Host-pathogen-vector continuum in a changing landscape: Drivers of *Bartonella* prevalence and evidence of historic spillover in a tropical multi-host community

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Abstract

Our understanding of pathogen spillover is largely based on viral systems associated with bats. Bacterial infections of zoonotic origin also pose a significant public health burden, many of which are associated with small mammals like rodents that live abundantly among humans. When ecologically different species of small mammals are brought in contact with each other due to various factors, including habitat modification, there is potential for bacterial spillover within the host community and subsequently to humans. Small mammals and their ectoparasite communities present a unique system to investigate the eco-epidemiology of multi-host pathogens, which can inform specific bacterial spillover determinants and their interplay. In a rainforest-human-use mosaic, we applied ecological and evolutionary analysis to investigate *Bartonella* spp. across small mammal and ectoparasite communities.

We observed substantial overlap among small mammal communities in different habitat types, predominantly driven by habitat generalists. Most ectoparasites were generalists, infecting multiple hosts, and several host species displayed polyparasitism, i.e., they were infected by multiple ectoparasites. We observed high *Bartonella* prevalence at both study sites – a forest-plantation mosaic (47.4%) and a protected area (28.8%). Seven of the ten ectoparasite morphotypes sampled were also positive for *Bartonella*, following the prevalence trend in their hosts. A Generalised Linear Model (GLM) revealed an independent association between aggregated ectoparasite load in species and *Bartonella* prevalence, implicating ectoparasites in transmission. *Bartonella* lineages from small mammals were host-specific, while ectoparasites showed no host-specific associations. They carried *Bartonella* associated with other hosts, indicating the potential for cross-species

transmission. Phylogenetic ancestral trait reconstruction of *Bartonella* haplotypes suggests historic spillover events in the small mammal community, validating the potential for contemporary spillover. These results highlight infection risk from such underdiagnosed agents in the landscape, and the necessity to disentangle complex multi-host multi-vector systems to understand their epidemiological consequences.

1. Background

Large-scale modification of natural habitats is associated with biodiversity loss and ecosystem services [1]. Other unexpected consequences, such as an elevated risk of zoonotic infections, are poorly acknowledged and understood, especially in biodiverse tropical systems. Both theoretical and empirical studies demonstrate that land-use change and associated habitat perturbations can result in modified communities of zoonotic hosts as a result of animals moving across habitat boundaries [2,3]. As a consequence, there is potential for pathogen spillover between animals did not previously co-occur, i.e. from reservoir hosts to incidental hosts, directly or indirectly through intermediate hosts and vectors [4,5].

Spillover between wildlife can lead to the emergence of several zoonoses [4], and has been implicated in several past epidemics, including SARS-CoV-1 [6]. Pathogen sharing between animal host communities can lead to the recombination and evolution of new variants with altered host ranges, vector specificities, and pathogenic potential [7]. A spillover event, however, is a complex and non-frequent process with numerous ecological and evolutionary filters that vary in space and time, including the distribution of reservoir hosts, pathogen prevalence, and infection intensity [8]. For example, a high density of reservoir hosts elevates direct interactions, leading to density-dependent transmission among the reservoir population and to the other susceptible members of the community [9]. Additionally, in the case of vector-borne pathogens, ectoparasites also respond to host densities and influence pathogen prevalence in reservoirs and incidental hosts [10].

Bats and small mammals (rodents and shrews) are the best-known reservoir taxa for zoonotic pathogens [11]. Small mammals, however, carry especially high numbers of pathogens [12,13] because they are disproportionately diverse within mammalian communities [14], even more so than bats. Small mammals also differ from bats in that they often increase (rather than decrease) in abundance in a modified landscape, resulting in the elevated prevalence and transmission risk of associated zoonoses in the landscape [15,16]. Small mammal densities are known to locally increase, for example, when large herbivore densities decrease [17], leading in turn to an increase in pathogen prevalence [18]. In addition, small mammals with generalist natural histories (often reservoirs) tend to move across habitat boundaries where they interact with incidental hosts [4,19], thereby moving pathogens across these boundaries. We expect such processes to be especially prevalent in tropical regions, as they harbour some of the richest small mammal communities [20], the highest rates of habitat modification [21,22], and therefore the highest predicted risk of zoonotic infections [23,24].

To understand the zoonotic consequence of small mammals and their ectoparasites in changing landscapes, we must first understand how their communities are structured and how they have responded (and continue to respond) to land-use change and habitat modification. In this study, we characterize differences in host community structure, ectoparasite community structure, and pathogen prevalence in a human-dominated rainforest-plantation landscape in South India, part of the Western Ghats biodiversity hotspot. We used *Bartonella*, a generalist zoonotic bacterial pathogen, as a model system to understand variation in prevalence and transmission dynamics in the landscape. We sampled small mammal communities and their ectoparasites in a forest-plantation mosaic

and a relatively undisturbed protected area in the landscape to address the following questions – i) How are small mammal communities structured in a forest-plantation mosaic and relatively less disturbed protected area? ii) Is there any difference in *Bartonella* prevalence between these two communities? iii) What are the main drivers of *Bartonella* prevalence and transmission in the landscape? (iv) and finally, do we find evidence for spillover, detected as shared *Bartonella* haplotypes between members of these communities? We began with the expectation that the forest-plantation mosaic would have higher small mammal densities and *Bartonella* prevalence than the protected area [9,15]. We also expected that *Bartonella* haplotypes would be specific to host species [25] while limited spillover (vector-mediated spillover) among hosts that occupy the same habitats [26].

