

1 **The ecology of Nipah virus in Bangladesh: a nexus of land use**
2 **change and opportunistic feeding behavior in bats**

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19

20 **Abstract**

21 Nipah virus is a bat-borne paramyxovirus that produces yearly outbreaks of fatal
22 encephalitis in Bangladesh. Understanding the ecological conditions that lead to spillover from
23 bats to humans can assist in designing effective interventions. To investigate the current and
24 historical processes that drive Nipah spillover in Bangladesh, we analyzed the relationship
25 between spillover events and climatic conditions, the spatial distribution and size of *Pteropus*
26 *medius* roosts, and patterns of land use change in Bangladesh over the last 300 years. We found
27 that 53% of annual variation in winter spillovers is explained by winter temperature, which may
28 affect bat behavior, physiology, and human risk behaviors. We infer from changes in forest cover
29 that a progressive shift in bat roosting behavior occurred over hundreds of years, producing the
30 current system where a majority of *P. medius* populations are small (median of 150 bats), occupy
31 roost sites for 10 years or more, live in areas of high human population density, and
32 opportunistically feed on cultivated food resources – conditions that promote viral spillover.
33 Without interventions, continuing anthropogenic pressure on bat populations similar to what has
34 occurred in Bangladesh could result in more regular spillovers of other bat viruses, including
35 Hendra and Ebola viruses.

36

37 **Keywords:** zoonotic disease; spillover; One Health; urbanization; *Pteropus*

38

39 **Introduction**

40 Zoonotic infections pose an increasing threat to human health [1,2], yet for many
41 zoonoses we have a poor understanding of the biological factors that determine when and where
42 animal hosts are infectious and pose a risk for spillover into human populations [3]. Spillover
43 events often appear sporadic in space and time and repeated outbreaks are rare. This low
44 replication makes it difficult to ascertain the natural history of pathogens. Moreover, rapid
45 response to outbreaks of novel infectious diseases is facilitated when data on related pathogens
46 have been collected through surveillance in animal hosts [4]. Only through long-term
47 surveillance efforts that integrate knowledge of reservoir host ecology, routes of pathogen
48 spillover, and the nature of human-animal interactions can we develop an understanding of the
49 ecology of emerging infections and manage the risk of spillover [3]. Our goal in this study was to
50 assess the ecological conditions that affect the spillover of Nipah virus from fruit bats to humans
51 in Bangladesh based on almost two decades of outbreaks.

52 Nipah virus (family *Paramyxoviridae*, genus *Henipavirus*) is hosted by various *Pteropus*
53 fruit bat species with partially overlapping ranges across countries of South and Southeast Asia
54 [5–17] and potentially the Philippines, where an outbreak of illness in humans and horses from a
55 Nipah-like virus occurred [18]. The range of henipaviruses including Hendra [19], Cedar [20],
56 and others [21–23] extends throughout the geographic range of pteropodid bats to Australia,
57 Indian Ocean islands, and sub-Saharan Africa [24]. These data, combined with limited evidence
58 of pathology in henipavirus-infected bats [25,26], suggest that henipaviruses have had a long
59 association with their bat reservoirs that spans the dispersal of pteropodid bats out of Southeast
60 Asia to other regions [27–31].

61 Distinct outbreaks of Nipah virus infection have highlighted that the same pathogen may
62 use multiple routes to spillover. Nipah virus was first discovered following an outbreak of febrile
63 illness in pigs, pig farmers, and abattoir workers in Malaysia and neighboring Singapore between
64 September 1998 and May 1999 [32–35]. The outbreak ended only after Malaysia established
65 widespread surveillance of pigs, resulting in the culling of over one million animals [36].
66 Outbreaks of Nipah virus infection in Bangladesh have a very different ecological pattern. Since
67 2001 when the first cases of human encephalitis in Bangladesh and India were linked to Nipah
68 virus [5,37], outbreaks have been reported almost every year in Bangladesh and more
69 sporadically in neighboring India [38,39]. Outbreaks in Bangladesh are seasonal, with cases
70 occurring between December and April [40] and cluster primarily in the central and northwest
71 districts of the country. Unlike the outbreaks in Malaysia, those in Bangladesh do not involve an
72 intermediate animal host and are instead linked to drinking fresh or fermented sap (*tari*) from
73 silver date palm trees (*Phoenix sylvestris*) [41–43]. Geographic variation in observed spillover
74 frequency across Bangladesh is partly explained by the proportion of households that drink fresh
75 date palm sap [44] and the distance to the nearest hospital where systematic Nipah virus
76 surveillance occurs [40]. The independence of these spillover events is supported by the genetic
77 variability among Nipah virus sequences from humans and bats in Bangladesh collected from
78 separate outbreaks, contrasting with the more homogeneous sequences from Malaysia [45].
79 Lastly, human-to-human transmission of Nipah virus occurs in Bangladesh [46,47] with an
80 average reproduction number (the average number of secondary cases per case patient) of 0.33
81 (95% confidence interval [CI]: 0.19–0.59) estimated over 2001–2014 [47] or 0.2 (95% CI: 0.1–
82 0.4) over 2007–2018 [38]. Human-to-human transmission of Nipah virus has also been reported
83 during Nipah virus outbreaks in India in 2001, 2007, and 2018 [37,39,48,49]. Although human-

84 to-human transmission was not widely acknowledged in Malaysia at the time of the outbreak
85 [34], methods for detecting such transmission events (e.g., contact tracing) may not have been in
86 place. Additionally, numerous cases reported in the literature had no contact with pigs,
87 suggesting human-to-human transmission may be an alternative explanation [35,50,51]. Thus,
88 the extent of human-to-human transmission that occurred during the Malaysian Nipah virus
89 outbreak remains unclear.

90 One striking similarity between Nipah virus ecology in Bangladesh and Malaysia is that
91 spillovers were facilitated by human resource supplementation in modified landscapes [52]. In
92 Malaysia this involved planting fruit trees in close proximity to piggeries [53,54] whereas in
93 Bangladesh the key resource appears to be date palm sap. *Pteropus medius* (formerly *P.*
94 *giganteus*) frequently visit date palm trees to consume sap, potentially contaminating sap by
95 licking the shaved area of the tree, urinating or defecating in the collection pots, or in some
96 cases, becoming trapped and dying in the pot [42,55,56]. Visits by *P. medius* are highest during
97 winter months (Islam et al., in preparation) when date palm sap is primarily harvested to drink
98 fresh (October to March or April) [41,55,57] and when other available cultivated fruit resources
99 for bats are low [58]. While *Phoenix sylvestris* is a native species in Bangladesh [59–62], date
100 palm sap would not be available to bats if trees were not tapped by sap collectors. *P. medius* is
101 found throughout Bangladesh and bats shed Nipah virus in their urine in all seasons [63]. Nipah
102 virus can remain infectious at 22 °C in neutral pH bat urine for up to four days and artificial sap
103 (13% sucrose, 0.21% bovine serum albumin, pH 7) for over one week [64,65]; most fresh sap
104 and fermented *tari* is consumed within hours of collection [41,43,55]. While the prevalence of
105 Nipah virus shedding in *P. medius* is generally low [63], presenting a bottleneck in spillover, the
106 risk of foodborne transmission increases for communities with higher sap consumption [44].

107 These patterns imply that the spatiotemporal clustering of Nipah spillovers is a convergence of
108 human and bat consumption behavior, wherein the risk of consuming sap contaminated with
109 Nipah virus shed from bats is highest during winter when most sap is consumed by humans, and
110 in regions with high rates of sap consumption.

111 However, there are still aspects of Nipah virus ecology in bats and their interface with
112 human populations that are unclear. First, there is substantial year-to-year variation in the
113 number of Nipah virus spillover events in Bangladesh [38] that may be explained by ecological
114 factors influencing bat behavior and viral shedding. Cortes et al. [40] showed that differences in
115 winter temperature can explain variation in Nipah virus spillovers, but this analysis only covered
116 the period 2007–2013 and missed the decrease in spillovers observed after 2015 [38]. Second,
117 we lack comprehensive information on the population biology, roosting and feeding behavior,
118 and movement ecology of *P. medius* in Bangladesh. Like other *Pteropus* spp. bats, *P. medius*
119 populations appear to be in decline due to hunting and habitat loss [66–68], but *P. medius* also
120 appears to thrive in the human-dominated landscapes of Bangladesh. This adaptability derives
121 from the opportunistic feeding habits of *Pteropus* species and their ability to forage over large
122 areas [63,69–71]. Even though Bangladesh is already the most densely populated country that is
123 not a small city-state or island [72], more *P. medius* roosts in Bangladesh are found in areas with
124 higher human population density, forest fragmentation, and supplemental food resources from
125 residential fruit trees [73,74]. However, villages with Nipah virus spillovers did not have more *P.*
126 *medius* roosts or total bats in the village or within 5 km of the village boundary than villages
127 where spillovers have not been detected [44]. National surveys of *P. medius* roost sites and
128 population trends, including mapping of food resources used by bats, would provide a better
129 understanding of *P. medius* interactions with humans. Lastly, we lack a historical perspective on

130 how land use changes in Bangladesh may have influenced *P. medius* populations and behavior,
131 thereby setting the stage for the emergence of Nipah virus. Analysis of these aspects of Nipah
132 virus ecology will provide clearer insights into the potential drivers of Nipah virus spillover from
133 bats.

