1   RH: microclimate refugia in Amazonia

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3   Climate trends and behavior of an avian forest specialist in central Amazonia indicate

4   thermal stress during the dry season

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16   *Abstract.* Rainforest loss threatens terrestrial insectivorous birds throughout the world's tropics.

17   Recent evidence shows these birds to be declining in undisturbed Amazonian rainforest, possibly

18   due to climate change. Here, we first addressed whether Amazonian terrestrial insectivores were

19   exposed to climate change using 38 years of climate data. We found that climate has changed in

20   central Amazonia, especially in the dry season, which was ~1.3°C hotter and 21% drier in 2019

21   than in 1981. Second, to test whether birds actively avoided hot and dry conditions, we used field

22   sensors to identify ambient extremes and prospective microclimate refugia within undisturbed

23   rainforest from 2017 – 2019. Simultaneously, we examined how tagged Black-faced Anthrushes

24   (*Formicarius analis*) used this space. We collected 1.4 million field measurements quantifying

25   ambient conditions in the forest understory, including along elevation gradients. For 11 birds, we

26   obtained GPS locations to test whether birds adjusted their shelter use ($n = 2,724$) or elevation (n

27    $= 640$) across seasonal and daily cycles. For four additional birds, we collected >180,000 light

28   and temperature readings to assess exposure. Field measurements in the modern landscape

29   revealed that temperature was higher in the dry season and highest on plateaus. Thus, low-lying

30   areas were relatively buffered, providing microclimate refugia during hot afternoons in the dry

31   season. At those times, birds entered shelters and shifted downslope, reducing their thermal

32   exposure by 50%. Because climate change intensifies the hot, dry conditions that antthrushes

33   avoid, our results are consistent with the hypothesis that climate change lowers habitat quality

34   for terrestrial insectivores. This sensitivity may be related to their declines within 'undisturbed'

35   Amazonian rainforest.

36

37   *Key words: behavioral thermoregulation; climate change; microclimate refugia; seasonality;*

38   *soil temperature; soil moisture; terrestrial insectivores.*

39

40   INTRODUCTION

41   Amazonia is the largest tropical forest and harbors a substantial portion of global

42   biodiversity. At over 7 million km^2, nearly equivalent to the continent of Australia, it contains

43   ~10% of described vertebrate species (IUCN, 2020; Silva et al., 2005). Rampant deforestation in

44   the region has motivated research on the consequences of clearing and fragmentation for

45   rainforest biota, including the avifauna (Bierregaard & Gascon, 2001; Peres et al., 2010;

46   Stouffer, 2020). Ground-foraging insectivores are consistently among the species that respond

47   most strongly to landscape disturbance. For example, experimental forest isolation led to attrition

48   of terrestrial insectivores from fragments in central Brazil, with extinctions inversely

49   proportional to fragment size (Stouffer & Bierregaard, 1995; Stratford & Stouffer, 1999). Similar

50   patterns materialized in Ecuador (Canaday, 1996; Canaday & Rivadeneyra, 2001) and elsewhere

51   in the Neotropics (Sekercioglu et al., 2002; Sigel et al., 2006, 2010; Visco et al., 2015). Strong

52   sensitivity to forest disturbance thus makes terrestrial insectivores representatives of biodiversity

53   within intact rainforest.

54   New studies have uncovered declines of terrestrial insectivores in what should be

55   undisturbed Amazonia. In Ecuador, abundance of these species decreased markedly over a 14-

56   year interval (Blake & Loiselle, 2015). Almost 2000 km away, a similar trend was recently

57   described from the central Amazon: over four decades, terrestrial insectivores vanished from

58   over half of primary forest sites and their relative abundance dropped substantially (Stouffer et

59   al., 2020). In that study, terrestrial insectivores declined fastest among 12 ecological guilds

60   examined, followed closely by near-ground insectivores. To document such population trends is

61   very challenging; it requires long-term sampling using standardized methods to survey elusive

62   species (Robinson et al., 2018). Within Amazonia, these two studies comprise the best available

63   information on population trends of rainforest birds in the absence of direct disturbance.

64   Alarmingly, both suggest that ground-foraging insectivores—already sensitive to landscape

65   processes—are in trouble.

