1   **Local temperature and ecological similarity drive**

2   **distributional dynamics of tropical mammals worldwide**

3

4   **Short title:** Tropical mammal distributional dynamics

5

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53   **Biosketch**

54

55   Lydia Beaudrot is a community and macroecologist whose research focuses on

56   understanding the determinants of community composition, particularly for tropical

57   mammals. Beaudrot combines observational data with statistical modeling approaches to

58   investigate questions at the interface of ecological theory and conservation biology

59

60   **Acknowledgements**

75

76   **Author Contributions**

77

78   LB, MA, JPL, and JA conceived the project idea.

79   MA, LB and JPL designed the analysis.

80   PAJ, CF, EL, TO, FR and DS contributed TEAM data.

81   LB, MA, JPL and AZ conducted the analysis.

82   LB, JPL and MA wrote the manuscript with contributions from all the authors.

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8

9 **Abstract**

10

11 **Aim**: Identifying the underlying drivers of species' distributional dynamics is critical for

12 predicting change and managing biological diversity. While anthropogenic factors such

13 as climate change can affect species distributions through time, other naturally occurring

14 ecological processes can also have an influence. Theory predicts that interactions

15 between species can influence distributional dynamics, yet empirical evidence remains

16 sparse. A powerful approach is to monitor and model local colonization and extinction—

17 the processes that generate change in distributions over time—and to identify their abiotic

18 and biotic associations. Intensive camera-trap monitoring provides an opportunity to

19 assess the role of temperature and species interactions on the colonization and extinction

20 dynamics of tropical mammals, many of which are species of conservation concern.

21 Using data from a pan-tropical monitoring network, we examined how short-term local

22 temperature change and ecological similarity between species (a proxy for the strength of

23 species interactions) influenced the processes that drive distributional shifts.

24

25 **Location**: Tropical forests worldwide

26

27 **Time period**: 2007 - 2016

28

29 **Major taxa studied**: Terrestrial mammals

30

31 **Methods**: We used dynamic occupancy models to assess the influence of the abiotic and

32 biotic environment on the distributional dynamics of 42 mammal populations from 36

33 species on 7 tropical elevation gradients around the world.

34

35 **Results**: Overall, temperature, ecological similarity, or both, were linked to colonization

36 or extinction dynamics in 30 populations. For six species, the effect of temperature

37 depended upon the local mammal community similarity. This result suggests that the way

38 in which temperature influences local colonization and extinction dynamics depends on

39 local mammal community composition.

40

41 **Main conclusions**: These results indicate that varying temperatures influence tropical

42 mammal distributions in surprising ways and suggest that interactions between species

43 mediate distributional dynamics.

44

45 **Keywords**: species distribution, range shift, species interactions, coexistence, dynamic

46 occupancy modeling, imperfect detection, occupancy-environment association

47 **Introduction**

48

49   Across ecosystems and taxa, species distributions shift over time in response to

50 natural conditions and anthropogenic threats. Identifying the underlying drivers of these

51 shifts is critical for predicting the future of biological diversity in a changing world.

52 Because abiotic conditions such as ambient temperature determine the geographic

53 locations where species can persist (Buckley et al., 2012), attempts to predict species

54 distributions often focus on climate associations alone (Pacifici et al., 2015). Other

55 factors such as species interactions and dispersal also influence where species occur

56 (Araujo & Peterson, 2012). Species often inhabit a subset of the range of abiotic

57 conditions they can tolerate because biotic interactions and dispersal limitation can

58 prevent species from "filling" their potential distributions. (Araujo & Pearson, 2005;

59 Schloss et al., 2012; Urban et al., 2013). Moreover, theory predicts that biotic processes

60 such as competition can significantly affect distributional shifts (Brooker et al., 2007;

61 Urban et al., 2012); nonetheless, empirical evidence remains sparse (Svenning et al.,

62   2014). In particular, a fundamental premise of biology is that competition between

63   species increases with their ecological similarity (Darwin, 1859; Swenson, 2013). A

64   species may therefore be less likely to colonize areas already occupied by ecologically

65   similar species and more likely to experience local extinction where ecological similarity

66   is high (Diamond, 1975; Strauss et al., 2006). Here, we incorporate ecological similarity

67   as a proxy for the strength of species interactions in empirical, process-based models to

68   simultaneously test the role of temperature, species interactions and their interdependence

69   in local colonization and extinction dynamics.

70   Identifying the determinants of species distributions involves combining process-

71   based models with high-resolution data over space and time, both of which are often

72   lacking. Instead, most current approaches to understand species distributions rely on

73   correlative models that infer distribution patterns based on occupancy-environment

74   relationships at a single snapshot in time (Pacifici et al., 2015). Such 'snapshot

75   approaches' suffer from multiple shortcomings (Araujo & Peterson, 2012). One key issue

76   is their assumption that observed distributions reflect the entire range of environmental

77   conditions a species can tolerate and therefore that species distributions are in equilibrium

78   (Araujo & Pearson, 2005). However, this spatial equilibrium assumption is rarely met, in

79   part because of temporal changes in the environment. A more robust alternative approach

80   is to monitor and model local colonization and extinction—the processes that generate

81   distributional shifts over time (Kery et al., 2013; Yackulic et al., 2015). The sequential

82   nature of time-series data enhances inference about causality because effects cannot

83   precede causes (Dornelas et al., 2013).

84   A crucial challenge for understanding how global patterns of diversity may

85   change under future conditions is to identify how the environment affects local

86   colonization and extinction dynamics of data deficient species. In particular, the extent to

87   which tropical species currently respond to climate remains largely unknown (Lenoir &

88   Svenning, 2015) but see (Freeman & Freeman, 2014; Duque et al., 2015), in large part

89   because reliable long-term data are lacking, particularly for some of the most threatened

90   species, which include many mammals (Schipper et al., 2008; Feeley & Silman, 2011;

91   Dornelas et al., 2014). Endothermy—the state of being warm blooded—buffers mammals

92   from changes in temperature (Buckley et al., 2012); most tropical mammals currently

93   experience temperatures within their range of thermal tolerance (Khaliq et al., 2014).

94   However, temperature increases are projected to push many tropical mammal species

95   beyond their thermoneutral zones this century (Khaliq et al., 2014). Moreover, examining

96   the role of biotic interactions, particularly competitive interactions, in local colonization

97   and extinction is especially important for tropical species because interactions may be

98   stronger in the tropics than at higher latitudes (MacArthur, 1972; Schemske et al., 2009;

99   Roslin, 2017) but see (Moles et al., 2011; Moles & Ollerton, 2016). Accordingly, tropical

100   mammals may be less likely to colonize areas where competitors—larger-bodied species

101   with similar activity patterns and diets (French & Smith, 2005)— occur than where

102   competitors are absent. Uncovering if and how temperature and species interactions

103   currently influence tropical mammal distributions can provide essential information for

104   modeling future shifts. Lastly, rapid human population growth and the natural resource-

105   based economies of many developing countries subject tropical forests to accelerating

106   rates of deforestation (Margono et al., 2014). Conversion of forested habitat to other land

107   uses is one of the greatest extinction threats for tropical wildlife (Pimm et al., 2014). We

108   therefore investigated whether change in forest cover influenced local colonization-

109   extinction dynamics.