2. Methods

(a) Field sampling

We carried out this study in two sites in the central Western Ghats: i) Kadamane, a mixed-use, forest-plantation mosaic in the Karnataka state in India and ii) Kudremukh National Park, a relatively less disturbed protected area in the same state **(Figure 1)**. We sampled small mammals (rodents and shrews) from different land-use types in Kadamane and Kudremukh between 2016 and 2021. Kadamane was sampled three times during this period (2016, 2017 and 2018) and Kudremukh was sampled once in 2021. In Kadamane, we sampled in forest fragments, grasslands, tea plantations, abandoned plantations (cardamon and coffee) and human habitation. In Kudremukh, we sampled forests, grasslands, and human habitation (a partially occupied township adjacent to Kudremukh National Park). In both sites, sampling was conducted during dry months between January- April.

We used medium-sized Sherman traps in a grid framework to capture small mammals. A trapping grid consisted of 10 trapping lines, each line consisting of 10 traps separated by 10 metres, covering one hectare in total. An additional 20 traps were placed on trees to capture arboreal species in forests and abandoned plantations. Trapping efforts were proportionately divided based on the area occupied by each land-use type. Each grid was sampled for four consecutive days during each trapping session. All traps were baited using peanut butter and locally available seeds. Traps were checked twice a day (morning and evening) for captured individuals. Captured individuals were anesthetised using Isoflurane for collecting measurements and samples. Small mammal species were first identified in field with the help of taxonomic keys and field guides [27–29]. In addition, ear clippings were collected to confirm species identification through molecular methods. We collected dried blood spots from every captured individual in 2018 and 2021 to screen for pathogens. To detect and collect ectoparasites, captured individuals were combed on a white paper for 2-3 minutes. All individuals were marked and released at the site of capture after sample collection (except in 2018; individuals were sacrificed for harvesting organs to screen for various pathogens).

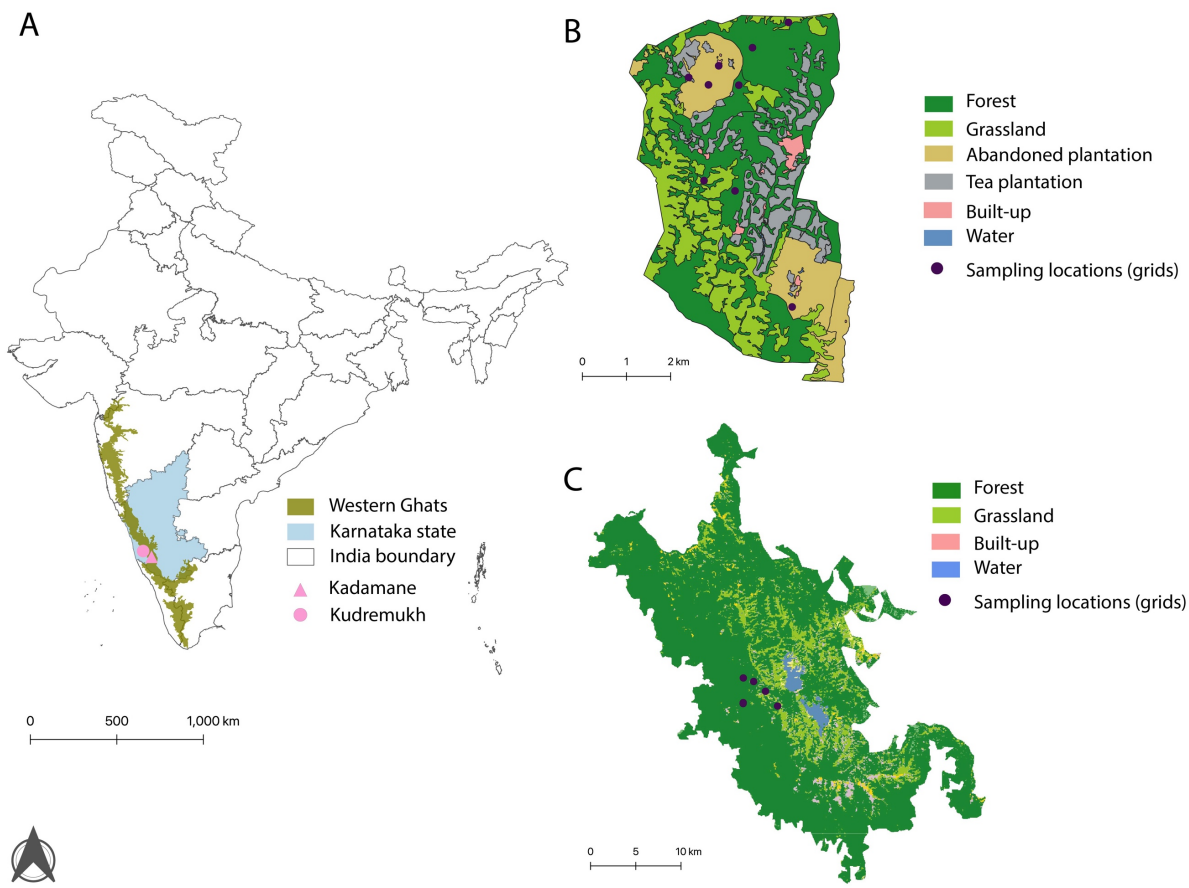

Figure 1: Map of the study area. A) India with Western Ghats and the Karnataka state boundary marked. (B) Land-use map of Kadamane forest-plantation mosaic with sampling locations marked. (C) Land-use map of Kudremukh National Park with sampling locations marked.

(b) Small mammal community

DNA was extracted from ear clippings using DNeasy Blood & Tissue Kit (Qiagen), following which 1140 bp of Cytochrome b (Cytb) gene was amplified and sequenced [30]. Maximum likelihood phylogenetic trees were constructed to identify cryptic *Mus* species and validate morphological species identification. All the other species were identified morphologically and validated using BLAST (blast.ncbi.nlm.nih.gov) similarity scores of Cytb sequences.

Based on species identification, we created a species abundance matrix for each land-use type, followed by a distance matrix using the Morisita-Horn index, a standard beta diversity measure to calculate dissimilarity [31]. The beta diversity index was plotted following hierarchical clustering to visualise the dissimilarly between small mammal communities in different land-use types and sampling grids. We also calculated the relative abundance of each small mammal species in each land-use type to understand species-habitat associations. The community ecology package Vegan [32] in R was used for this analysis.

