are older individuals who might have accumulated more parasites over time, or may be more susceptible due to immunosenescence at an older age (Zohdy, S., 2012. Senescence ecology: aging in a population of wild Brown Mouse Lemurs (*Microcebus rufus*). Academic dissertation, University of Helsinki, Finland). However, Klein et al. (2018), who compared ectoparasite prevalences on juvenile and adult gray (*M. murinus*) and golden-brown mouse lemurs (*M. ravelobensis*) in ANK, could not find significant differences. Few studies related body mass to parasite load in lemurs. While Hokan et al. (2017) did not find significant correlations between body mass and ectoparasite infestations or microfilarial parasite prevalence in Milne-Edward's sportive lemurs (*Lepilemur edwardsi*) and western woolly lemurs (*Avahi occidentalis*), Klein et al. (2019) detected a higher prevalence of microfilarial blood parasites in *M. murinus* and *M. ravelobensis* with increasing body mass. An accumulation of parasites over time in host individuals with high body mass is likely to be the main cause of our observations in the stationary and directly transmitted Atopomelidae mites for two reasons. First, Atopomelidae fur mites feed on scales and skin particles and are therefore not exposed to the immune mechanisms of the host. Second, mouse lemurs suffer from very high mortality rates in northwestern Madagascar (Radespiel et al., 2001; Lutermaun et al., 2006), which keeps the average adult lifespan rather low (Radespiel et al., 2019), limiting possible effects of immunosenescence in these populations. With regard to the “well-fed host hypothesis”, observations for nest-associated Laelaptidae mites are more likely to be explained with direct selection of high quality hosts by the parasite among the members of a sleeping group. Masked host species effects due to general differences in body mass between the studied host species, such as between mouse lemurs and *R. rattus*, can be excluded since body mass was standardized within each species.

4.3. Effects of host population density on ectoparasites

Data on the effects of host population density on the hosts parasite prevalence in lemurs and rodents are scarce. However, many studies on other host taxa described that high host population densities are associated with higher parasite prevalence and parasite species richness (primates – Mbona and McPeck, 2009; other mammals – Wilson et al., 1985; Arneberg et al., 1998; Arneberg, 2002; Stringer and Linklater, 2015; reptiles – Coates et al., 2016). Host-specific parasites are particularly likely for such a hosts population density effect which could explain the positive effect of increasing

host population density on sucking lice infestation risk. A positive effect on directly transmitted sucking lice may thus be directly related to higher frequencies of social contact in larger populations.

The infestation risk of indirectly transmitted parasites such as the less host-specific ticks may also rise, if higher general host densities lead to proliferating parasite populations via enhanced feeding rates (Anderson and May, 1978; May and Anderson, 1978; Arneberg et al., 1998; Arneberg, 2002; Mbori and McPeck, 2009). Alternatively, according to the “crowding-stress hypothesis”, host susceptibility to parasite infection might increase due to physiological stress resulting from intraspecific competition in higher density populations (Lindsey et al., 2009). Trombiculidae mites were not affected by host population density and were also the least host-specific of all ectoparasites in this study. These findings are congruent with the observation that birds and reptiles may also be accepted as hosts by members of this family (Morand and Krasnov, 2007).

Although Atopomelidae and Laelaptidae species were found to be fairly host-specific, no host population density effect could be shown for these taxa. We are not able to explain our results for the atopomelid mites, but Laelaptidae, as nest-associated parasites, might be dependent in their abundance rather on the size of their hosts sleeping group than on population density per se. Sleeping group sizes are, however, known to be rather stable at least in mouse lemurs (Weidt et al., 2004) and may therefore not depend on host population density.