110   Here, we assess abiotic and biotic drivers of local colonization-extinction

111   dynamics of mammals along elevational gradients in seven tropical forests. We test for

112   occupancy-environment associations with temperature and ecological similarity through

113   time. Elevational gradients provide a tractable opportunity to study how abiotic and biotic

114   factors drive distributional dynamics (Malhi et al., 2010; HilleRisLambers et al., 2013).

115   Background climate often varies systematically along elevational gradients, constituting a

116   natural laboratory to address questions about the role of climate in species distributions

117   (Sundqvist et al., 2013). Species occurrences can be more comprehensively documented

118   along elevational than latitudinal gradients because of their smaller spatial area. Finally,

119   the shorter distances encompassed by elevational gradients relative to latitudinal

120   gradients largely control for dispersal limitation (Hargreaves et al., 2013).

121

122   **Methods**

123

124   Field sites and data collection

125   We analyzed over 400,000 camera-trap observations sampled along seven

126   elevational gradients from three continents by the Tropical Ecology Assessment and

127   Monitoring (TEAM) Network (Figure 1). TEAM is a global monitoring network

128   comprised of three core partners (Conservation International, Wildlife Conservation

129   Society, Smithsonian Institution) and numerous academic and local partners. TEAM was

130   established in 2002 to monitor long-term trends in biodiversity, land use and climate in

131   tropical forests throughout the world. TEAM surveys terrestrial (i.e., ground-dwelling)

132   tropical mammal populations on an annual basis, using a standardized protocol with

133   large-scale arrays of permanent camera-trap points (Jansen et al., 2014). This provides

134   fine-grained data replicated over a large spatial extent, which are rarely available in the

135   tropics (Beck et al., 2012). The camera traps also record the temperature each time a

136   photograph is taken, providing local-scale information on temperature in regions of the

137   world for which high-resolution climate data are lacking.

138   We analyzed data from seven TEAM study sites that spanned elevation gradients

139   of more than 500m (Supplemental Table 1). These sites were located in tropical forests

140   on three continents (Figure 1). The study sites were: Bwindi Impenetrable Forest (BIF) in

141   Uganda, Nam Kading (NAK) in Lao PDR, Pasoh Forest Reserve (PSH) in Malaysia,

142   Ranomafana (RNF) in Madagascar, Udzungwa (UDZ) in Tanzania, Volcan Barva (VB)

143   in Costa Rica, and Yanachaga- Chimillen National Park (YAN) in Peru. We use the term

144   "site" throughout the manuscript to refer to these overall TEAM study sites. Individual

145   camera trap sampling points are referred to as sampling points or camera traps. All

146   camera trap data were collected between 2007 and 2016.

147   At each study site, 60 camera traps were deployed at a density of 1 camera per 1

148   or 2 km^2 (Supplementary Table 1). TEAM has defined the sampling units as a grid of 2

149   km^2 cells assuming that animals within the sampling unit have non-zero probabilities of

150   encountering the camera trap given their movement patterns and density (TEAM

151   Network, 2011). Each camera trap was deployed for 30 consecutive days during the dry

152   season, defined as months with < 100 mm average rainfall, or the drier part of the year at

153   sites with no dry season. Camera trap images were identified by TEAM personnel

154   following the standard IUCN Red List (IUCN, 2014) and managed via custom

155   cyberinfrastructure (Fegraus et al., 2011; Baru et al., 2012). TEAM monitors all ground-

156   dwelling and predominately ground-dwelling mammals greater than 100 g in body mass.

157   Of the 163 mammal populations monitored at these sites, the 62 populations with more

158   than 5 detections annually were examined in this study. For a complete list of species

159   monitored, see Beaudrot et al. (2016).

160

161   Occupancy modeling

162   We modeled population-specific local colonization and extinction along

163   elevational gradients using dynamic (multi-season) occupancy models (MacKenzie et al.,

164   2003). This model is an appropriate and robust tool because it accounts for imperfect

165   detection by camera traps (MacKenzie et al., 2006; Royle & Dorazio, 2008) and makes

166   few assumptions about equilibrium or pseudo-equilibrium (Clement et al., 2016). The

167   dynamic occupancy modeling approach has a similar sampling scheme as Pollock's

168   robust design for mark-recapture studies (Pollock, 1982). This design is composed of two

169   sampling periods, primary and secondary, in which a series of detections or non-

170   detections are recorded (Supplemental Figure 1). Among primary periods the population

171   is allowed to be open for colonization or extinction. Our primary periods consisted of

172   years; thus, colonization and extinction occurred on an annual basis. Secondary periods

173   consisted of 24-hour intervals within the annual 30-day camera-trap sampling period,

174   which we further combined into six days of sampling to increase the number of

175   detections per secondary period and aid model convergence. This sampling scheme

176   assumes a population was closed to local colonization and extinction during the 30-day

177   period each year when the camera traps were deployed.

178   In a dynamic occupancy modeling framework, collecting data during primary and

179   secondary periods allows the ecological process, which is occupancy, to be modeled

180   separately from the observation process, which is detection. Indeed, these processes must

181   be modeled separately to estimate detection probability. The ecological process involves

182   three parameters: initial occupancy probability, local colonization probability and local

183   extinction probability. The observation process involves one parameter: detection

184   probability. Detection probability is important because animals may not be detected even

185   though they are present. Occupancy estimates that do not account for imperfect detection

186   may be biased and underestimate occupancy (MacKenzie, 2006).

187   The occupancy and observation processes can be modeled as latent and observed

188   random variables such that:

$$z_{1,i} \sim Bern(\psi_1) \tag{1}$$

$$(z_{t,i}|z_{t-1,i} = 0) \sim Bern(\gamma_{t-1}) \text{ for } t = 2,\ldots,T, \tag{2}$$

189

$$(z_{t,i}|z_{t-1,i} = 1) \sim Bern(1 - \epsilon_{t-1}) \text{ for } t = 2,\ldots,T, \tag{3}$$

$$h_{t,ij}|z_{t,i} \sim Bern(z_{t,i}p_{tj}) \tag{4}$$

190   where, $z_{t,i}$ represents occupancy in time t at site i, $h_{t,ij}$ the detection history and p_{tj} the

191   probability of detection. These equations describe occupancy as a Bernoulli process. In

192   the first primary period the probability of occupancy is given by ψ_t. If the species was not

193   detected in site i in the previous primary period, then the probability of the species being

194   colonized at time t is γ_t. If the species was detected in the previous primary period, then

195   the probability of detecting it again is given by 1- ε_t (i.e., one minus the probability of

196   local extinction). The probability that a site is occupied depends upon whether it was

197   occupied in the previous time step, thus dynamic changes in occupancy are treated as a

198   first-order Markov process. Initial occupancy, colonization, and extinction can also be

199   modeled using covariates through a logit model of the form logit(π_t)=$\beta_0 + \beta_1 x_t$, where π_t is

200   a Bernoulli distributed variable that represents initial occupancy (ψ_t), colonization (γ_t) or

201   extinction probabilities (ε_t), and x_t represent covariates.