We used a Capture-Mark-Recapture approach [33] to estimate densities of the four most common small mammals by creating individual capture histories in forest and grassland. Since abandoned plantations and forests had similar vegetation structure and small mammal communities, we grouped them under 'forests' for this analysis (to obtain adequate sample size). We assumed a closed population with varying capture probability to estimate population size following a customised log-linear model [34]. Density (number of individuals per hectare) for each species was estimated after accounting for the number of grids sampled in each habitat. We used R package *Rcapture* for this analysis [34].

(c) Ectoparasite community

Ectoparasites were brought back to the laboratory in 100% ethanol. Mites, ticks, and fleas were segregated using a stereo-zoom microscope. We identified ticks and fleas to the genus level under a high-resolution microscope with the help of taxonomic keys and monographs [35–37]. Mites were mounted on a slide for observation under the microscope and identified through descriptions in a monograph [38]. We serially named and counted individual ectoparasites that belonged to the same morphotypes (potentially species).

175 We constructed a distance matrix based on ectoparasite abundance per individual small
176 mammal species [39]. We used this matrix for a Principal Coordinate Analysis (PCoA) in R
177 [40], and plotted the clustering using ggplot2 [41] to understand overlap in ectoparasite
178 communities between small mammal species (the first two PCoA axes). We also estimated
179 ectoparasite density, or the mean number of each morphotype per host species in forests
180 (including abandoned plantations), grasslands, and built-up areas. The infestation rate, i.e.,
181 frequency of ectoparasite (mites, ticks, and fleas) occurrence in each host species and
182 habitat, was recorded as aggregated ectoparasite load.
183
184 **(d) *Bartonella* screening and prevalence estimation**
185 To detect *Bartonella* in small mammals, DNA was extracted using QIAamp DNA Mini Kit
186 (Qiagen) from the dried blood spots (DBS) collected in 2018 (Kadamane) and 2021
187 (Kudremukh), and screened for *Bartonella* specific *rpoB* gene (825 bp) using conventional
188 PCR [42]. *Bartonella* prevalence in the Kadamane samples was reported previously [43].
189
190 To detect *Bartonella* in ectoparasites, ectoparasite were pooled, mechanically
191 homogenised, and DNA was extracted using DNeasy Blood & Tissue Kit (Qiagen). A pool
192 contained 1-10 individual ectoparasites (mean = 3.06) belonging to same morphotype
193 collected from the same individual small mammal. We used PCR reagents as follows- 25 µl
194 reaction mixture composed of 6 µl of template DNA, 12.5 µl of 1X HotStarTaq Master Mix
195 (Qiagen), 1 µl each of 5 µM primers and 4.5 µl of nuclease-free water. PCR products were
196 visualized on a 1.5% agarose gel stained with GelRed Nucleic Acid Gel Stain (Biotium Inc)
197 with reference to negative and positive controls set along the test samples. Positive samples
198 were purified using AMPure XP magnetic beads (Beckman Coulter) and sequenced.

199 Sequences were verified for *Bartonella* after comparing with the reference database (NCBI)
200 using BLAST [44]. All *Bartonella* sequences generated in this study have been deposited in
201 GenBank under accession number OR574780-OR574826.
202
203 Prevalence was calculated as the proportion of positive individuals against the number of
204 individuals tested. Small mammal species with low sample sizes were grouped as 'others' in
205 the prevalence calculation. While calculating the overall prevalence, we included two forest
206 grids from Kudremukh twice (randomly selected) to compensate for additional trapping
207 effort in Kadamane (abandoned plantations) and make it comparable to Kudremukh. We
208 calculated 95% confidence intervals (Wilson interval) associated with the prevalence using
209 the R package *Hmisc* [45]. Prevalence in ectoparasite pools was represented as the
210 proportion of positive pools among the total number of ectoparasite pools tested.
211
212 **(e) Ecological correlates of *Bartonella* prevalence**
213 We used a Generalized Linear Model (GLM) to understand drivers of *Bartonella* prevalence
214 among small mammals in the landscape. We modelled prevalence as the incidence of
215 *Bartonella* (presence/absence) in each individual small mammal as a function of the
216 sampling site, aggregated ectoparasite load (the proportion of all individuals of the species
217 with any ectoparasite presence - mites, ticks, and fleas - within the relevant habitat-site
218 combination), and the density of the small mammal species itself. We assumed a binomial
219 error distribution as our response consisted of 0s and 1s. We restricted this analysis to the
220 10 species-habitat-site combinations that contained data from more than three individuals
221 of the species, together comprising 196 individuals of five species. We also examined host
222 species identity and habitat type as covariates but dropped them because the models did

223 not converge. The covariate 'aggregated ectoparasite load' is the frequency of ectoparasite
224 occurrence in each species and habitat, and is not ectoparasite density per individual small
225 mammal. We considered this a more reliable measure than raw ectoparasite densities since
226 it is possible to occasionally encounter individuals with heavy infestation in the community
227 and this might potentially influence our inference.
228
229 **(f) Phylogenetic analysis**
230 We generated a consensus of forward and reverse sequences for the partial *rpoB* sequence.
231 These sequences were aligned with known *Bartonella* species sequences from the NCBI
232 database, and sequences reported in Ansil et al 2021 (accession number MT787671-
233 MT787733) [43]. A 773 bp alignment was created using MUSCLE in MEGA 7.0.26 [46].
234 Sequences generated from the ectoparasites were also included in this alignment.
235 Alignment was codon-optimized and tested for the appropriate nucleotide substitution
236 models using PartitionFinder 2.1.1 [47]. We performed a Bayesian phylogenetic analysis
237 using this alignment in BEAST 1.8.4 [48]. The phylogeny was run for 10^8 Markov Chain
238 Monte Carlo (MCMC) cycles. Effective sample sizes (ESS) and parameter convergence of
239 MCMC sampling were assessed using Tracer 1.6.0 [49]. The resulting trees were summarised
240 into a consensus tree after 25% burnin, and were visualized and annotated using FigTree
241 1.4.4 [50]. Internal nodes of the tree are marked and coloured based on the Posterior
242 Probability (PP).
243