134 The objective of this study was to describe the ecological factors that produce frequent
135 spillover of Nipah virus, including climate effects on bat behavior or physiology, the geography
136 of bat roosting sites in Bangladesh, and the relationship between historical land use change and
137 bat roosting behavior. Following the results of Cortes et al. [40], we hypothesized that Nipah
138 virus spillovers would have a strong relationship with winter temperature that explains annual
139 variation in spillover numbers between 2001–2018. Regarding *P. medius* roosting sites, we
140 hypothesized that spatial variables related to climate, human population density, land use, and
141 anthropogenic food resources such as fruit trees and date palm trees could explain variation in
142 the occupancy and size of roosting bat populations. Finally, we hypothesized that land use
143 change, specifically the loss of primary forests, has been a continuous process throughout human
144 occupation of the region that was accelerated during British occupation. This progressive loss of
145 forests likely led to a shift in roosting sites toward more urban areas closer to anthropogenic food
146 resources, a condition that facilitates spillover but predates the first recognized outbreaks of
147 Nipah virus infection by many years. By assessing these patterns, we develop a more
148 comprehensive view of Nipah virus ecology in Bangladesh and provide a path forward for
149 research and management of this system.

150

151 **Materials and Methods**

152 *Nipah virus spillover events*

153 To investigate the spatial and temporal patterns of Nipah virus spillover in Bangladesh,
154 we compiled data on the number of spillover events and affected administrative districts during
155 2001–2018. Cases prior to 2007 were detected through community investigations following
156 reports of clusters of encephalitis. Cases from 2007 onward reflect those identified through
157 systematic surveillance for Nipah virus infection at three tertiary care hospitals combined with
158 investigations of all cases detected to look for clusters, as well as any reports of possible
159 outbreaks through media or other information sources [38]. Independent spillover events were
160 defined as index cases of Nipah virus infection within a given outbreak year. This definition
161 excludes cases that resulted from secondary human-to-human transmission following spillover.

162

163 *Climate data*

164 Expanding on the results from Cortes et al. [40] showing associations between climate
165 and the number of spillover events during 2007–2013, we used data from 20 weather stations in
166 Bangladesh. Mean temperature at three-hour intervals and daily precipitation between 1953–
167 2015 were obtained from the Bangladesh Meteorological Department. Daily temperature and
168 precipitation summary data from 2015 onwards were obtained from the National Climatic Data
169 Center [75] and merged with the older data. We also downloaded monthly indices for three
170 major climate cycles that lead to temperature and precipitation anomalies in the region: the
171 multivariate ENSO index (MEI) for the El Niño–Southern Oscillation, the Indian Ocean dipole
172 mode index (DMI), and the subtropical Indian Ocean dipole index (SIOD). Data were retrieved
173 from the Japan Agency for Marine–Earth Science and Technology Application Laboratory [76]

174 and the National Oceanic and Atmospheric Administration Physical Sciences Laboratory [77].
175 Based on the frequency of Nipah virus spillovers occurring in winter, we focused on weather
176 summary statistics for each year that covered the period from the start of the preceding
177 December to the end of February of a focal outbreak year. We calculated the mean and recorded
178 the minimum temperature over all stations, the percentage of days below 17 °C, and the
179 cumulative precipitation from all stations over the focal period. The choice of 17 °C was
180 arbitrary but represents an upper bound for relative coolness during winter that does not produce
181 any zeros. Mean winter MEI, DMI, and SIOD values were also calculated for each year.

182

183 *Survey of bat roost sites and food resources*

184 The spatial distribution of *Pteropus medius* in Bangladesh was inferred from a country-
185 wide survey of villages as part of investigations regarding risk factors for Nipah spillover
186 performed over the winters of 2011–2012 and 2012–2013 [44]. Briefly, trained teams of data
187 collectors interviewed key informants within villages, who identified known bat roost sites (both
188 occupied and unoccupied) in the village and within 5 km of the village and reported details of the
189 duration of roost occupancy and perceived population trends. The interviewers also mapped the
190 location and number of date palm trees (*Phoenix sylvestris*) and known feeding sites that bats
191 were reported to visit within 500 m of the villages. Feeding sites included fruit trees planted in
192 orchards or in residential areas: jujube (*Ziziphus mauritiana*), banana, mango, guava, lychee, star
193 fruit, jackfruit, papaya, sapodilla (*Manilkara zapota*), mulberry, hog plum (*Spondias mombin*),
194 Indian olive (*Elaeocarpus serratus*), and other species.

195

196 *Spatial covariates of bat roost sites*

197 To evaluate spatial covariates that could explain the occupancy (presence/absence of
198 bats) and abundance (estimated population size) of bats living in mapped roost sites, we
199 extracted data from available raster surfaces describing human population density, land use,
200 bioclimatic variables (e.g., mean annual temperature and precipitation), elevation, slope, and
201 forest cover. Spatial covariate raster files were downloaded from WorldPop [78,79], the
202 Socioeconomic Data and Applications Center (SEDAC) [80], WorldClim [81], and a study on
203 global forest cover change [82]. We also calculated the distance from an index roost site to the
204 nearest village, neighboring roost, date palm tree, and feeding site, and the number of villages,
205 other mapped roosts, date palm trees, and feeding sites within a 15 km radius around each roost.
206 Average nightly foraging distances of individual *P. medius* in two colonies in Bangladesh were
207 estimated to be 10.8 km and 18.7 km, so 15 km was chosen to represent the distance a bat might
208 expect to travel to reach a suitable feeding site [63]. The number of potential covariates was
209 initially reduced by removing variables that were colinear (Pearson's correlation greater than
210 0.7). Descriptions, sources, spatial resolution, and distribution statistics for all 32 covariates are
211 provided in Table A1.

212

213 *Historical land use data*

214 Given the reliance of *P. medius* on tall trees for roosting and various native and cultivated
215 fruit trees for food, we gathered data on historical changes in land use, particularly forested
216 lands, across Bangladesh from data sources covering separate but overlapping time periods.
217 Reconstructed natural biomes and anthropogenic biomes from 1700–2000 were extracted from
218 rasters produced by Ellis et al. [83] using the HYDE 3.1 data model [84] and available from

219 SEDAC. We reclassified their land use subcategories into three primary categories: dense
220 settlements, consisting of urban and suburban areas with high human population density (>100
221 persons/km² for settlements, >2500 persons/km² for urban areas); rice villages and other
222 croplands or rangelands; and forested areas, including populated woodlands and remote forests.
223 Land use data for the years 1992, 2004, 2015, and 2018 were downloaded from the Organisation
224 for Economic Co-operation and Development (OECD) land cover database [85], derived from
225 European Space Agency Climate Change Initiative Land Cover maps [86]. Data for 1990 and
226 2016 were provided by the World Bank [87]. Land cover over the period 1930–2014 came from
227 an analysis by Reddy et al. [88]. Finally, forest cover from 2000 and subsequent forest loss as of
228 2017 were calculated from maps produced by Hansen et al. [82] using the R package *gfcanalysis*
229 [89,90]. For the calculations from Hansen et al. data, we chose a cutoff of 40% forest cover
230 density to match the definition of dense forests used by Reddy et al. Across these datasets, we
231 calculated the percentage of Bangladesh’s total land area (147,570 km² [88]) that was classified
232 as forest.

233

234 *Statistical analysis*

235 Separate Nipah virus spillover events were clustered geographically by the latitude and
236 longitude of affected administrative districts and temporally by the date of illness of each index
237 case using a bivariate normal kernel via the R package *MASS* [91]. To examine the association
238 between Nipah virus spillovers and climate variables, separate generalized linear models were
239 produced that examined climate summary statistics and the number of spillover districts or
240 independent spillover events assuming a Poisson distribution for each response. Model selection
241 was performed to choose the best fitting combination of climate covariates according to Akaike’s

242 information criterion corrected for small sample sizes (AICc) [92] using the R package *MuMIn*
243 [93].