202   Covariates were selected to test the effects of abiotic and biotic factors on local

203   colonization and extinction. Covariate measurements are described in more detail below.

204   We used two types of covariates: sampling point covariates (Elevation, Forest Loss,

205   Forest Gain, Biotic) and covariates that were both sampling point and time-dependent

206   (Tmin, Tmax, Tvar). Sampling point covariates differed between sampling points (i.e.,

207   camera traps) but did not change over time. Thus, each camera trap had a single (i.e.,

208   constant) value of elevation, forest loss and forest gain for the study. For each population,

209   each camera trap had a single (i.e., constant) biotic value for the study. Sampling point-

210   and time-dependent covariates changed annually between sampling points and between

211   years. Thus, each camera trap had a different annual value for Tmin, Tmax and Tvar.

212 These values were the minimum, maximum and variance of the temperatures recorded at

213 a camera trap during the 30 days of sampling in a year (see details below).

214   We parameterized the models using maximum likelihood and used AIC_c model

215 selection (Burnham & Anderson, 2002) to test hypothesized relationships between local

216 colonization-extinction dynamics based on the most parsimonious combination of forest

217 cover change, temperature and/or biotic interaction covariates. All models included in the

218 model set are listed in Supplementary Table 2. We used an intercept-only model (no

219 covariates) as a null dynamic occupancy model. For initial occupancy, we conducted

220 model selection with and without elevation as a covariate because whether a site was

221 occupied at the beginning of the study may vary with elevation for some species but not

222 others. That is, some species may be more likely to occur at certain elevations whereas

223 other species may be equally likely occur at all elevations. For detection, models

224 contained forest cover change, temperature and/or biotic interaction as covariates. We

225 included covariates of colonization and extinction as covariates for detection because

226 variation in abundance can be a chief determinant of detection probability (Royle &

227 Nichols, 2003). We modeled both linear and quadratic terms for elevation and

228 temperature covariates because a range of ideal conditions for a species could result in

229 non-monotonic relationships (e.g. initial occupancy or colonization is highest at

230 intermediate temperatures).

231   Colonization and extinction were modeled as single parameters rather than year-

232 specific parameters. We explored year effects on colonization and extinction in an

233 attempt to explore non-stationarity (i.e. that occupancy is not approaching equilibrium).

234 However, models with year effects, except for a small number of populations, did not

235 converge.

236   We used condition numbers as a way to ensure adequate model fit. Condition

237 numbers provide data on how much information is lost when a problem is solved

238 numerically rather than analytically. Models with a condition number $> 10^4$ are indicative

239 of parameters that are unidentifiable or models with optimization problems (Cheney &

240 Kincaid, 2008) (p. 640). Therefore, we chose the combination of a condition number <

241 5000 and small standard errors as a conservative way of selecting models with which to

242 make inferences in this study. This ensured that the model selected through AICc model

243 selection had an appropriate fit to the data. Populations were included in our results if the

244 null model and at least one non-null model had a condition number less than 5000. Odds

245 ratios were used to interpret the strength of local colonization and extinction covariates in

246 the best model of each population. All modeling was conducted in R using the library

247 "unmarked" (Fiske & Chandler, 2011; R Development Core Team, 2016).

248

249 Forest cover change

250   Hansen et al. (2013) used Landsat images to produce a global dataset

251 characterizing forest extent and change (i.e., loss or gain) at a 30 m resolution. We used

252 the Global Forest Change product from Hansen et al. (2013) and applied a 75% threshold

253 to the 2000 forest cover layer to produce a forest/non-forest map for the year 2000. We

254 took into account the forest loss layers in the product to calculate forest-non-forest maps

255 for each camera trap location for the five years prior to the onset of camera trap

256 monitoring. We calculated the percent of forest lost in a 30m, 60m and 120m buffer

257 surrounding each camera trap location to quantify forest cover change because we were

258 interested in the role of local change (Supplemental Figure 2). Because camera traps were

259 deployed at a density of 1 camera per 1 or 2 km^2, buffers of larger sizes that overlapped

260 between camera traps would not provide meaningful information. To capture the greatest

261 variation in forest cover, we used the 120m buffer for camera trap specific forest cover

262 loss as a covariate of local colonization, extinction and detection in the dynamic

263 occupancy models. We also calculated percent forest gain over the 2000-2012 period for

264 the buffers around each camera. We used the 120m buffer of forest gain as a covariate of

265 local colonization, extinction and detection (Supplemental Table 2).

266

267 Temperature and elevation

268   We considered three aspects of temperature on local colonization and extinction

269 that have been shown to influence distributions of other taxa: temperature minimum

270 (T_{min}) (Warren & Chick, 2013), temperature maximum (T_{max}) (Welbergen et al., 2008),

271 and temperature variance (T_{var}) (Thompson et al., 2013). Temperature measurements

272 were taken from the camera traps during times of active sampling, providing highly local,

273 site-specific temperature data with a precision of one degree Celsius every time a camera

274   was triggered. The temperature data measured conditions at each camera trap during

275   times of animal activity and are thus biased against conditions that animals avoided.

276   Because both the precision of the data and potential bias towards animal activity reduce

277   the likelihood of detecting responses to temperature, this approach produced conservative

278   results.

279   We inspected the temperature data and removed outliers that indicated faulty

280   temperature sensors (i.e., $> 40\ °C$; $N = 3$ cameras). Faulty temperature sensors within the

281   normal temperature range would have been undetected. We then calculated the

282   temperature minimum, maximum, and variance for each year at each camera trap

283   sampling point using camera trap specific temperature records. We used these sampling

284   point- and time-dependent measurements as covariates of local colonization, local

285   extinction and detection.

286   We also calculated temperature trends to assess patterns in temperature change

287   over time at the 7 TEAM sites. Specifically, we calculated the trend in temperature for

288   each camera trap at each TEAM site. We ran a linear regression for the annual

289   temperature values at each camera trap as a function of time. We then extracted the slope

290   of the linear regression and used this as the temperature trend for a camera trap. To

291   examine whether temperature trends showed consistent warming at a TEAM site, we

292   plotted the distribution of camera trap specific trends per TEAM site (Figure 2).