244 **(g) Host- *Bartonella* association**

245 We also constructed a tanglegram using sequence data from the hosts (Cytb) and *Bartonella*
246 (*rpoB*) in TREEMAP [51] to understand host- *Bartonella* haplotype association. We visually
247 analysed the resulting co-phylogeny for potential host switching (spillover) events.
248 A separate alignment was constructed using unique *Bartonella* haplotypes and considered
249 for a Bayesian phylogenetic ancestral trait reconstruction. We restricted this analysis to
250 unique haplotypes recovered from each host species. We included one additional sequence
251 from *Mus cf. fernandoni* to avoid over-representation and subsequent biases from *Rattus*
252 *satarae* sequences. We used six identified host states as traits to estimate host probabilities
253 for all ancestral nodes in BEAST 1.8.4 [48]. The resultant phylogeny was summarised and
254 annotated as described before.

255

256 ## 3. Results

257 **(a) Small mammal community assembly**

258 We recorded 11 small mammal species, of which nine were rodents, and two were shrews
259 **(Table S1).** The rodent species were *Rattus satarae*, *Rattus rattus*, *Mus cf. fernandoni*, *Mus*
260 *cf. famulus*, *Mus cf. terricolor*, *Golunda ellioti*, *Vandeleuria nilagirica*, *Platacanthomys*
261 *lasiurus*, and *Funambulus tristriatus*. The two shrew species were *Suncus niger* and
262 *Crocidura horsfieldii*. The three *Mus* species were morphologically similar and could only be
263 differentiated using their phylogenetic clustering **(Figure S1)**. The average genetic distances
264 (p distances) for *M. cf. fernandoni*, *M. cf. famulus*, and *M. cf. terricolor* from their respective
265 parent species, for example *M. cf. fernandoni* vs *M. fernandoni*, were 0.05, 0.07 and 0.09,
266 respectively.

267

Among the land-use types sampled, five species of small mammals were observed in forests in Kadamane, and grasslands in Kadamane and Kudremukh. Three species were observed in forests in Kudremukh and in built-up habitats at both sites. Tea plantations were the most species-poor land-use type, with only one species (*M. cf. famulus*) captured once in 2016. Based on the hierarchical clustering of beta diversity, forests (FR16, FR17, FR18 and FR21) and abandoned plantations (AP16, AP17 and AP18) showed similar community assemblages with minimal dissimilarity (<20%); the forest community from Kudremukh (FR21) was also a part of this cluster **(Figure 2A)**. The grassland cluster altogether showed 40% dissimilarity with the forest-abandoned plantation cluster while maintaining moderate dissimilarity (<20%) between years (GL16, GL17, GL18) and sites (GL21). Built-up habitats were the most dissimilar (60%) to other land-use types, although they retained two species (*S. niger* and *M. cf. famulus*) detected in the other land-use types. We were able to estimate densities for four (of eleven) common small mammal species (*Rattus satarae*, *M. cf. fernandoni*, *M. cf. famulus* and *M. cf. terricolor*). These densities are reported in Supplementary results and in **Figure S2.**