244 The importance of spatial covariates in explaining variation in the occupancy and
245 abundance of bats at roost sites was assessed through a combination of linear modeling and
246 machine learning. The covariates were standardized, and data were split into two sets: an
247 occupancy dataset of 488 mapped roost sites with a binary variable describing whether bats were
248 currently present or not and an abundance dataset of 323 mapped roost sites with the estimated
249 count of bats at each currently occupied roost at the time of the interview. Both datasets were
250 split into training (80%) and testing (20%) sets for validation of models [94]. Generalized linear
251 models (GLMs) were fit with all potential covariates, assuming a binomial distribution for roost
252 site occupancy and a negative binomial distribution for roost counts, which was chosen because
253 of the observed overdispersion of the data, with a variance:mean ratio greater than unity. Due to
254 the large number of potential covariates, least absolute shrinkage and selection operator (lasso)
255 regularization was implemented to reduce the number of covariates and minimize prediction
256 error [95]. We also used random forests to perform covariate selection and assess explanatory
257 power [96]. This machine learning method constructs many decision trees using random subsets
258 of the response variable and covariates then averages the predictions. This method of
259 constructing and averaging a set of uncorrelated decision trees reduces overfitting relative to
260 single decision trees. Linear modeling and random forests were performed in R using the
261 packages *caret*, *glmnet*, and *ranger* [97–99].

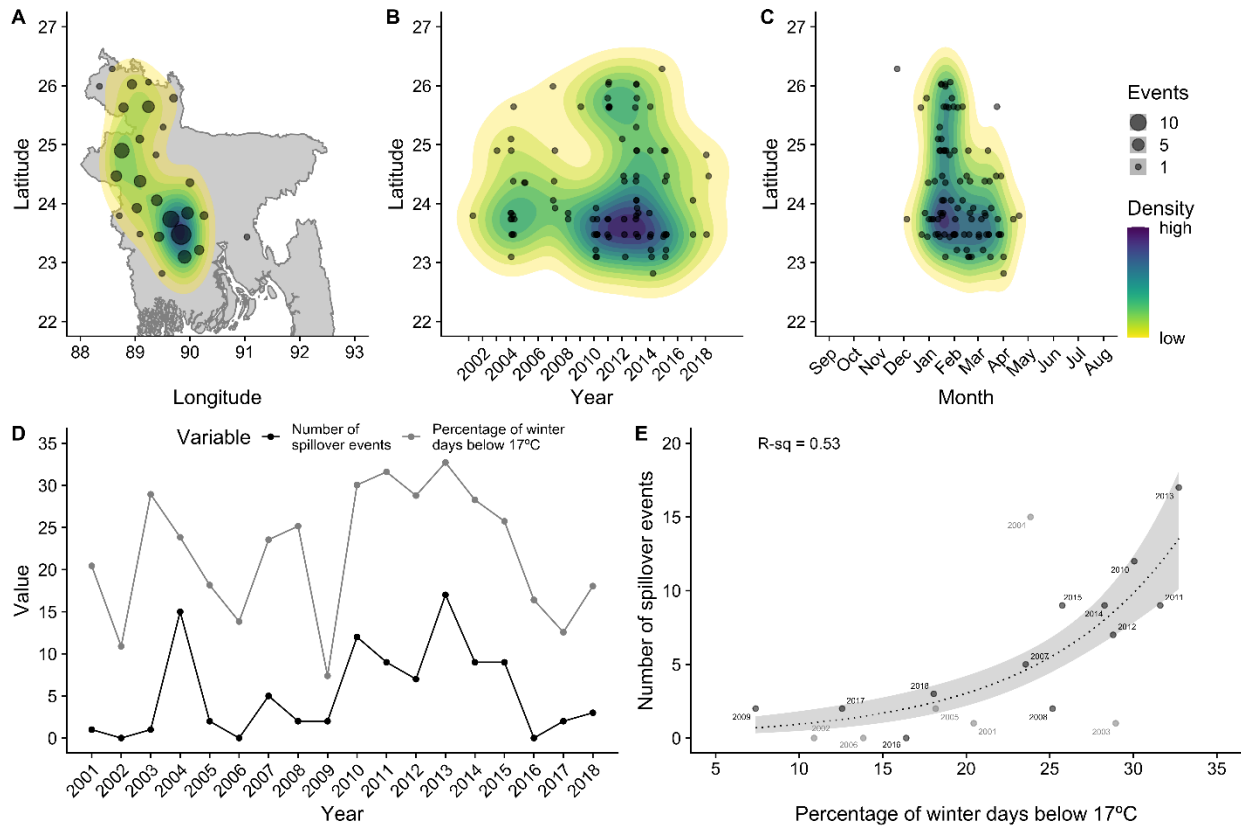
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263 **Results**

264 *Spatiotemporal patterns of Nipah virus spillover*

265 Based on 183 spillover events from 2001–2018, we confirmed previous analyses
266 [38,40,44] showing that Nipah virus spillovers are spatially clustered within districts in the
267 central and northwest regions of Bangladesh (Figure 1A). Outbreak years vary in the intensity of
268 spillover and winter is the primary season when spillovers occur throughout the country (Figure
269 1B,C), although there are occasional events in early spring in central Bangladesh. With the
270 exception of 2002, 2006, and 2016, Nipah virus spillovers have been observed every year since
271 the virus was first identified in 2001, and as observed by Nikolay et al. [38], more spillovers
272 were observed between 2010–2015 than before or after this period (Figure 1D). In accordance
273 with previous work [40] covering 2007–2013, we confirmed that much of this yearly variation in
274 spillover events (53%) can be explained by winter weather over the longer period 2001–2018.
275 Mean winter temperature, minimum winter temperature, and the percentage of days below 17 °C
276 all showed statistically significant associations with yearly spillover events and the number of
277 affected districts ($P < 0.001$; Figures A1–A3). There were no significant associations with
278 cumulative winter precipitation ($P > 0.05$; Figure A4) or the three climate oscillation indices
279 (MEI, DMI, and SIOD; Figure A5). The percentage of days below 17 °C was chosen as the
280 single best fitting covariate for both outcomes according to AICc (Tables A2–A3), showing that
281 colder winter temperatures were associated with more spillovers and more affected districts
282 during 2010–2015, followed by fewer spillovers and affected districts during the relatively
283 warmer period of 2016–2018 (Figure 1D,E; Figure A3). Sensitivity analysis of the association
284 between spillovers and the number of winter days below a certain temperature threshold
285 confirmed that the relationship was strongest at thresholds of 16 to 18 °C, but was statistically

286 significant for thresholds ranging from 15 to 20 °C. We note that spillover observations prior to
287 2007 mostly appear as undercounts relative to those expected by the winter temperatures (Figure
288 1E; Figures A1–A3), which may be attributed to the lack of systematic surveillance during that
289 period [38].



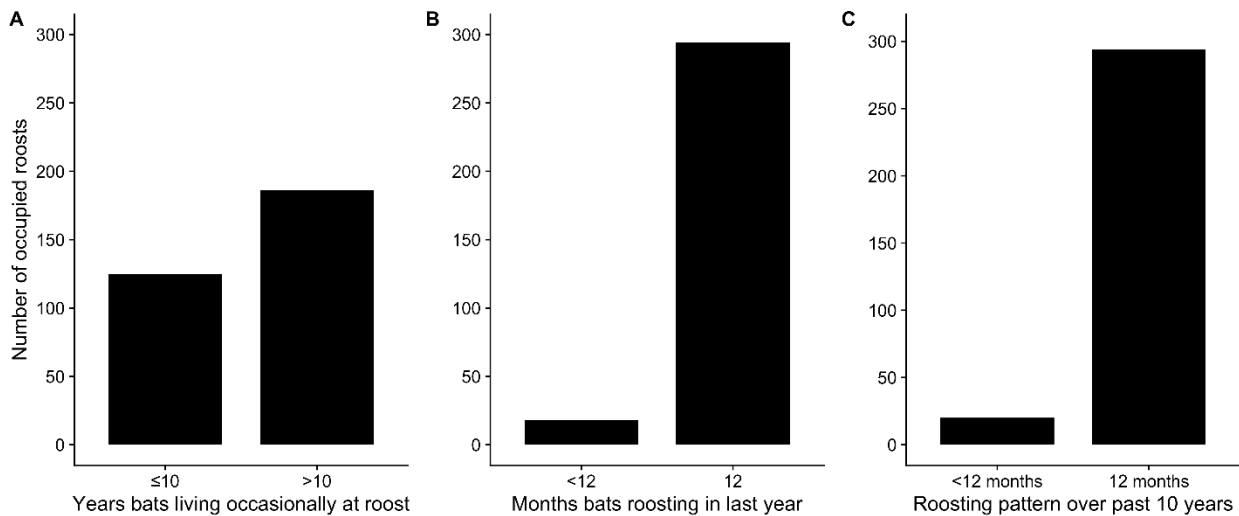
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291 **Figure 1.** Spatiotemporal patterns of Nipah virus spillover events across Bangladesh, 2001–
292 2018. Color contours in panels A–C show the spatial density of events estimated with a bivariate
293 normal kernel. Panels D–E show the variation in the number of Nipah spillover events across
294 years and the association with cold winter temperatures. Gray dots in panel E show the years
295 before systematic Nipah virus surveillance.
296