293   Elevation data were extracted from the void filled Shuttle Radar Topography

294   Mission (SRTM) digital elevation model (90 m resolution with vertical accuracy of 4-7 m

295   (Gorokhovich & Voustianiouk, 2006)) from the Consortium for Spatial Information

296   (CGIAR-CSI) (Jarvis et al., 2008) for the geographic coordinates of each camera trap.

297

298   <u>Ecological similarity of local mammal community composition</u>

299   We tested for potential species interactions by including an index of ecological

300   similarity as a predictor of local colonization and extinction dynamics. In the absence of

301   direct information on competitive interactions, measures of ecological similarity —

302   namely, ecological traits such as diet, body size and activity pattern, and the degree of

303   evolutionary relatedness in local communities (Cavender-Bares et al., 2009; Uriarte et

304 al., 2010; Cadotte et al., 2013) — can serve as a proxy of the amount of biotic resistance

305 encountered as distributional dynamics occur.

306 For each camera-trap point at each TEAM site and for each species, we computed

307 an ecological similarity index between the focal species being modeled and all other

308 mammal species observed at the camera-trap point. This index combined phylogenetic

309 and functional trait distances in a single, continuous index (Cadotte et al., 2013). We

310 chose to combine phylogenetic and functional trait information because phylogenies and

311 traits can provide different and sometimes complementary information. By combining the

312 two sources of information together, we sought to overcome the weaknesses of each

313 individual approach (Cadotte et al., 2013).

314 We used a phylogenetic tree of mammals (Fritz et al., 2009) to estimate

315 phylogenetic distances between all pairs of species observed at each TEAM site. Because

316 this phylogenetic tree was not fully resolved, we used a set of 100 trees wherein

317 polytomies were randomly resolved (Kuhn et al., 2011). Then branch lengths were

318 averaged over these 100 trees to create a pairwise matrix of phylogenetic distances.

319 To estimate functional-trait distances, we used trait data on body size and dietary

320 guild from Beaudrot et al. (2016), data on activity pattern from PanTHERIA (Jones et al.,

321 2009) and the R package "FD" (Laliberte & Shipley, 2011). Body-mass data were

322 continuous (in grams) whereas dietary-guild data (herbivore, omnivore, insectivore or

323 carnivore) and activity pattern data (diurnal only, nocturnal only, other) were categorical.

324 We calculated a Gower-distance matrix because the Gower-distance can integrate

325 continuous and categorical data into a single-distance metric (Gower, 1971). The body

326 mass, dietary-guild and activity pattern data were weighted equally in the Gower-distance

327 matrix.

328 We combined the phylogenetic (PDist) and functional-trait-distance (FDist)

329 matrices into a single-distance matrix (FPDist) weighing the two input matrices equally

330 (Cadotte et al., 2013) such that:

331

$$FPDist = (aPDist^p + (1-a)FDist^p)^{1/p}, \qquad (4)$$

332

333   where a and p are weighting factors (Cadotte et al., 2013). We used a = 0.5 to weight the

334   phylogenetic and functional trait distances evenly in the FPDist calculation. We used p =

335   2 to calculate a Euclidean distance from the combined functional and phylogenetic

336   distances.

337   One shortcoming of functional and phylogenetic distances is that they are

338   sensitive to variation in species richness (i.e. in the local community size). We therefore

339   standardized FPDist for our ecological dissimilarity index (EDI) to eliminate the

340   sensitivity to variation in species richness (see (Uriarte et al., 2010) for a similar

341   approach). To standardize the EDI, we created null models wherein artificial

342   communities were simulated and their EDI recalculated each time. For each species and

343   community combination, we generated 1000 simulated EDI values. The standardized EDI

344   was calculated using the following formula:

345

346            $- (EDI_{obs} - \text{mean } EDI_{null} / \text{SD } EDI_{null.}).$ (5)

347

348   We used the mean distance between the focal species and the other species observed at a

349   camera trap as a covariate of local colonization, local extinction and detection. Positive

350   values for the standardized index indicate ecological dissimilarity, whereas negative

351   values indicate ecological similarity.

352   Dendrograms illustrate the ecological similarity measured within mammal

353   communities at each TEAM site (Supplemental Figure 2). We used the unweighted pair

354   group method with arithmetic mean (UPGMA) clustering method, which calculates the

355   mean distance between clusters as the distance between each cluster point and all other

356   points in a different cluster. A new cluster forms from the two clusters with the lowest

357   mean distance (Fielding, 2007). Species that are more ecologically similar at a TEAM

358   site are closer together in the site-level dendrograms.

359

360   **Results**

361

362   Forty-two populations representing 36 species had sufficient data for successful

363   model convergence (Supplementary Table 3). Of these 42 populations, the null model

364 (without covariates) was the best model for 12 populations. Thirty populations had best

365 models with biotic and/or temperature covariates for local colonization and/or extinction

366 (Table 1). All seven tropical forest study sites had mammal populations with best models

367 containing biotic and temperature covariates for local colonization and/or extinction

368 (Supplementary Table 1).

369

370 Forest cover change

371 There was little change in forest cover during the period examined, presumably

372 because the camera traps were located within protected areas. Only 3 of the 7 study sites

373 (i.e., BIF, PSH, UDZ) had measurable change in forest loss or gain within a 30m buffer

374 of the camera traps (Supplementary Figure 1). None of the best models for any

375 population contained forest cover change (Table 1).

376

377 Temperature

378 Temperature trends at individual camera trap locations varied substantially

379 despite a lack of overall study site-level warming during the study period (Figure 2).

380 Local colonization and extinction dynamics of the majority of populations in this study

381 responded to changes in local (i.e., camera trap specific) temperature (Table 1), but the

382 direction and magnitude of this change varied among populations (Figure 3, Figure 4).

383 In many instances, odds ratios of local colonization and extinction estimates ($\pm$

384 SE) indicated that animals were less likely to occupy areas as they warmed. For example,

385 the colonization probability of the black agouti (Dasyprocta fuliginosa, Yanachaga, Peru)

386 decreased on average 3.41 ± 0.30 times for a unit increase in scaled minimum

387 temperature. (All interpretations correspond to scaled covariates because covariates were

388 scaled and centered to aide in model convergence.) We found similar patterns in the

389 Central American agouti (Dasyprocta punctata, Volcan Barva, Costa Rica), and

390 Svynnerton's bush squirrel (Paraxerus vexillarius, Udzungwa, Tanzania), which

391 decreased 3.51 ± 0.31 and 9.58 ± 0.12 times respectively for a unit increase in scaled

392 minimum temperature (Figure 3).