66   Why are terrestrial insectivores disappearing from intact forest? Research in disturbed

67   landscapes offers a place to start. Hypothesized explanations range from vulnerability to

68   changing forest structure (Laurance et al., 2002; Stratford & Stouffer, 2015), reduction in forest

69   patch area (Stouffer, 2007), and several other factors (Powell et al., 2015; Visco et al., 2015).

70   Notably, the 'microclimate hypothesis' posits that non-forest areas and forest edges harbor

71   altered microclimates (*sensu* Chen et al., 1999) that are unsuitable for terrestrial insectivores,

72   which are associated with shaded, cool, and wet conditions within forest interior. Isolated forest

73   patches gain abnormal microclimate as a consequence of edge effects—they become brighter,

74   hotter, drier, and these conditions grow more variable (Laurance et al., 2002). Anomalies were

75   identified as most detrimental to organisms in stable environments, because ecological theory

76   predicts that physiology is shaped by the conditions under which it evolved (Janzen, 1967). This

77   notion is supported both for endotherms and ectotherms, as animals that display the narrowest

78   physiological tolerances tend to reside in the tropics (Huey et al., 2009; Porter & Kearney, 2009),

79   where temperature and precipitation are relatively stable throughout the year. Within Amazonia,

80   terrestrial insectivores inhabit the most stable of environments—the floor of the forest interior,

81   removed from both edge effects and the hotter, brighter, drier canopy >20 m above the ground.

82   Here, temperature and light intensity near forest edge and the canopy climb, while the reverse

83   occurs for water availability (Kapos, 1989; Scheffers et al., 2013; Sheldon et al., 2018; Walther,

84   2002). Thus, in the absence of edge effects, pristine forest appears to deliver optimal

85   environment for terrestrial insectivores.

86   However, even large tracts of primary forest may be disturbed. Human activities cause

87   the climate to diverge from historical norms across the globe. In the tropics, climate models

88   forecast abnormally high temperatures (Mora et al., 2013; Neelin et al., 2006) and more

89   temperature fluctuations (Bathiany et al., 2018). In Amazonia, average temperature has climbed

90   ~0.05°C year^{-1} since 1973 (Almeida et al., 2017). In contrast with consistent warming,

91   precipitation is more spatially variable. Shifts in rainfall regimes are sometimes manifested

92   through wetter wet seasons, but dry seasons are often drier and longer (Almeida et al., 2017; Fu

93   et al., 2013), with droughts predicted in the future (Neelin et al., 2006). Climate change has

94   already been linked to changes to forest structure by amplifying tree mortality, abundance of dry-

95   affiliated species, and biomass of lianas (Aleixo et al., 2019; Esquivel-Muelbert et al., 2019;

96   Laurance et al., 2014). Evidence is hence mounting that today's terrestrial insectivores occupy a

97   hotter and drier Amazonia than just a few decades ago, with conditions increasingly aligned with

98   forest fragments.

99   The Biological Dynamics of Forest Fragments Project (BDFFP) offers the opportunity to

100   assess the impacts of climate change on terrestrial insectivores. Located just north of Manaus,

101   Brazil (Figure 1), the BDFFP is the nexus of research on the Amazon rainforest (Laurance et al.,

102   2018), including birds (Stouffer, 2020), and is one of the sites where terrestrial insectivores

103   declined in primary forest (Stouffer et al., 2020). Here, we address two objectives while drawing

104   on extensive research on terrestrial insectivores in local disturbed and undisturbed landscape.

105   First, we assess evidence for exposure of terrestrial insectivores to climate change *in situ* using

106   38 years of data from a climate reanalysis focused on our study site rather than broad regional

107   patterns. Second, to test our hypothesis that hot and dry conditions are unsuitable for birds, we

108   use field sensors to identify cyclic periods of ambient extremes and prospective microclimate

109   refugia, while simultaneously tracking the behavior of Black-faced Antthrush (*Formicarius*

110   *analis*), a terrestrial insectivore. These results reveal that birds emblematic of undisturbed

111   Amazonia attempt to avoid the very conditions which climate change exacerbates within primary

112   forest thought to be intact.