297 *Spatial distribution and sizes of Pteropus medius roosts*

298 Interviewers mapped a total of 474 roost sites in and around 204 villages, 315 that were
299 occupied at the time of the interview and 159 that were unoccupied. According to interviewees,
300 most occupied roosts (186, 59%) were reported as being at least occasionally occupied for more
301 than 10 years, with an average occupancy duration of 8.5 years (Figure 2A). The majority (294,
302 93%) of roosts were reported to be continuously occupied every month within the last year, with
303 an average duration of 11.6 months (Figure 2B). This pattern of continuous occupancy was
304 reported by interviewees to have been similar over the last 10 years (Figure 2C). Interviewees
305 generally could not recall what season bats began roosting at sites, but when reported, roosts
306 were first occupied more frequently in winter than other seasons (Figure A6A). When
307 considering intermittently occupied roost sites (<12 months of occupancy in a year), bats were
308 also more likely to be present at roost sites during winter (Figure A6B).

309

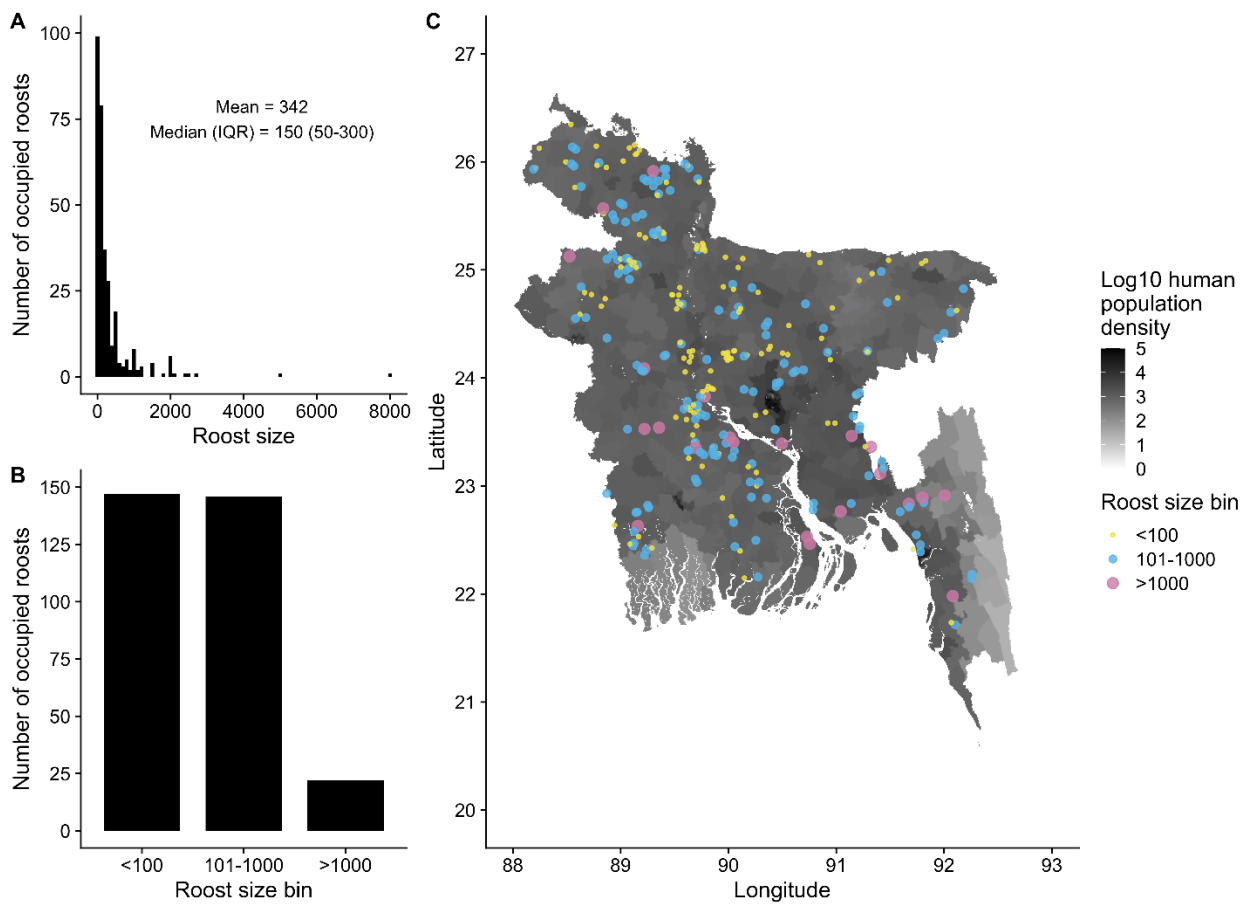


310

311 **Figure 2.** Duration of occupancy of *Pteropus medius* populations at occupied roost sites.
312 According to interviewees, occupied roosts were most frequently occupied for more than 10
313 years (A) and for 12 months out of the year (B). Continuous roost occupancy was similar over
314 the past 10 years (C).

315

316 The size of occupied roosts varied widely, from only one bat to an estimated 8,000 bats at
317 one roost in west-central Bangladesh, with a median size of 150 bats (Figure 3A,B). Studies of *P.*
318 *medius* demonstrate that this distribution of individual roost sizes is similar to those reported in
319 Pakistan, India, Nepal, and Sri Lanka [100–106]. This contrasts with reports of much larger
320 roosts of thousands of *P. lylei* in Cambodia and Thailand [13,107], and roost sizes of *P. alecto*
321 and *P. poliocephalus* in Australia estimated in the tens of thousands [108–110].
322



323

324 **Figure 3.** Size and geographic distribution of *Pteropus medius* populations at occupied roost
325 sites (N = 307) in Bangladesh. Roost sizes varied widely from 0 to 8,000 bats (A) but most
326 roosts contained fewer than 1,000 bats (B). Roosts of varying size were observed throughout the
327 country (C) where human population density is high (1,134 persons/km² in the whole country in
328 2010).
329

330 Roost sizes did not appear to be spatially clustered, such that large and small roosts are
 331 intermixed throughout the country (Figure 3C). The clustering of roosts in the central and
 332 northwest regions of Bangladesh appears to be a spatial artefact of the sampling design, which
 333 targeted roost sites predominantly in and nearby villages where Nipah virus spillover events have
 334 occurred (Figure A7). Following model selection using lasso, the remaining spatial covariates
 335 generally had poor explanatory power for roost occupancy (presence/absence of bats) and
 336 abundance (roost size), with R^2 of 15% or less for testing and training sets (Table 1). AUC was
 337 70% or less for models of occupancy, which indicates poor discriminatory power for predicting
 338 occupied and unoccupied roosts [111].
 339

340 **Table 1.** Performance metrics of GLM and random forests of bat roost occupancy and
 341 abundance.

Response variable	Set	Model	Response error	RMSE	MAE	R²	AUC
Occupancy (presence/absence of bats)	Training (n = 380)	GLM	0.48	0.45	0.42	0.12	0.7
		Random forest		0.48	0.41	0.04	0.61
	Test (n = 94)	GLM	0.46	0.46	0.43	0.02	0.59
		Random forest			0.51	0.43	0
Abundance (roost size)	Training (n = 255)	GLM	670	631	314	0.14	
		Random forest			643	312	0.09
	Test (n = 60)	GLM	744	711	320	0.1	
		Random forest			709	327	0.08

342 RMSE – root mean square error, MAE – mean absolute error, AUC – error under the receiver
 343 operating characteristic curve.
 344

345 These results broadly indicate that bat roosts are not linearly associated with the available
346 covariate data and largely reflect the geography of nearby villages that were surveyed (Tables
347 A5–A6). For example, an average roost site is situated in an area with high human population
348 density, close to inland water bodies, with a nearby feeding site (fruit trees) or date palm tree
349 within 5 km, and numerous feeding sites or date palm trees within a 15 km radius around the site
350 (Table 2; Figure A8). This pattern is consistent with Bangladesh as a whole, where human
351 population density is high everywhere (Figure 3C) and villages contain numerous potential fruit
352 and date palm trees that could attract bats (Figure A7). Only seven out of 474 roost sites had no
353 date palm trees or feeding sites within 15 km of the roost site. However, all of these roost sites
354 had a date palm tree or feeding site within 25 km of the roost site. Roost sizes showed similarly
355 static distributions compared to the other 28 covariates assessed (Table A1; Figures A9–A11).
356 Similar to other studies of *P. medius*, roost sites were close to water bodies (Table 1)
357 [101,102,105], but distance to water did not explain variation in the occupancy or abundance of
358 bats at roost sites (Tables A5–A6).