393 Other species were more likely to go locally extinct with increasing temperatures.

394 For example, the Malagasy civet (Fossa fossana, Ranamofana, Madagascar) and ring-

395   tailed coati (Nasua nasua, Yanachaga, Peru) were 1.8 ± 2.10 times and 3.72 times,

396   respectively, more likely to go locally extinct with a unit increase in scaled minimum

397   temperature. Furthermore, the African giant pouched rat (Cricetomys gambianus,

398   Udzungwa, Tanzania) was 2.32 ± 0.97 times more likely to go locally extinct with a unit

399   increase in scaled maximum temperature. These results suggest that a number of tropical

400   mammal populations moved away from warmer microhabitat conditions.

401   In other cases, areas that got hotter were more likely to be occupied. For instance,

402   the colonization probability of the lesser mouse-deer (Tragulus kanchil, Nam Kading,

403   Lao PDR) increased 17.20 ± 0.41 times with a unit increased in scaled maximum

404   temperature. We found a similar pattern for the red brocket (Mazama americana,

405   Yanachaga, Peru), bushpig (Potamochoerus larvatus, Udzungwa, Tanzania), chimpanzee

406   (Pan troglodytes, Bwindi, Uganda) and L'hoesti's monkey (Cercopithecus lhoesti,

407   Bwindi, Uganda), which were 2.38 ± 1.26, 2.21 ± 1.31, 1.43 ± 0.57 and 1.30 ± 0.60

408   times, respectively, more likely to colonize a site with a unit increased in scaled

409   maximum temperature. Local extinction decreased 1.59 ± 0.42 times for the Asiatic

410   brush-tailed porcupine (Atherurus macrourus, Nam Kading, Lao PDR), 1.65 ± 0.47 times

411   for the lowland paca (Cuniculus paca, Volcan Barva, Costa Rica) and 3.70 ± 0.33 times

412   for black-fronted duiker (Cephalophus nigrifrons, Bwindi, Uganda) with a unit increase

413   in scaled minimum temperature. The probability of extinction also decreased 2.11 ± 0.45

414   times for the bushy-tailed mongoose (Bdeogale crassicauda, Udzungwa, Tanzania) and

415   29.10 ± 0.58 times for the chimpanzee (Pan troglodytes, Bwindi, Uganda) with a unit

416   increase in scaled maximum temperature (Figure 4).

417   As scaled local temperature variance increased by one unit, local colonization

418   increased 16.67 ± 26.45 times for African golden cat (Caracal aurata, Bwindi, Uganda)

419   and 2.80 ± 4.25 times for the common treeshrew (Tupaia glis, Pasoh, Malaysia). In

420   contrast, local colonization declined 2.66 ± 0.40 times for tayra (Eira Barbara,

421   Yanachaga, Peru) and 210.66 ± 0.17 times for the collared peccary (Pecari tajacu,

422   Volcan Barva, Costa Rica) (Figure 3). For lesser mouse deer (Tragulus kanchil, Pasoh,

423   Malaysia), local extinction decreased 8.41 ± 0.20 times as scaled temperature variance

424 increased one unit (Figure 4). These findings reinforce the importance of accounting for

425 temperature variability when modeling species distributions (Vasseur et al., 2014).

426

427 Ecological similarity

428   Competition with ecologically similar species influenced local colonization and

429 extinction dynamics for some species. Specifically, lowland paca (Cuniculus paca,

430 Yanachaga, Peru), were 1.77 ± 0.86 times less likely to colonize areas occupied by

431 ecologically similar species – their potential competitors (Figure 3). Black-fronted duiker

432 (Cephalophus nigrifrons, Bwindi, Uganda) and Malagasy civet (Fossa fossana,

433 Ranamofana, Madagascar) were 3.49 ± 0.24 and 4.57 ± 0.11 times, respectively, more

434 likely to experience local extinction in areas occupied by ecologically similar species

435 (Figure 4).

436   Other species were more likely to colonize areas already occupied by ecologically

437 similar species. For instance, chimpanzees (Pan troglodytes, Bwindi, Uganda), Asiatic

438 brush-tailed porcupine (Atherurus macrourus, Pasoh, Malaysia), L'Hoesti's monkey

439 (Cercopithecus lhoesti, Bwindi, Uganda), and lesser mouse-deer (Tragulus kanchil, Nam

440 Kading, Lao PDR) were 3.06 ± 0.001, 5.61, 6.85 ± 0.60 and $>10^8 \pm 0.26$ times,

441 respectively, more likely to colonize areas with ecologically similar species (Figure 3).

442 Furthermore, chimpanzee (Pan troglodytes, Bwindi, Uganda), bushpig (Potamochoerus

443 larvatus, Bwindi, Uganda), and lowland paca (Cuniculus paca, Volcan Barva, Costa

444 Rica) were 550.54 ± 0.0007, 16.62 ± 7.97 and 2.06 ± 0.78 times, respectively, less likely

445 to go locally extinct in areas occupied by ecologically similar species (Figure 4).

446

447 Synergistic effects of temperature and ecological similarity

448   For six species, local colonization-extinction dynamics were contingent on both

449 temperature and ecological similarity (i.e., the best model contained an interaction term,

450 see Supplementary Table 3). For these species, the way in which temperature influenced

451 local colonization and extinction dynamics depended on how ecologically similar the

452 local mammal community was to the focal species. Specifically, red brocket (Mazama

453 temama, Volcan Barva, Costa Rica) and servaline genet (Genetta servalina, Udzungwa,

454 Tanzania) moved into areas with ecologically similar species as maximum temperatures

455   got hotter but colonized areas with ecologically dissimilar species where maximum

456   temperatures cooled over time. As minimum temperatures warmed, Abbott's duiker

457   (Cephalophus spadix, Udzungwa, Tanzania) and yellow-backed duiker (Cephalophus

458   silvicultor, Bwindi, Uganda) were more likely to go locally extinct in areas with

459   ecologically similar species. Lastly, as temperature variance increased, Sanje monkey

460   (Cercocebus sanjei, Udzungwa, Tanzania) and nine-banded armadillo (Dasypus

461   novemcinctus, Volcan Barva, Costa Rica) were more likely to both colonize and go

462   extinct in areas with ecologically similar species as temperature variance increased. Nine-

463   banded armadillos were more likely to colonize and go extinct in areas with ecologically

464   dissimilar species when local temperatures were more stable (i.e., when temperature

465   variance decreased) (Figure 5).

466

467   **Discussion**

468

469   We tested for the influence of local temperature, ecological similarity and forest

470   cover change as drivers of local colonization and extinction dynamics – the processes

471   underlying distributional shifts – in tropical mammals. We found that local temperature

472   change was associated with important effects on these dynamics for many, but not all,

473   species, and responses to local temperature were highly variable. Moreover, ecological

474   similarity also affected local colonization and extinction dynamics, suggesting that inter-

475   specific biotic interactions can act as a barrier (sensu "biotic resistance" (Levine et al.,

476   2004)) for some tropical mammal species. Nevertheless, we did not find consistent

477   support for the prediction that species would have lower colonization and higher

478   extinction in areas with ecologically similar mammals. Instead, a number of populations

479   had the opposite response: higher colonization and lower extinction probabilities in areas

480   with ecologically similar species. None of the populations responded change in forest

481   cover, likely because of the small amount of change observed.