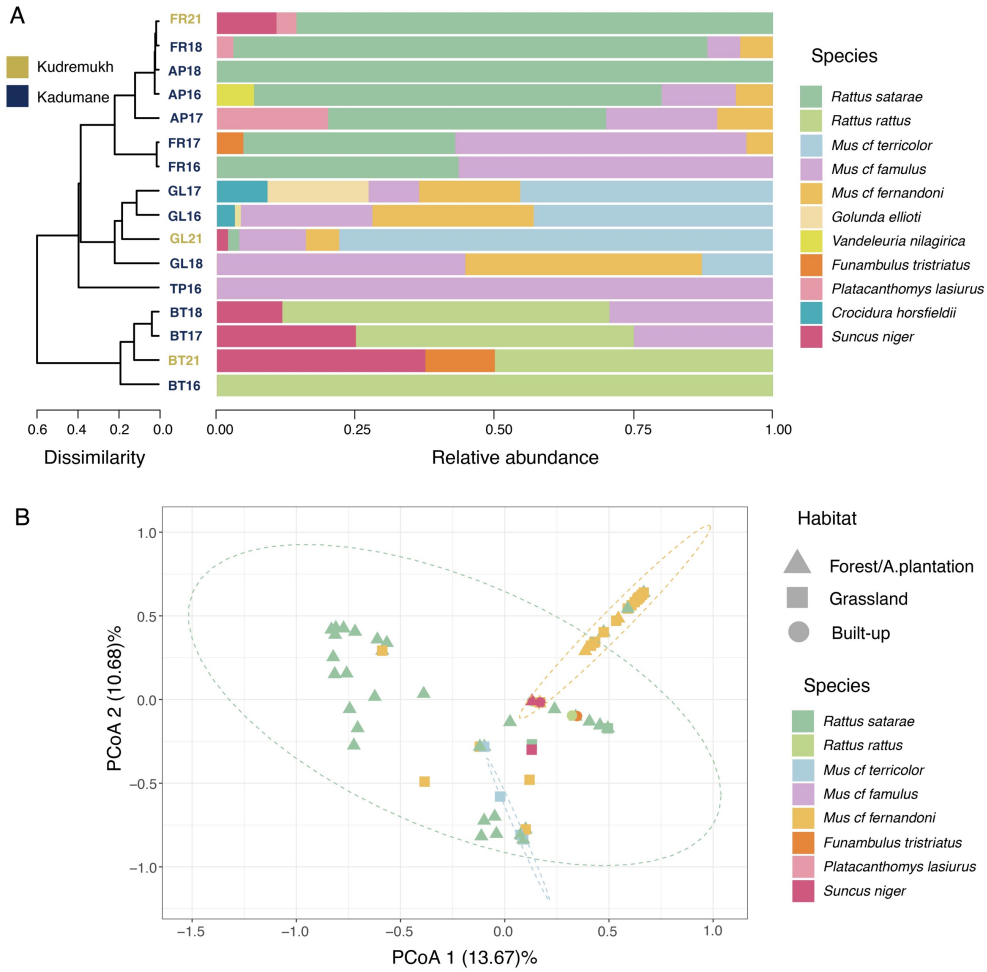

Figure 2: Community structure of small mammals and their ectoparasites. A) Community dissimilarity based on beta diversity and relative abundance. Left: a dendrogram showing dissimilarity index between land-use types during different sampling years. Abbreviations; FR- Forest, GL-Grassland, AP-Abandoned plantations, TP-Tea plantations, and BT-Built-ups. Right: Relative abundance of different species captured in different land-use types. B) Principal Coordinate (PCoA) plot showing ectoparasite community structure across different small mammals and habitats.

(c) Ectoparasite assemblage

Ten ectoparasite species were recorded from the small mammal community; two species of mites belonging to the genus *Laelaps*, three species of ticks belonging to the genus *Rhipicephalus*, *Ixodes* and *Haemaphysalis* and five species of fleas belonging to the genus *Xenopsylla* **(Table S2)**. Since more than one species was detected under *Laelaps*

298 (mites) and *Xenopsylla* (fleas), these morphotypes were named serially *(e.g. Xenopsylla sp 1,*
299 *Xenopsylla sp 2* and so on). Only one morphotype each was identified from three tick
300 genera. Interestingly, six ectoparasites species (60%) were detected in multiple hosts
301 (generalists) and six of eight small mammals sampled (75%) were polyparasitic (infested
302 with two or more ectoparasite species).
303
304 Our principal coordinate analysis (PCoA) revealed significant overlap and variation in
305 ectoparasite communities hosted by small mammals (**Figure 2B**). *R. satarae* showed
306 significant variation in ectoparasite community along the PCoA axis 1 and 2 (13.67 % and
307 10.68 % explained, respectively), while *M. cf.* fernandoni predominantly displayed identical
308 ectoparasite community. However, Individuals from *R. rattus*, *F. tristriatus*, *M. cf.*
309 *fernandoni*, *M. cf. terricolor*, and *S. niger* also had similar ectoparasite communities to *R.*
310 *satarae*. We also estimated the mean density of each ectoparasite morphotype recovered
311 from each small mammal species per habitat and this is presented in Supplementary results
312 and in **Figure S2**.
313
314 **(d) *Bartonella* prevalence in small mammals**
315 We detected *Bartonella* in five species of small mammals in the community: *R. satarae*, *R.*
316 *rattus*, *M. cf. fernandoni*, *M. cf. famulus,* and *S. niger* (**Table 1**) with varying prevalence (0-
317 75.8%). In both sites, *R. satarae* showed high prevalence (75.8% in Kadamane and 72% in
318 Kudremukh). *M. cf. fernandoni* showed 54.5% (n=22) in Kadamane and 40% (n=5) in
319 Kudremukh. One individual of *M. cf. famulus* was positive in Kadamane (3.8%, n=26), while
320 Kudremukh individuals were negative (n=3). We did not observe any significant site level
321 difference in prevalence for common species (*R. satarae* and *M. cf. fernandoni*) and overall

322 community **(Figure 3A)**. Other species, such as *R. rattus* and *S. niger* had low prevalence, but
323 also low sample sizes, hence we have minimal confidence in their prevalence estimates.
324 Interestingly, despite sufficient sample size, all the *M. cf. terricolor* were negative for
325 *Bartonella*. Pooled ectoparasite positivity was largely correlated with prevalence in small
326 mammals, albeit was slightly lower in every case. Positivity in specific ectoparasite
327 morphotypes are provided in **Table S3.**
328
329 **Table 1:** Prevalence of *Bartonella* in small mammal blood and ectoparasites collected from
330 Kadamane and Kudremukh. Positivity reported here for ectoparasites is not true prevalence
331 since individual ectoparasites are pooled for screening.
332

	***Bartonella* prevalence; number of positives / number of samples tested (%)**			
	Dried blood spot (DBS)		Pooled ectoparasites	
	Kadamane	Kudremukh	Kadamane	Kudremukh
Rattus satarae	50/66 (75.8)	18/25 (72)	24/71 (33.8)	6/24 (25)
Rattus rattus	0/10 (0)	1/4 (25)	-	0/3 (0)
Mus cf. fernandoni	12/22 (54.5)	2/5 (40)	9/29 (31)	0/6 (0)
Mus cf. famulus	1/26 (3.8)	0/3 (0)	0/1 (0)	-
Mus cf. terricolor	0/6 (0)	0/37 (0)	-	0/7 (0)
Platacanthomys lasiurus	-	0/1 (0)	-	0/1 (0)
Funambulus tristriatus	-	0/1 (0)	0/2 (0)	0/2 (0)
Suncus niger	0/2 (0)	2/4 (50)	0/1 (0)	1/2 (50)
Total	63/132 (47.4)	23/80 (28.8)	33/102 (32.4)	7/45 (15.6)