4.4. Edge effects and fragmentation responses in ectoparasites

It was expected that reduced host immune defense, due to increasing stress and lacking resources in forest fragments, would lead to higher ectoparasite prevalences in such sites. Although higher prevalences in forest fragments could be confirmed for Laelaptidae mites, no such effect was observed for sucking lice and Atopomelidae mites. Ticks and Trombiculidae mites were even found in higher prevalences in the continuous forests. Furthermore, our results showed that all parasite species, with the exception of Atopomelidae mites, showed decreasing prevalences in proximity to the forest edge, which is closely linked to fragmentation. It is known that abiotic factors such as temperature, humidity, ultraviolet radiation and air speed differ between the forest edge and the interior of the forest (Kapos, 1989; Murcia, 1995). In our study, forest fragments and the continuous forest bordered a savannah matrix that was hotter and dryer than the forest itself. High temperatures and lower humidity at the edge may challenge and reduce successful ectoparasite reproduction and development, and increase adult mortality, particularly of environmental stages of temporary parasites. Negative edge effects on ectoparasites were first mentioned by Piloosof et al. (2012) investigating bat flies on neotropical bats, but have not yet been described in Malagasy ecosystems and for ectoparasites on primates in general. In particular, environmental temporary parasite stages may have specific ecological requirements (e.g., temperature, humidity) to facilitate development and survival (Kakuda et al., 1990). However, stationary parasites may also respond to changing environmental factors. For example, Moyer et al. (2011) reported that sucking lice are less abundant on avian hosts in habitats with low humidity. In the present study, both temporary (ticks, Trombiculidae, Laelaptidae) and stationary (sucking lice) ectoparasites showed an increasing prevalence with increasing distance from the forest edge. A difference between these two types of parasites could be seen only in the steepness of the response to increasing distance from the edge. Temporary parasites showed rather low overall prevalences at the forest edge (<25%), and prevalences increased gradually to more than 75% at a distance of approximately 750 m from the

edge. In contrast, the stationary sucking louse prevalence at the edge started with higher values of approximately 40% and increased more slowly to beyond 90% when reaching a distance of 750 m from the forest edge. A certain buffering function of the homeothermic hosts body surface for sucking lice on hosts living close to the edge is likely to explain these differences. Overall, ectoparasite prevalences and EPSR were observed to increase up to a distance of 750 m from the forest edge. Beyond that distance, prevalences remained rather stable at about 75–100% for ticks, and about 100% for Trombiculidae and sucking lice. The ectoparasite edge effects were thus found to penetrate up to 750 m deep into the forest interior. Negative effects of proximity to the forest edge were also shown for Laelaptidae mites, although these mites were mostly found in forest fragments. Since transects in our set of forest fragments just reach a maximum length of 490 m, estimating the range of forest edge effects for this parasite is difficult.

This study suggests that parasite-related edge effects reach deeper into the forest than most of the previously described biotic and abiotic edge effects (e.g. McGoogan, K.C., 2011. Doctoral thesis, cited earlier). Circular forest fragments would need a minimum size of more than 200 ha to provide a minimum of 1 ha of “forest interior” according to this parasite-related edge effect. However, the largest forest fragment sampled in this study was only 114.6 ha in size and not circular at all. Given the relatively small fragment size (0.04–114.6 ha) and the associated short distances of capture points to the next edge (0–206 m) in all studied fragment transects, abiotic factors such as temperature or humidity were influenced by the proximity to one or even multiple edges. This suggests that parasite-related edge effects were omnipresent across our studied fragmented landscapes.

Three parameters were used to further evaluate the impact of forest fragmentation on parasite load and ectoparasite communities: forest patch size, the percentage of edge habitat (=50 m edge zone) in fragments and the comparison of continuous forest sites with forest fragments (forest type). These parameters revealed clear fragmentation effects in temporary ectoparasites. Tick and Trombiculidae mite infestations were more abundant in continuous forest sites than in fragments, and prevalence increased with increasing forest patch size, and with a decreasing proportion of the 50 m edge zone in forest fragments. In edge proximity, temporary parasites staying in the open vegetation (i.e., ticks, Trombiculidae) are more exposed to abiotic environmental changes than those associated with nests, such as Laelaptidae (Strandtmann, 1949; Allred and Roscoe, 1957; Morand and Krasnov, 2007; Orlova and Yakimenko, 2016). Laelaptidae feed on their hosts in their sheltered sleeping sites, mostly wooden tree holes (Morand and Krasnov, 2007). Consequently, Laelaptidae showed no negative fragmentation effect, but even higher prevalences in fragments than in the continuous forest sites. Wooden tree holes of good quality might be rare in degraded forest fragments and therefore used by the hosts with higher reuse-frequency than in the continuous forest (Bolívar-Cimé et al., 2018), leading to proliferating Laelaptidae populations in fragments. In contrast, effects of fragmentation parameters on stationary ectoparasites were less pronounced. For Atopomelidae mites, no effects of habitat-related factors were observed. However, a negative effect of an increasing proportion of edge habitat in forest fragments and proximity to the forest edge on sucking louse infestations indicates that fragmentation can also affect stationary parasites. Given the observed negative fragmentation effects on several ectoparasite taxa, it is not surprising that EPSR was higher in the continuous forest and in larger forest patches with a lower percentage of the 50 m edge zone. Negative fragmentation and edge effects on EPSR may even be aggravated by stochastic local extinctions of parasite species in habitat fragments while host populations may still remain viable (Bush et al., 2013). When host populations decrease