482   Positive species interactions can facilitate colonization and reduce local extinction

483   (Bruno et al., 2003), yet have rarely been considered when examining the drivers of

484   distributional change (Crotty & Bertness, 2015). In particular, species interactions that

485   improve habitat conditions (i.e., habitat amelioration) or reduce predation (i.e.,

486   associational defenses) can promote persistence and expand the area where a species

487   occurs (Bertness & Callaway, 1994). Contrary to our expectation for competition

488   between ecologically similar species, positive interactions with ecologically similar

489   species could have affected distributional dynamics for some species in this study. For

490   example, local extinction probability was lower for both chimpanzees and bushpigs at

491   camera traps with ecologically similar species. Chimpanzees are dominant to other

492   primate species due to their large body size, and have access to the highest nutritional

493   quality fruit when feeding in proximity (Houle et al., 2010). Chimpanzees may cue in on

494   other primate species feeding as a signal of food availability thereby benefiting from

495   ecologically similar species. As another example, bushpigs are ecologically similar to

496   several primate species at Bwindi in Uganda (Supplementary Figure 3). They have been

497   observed to forage for fallen fruits under fruiting trees as primates feed and drop fruits to

498   the ground (Ghiglieri et al., 1982). Bushpigs can therefore benefit from some frugivorous

499   primates via increased access to food.

500   Importantly, the influence of temperature on local colonization and extinction

501   depended on mammal community similarity for several species demonstrating that these

502   factors can have synergistic effects. The relative influence of these factors can therefore

503   change depending on the environmental and community context (Lessard et al., 2012;

504   Lessard et al., 2016). Furthermore, of the 6 species for which we modeled populations at

505   multiple TEAM study sites, none exhibited consistent relationships with temperature

506   across study sites (Supplementary Table 3). Similar inconsistencies in species responses

507   to temperature have also been found for temperate mammals (Rowe et al., 2015). This

508   highlights the context dependency of species responses to changing temperature,

509   potentially due to differences in local community composition. Local mammal

510   communities differed not only between camera traps but also between TEAM study sites.

511   We suggest that differences in local community composition may play an important and

512   often unaccounted for role in influencing distributional dynamics.

513   That changing temperature and ecological similarity simultaneously and

514   synergistically affected local colonization and extinction dynamics has fundamental

515   implications for climate-change research. Most models still rely on the environmental

516   affinities of species alone to forecast species distributions while ignoring the potential

517 role of biotic interactions (Urban et al., 2016), despite considerable implications (Araujo

518 & Luoto, 2007; Blois et al., 2013; Wisz et al., 2013; Pacifici et al., 2015). Very few

519 studies show a direct link between climate change and site-level extinctions, yet changes

520 in species interactions have been a commonly identified proximate driver of site-level

521 extinctions (Cahill et al., 2013). Novel competitors can reduce fitness (Alexander et al.,

522 2015) and variation in competitive ability has been shown through simulations to drive

523 site-level extinctions (Urban et al., 2012). While an increasing number of studies

524 incorporate biotic interactions to species distributions models, few studies have provided

525 empirical support for the role of species interactions affecting shifts. The fact that the

526 ecological similarity of the local mammal community influenced the local colonization

527 and extinction dynamics of numerous populations in this study suggests that species

528 interactions likely influence tropical mammal distributions. Our empirical results are

529 consistent with theoretical predictions and simulation studies indicating that interactions

530 between species can affect the colonization of new areas (Brooker et al., 2007; Urban et

531 al., 2012) and therefore indicate that the inclusion of species interactions in species

532 distribution modeling is vital, yet the context dependency of our results highlights the

533 complexities of such requirements.

534 We documented the drivers of local colonization and extinction dynamics in

535 species of conservation concern, but multiple factors limited our assessment. First, even

536 with intensive sampling most species were rare and insufficient detection of rare species

537 inhibits estimation of occupancy dynamics for many of the species monitored by TEAM

538 (Beaudrot et al., 2016). Second, the time span of this study (5 - 9 years) is short in

539 comparison with some mammalian life spans. Furthermore, the distributions of some

540 tropical mammals may shift in response to fluctuations in food availability (Marshall et

541 al., 2014). Changes in temperature and precipitation may trigger phenological changes

542 (Wright, 1996) that modify resource availability and habitat quality, which may

543 ultimately drive local colonization-extinction dynamics. Other unmeasured factors, such

544 as natural disturbance (Sheil, 2016), rainfall, humidity and cloud cover could have also

545 affected local colonization-extinction dynamics. In addition, shared habitat preferences

546 between ecologically similar species may have driven local colonization-extinction

547 dynamics rather than species interactions. Lastly, we did not find an effect of forest cover

548 change, likely because camera traps were located within protected areas, but other forms

549 of anthropogenic disturbance at TEAM sites, such as edge effects and hunting, may have

550 affected mammal populations (Mugerwa et al., 2013; Hegerl et al., 2017).

551 We found that the local colonization and extinction dynamics of tropical forest

552 mammals are strongly associated with changes in local temperature and our results

553 further suggest that local mammal-community composition can affect these dynamics.

554 This paper highlights the importance of long-term, standardized studies of mammal

555 communities for understanding the role of species interactions and the environment in

556 distributional dynamics. We conclude that considering the influence of species

557 interactions is essential in climate change projections as they are increasingly

558 incorporated into tropical land management, vulnerability assessments and conservation

559 planning.

560

561 **Data availability statement:** All TEAM data are open source data. They are available at

562 http://www.teamnetwork.org/data/query and will be available through

563 wildlifeinsights.org in the future.

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565

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823

824

825 **Table 1**. **Summary of best models**. The number of populations with best-fit models with

826 and without covariates are shown. Supplemental Table 2 contains the model set and

827 Supplemental Table 3 contains the best-fit models for each population.

Best model	Number of populations
Null	12
Covariate	30
Biotic	*3*
Temperature	*13*
Temperature & Biotic	*14*
Forest Cover Change	*0*

828

829

830 **Figure Legends**

831

832 **Figure 1. Location of 7 TEAM study sites** with elevation ranges > 500 m sampled by

833 camera traps. Each study site had 60 camera traps at a density of 1 camera per 1-2 km^2.