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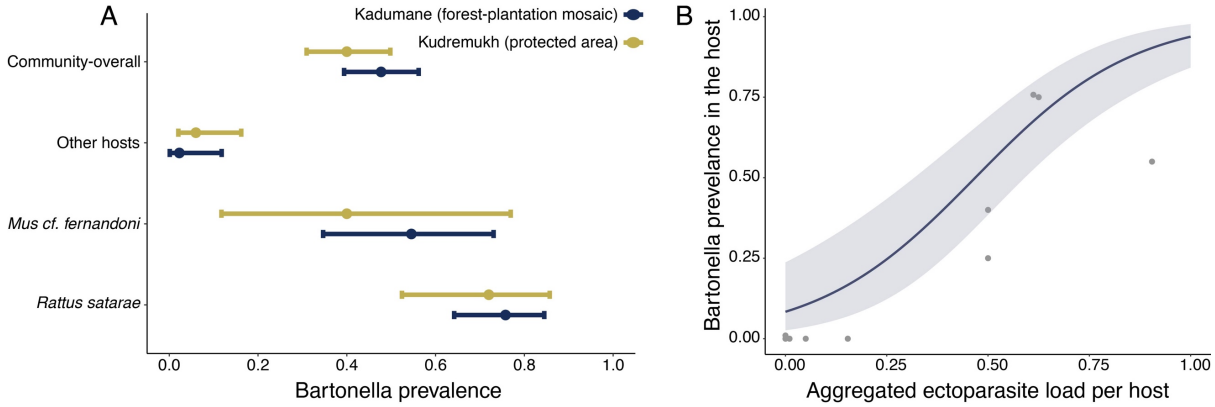

Figure 3: (A) *Bartonella* prevalence in small mammal hosts in Kadamane and Kudremukh. 'Other hosts' include small mammal species showed low *Bartonella* positivity and had low sample sizes. (B) *Bartonella* prevalence positively correlated with aggregated ectoparasite densities within a species at each habitat site. The trend line indicates predicted *Bartonella* prevalence with respect to aggregated ectoparasite load. The shaded area represents the confidence intervals of the predicted prevalence estimate.

(e) Factors affecting *Bartonella* prevalence

Bartonella prevalence within a population was proportional to aggregated ectoparasite load within a species at each habitat site (mites, ticks, and fleas; GLM, $p<0.05$**, Figure 3B**). Surprisingly, host densities and sampling locations were poorly correlated with *Bartonella* prevalence (**Table 2**). A second GLM with host species identity and habitat type as additional covariates did not converge; hence we tested these variables separately and found them not significant.

352 **Table 2:** Results of Generalised Linear Model (GLM) examining drivers of *Bartonella*
353 prevalence. Significant variables are marked with (*)
354

	Estimate	Std. Error	Z value	Pr(>|z|)
Intercept	-1.633595	1.05266	-1.554	0.120
Host density	-0.07574	0.06711	-1.129	0.259
Site	-0.47880	0.72288	-0.662	0.508
Aggregated ectoparasite load	5.10933*	0.96562	5.291	1.21e-07 **

355

356

357 **(f) Phylogenetic analysis**

358 Phylogenetic analysis (*rpoB*) revealed eight distinct *Bartonella* lineages (BL1-BL8) from small
359 mammals and ectoparasites. We found that five lineages among them (BL1-BL5) were
360 phylogenetically related to known zoonotic *Bartonella* species (**Figure 4A**). We observed
361 three lineages in *R. satarae* (BL1, BL6 and BL7) and two lineages in *M. cf. fernandoni* (BL4
362 and BL8). BL1 included *Bartonella* sequences from *R. satarae* and ectoparasites (*Laelaps sp*
363 *1, Rhipicephalus sp, Ixodes sp, Xenopsylla sp 1, and Xenopsylla sp 5*). Interestingly,
364 sequences from *Laelaps sp 1* and *Xenopsylla sp 5* in this lineage were not collected from *R.*
365 *satarae* but *M. cf. fernandoni* and *S. niger* respectively. BL2 consisted of a single sequence
366 collected from *R. rattus*, and closely related to BL1. These two lineages were
367 phylogenetically related to *B. queenslandensis*. BL3 consisted of two sequences, one from *S.*
368 *niger* and the other from *Laelaps sp 1* collected from *M. cf. fernandoni*. This lineage was
369 related to *B. tribocorum*. BL4 consisted of *Bartonella* sequences from *M. cf. fernandoni*, *M.*
370 *cf. famulus,* and ectoparasites (*Laelaps sp 1, Rhipicephalus sp, Ixodes sp, Haemaphysalis sp,*
371 *and Xenopsylla sp 3*). In this lineage, the *Haemaphysalis sp* was recovered from *R. satarae*
372 and not from any of the *Mus* species. BL5 was a single sequence from *F. tristriatus* (reported

373 in Ansil et al. 2021, accession number- MT787671), forming a sister lineage to BL4. We
374 included this sequence in our analysis since it was collected during our study in Kadamane.
375 The remaining lineages (BL6-BL8) were related to non-pathogenic *Bartonella* species. BL6
376 comprised sequences from *R. satarae* (second lineage from *R. satarae*) and *Ixodes sp*
377 recovered from them. This lineage was related to *B. phoceensis*. BL7 and BL8 were two
378 distinct lineages from *R. satarae* (third lineage from *R. satarae*) and *M. cf. fernandoni*
379 (second lineage from *M. cf. fernandoni*), respectively. Both these lineages were
380 phylogenetically related to *B. thailandensis*.
381
382 **(g) Host-*Bartonella* association and historic spillover**
383 The co-phylogeny of small mammals and *Bartonella* predominantly displayed host-specific
384 lineages **(Figure S4)**. However, one *Bartonella* lineage from *M. cf. fernandoni* was observed
385 to be phylogenetically related to *Bartonella* sequences from *R. satarae*. Our phylogenetic
386 ancestral trait reconstruction revealed a high probability (0.87) of *R. satarae* being the host
387 state of the common ancestor of these lineages **(Figure 4B)**, suggesting a potential past
388 spillover event. Similarly, we also observed a moderately high probability (0.73) of *R.*
389 *satarae* being the host state for the *Bartonella* sequence from *R. rattus* and the remote
390 common ancestor (0.8) of the *Bartonella* community level phylogeny. We found no
391 evidence for contemporary *Bartonella* spillover or sharing between small mammal hosts.