359

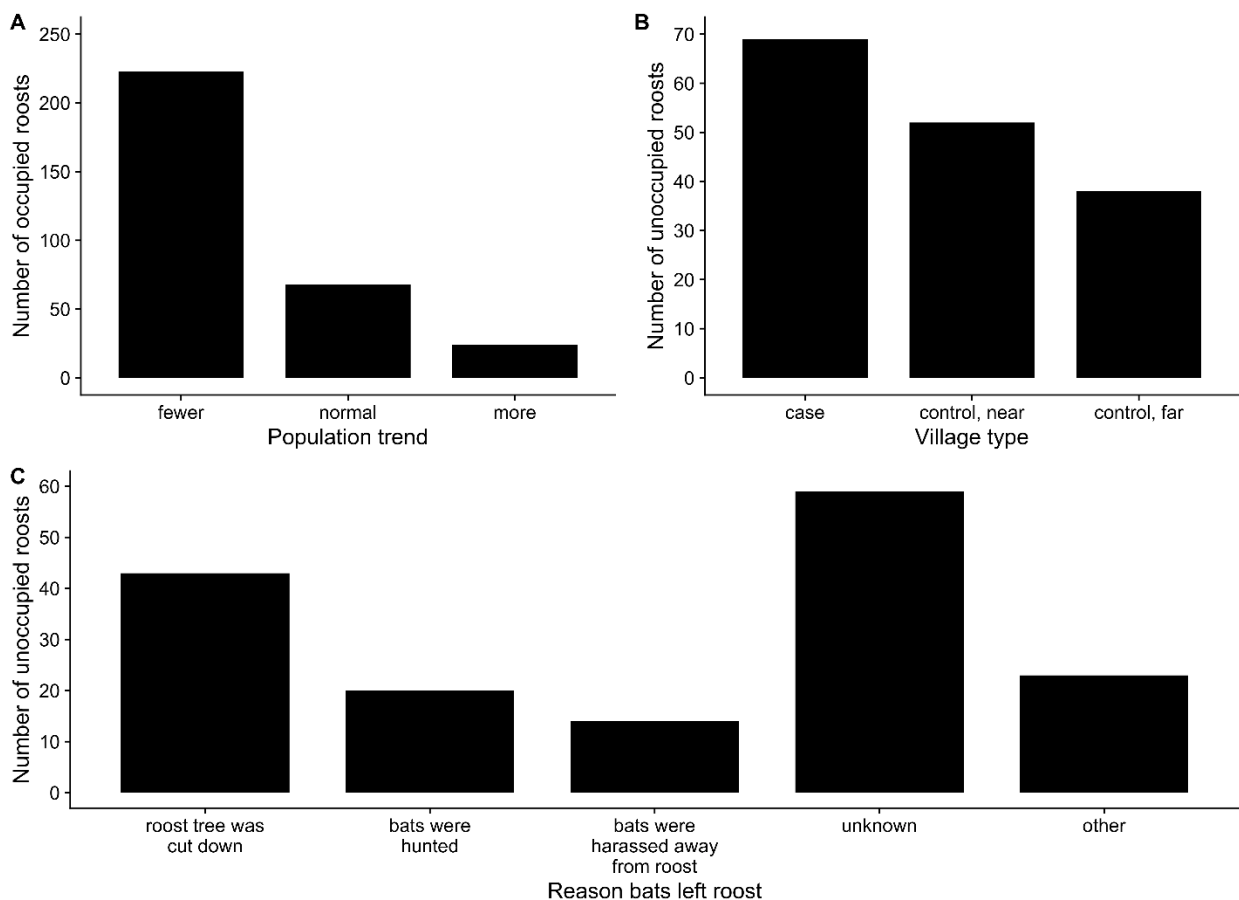
360 **Table 2.** Distribution of select spatial covariates across all mapped roost sites.

Covariate	Median (IQR)
Human population density (persons/km ²)	996 (858–1,260)
Distance to nearest inland water (km)	0.6 (0.3–1)
Distance to nearest feeding site (km)	2 (0.9–3.6)
Distance to nearest date palm tree (km)	1.2 (0.2–2.7)
Number of feeding sites within 15 km of roost site	11 (3–20)
Number of date palm trees within 15 km of roost site	80 (29–307)

361

362 Despite the widespread distribution of bat roost sites and the presence of some relatively
363 large roosts (>1,000 bats), interviewees report that, with respect to their own memory, most
364 roosts are decreasing in size (Figure 4A). These patterns support anecdotal reports of decreasing

365 *P. medius* populations from biologists and bat hunters, a trend attributed to cutting of roost trees
366 and overhunting [66,67]. Local Nipah virus spillover investigation teams have reported that
367 village residents will often cut down roost trees within villages after an outbreak [44]. In support
368 of this, we observed that roost sites in and around Nipah virus case villages had more unoccupied
369 roosts than control villages that were either near (>5 km) or far (>50 km) from case villages
370 (Figure 4B). Besides cutting down roost trees, interviewees listed a number of other reasons that
371 bats left a roost site, including that bats were hunted, or bats were harassed with rocks, mud,
372 sticks, or gunfire (Figure 4C).
373



374

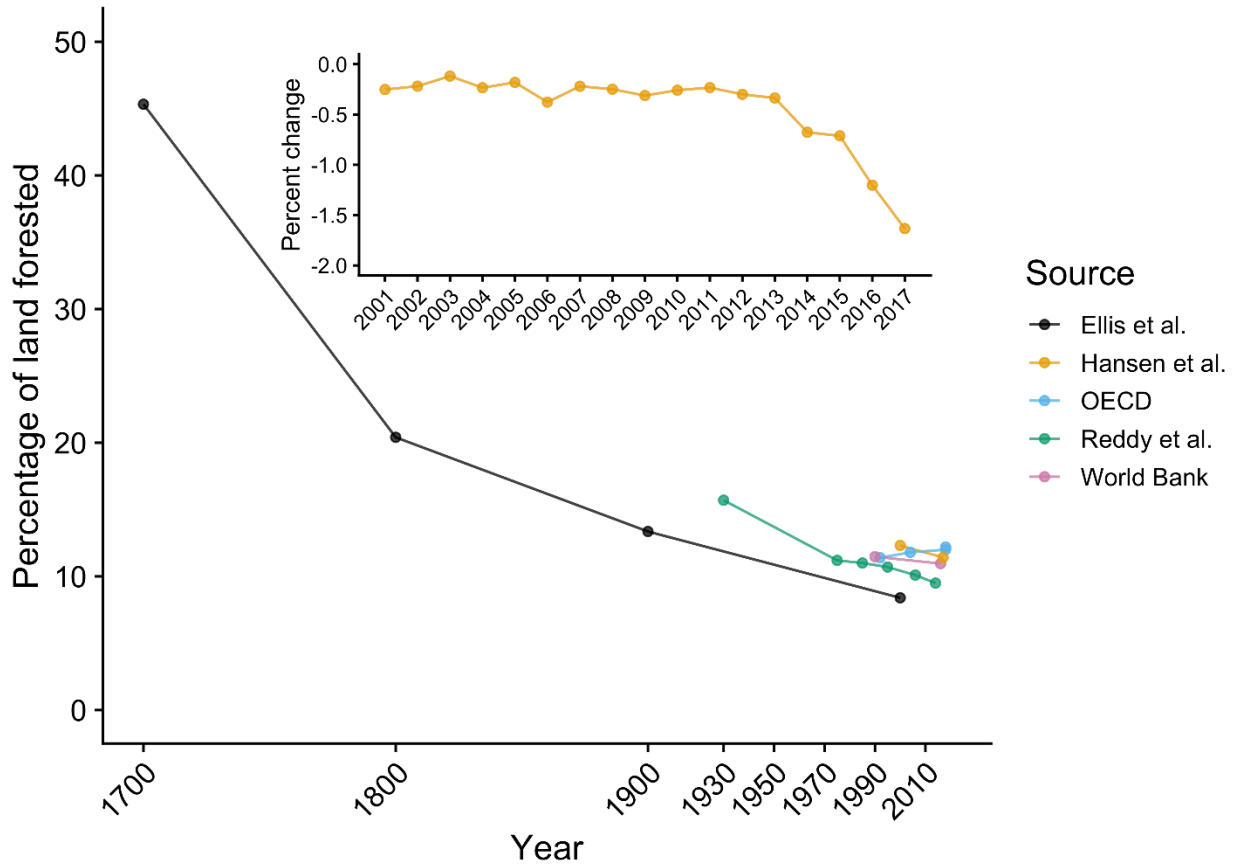
375 **Figure 4.** Reported trends for *Pteropus medius* populations at occupied roost sites (A);
376 distribution of unoccupied roost sites across Nipah virus case villages and control villages (B);
377 and reported reasons for bats no longer occupying roost sites (C).