113

114   MATERIALS AND METHODS

115   *Study area, seasonality, and climate*

116   The BDFFP typifies forests of lowland Amazonia. The project spans approximately

117   1,200 km^2 of which ~95% in 2017 was covered with *terra firme* forest (Rutt et al., 2019),

118   growing on nutrient-poor soils of the Guiana Shield (Gascon & Bierregaard, 2001). We collected

119   data within continuous primary forest at the Cabo Frio and Camp 41 camps (Figure 1). Both

120   areas have topography characterized by moderate relief where stream valleys dissect upper-

121   elevation plateaus often located ~100 m higher, creating a highly reticulated landscape (Figure

122   1B).

123   Temperature and precipitation are high throughout the year but vary seasonally. The

124   region experiences an annual cycle of predictable rainfall fluctuation (Fu et al., 2013). The main

125   goal of this study was to assess whether birds are sensitive to hot and dry conditions; we

126   delineated the seasonal cycle at the BDFFP to understand when birds are expected to respond. To

127   do so, we compiled climate data for 38 years from the ERA5-Land reanalysis (Copernicus

128   Climate Change Service, 2017) for the area where birds were historically sampled (Stouffer et

129   al., 2020). ERA5-Land uses satellite and land-based records with a climate model to estimate

130   several climate values at 9 km resolution. We summarized precipitation and temperature at 2 m

131   above ground level within ~4,000 km^2 surrounding the study sites (Figure 1), yielding monthly

132   summaries from 1981 to 2019, and then used generalized additive models (GAMs; see *Statistical*

133   *analyses*) to quantify the annual climate cycle. Our models revealed August to be the middle of

134   the dry season, when precipitation is about a third of the total rainfall in March and April, the

135   wettest months (Figure 2). Temperatures peak slightly after the driest period—they are ~1.5°C

136   higher around October than in the middle of the wet season (Figure 2).

137   Is the BDFFP experiencing climate change? To answer this question, we grouped the

138   ERA5-Land monthly summaries by season: Jun – Nov (dry) and Dec – May (wet). These

139   seasonal classifications were based on our within-year analysis (Figure 2) and follow past

140   designations for the BDFFP (Stouffer et al., 2020). Climate covariates were modeled with GAMs

141   to determine whether climate change occurred at our site and if climate extremes varied by

142   season.

143

Microclimate refugia

145   Ambient extremes can manifest in time and space. Seasonal climate suggests that

146   extremes generally occur during the dry season at the BDFFP (Figure 2). Ambient conditions

147   thus often differ the most between about August and March—intervals that define the trough and

148   crest of the annual rainfall and temperature cycles. Dry season, and especially dry season

149   afternoons, are generally the hottest and driest periods in Amazonia. However, these extremes

150   may be reduced in microclimate refugia—localized areas that remain relatively cool and wet. For

151   example, in primary rainforest in the Philippines, the rate of temperature change in dense

152   vegetation and tree cavities was 43% relative to ambient temperature, and exposure to extreme

153   temperatures occurred over intervals that were 22 times longer (Scheffers et al., 2014). In

154   addition to this physical shelter, topography may also buffer ambient extremes. Temperature

155   drops with increasing elevation at large scales—a fact of little consequence in most of low-

156   elevation Amazonia. In contrast, at the BDFFP landscape, valleys likely remain wetter and

157   cooler. The bottoms of these 'micro-catchments' usually contain streams that are maintained by

158   groundwater throughout the year (Epron et al., 2006; Tomasella et al., 2008). Aside from direct

159   cooling, water buffers against temperature change (Davis et al., 2019; Elsenbeer, 2001; Fridley,

160   2009), and wetter soils allow evapotranspiration to occur when drier areas may lead to stomatal

161   closure (Aleixo et al., 2019). Hence, we expected ambient extremes to arise in the afternoons of

162   the dry season, with physical cover and valley bottoms offering buffered microclimates.