Figure 4: A) Bayesian phylogenetic inference of *Bartonella* based on 773 bp of *rpoB* sequences. Nodes are coloured based on posterior probability, and monophyletic clades are collapsed for easy visualization. B) Bayesian phylogenetic inference showing ancestral host state of different *Bartonella* haplotypes. Each colour represents a specific host, and the number at the common ancestor nodes indicates the probability for the corresponding host state.

400 ## 4. Discussion

401 We characterized small mammal communities, their ectoparasites, and their links with
402 *Bartonella* at two contrasting sites in the Western Ghats. We demonstrated that different
403 small mammal host species and ectoparasites, with specific *Bartonella* lineages, often co-
404 occur. We also show that ectoparasites can be vectors for multiple *Bartonella* lineages, as
405 the *Bartonella* prevalence in the community was driven by aggregated ectoparasite load in
406 small mammals. Additionally, we present evidence of a historic *Bartonella* spillover event
407 between two abundant hosts in the community and substantiate the potential for
408 *Bartonella* sharing between hosts, possibly through their ectoparasites.

409

410 **(a) Host communities are largely similar across land-use types**

411 Our results revealed a substantial similarity in host communities between different land-use
412 types. This similarity was predominantly driven by a few species that occur in multiple land-
413 use types within the landscape in varying densities [52]. Species such as *M. cf.*
414 *famulus* and *S. niger* were recorded in multiple land-use types (forests, grassland, and built-
415 up), indicating their potential for being habitat generalists [53] hence driving similarities
416 between communities. Such generalist invasions are observed in many tropical communities
417 [54,55]. For example, *M. musculus*, a common small mammal that inhabits human
418 habitation, has been observed to colonize forest fragments next to plantations in the
419 southern Western Ghats [56]. Such colonization is potentially due to high densities of the
420 colonizing species [57], possibly because of favourable eco-climatic variables (e.g. lack of
421 competition) in native habitats [58] and habitat edges, leading to further homogenised
422 species assemblages [59].

423

Surprisingly, small mammal communities in forests (protected area and forest-plantation mosaics) showed no significant difference. Similarly, forests and abandoned plantations in Kadamane also had similar community, dominated by *R. satarae*, an endemic small mammal, and known *Bartonella* host. [43]. Because of their community similarity, we treated these two habitats as the same, and were able to use small mammal density estimates to better understand prevalence. Other species in forests/abandoned plantations (e.g. *M. cf. fernandoni*) exhibited lower densities, potentially due to the over-dominance of *R. satarae* in these land-use types. Comparable trends in small mammal abundance was observed in human-use habitats [54,60], where species with generalist life history adapt well to habitat changes and achieve high densities, while driving inferior competitors to lower densities [61]. Such communities in tropical systems are also observed to have low species diversity [54,61].

Despite species overlap in community, we observed significantly high densities of specific species in specific land-use types (e.g. *R. satarae* in forests and *M. cf. terricolor* in grasslands) indicating their preferred land-use types, similar to that observed in many other ecological communities [62]. We found that grasslands were dominated by *Mus* species; *M. cf. fernandoni*, *M. cf. famulus* and *M. cf. terricolor*. Previous studies from the landscape morphologically identified *M. cf. fernandoni* as *M. musculus* and the latter two as *M. booduga* [43]. Phylogenetic analysis suggests that they are distinct lineages related to *M. fernandoni* (a Sri Lankan species), *M. famulus* and *M. terricolor*, respectively. Their high genetic distances with their potential parent species (see results) suggest that these three *Mus* species could be new lineages in the Western Ghats.

448 Interestingly, all these three *Mus* species showed variation in annual densities, potentially a
449 signature of annual population oscillations [63,64]. Long-term studies with multiple spatial
450 replicates are required to better understand signals of annual or multiannual population
451 dynamics, which can be further correlated with eco-climatic variables in the region to
452 understand drivers of variation in small mammal populations at a local scale. Such intra- and
453 inter-annual variations in host densities are important determinants of 'zoonotic hazard',
454 which contributes to spillover risk through its overlap with exposure and vulnerability [65].
455 This reiterates the importance of detailed ecological studies to understand spillover
456 dynamics.
457
458 **(b) Diverse ectoparasites are shared among small mammals in the community**
459 Our results show that ectoparasite diversity and density in the landscape are centred
460 around abundant, large-bodied and synanthropic species. Specifically, *R. satarae* and *R.*
461 *rattus* were large-bodied small mammals with high richness of ectoparasites, consistent
462 with the positive correlation observed between body size and parasitism [66]. Similarly, *R.*
463 *satarae* and *M. cf. fernandoni* (two abundant species) were also detected with multiple
464 ectoparasites (polyparasitism), often with high densities supporting density dependent
465 parasite transmission and uptake [67]. Earlier studies from south India also observed high
466 diversity of ectoparasites, predominantly from synanthropic and habitat generalist small
467 mammals [68]. Broadly, our results strongly imply that specific host traits [69] affect
468 ectoparasite distributions, including diversity and polyparasitism. Additionally, the large
469 distribution ranges of these species provide opportunities to acquire new ectoparasites
470 (through horizontal transmission) from other overlapping small mammals [70], driving
471 ectoparasite richness on them [71]. In addition to polyparasitism, our results revealed some