378

379 *Historical land use change in Bangladesh*

380 According to the collated data, the majority of forest loss in Bangladesh occurred prior to
381 the 20th century but has steadily continued to the present (Figure 5). Prior to human occupation
382 of the land area comprising Bangladesh, the whole country was likely covered in dense tropical
383 forest, similar to neighboring countries in Southeast Asia [83]. Evidence of human occupation in
384 Bangladesh dates back at least 20,000 years, rice cultivation and domesticated animals occurred
385 before 1500 BCE, and sedentary urban centers were seen by the fifth century BCE [112].
386 Clearing of land for rice cultivation continued through to the 16th century CE, by which time rice
387 was being exported from the Bengal delta to areas of South and Southeast Asia. During Mughal
388 rule over the Bengal delta starting in the 1610, the Ganges (Padma) River shifted eastward, so
389 Mughal officials encouraged colonists to clear forests and cultivate rice in eastern Bangladesh
390 [112]. Thus, much of the native forests in Bangladesh had been converted to cultivated land prior
391 to 1700 (Figure 5).

392



393

394 **Figure 5.** Historical change in forested land area in Bangladesh according to available sources.
395 Inset displays the rate of dense forest loss (annual percent change) since 2000, with a recent
396 increase in this rate of decline, drawn from Hansen et al. [82]. A cutoff value of 40% was used to
397 define dense forests. Only gross forest loss is displayed, since data on forest gain only covers the
398 period 2000–2012.
399

400 Following the Battle of Plassey in 1757, the British East India Company took control of
401 the country and established Permanent Settlement, a system of land taxation that set a fixed tax
402 burden for landholders (zamindars). While the intention was that the fixed tax rates would allow
403 zamindars to invest more in agricultural development of the land through better seeds, irrigation,
404 and tools, this never materialized. Since the British would auction the zamindar's land if they fell
405 behind on their tax obligation, land became a valuable commodity that was bought and sold by
406 wealthy bureaucrats and zamindars. This fostered a hierarchical system where the peasantry

407 working the land paid rent but had no property rights, while landowners were only attached to
408 the land through a series of intermediary managers. To meet their tax obligation and collect rent
409 from tenant farmers, landowners encouraged cultivation of cash crops (cotton, indigo, sugarcane,
410 silk, tea, tobacco, and jute) meant for export in the global market. Agrarian production increased
411 not through agricultural intensification of already cultivated land, but through clearing of native
412 forest. Forest cover declined dramatically during the 1700s and 1800s (Figure 5; Figure A12)
413 and the system of Permanent Settlement existed with some modifications until the 1950s [112].

414 Production of sugar for export and local consumption came predominantly from
415 sugarcane during the colonial period, but a minor proportion (perhaps 10–15%) was produced
416 from date palm sap from cultivated *Phoenix sylvestris*. While historically date palm sugar was
417 used locally for the preparation of sweetened foods, it became integrated into the global sugar
418 trade starting in 1813 and the value of date palm sap increased. The number of date palms in
419 Bangladesh increased rapidly from the 1830s and remained high until at least the early 1900s,
420 propelled by British encouragement of landowners and the development of mills by the British to
421 produce sugar from date palm sap [61]. Roughly 1,370 metric tons of raw sugar (*gur*) was
422 produced from date palm sap on average during 1792–1813 in Bangladesh, which increased to
423 38,000 tons of *gur* in 1848 and 162,858 tons by 1905, and then decreased to 66,930 tons by 1911
424 [61]. The most recent figures from the Bangladesh Bureau of Statistics for 2016–2017 put the
425 area of Bangladesh under date palm cultivation for sap at 20.8 km² with a production of 169,056
426 metric tons of palm sap (perhaps 10% of which might be converted to *gur*) [113,114]. This is
427 compared to 920 km² under sugarcane producing 3,862,775 tons of sugarcane juice during the
428 same year [113].

429 Today, Bangladesh has less than 14% of its forest remaining (Figure 5) and the only
430 dense forests are restricted to the southwestern mangrove forests of the Sundarbans and the
431 southeastern forests of the Chittagong Hill Tracts (Figure A12). The portion of the Sundarbans in
432 Bangladesh is a protected as the Sundarban Reserve Forest containing three large wildlife
433 sanctuaries. The region of the Chittagong Hills had enjoyed a level of political autonomy during
434 Mughal rule and was also the last part of Bangladesh to come under state rule after the British
435 invaded in 1860 but retained some regional autonomy in their system of taxation and land rights
436 [112]. Combined with the more rugged terrain of this region, intensification of industrial forestry
437 and agricultural production was delayed until the 1900s, and this region remains one of the least
438 populated areas of the country (Figure 3). These conditions have thereby preserved much of the
439 primary forest until the present (Figure A12). The conditions in neighboring Myanmar were
440 similar, as the British did not begin their rule of the country until 1824. Prior to British rule,
441 Myanmar's agricultural economy was not as export-focused compared to Bangladesh, but this
442 shifted towards intensified production of rice for export during the colonial period [115]. Partly
443 due to a delayed agricultural intensification imposed by the British, trees still cover around half
444 of Myanmar's land area [85] and the population density was only 77 persons/km² in 2010 [72].

445 Recent deforestation in Bangladesh has continued at a steady pace, with a net rate of
446 0.75% or less per year during 1930–2014 [88], and is concentrated in eastern Chittagong
447 Division (Figure A13). However, there has been a rise in deforestation since 2013 (Figure 5
448 inset). Additionally, felling of tall trees continued even in largely deforested areas of Bangladesh
449 for the purpose of curing tobacco leaves and brick burning [67]. Since *P. medius* relies on tall
450 tree species such as banyan (*Ficus benghalensis*) to form large roosts [73], the loss of single tall
451 trees can scatter bats into ever smaller populations.

452

453 **Discussion**

454 *Historical land use change, bat ecology, and Nipah virus spillover*

455 Given the nearly two decades of research on Nipah virus in Bangladesh, there are facets
456 of its ecology that are now clear. Historical patterns of forest loss have drastically diminished
457 native habitat for fruit bats. *Pteropus medius* bats now live in mostly small, resident roosts in
458 close proximity to humans and opportunistically feed on cultivated food resources. These
459 gradual but dramatic changes have produced a system that facilitates spillover of a bat-borne
460 virus. The consequence is almost annual spillover of Nipah virus in winter months following
461 consumption of raw or fermented date palm sap that has been contaminated with bat excreta
462 containing Nipah virus.