834 The map includes the elevation range in meters, the number of species analyzed, the

835 number of years of data and the distribution of camera trap temperature measurements in

836 degrees C for each TEAM study site. Vertical lines within temperature distributions

837 depict the minimum, median, and maximum temperature for each TEAM site. See

838 Supplementary Table 1 for additional site information.

839

840 **Figure 2. Distribution of temperature trends at individual camera traps**. Each

841 camera trap recorded the temperature when it took a photograph, providing highly local,

842 camera trap-specific temperature data. We show the distribution of slopes of temperature

843   trends over time for each of the 60 camera traps at each of the 7 TEAM sites for

844   temperature a) maximum b) minimum and c) variance. Temperature did not change

845   during the study period at TEAM sites overall. However, temperature changed over time

846   at many individual camera traps. Darker shading depicts higher densities of camera traps

847   with a given temperature trend. Black tick lines indicate the minimum, median and

848   maximum trend for each variable and site. Median values at zero indicate the lack of an

849   overall temperature trend at the TEAM site level. The extent of variation in positive and

850   negative trends, shown by the variances in the distributions, denotes temperature

851   increases and decreases during the study period at the local camera trap scale. An

852   individual temperature trend was calculated as the slope of a linear regression of

853   temperature values over time at a camera trap. Standardized beta coefficients from the

854   linear regressions are shown. Three letter TEAM site codes correspond to Figure 1.

855

856   **Figure 3. Influence of temperature and ecological similarity on local colonization**

857   **probabilities.** Predicted values (black line) and 95% confidence intervals for temperature

858   minimum (Tmin, orange shading), temperature variance (Tvar, yellow shading),

859   temperature maximum (Tmax, red shading), and ecological similarity (Biotic, blue

860   shading) for species with top models containing covariates as predictors of local

861   colonization and $\Delta AIC_c > 2$ from the null model. Variables have been scaled and

862   centered, thus positive and negative values represent increases and decreases from the

863   mean. Positive values for the biotic index indicate ecological dissimilarity of the local

864   mammal community to the focal species, whereas negative values indicate ecological

865   similarity. Confidence intervals are too small to be seen for Tragulus kanchil (NAK).

866   Three letter site codes correspond to Figure 1.

867

868   **Figure 4. Influence of temperature and ecological similarity on local extinction**

869   **probabilities.** Predicted values (black line) and 95% confidence intervals for temperature

870   minimum (Tmin, orange shading), temperature variance (Tvar, yellow shading),

871   temperature maximum (Tmax, red shading), and ecological similarity (Biotic, blue

872   shading) for species with top models containing covariates as predictors of local

873   extinction and $\Delta AIC_c > 2$ from the null model. Variables have been scaled and centered,

874 thus positive and negative values represent increases and decreases from the mean.

875 Positive values for the biotic index indicate ecological dissimilarity of the local mammal

876 community to the focal species, whereas negative values indicate ecological similarity.

877 Confidence intervals are too small to be seen for Nasua nasua (YAN). Three letter site

878 codes correspond to Figure 1.

879
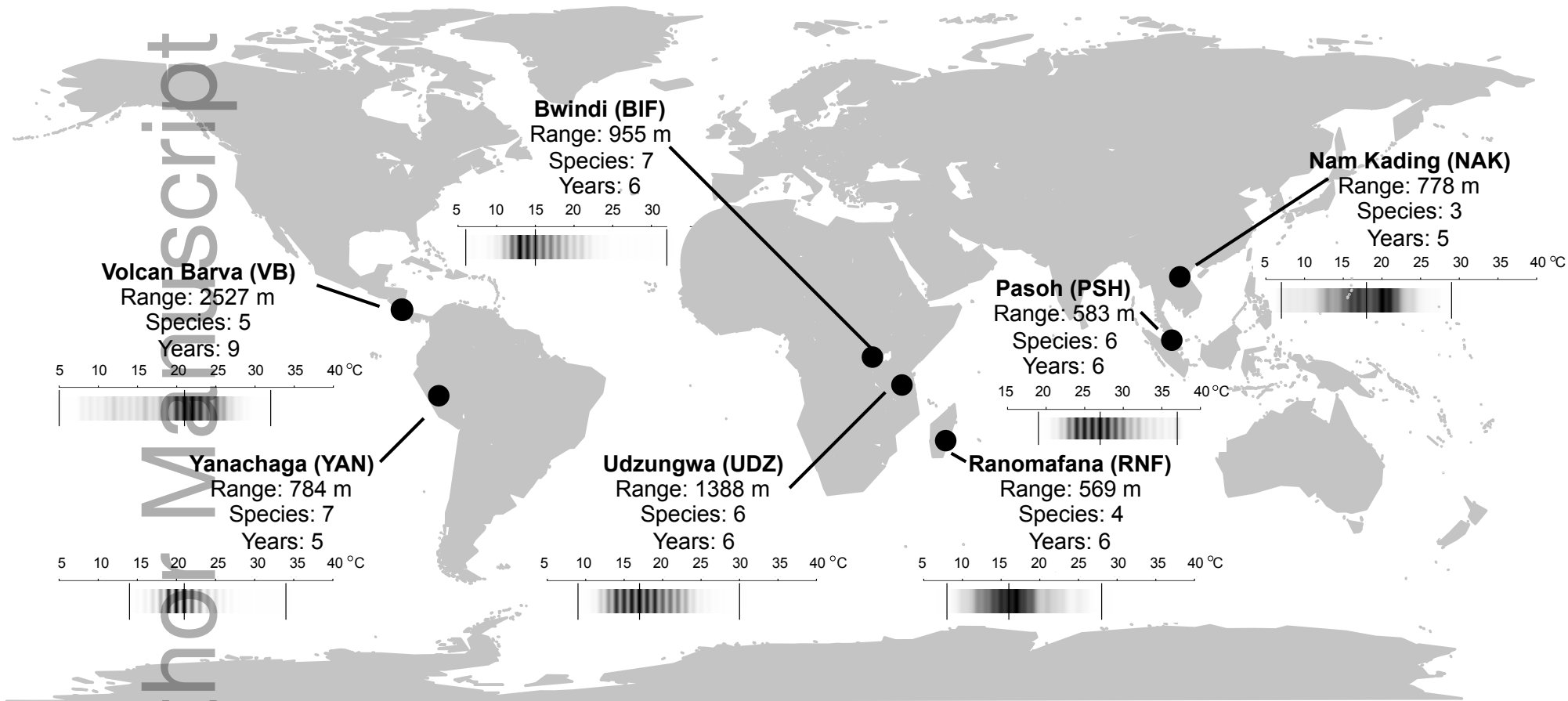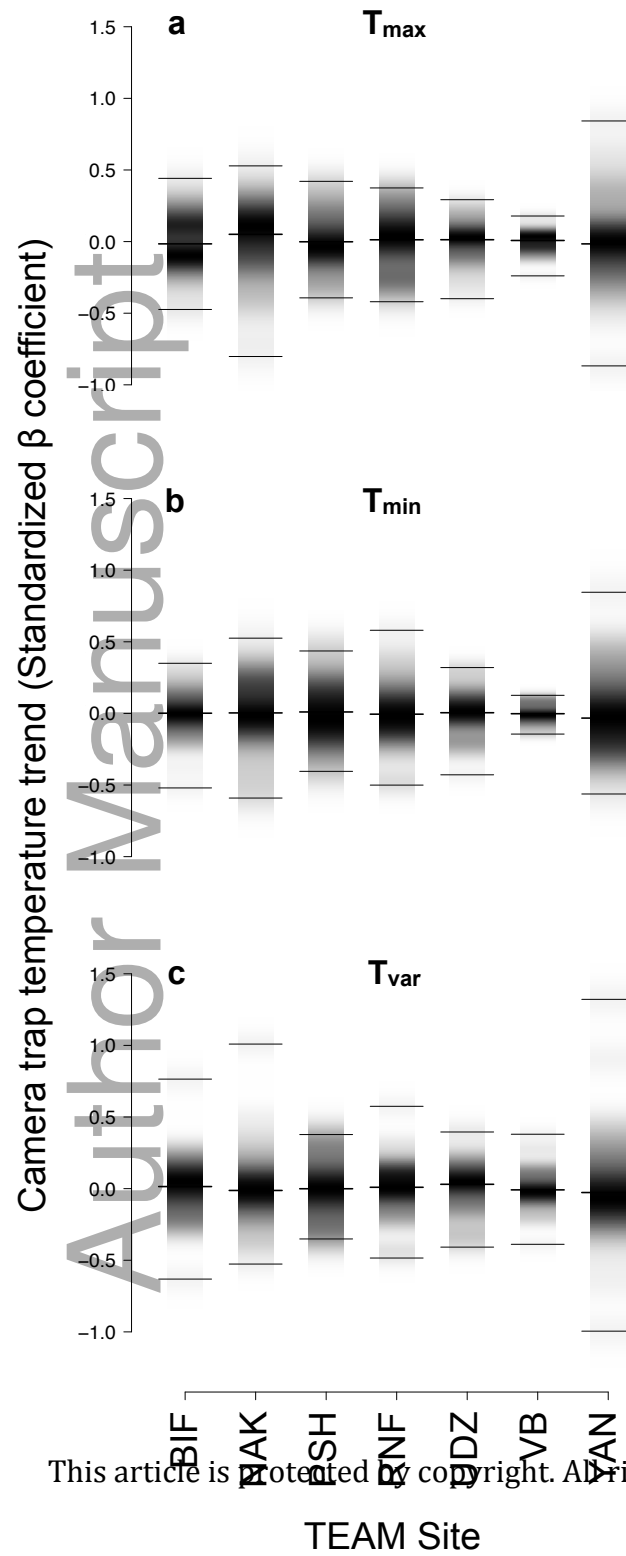
880 **Figure 5**. **Synergistic influences of temperature and ecological similarity on local**