163   We empirically identified microclimate refugia with field measurements. The buffering

164   property of physical cover in a rainforest setting was revealed elsewhere (Scheffers et al., 2014);

165   here we focused on elevational refugia within Amazonian micro-catchments (Tomasella et al.,

166   2008). To determine whether valleys buffered ambient extremes, we measured temperature and

167   soil moisture along three elevational transects with a total of nine datalogging stations (Figure 1,

168   Appendix 1). We selected transects along slopes in primary forest based on LiDAR elevation

169   data, and placed stations away from treefall gaps such that each transect held one station at the

170   valley bottom (level 1), mid-slope (level 2), and plateau (level 3). The nine stations were thus

171   evenly classified by elevation, embedded within transects spanning ~600 m of length and ~40 m

172   in elevation (Appendix 1). Each station contained one logger (TrueLog100) and one sensor

173   (SMT100), both manufactured by Truebner (Truebner GmbH, Neustadt, Germany). We inserted

174   sensors fully into the ground; temperature and water content readings thus correspond to the

175   topmost 11 cm of soil—a relevant stratum for birds that seldom leave the forest floor. Loggers

176   were programmed to measure temperature (°C) and soil moisture (% volumetric water content)

177   every 10 min for the duration of sampling. We assigned the sampling periods to be Aug – Nov

178   (dry season; DS) and Feb – May (wet season; WS). We chose these months because they fell

179   within the DS or WS based on historical rainfall data (Figure 2), contain the most bird

180   observations, and are of equal length for the analysis of microclimate conditions. Aside from

181   automated measurements at these nine locations, we manually sampled stream temperature

182   across a broader area. These 53 samples were collected evenly throughout daylight hours over 32

183   days within 21 Jun – 13 Sep 2019 in the two study areas (Figure 1) and represented the effect of

184   stream temperature on valley-bottom microclimate in the DS.

185

186   *Tracking bird behavior*

187   We expected birds to seek microclimate refugia during the DS, as vagile animals can

188   exploit heterogeneity within their habitat to maintain optimal body temperature by behavioral

189   thermoregulation (Cowles & Bogert, 1944; Huey et al., 2003; Porter et al., 1973; Stevenson,

190   1985). To assess whether this occurred, we used the WS as the baseline for comparison, and

191   tested our prediction that birds used shelter more and shifted to lower elevations in the DS.

192   We selected *Formicarius analis* as a representative terrestrial insectivore. The BDFFP

193   contains 13 species of terrestrial insectivores (Stouffer, 2007), but only *F. analis* is both

194   adequately common and sufficiently large to carry GPS devices (Johnson & Wolfe, 2017; Rutt et

195   al., 2017). The species is a permanent resident that maintains a year-round territory defended by

196   a mated pair, but territory stability can fluctuate among years (Stouffer, 2007). As with nearly all

197   terrestrial insectivores, capture rates of *F. analis* displayed a declining trend since the early

198   1980s (Stouffer et al., 2020).

9

199   We caught territorial birds with target-netting. First, we located birds by broadcast of

200   conspecific playback to elicit a vocal response of a local territory owner. After detection, we set

201   two or more 12-m mist nets (32 mm mesh) arranged in a 'V' formation with the playback in the

202   center. When the focal bird approached playback, a concealed operator then flushed the bird into

203   nets. We then repeated the capture process the following year to recover devices. Initial trapping

204   and data recovery required 257 days (136 at Camp 41 and 121 at Cabo Frio) spread across 12

205   months in three years: 2017 (Jun – Aug), 2018 (Jun – Oct), and 2019 (Jun – Sep). At each

206   capture occasion, we took standard morphometric measurements and outfitted birds with either

207   GPS or biologging tags. Because age and sex is difficult to determine for this species (Johnson &

208   Wolfe, 2017), we assumed all captured birds were adult males due to their territorial responses to

209   song playback. For details about tag fitting, materials, and the lack of detrimental effects of

210   tagging on study birds, see Jirinec et al. (In press).

211   We tracked bird positions in space and time with archival GPS tags (PinPoint-50; Lotek,

212   Newmarket, Ontario, Canada). Tag configuration ('SWIFT' fixes) maximized the number of

213   locations at the expense of greater location error and occasionally large outliers. SWIFT fixes

214   involved a 12-second timeout after which devices either acquired sufficient GPS signal to

215   determine location (fix = success) or not (fix = fail). We programmed tags to attempt four fixes a

216   day (07:00, 10:00, 13:00, 16:00 local time) over one month in each of the two seasons. This

217   scenario allowed us to compare a similar number of locations (up to 124 fixes per season) for

218   each bird. In 2017 and 2018, we deployed a total of 18 GPS tags, of which we recovered 11 in

219   subsequent years. Recovered tags contained locations from eight birds in the 2017 DS – 2018

220   WS cycle and three birds in the 2018 DS – 2019 WS cycle (Figure 2). Using successful fixes, we

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221   extracted elevation from a 12-m WorldDEM (Riegler et al., 2015) to determine whether birds

222   reduced their exposure to ambient extremes by moving downslope.