472 broad ectoparasite-host association patterns. Mites (*Laelaps sp 1*) were predominantly
473 associated with *M. cf. fernandoni*, while ticks (*Rhipicephalus sp*, *Ixodes sp*, and
474 *Haemaphysalis sp*) were associated with *R. satarae* and other *Mus* species. In contrast to
475 these group-specific generalities, fleas were relatively species-rich and detected in most
476 small mammals, possibly due to their ability to move from one host to another [72].
477
478 Several ectoparasites (e.g. *Rhipicephalus sp*, *Xenopsylla sp 1*) showed a wider host range,
479 presumably due to their ability to infect multiple locally available hosts [73]. As observed
480 elsewhere [74], host sharing was the predominant pattern observed in the community. Such
481 generalist ectoparasites can facilitate the transmission of pathogens between hosts [75],
482 making their ecology a crucial part of vector-borne pathogen dynamics. Additionally, known
483 reservoir hosts such as *R. rattus* with multiple fleas (as demonstrated in this study) imply
484 potential for spillover and risks of vector-borne diseases to humans and other wildlife in the
485 landscape [76].
486
487 **(c) Aggregated ectoparasite load drives *Bartonella* prevalence in the small mammal**
488 **community**
489 Corroborating with the earlier findings [26,77], we observed a high *Bartonella* prevalence in
490 the small mammal community with *R. satarae* and *M. cf. fernandoni* as two primary hosts in
491 both sites. All three ectoparasite groups (mites, ticks and fleas) collected from these primary
492 hosts displayed similar prevalence trends, suggesting *Bartonella* transmission between hosts
493 and ectoparasites. Lower habitat heterogeneity and higher ungulate density should lead to
494 low host density and pathogen prevalence in Kudremukh (see Faust et al., 2018; Young et
495 al., 2014), but this prediction is not evident in our data.

While we expected host density and ectoparasitism to drive prevalence [9,78], we found only aggregated ectoparasite load per species explains *Bartonella* prevalence. High vector densities in the environment (not on a specific host) are known to elevate pathogen transmission (density-dependent transmission), impacting prevalence and risk of infection [79]. Our results spotlight ectoparasite communities and their dynamics, which are even less known than host dynamics. Unfortunately, ecological drivers of aggregated ectoparasite load remain poorly understood. Longitudinal sampling targeting larger sample size from each representative species in combination with ecological models incorporating additional appropriate variables, e.g. host traits, season, etc., might help explain variance in aggregated ectoparasite load. We caution that other variables previously shown to influence pathogen prevalence, like seasonality [9] and environmental stressors [80] were unavailable in our study.

(d) Evidence of historic spillover in the community provides clues to potential future *Bartonella* spillover.

Characterizing *Bartonella* diversity in small mammals is crucial from a public health perspective, as small mammals maintain several zoonotic species from these genera [81]. For example, endemic *Bartonella* variants such as *B. bacilliformis* (carrion's disease) are fatal and cause serious mortality [82]. Five *Bartonella* lineages from this study showed phylogenetic affinity to known zoonotic species such as *B. queenslandensis* and *B. tribocorum*. Additionally, presence of these lineages in ectoparasites suggest possible transmission of *Bartonella* among hosts, and potentially to humans. Interestingly, while hosts carried single *Bartonella* lineages, ectoparasites (on a given host) carried a higher

520 diversity of *Bartonella* (e.g. *Xenopsylla sp* 5 carried *Bartonella* associated with *S. niger* and *R.*
521 *satarae*), enhancing probability for cross-species transmission, given vector competency.
522
523 Cross-species pathogen transmission, especially vector-borne pathogens, among wildlife is
524 more common than previously thought [83]. Our ancestral trait reconstruction for
525 each *Bartonella* lineage suggests *R. satarae* as the ancestral host for several lineages with a
526 medium to high probability. In fact, two lineages (BL7 and BL8), are consistent with spillover
527 occurred in the past from *R. satarae* to *M. cf. fernandoni*. Interestingly, these two species
528 are the major *Bartonella* carriers (high prevalence) and harbour multiple haplotypes
529 indicating they could be potential reservoirs. We did not identify instances of contemporary
530 spillover. However, evidence of potential historic spillover suggests that species that share
531 habitat and other resources could be particularly vulnerable [84]. The communities we
532 studied include many small mammals and their ectoparasites that overlap between
533 habitats, increasing the likelihood of such inter-species transmission [85]. In addition,
534 generalist hosts move across multiple habitats, also carrying generalist ectoparasites likely
535 to further drive pathogen spillover in the landscape [86]. Such pathogen movement
536 between host species could provide an opportunity for the evolution of new virulent
537 variants through recombination [4], similar to those observed in other pathogens [6].
538

539 **Conclusion**

540 We used an ecological and evolutionary approach to disentangle the complex relationship
541 between small mammal hosts, their ectoparasites, and pathogens in a tropical rainforest-
542 plantation landscape. Using systematic and tiered sampling, we determined factors that

influence *Bartonella* prevalence and transmission at a local scale. Our results indicate overlap in small mammal communities across different land-use types, predominantly driven by habitat generalists. These small mammals hosted a diverse ectoparasite community, often showing polyparasitism and host overlap. We observed a positive relationship between *Bartonella* prevalence and aggregated ectoparasite load per host, reiterating the role of ectoparasites as vectors for *Bartonella* transmission. While all the *Bartonella* lineages were host-specific, ectoparasites carried non-specific lineages from other hosts, indicating the potential for cross-species transmission. Evidence of a historic spillover event between two primary *Bartonella* hosts suggests a high chance for such spillovers in the community, especially when ectoparasites show wide host ranges and carry non-specific *Bartonella* lineages. Circulating potentially zoonotic diversity in these small mammals, including synanthropic hosts and their ectoparasites, amplifies the concern of zoonotic transmission. Increased density of generalist hosts and potential vectors due to habitat disturbances would further drive the likelihood of such transmissions. In summary, our study highlights the complex relationship between small mammals, ectoparasites, and pathogen ecology in multi-host, multi-parasite communities. At the same time, these results warrant focused research on bacterial vector-borne pathogens in small mammals to understand the zoonotic implications of undetected spillover in changing multi-host communities.

Ethics statement

This study and associated protocols were approved by National Centre for Biological Science Institutional Animal Ethics Committee (NCBS-IAEC-2016/10-[M], NCBS-IAE-2020/ 02[N]) and Institutional Biosafety Committee (TFR:NCBS:23_IBSC/2017).

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