881 **colonization and extinction dynamics.** Local colonization-extinction dynamics were

882 contingent on both temperature and ecological similarity for several species. This figure

883 depicts the interaction terms by showing the effect of ecological similarity on

884 colonization and extinction as temperature changed. For example, Mazama temama was

885 more likely to colonize areas with ecologically similar species as maximum temperature

886 increased, but more likely to colonize areas with ecologically dissimilar species as

887 maximum temperatures decreased. Temperature maximum (T_{max}), minimum (T_{min}) and

888 variance (T_{var}) have been scaled and centered, thus positive and negative values represent

889 increases and decreases from the mean. The green and purple shading show 95%

890 confidence intervals for the estimates of local colonization in ecologically similar and

891 dissimilar mammal communities, respectively, for two standardized values (-1, 1) of the

892 continuous ecological similarity index.

Bwindi (BIF)
Range: 955 m
Species: 7
Years: 6

Nam Kading (NAK)
Range: 778 m
Species: 3
Years: 5

Volcan Barva (VB)
Range: 2527 m
Species: 5
Years: 9

Pasoh (PSH)
Range: 583 m
Species: 6
Years: 6

Yanachaga (YAN)
Range: 784 m
Species: 7
Years: 5

Udzungwa (UDZ)
Range: 1388 m
Species: 6
Years: 6

Ranomafana (RNF)
Range: 569 m
Species: 4
Years: 6

Lesser mouse deer
Tragulus kanchil (NAK)

Lowland paca
Cuniculus paca (YAN)

Black agouti
Dasyprocta fuliginosa (YAN)

African golden cat
Caracal aurata (BIF)

Red brocket
Mazama americana (YAN)

Chimpanzee
Pan troglodytes (BIF)

Central American agouti
Dasyprocta punctata (VB)

Common treeshrew
Tupaia glis (PSH)

Bushpig
Potamochoerus larvatus (UDZ)

Brush-tailed porcupine
Atherurus macrourus (PSH)

Svynnerton's bush squirrel
Paraxerus vexillarius (UDZ)

Tayra
Eira barbara (YAN)

Chimpanzee
Pan troglodytes (BIF)

L'hoesti's monkey
Cercopithecus lhoesti (BIF)

Lowland paca
Cuniculus paca (YAN)

Collared peccary
Pecari tajacu (VB)

L'hoesti's monkey
Cercopithecus lhoesti (BIF)

Lesser mouse deer
Tragulus kanchil (NAK)

Probability of colonization $\hat{\gamma}$

Tmin   Tvar   Tmax   Biotic

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Malagasy civet
Fossa fossana (RNF)

Lesser mouse deer
Tragulus kanchil (PSH)

Chimpanzee
Pan troglodytes (BIF)

South American coati
Nasua nasua (YAN)

African giant pouched rat
Cricetomys gambianus (UDZ)

Bushpig
Potamochoerus larvatus (BIF)

Brush-tailed porcupine
Atherurus macrourus (NAK)

Bushy-tailed mongoose
Bdeogale crassicauda (UDZ)

Lowland paca
Cuniculus paca (VB)

Lowland paca
Cuniculus paca (VB)

Chimpanzee
Pan troglodytes (BIF)

Black-fronted duiker
Cephalophus nigrifrons (BIF)

Black-fronted duiker
Cephalophus nigrifrons (BIF)

South American coati
Nasua nasua (YAN)

Malagasy civet
Fossa fossana (RNF)

Probability of extinction $\hat{\varepsilon}$

Tmin Tvar Biotic

Tmin Tmax Biotic

Tmin Tmax Biotic

Tmin Tmax Biotic

Tmin Biotic Biotic

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Central American red brocket
Mazama temama (VB)

Yellow-backed duiker
Cephalophus silvicultor (BIF)

Local mammal community
- - - Similar
—— Dissimilar

Servaline genet
Genetta servalina (UDZ)

Abbott's duiker
Cephalophus spadix (UDZ)

Nine-banded armadillo
Dasypus novemcinctus (VB)

Nine-banded armadillo
Dasypus novemcinctus (VB)

Probability of colonization $\hat{\gamma}$

Probability of extinction $\hat{\varepsilon}$

Tmax

Tmin

Tvar

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