below a certain threshold, transmission becomes more unlikely and parasite populations are unable to perpetuate. Once locally extinct and host connectivity between fragments or to the continuous forest is reduced or lost, parasites may no longer be able to colonize the area again.

4.5. Conclusion

Our prediction of enhanced host susceptibility for ectoparasite infestations in fragmented habitats was not confirmed as neither higher ectoparasite prevalences in general nor higher EPSR were observed in forest fragments. In contrast, the results rather suggest that forest fragmentation and forest edges negatively affect ectoparasites and that these effects are stronger than those increasing host susceptibility in fragments. These findings demonstrate that temporary and stationary parasites possess their own autecology and depend on certain biotic and abiotic conditions in their environment. Such vulnerability of parasites towards environmental changes is alarming, as they provide invaluable ecosystem services (Hudson et al., 2006). Comparable to the role of predators, they are regulating their host's population dynamics and community structure (Marcogliese, 2004), influence species coexistence by affecting competition, predation and herbivory, and affect energy flow and complexity of food webs (Hatcher et al., 2012). The signals of disturbance in parasite infestation patterns generated by forest fragmentation and edge effects illuminated by this study raise sincere conservation concerns and should receive more attention from scientists within but also beyond the biodiversity hotspot of Madagascar. In parallel to the elevated risk of extinction of key hosts (Dunn et al., 2009; Poulin, 2010), continuous habitat loss and the increasing impact of habitat edges may eventually lead to a depletion of ectoparasite biodiversity which may also impair ecosystem integrity and stability (Poulin, 2010; Hatcher et al., 2012) in the future.

Acknowledgements

This study was conducted within the framework of the project INFRAGECO (Inference, Fragmentation, Genomics, and Conservation) funded by the BiodivERsA initiative of the European Community (no. 2015-138) and the German Federal Ministry of Education and Research (Bundesministerium für Bildung und Forschung) (grant no. 01LC1617A). We would like to thank the Direction du Système des Aires Protégées (DSAP, Madagascar) and Madagascar National Parks (MNP) for research permission in the Ankarafantsika National Park and the Mariarano region (research permit nos.: N°80/17/MEF/SG/DGF/DSAP/SCB.Rc, N°151/17/MEF/SG/DGF/DSAP/SCB.Rc, N°84/18/MEF/SG/DGF/DSAP/SCB.Rc., N°93/18/MEF/SG/DGF/DSAP/SCB.Rc). We thank Mamy Razafitsalama and Travis Steffens from Planet Madagascar, Shawn Lehman, the late Elke Zimmermann, the organisations Development and Biodiversity Conservation Action for Madagascar (DBCAM, Madagascar), Operation Wallacea (United Kingdom) and the people of Maevatanimbary, Andranohobaka, Ambarindahy, Mariarano, Ambolodihy and Antanambao for providing infrastructure and technical and logistical support. We are grateful for valuable assistance during fieldwork by Leonie Baldauf, Fernand Fenomanantsoa, Jack O'Connor, Quinn Parker, Olivia Pilmore-Bedford, Miarisoa Ramilison, Onjaniana Gilbert Razafindramasy, Simon Rohner and Harry Skinner. Additionally, we thank Oliver Schülke for valuable comments on data analyses and results, and Annette Klein for various advice including help with data analyses and parasite identification.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ijpara.2020.01.008>.

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