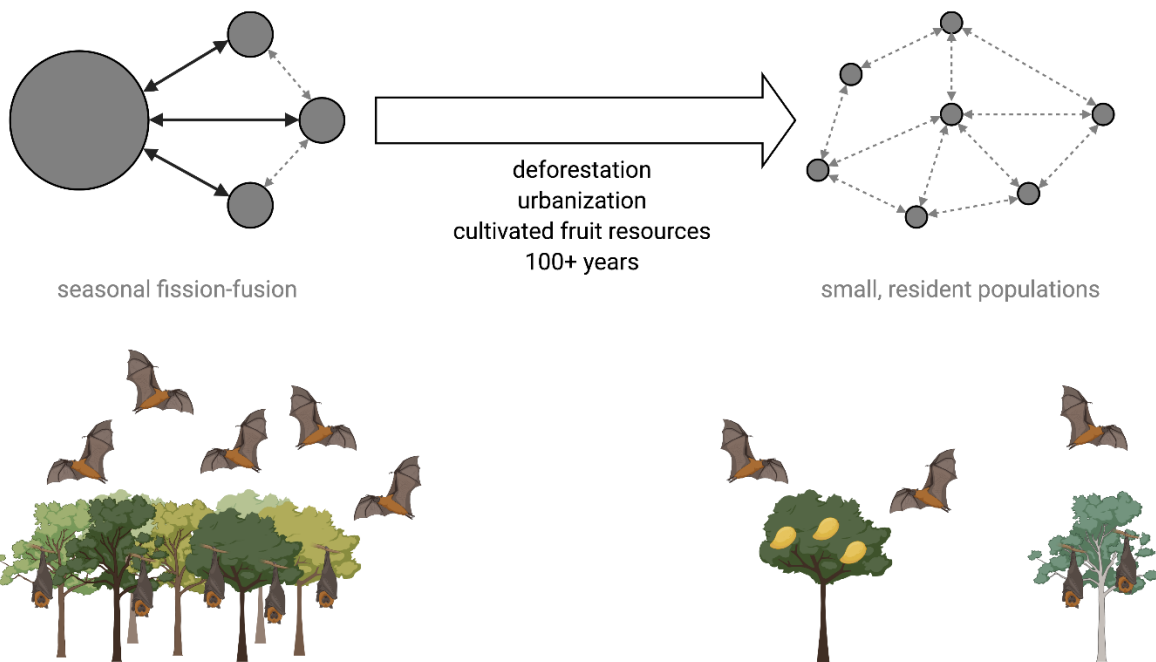
463 Our analysis suggests that the current state of the bat-human ecological system in
464 Bangladesh supports Nipah virus spillover: a mobile metapopulation of reservoir hosts living
465 amongst humans and sharing food resources that has likely existed for many years prior to the
466 first recognized outbreaks. While the loss of forests in Bangladesh is still occurring and
467 potentially affecting the distribution of *P. medius*, the majority of the land use change from forest
468 to cultivated areas occurred at least a century ago (Figure 5). Cultivation of date palm trees for
469 their sap and other products is a tradition that has likely been practiced for centuries [116], and
470 bats have been potentially consuming sap for an equal amount of time. Importantly, the date
471 palm sap industry was greatly expanded by the British during the late 19th and early 20th
472 centuries and continues at a similar scale to the present [61,113]. Time-calibrated phylogenetic
473 analyses indicate that Nipah virus has been circulating in *P. medius* in Bangladesh and India
474 since the 1950s or earlier [6,117,118]. Thus, none of the conditions that promote Nipah virus

475 spillover in Bangladesh are new. Spillovers almost certainly occurred in the past but were
476 undetected prior to the first isolation of Nipah virus in 1999 and the subsequent development of
477 diagnostic tests. Even recent outbreaks since surveillance was established in 2007 might be
478 missed. Hegde et al. found that because encephalitis case patients are less likely to attend a
479 surveillance hospital if it is distant from their home and if their symptoms are less severe, at least
480 half of all Nipah virus outbreaks during 2007–2014 were likely missed [119].

481 The ecological state of Nipah virus in Bangladesh has important similarities and
482 differences with the ecology of the related Hendra virus in *Pteropus* spp. in Australia. Spillover
483 events from bats primarily occur in the cooler, dry winter months in both Australia and
484 Bangladesh, and evidence from Australia suggests that this season is when bats are potentially
485 experiencing nutritional stress, are residing in small roosts close to humans, and are shedding
486 more viruses [24,120]. In contrast to *P. medius* in Bangladesh, *Pteropus* populations in Australia
487 exhibit a range of population sizes and behaviors, from large, nomadic groups that track
488 seasonally available nectar sources to small, resident colonies that feed on anthropogenic
489 resources [108]. The increasing incidence of Hendra virus spillovers is linked with periods of
490 acute food shortage that shift bats from nomadism to residency and drive bats to feed on
491 suboptimal food sources, thereby exacerbating stress and associated viral shedding (Eby et al., in
492 review) [121].

493 We propose that the systems of Nipah virus in Bangladesh and Hendra virus in Australia
494 represent distinct points on a continuum describing patterns of bat aggregation and feeding
495 behavior in a landscape of available roosting sites and food resources (Figure 6). One end of the
496 spectrum is characterized by seasonal shifts from smaller populations to large aggregations of
497 bats in response to transient pulses in fruit and nectar resources (fission-fusion). The other end of

498 the spectrum represents a permanent state of fission, where bats are distributed in small, mostly
499 resident roosts in a matrix of anthropogenic food resources. Bangladesh appears to fall at the
500 latter end of the spectrum, wherein historical land use change and urbanization removed the
501 native forest habitats that supported *Pteropus medius* populations, leaving limited roosting sites
502 but abundant cultivated fruits that are sufficient for sustaining small populations of bats.
503 Australia would traditionally have been on the opposite end of the spectrum, but loss of winter
504 habitat and urban encroachment may be pushing the system towards more permanent fission,
505 which could result in more consistent spillovers of Hendra virus (Eby et al. in review) [121].
506 Similar anthropogenic pressures acting on pteropodid bat populations in Southeast Asia or Africa
507 could push these systems into a state similar to Bangladesh, consequently increasing the risk of
508 henipavirus spillover [24].
509



510

511 **Figure 6.** Long-term shifts in pteropodid bat populations and seasonal movements due to
512 anthropogenic land use change. Black arrows show seasonal movements of bats into large
513 aggregations. Dashed gray arrows represent occasional bat movement between roost sites.
514

515 *Seasonality of date palm sap consumption and spillovers*

516 Beyond the broad ecological forces that facilitate henipavirus spillover from bats, there
517 are epidemiological patterns that will require further research to explain. Perhaps the most
518 complex are the causes of winter seasonality in Nipah virus spillovers. Recent evidence suggests
519 that bats shed Nipah virus at low levels throughout the year [63]. Date palm trees are also tapped
520 year-round for *tari* production but harvesting increases during winter months to meet increased
521 demand for *tari* and fresh sap [41,43]. Visits by *P. medius* to date palm trees are more frequent in
522 winter [56], even when date palms are tapped year-round for *tari* production (Islam et al., in
523 preparation). Therefore, the risk of viral spillover is always present, but may increase during

524 winter because bats are capitalizing on a resource when it is most available, thereby increasing
525 the probability that sap is contaminated during the winter harvest.

526 The observation that more Nipah virus spillovers occur during years with colder winters
527 indicates that climate is affecting one or more factors in the system: date palm physiology, bat
528 and human behavior, bat physiology and immunology that affect viral replication, or some
529 combination of these factors. Date palm sap collectors report that date palm sap is sweeter and
530 flows more freely during cooler weather [43,56,61]. These might be physiological responses of
531 *Phoenix sylvestris* to seasonal weather conditions (e.g., sugar or water is concentrated in the
532 trunk during cool, dry weather), yet no data are available on variation in sap flow or sugar
533 content for this species outside of winter months [61]. Harvesting date palm sap when it is
534 sweetest would be optimal not only for the collectors, but also for bats. Fewer cultivated fruits
535 are available during winter than other seasons [58], so bats may gravitate towards date palms
536 because it is readily available during a time of relative food scarcity. More surveys of *P. medius*
537 feeding behavior and the fruits they consume at different times of the year would be necessary to
538 assess this hypothesis [122]. Complementary experiments could be performed to evaluate
539 whether pteropodid bats perceive small differences in sugar concentration and modify their
540 feeding behavior in response to varying energy demands [123].

541 Another hypothesis, derived from research on Hendra virus in Australian bats, posits that
542 bats shed viruses more frequently during periods of nutritional stress that compromise bat
543 immune function [24,124]. Increased metabolic demands of thermoregulation during winter
544 when food resources are already limited could produce physiological and nutritional stress in
545 bats. Bats may seek out alternative foods (e.g., date palm sap) to compensate for this stress.
546 Whether *P. medius* are shedding more Nipah virus when they are experiencing physiological or

547 nutritional stress in winter is an open question. We need more documentation of body condition,
548 biomarkers of stress and immune function, or abortion rates among female bats to understand
549 any relationships between Nipah virus shedding, stress, and climate [24,125–127].

550 We also lack information on how seasonal bat movements might influence Nipah virus
551 spillover dynamics. Although our data suggest that most roost sites are continuously occupied
552 (Figure 2), there may still be some seasonal dynamics in bat population sizes as individuals make
553 occasional movements to use seasonally available resources or aggregate for mating. There is
554 evidence from India and Nepal that *P. medius* roost populations vary seasonally, with larger
555 populations in fall and winter than in summer [128,129]. This is mirrored by our data showing
556 winter is the season when more roosts were founded, and bats are present at intermittently
557 occupied sites (Figure A6). There is also evidence that *P. medius* home ranges contract during
558 the dry season (including winter) than the wet season [63]. Nevertheless, genetic data on *P.*
559 *medius* and Nipah virus in Bangladesh indicate that bat movements are common enough to
560 promote genetic admixture and spread distinct Nipah virus genotypes among geographically
561 distant *P. medius* populations [6]. To better understand how bat movements influence spillover
562 dynamics, we need more information on seasonal variation in bat population sizes at roost sites
563 and potentially individual movement tracking data, which could be used to parameterize
564 metapopulation models of Nipah virus transmission.

565

566 *Roost tree loss and Pteropus roosting behavior*

567 In addition to the causes of seasonality in Nipah virus spillover, more research is needed
568 to determine the effects of current deforestation and human disturbance on *P. medius*
569 populations. While historical patterns of deforestation and land use change have undoubtedly

570 reduced available habitat for pteropodid bats (Figure 5), the effects of current deforestation may
571 be easiest to measure at the scale of individual roost trees. If a single tree in a largely deforested
572 area has qualities that are preferred by bats and therefore supports a large population of bats, loss
573 of that tree could have a very large effect on the bat population but would contribute very little to
574 overall deforestation rates. Our statistical analysis was unable to explain substantial variation in
575 the occupancy and size of roosts using available data on spatial covariates, including land use,
576 human population density, bioclimatic variables, and distribution of cultivated fruit and date
577 palm trees (Table 1; Table A1). Similar results were observed for *P. medius* populations in Uttar
578 Pradesh, India [101]. Kumar and Elangovan [101] were unable to explain variation in colony size
579 using data on distance to human settlements, roads, or water bodies. However, they did find that
580 colony size increased with tree height, trunk diameter, and canopy spread. The majority of
581 colonies were found in tree species with wide canopies, including *Ficus* spp., mango, *Syzygium*
582 *cumini*, and *Madhuca longifolia* [101]. Hahn et al. [73] compared occupied roost trees to non-
583 roost trees within a 20x20 m area around central roost trees and found that *P. medius* in
584 Bangladesh favor tall canopy trees with large trunk diameters. Therefore, future efforts to
585 understand variation in *P. medius* population sizes across Bangladesh should collect more data
586 on characteristics of roost trees. Furthermore, the sampling design of our population meant that
587 no bat roosts could have been observed further than 5 km from a village, meaning that bat roosts
588 in remnant forested areas in the Sundarbans and Chittagong Hills were much less likely to be
589 included in the study (Figure A7). Further surveys of roost sites may reveal distinct roosting
590 patterns of *P. medius* populations living in these areas or in other areas within the range of *P.*
591 *medius* where human population density is lower and forested habitat is more intact.

592 Our survey data also indicate that many roost sites are frequently abandoned following
593 harassment, hunting, or removal of roost trees and that more unoccupied roosts are found near
594 villages that have experienced Nipah virus spillover (Figure 4). Presumably these bats disperse
595 and form new roosts or join existing roosts, but the new roost trees may be of lower quality than
596 the previous roost and only support a smaller population of bats. More granular data on the
597 cumulative effects of roost tree loss on average *P. medius* population sizes would refine our
598 conceptual model of shifting roosting behavior in pteropodid bats (Figure 6). Moreover,
599 movements of bats following abandonment of roost sites could have implications for Nipah virus
600 transmission dynamics. Dispersal of bats following roost tree loss or harassment could lead
601 infected bats to seed outbreaks elsewhere [124]. Therefore, reactionary cutting of roost trees in
602 villages with Nipah virus spillovers is counterproductive for spillover prevention and bat
603 conservation and should be discouraged.

604

605 *Possible interventions to prevent Nipah virus spillover*

606 Finally, there is a need to explore possible interventions to prevent Nipah virus spillover.
607 Without a vaccine for Nipah virus, much of the research has focused on mitigating the risk of
608 spillovers. Several studies in Bangladesh have centered on educating the public about the risks of
609 drinking raw date palm sap and methods for preventing bat access to date palm sap during
610 collection [130–132]. There is also a need for increased surveillance of bats and humans in close
611 contact with bats in Bangladesh and other areas within the range of *Pteropus* bats. These
612 enhanced surveillance efforts could include serosurveys of bat hunters, date palm sap collectors,
613 people who drink sap or eat fruits that have been partially consumed by bats, and people who
614 live in close proximity to bat roost sites [13,66,133,134]. While there has been no evidence that

615 consuming fruits partially eaten by bats is associated with Nipah virus spillover to humans in
616 Bangladesh and Cambodia [13,135], this route was believed to be the cause of the 1998–1999
617 outbreaks in pigs that led to human cases in Malaysia and Singapore [54]. A 2009 survey of
618 livestock in Bangladesh living nearby to *Pteropus* bat roosts also found henipavirus antibodies in
619 6.5% of cattle, 4.3% of goats, and 44.2% of pigs [136]. Animals were more likely to be
620 seropositive if they had a history of feeding on fruits partially eaten by bats or birds and drinking
621 date palm juice from Asian palmyra palms (*Borassus flabellifer*) [136]. Therefore, Nipah virus
622 transmission from livestock to humans in Bangladesh is a risk that should be explored with
623 additional serosurveys and efforts to limit contact of livestock with fruits and other materials
624 potentially contaminated with bat excreta.

625 Similar risks may apply in neighboring India where Nipah virus outbreaks have been
626 linked to fruit bats [48,137]. The index case of a 2007 Nipah outbreak in West Bengal was
627 reported to frequently drink date palm liquor (*tari*) and had numerous bats living in trees around
628 their home [48]. Researchers speculate that the 2018 and 2019 outbreaks in Kerala, India, may be
629 linked to consumption of partially eaten fruits [137]. However, this has not been confirmed via
630 detection of Nipah virus on partially eaten fruits or case-control studies [39,44]. The index case
631 associated with 23 cases of Nipah virus infection during the 2018 Kerala outbreak reported
632 possible contact with an infected baby bat, but this was also not confirmed [39]. Silver date palm
633 is not cultivated for sap in Kerala, but coconut palm and Asian palmyra palm are [39]. The
634 narrow-mouthed containers that are used to collect sap from these palm species are thought to
635 prevent bat access to the sap within the container [39] but might not prevent bats from accessing
636 and contaminating sap at the tapping site or from inflorescences. Additional studies using
637 infrared cameras to understand fruit bat feeding behavior around other palm trees harvested for

638 sap and possible intervention methods similar to those done in Bangladesh are warranted
639 [56,130]. Such information would help to clarify how Nipah virus is transmitted from fruit bats
640 to humans in India and allow for ecological comparison of outbreaks in these two neighboring
641 countries.

642 At a higher level, methods that limit human-bat contact through ecological interventions
643 may be beneficial. Plantations of fruit- and nectar-producing tree species could provide
644 alternative food for *P. medius*, such as cotton silk (*Ceiba petandra*, *Bombax ceiba*), Indian mast
645 tree (*Polyalthia longifolia*), and Singapore cherry (*Muntingia calabura*). Trees that produce fruit
646 year-round or specifically during winter could provide bats with the required nutrition that would
647 have been acquired from date palm sap or other cultivated fruits. In combination with methods to
648 prevent bat access to date palm sap, ecological interventions that would allow *P. medius*
649 populations to persist in Bangladesh and other areas while lowering the risk of Nipah virus
650 spillover should be explored.

651

652 **Conclusions**

653 The ecological conditions that produce yearly spillovers of Nipah virus in Bangladesh are
654 not a new phenomenon, but rather a culmination of centuries of anthropogenic change. The
655 opportunistic feeding behavior of *P. medius* has allowed populations to adapt to these modified
656 landscapes, persisting in small, resident colonies feeding on cultivated fruits. Shared use of date
657 palm sap by bats and humans is a key route for Nipah virus spillover during winter months.
658 Continued research on this system could reveal how bat behavior and physiology influence the
659 seasonality of Nipah spillovers and explore potential ecological interventions to prevent
660 spillover.

661

662 **Supplementary Materials:** The following are available online at www.mdpi.com/xxx,

663 Appendix A: Supplementary tables and figures.

664

665 **Author Contributions:** Conceptualization, E.G., R.P., and P.H.; data curation, C.M., E.G., and

666 H.S.; formal analysis, C.M.; visualization, C.M.; writing – original draft preparation, C.M.;

667 writing – reviewing and editing, all authors. All authors have read and agreed to the published

668 version of the manuscript.

669

670 **Funding:** C.M., E.G., S.L., R.K.P., P.J.H. were funded by the DARPA PREEMPT program

671 Cooperative Agreement D18AC00031; R.K.P. and P.J.H. by the U.S. National Science

672 Foundation (DEB-1716698); and R.K.P. by the USDA National Institute of Food and

673 Agriculture (Hatch project 1015891).

674

675 **Acknowledgments:** We thank Peggy Eby and Birgit Nikolay for early discussions on data

676 sources and analyses.

677

678 **Conflicts of Interest:** The authors declare no conflicts of interest.

679

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