223   While we used successful GPS fixes to measure elevation shifts, we applied both

224   successful and failed fixes to track shelter use. Because the precision of GPS tags was

225   insufficient to resolve microhabitat directly from x-y coordinates, we employed the inverse

226   probability of GPS fix as a proxy for shelter use. Dense vegetation and other physical barriers

227   hinder satellite signal, leading to relatively fewer locations within these areas (Di Orio et al.,

228   2003; Jiang et al., 2008; Recio et al., 2011). Although this reality is usually undesirable, here it

229   allowed us to track shelter use indirectly when we standardized the intervals over which tags

230   search for satellites (12 seconds). Because GPS signal varies little spatially and temporally

231   (*GPS.Gov: Space Segment*, 2020), the probability of successful GPS fix is inversely proportional

232   to the level of surrounding obstruction, with probability of fix near '1' in open sky and '0' inside

233   logs, stumps, or dense vegetation. To help validate this assumption, we radio-tracked a single *F.*

234   *analis* with VHF telemetry between 19 Jul and 24 Aug 2017, which allowed us to observe

235   behavior directly. If birds sought cover during ambient extremes, those times should coincide

236   with the lowest probability of GPS fix.

237   To quantify exposure to ambient conditions, we tracked birds with biologging tags

238   ('geolocators'; Intigeo-P65B1-11T-20deg, Migrate Technology, Cambridge, UK). Tags recorded

239   light intensity (lux) every 5 min and temperature (°C) every 15 min for two months each season.

240   Biologgers sampled light intensity atop a stalk to prevent feather shading, while thermometers

241   were embedded in tags that were flush with the bird's body (Appendix 2). Thus, light readings

242   represented direct exposure to light, while temperature was a combination of body and ambient

243   temperature. To better understand the relationship between tag measurements and ambient

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244   conditions, we sampled light and temperature with four biologgers that were placed near tagged

245   birds ~10 cm high in the understory of mature forest, at a mean elevation of 136 m (Figure 1,

246   Appendix 2). We also measured the body temperature of 36 unique birds by cloacal

247   measurements with a medical thermometer (upper temperature limit = 43.0°C). Measurements

248   were taken as soon as possible after capture to lessen any possible effect on body temperature

249   (Prinzinger et al., 1991). In 2017 and 2018, we deployed 13 biologgers on birds, of which we

250   recovered four in the following years. Light and temperature data came from three birds tracked

251   over the 2017 – 2018 seasonal cycle: Sep – Oct and Mar – Apr, and one bird tracked over the

252   2018 – 2019 cycle in Oct – Nov and Mar – Apr (Figure 2). Ambient loggers collected data in

253   concert with bird tags, providing an approximation of ambient conditions that birds were

254   exposed to. This allowed us to test for behavioral thermoregulation by comparing measurements

255   from identical devices on birds and in the environment.

256

257   *Statistical analyses*

258   To analyze climate and biologger data, we employed generalized additive models

259   (GAMs) implemented in R package 'mgcv' (Wood, 2020). GAMs are similar to linear models,

260   but allow for modeling of non-linear relationships in the response using smooth functions of

261   explanatory variables (Wood, 2017). Package 'mgcv' calculates an approximate p-value for the

262   smooth term; a low p-value constitutes evidence for a significant relationship—either positive or

263   negative—somewhere along the range of the covariate, and plot of the smooth should be

264   examined to interpret results (Wood, 2017).

265   To quantify annual seasonality and to test for climate change with ERA5-Land at the

266   BDFFP, we used GAMs that accounted for autocorrelated observations. We selected the cyclic

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267   cubic regression spline basis (bs = 'cc', k = 10) for annual seasonality models and the thin plate

268   regression spline basis (bs = 'tp', k = 10) for climate change models; all were fit with restricted

269   maximum likelihood and Gaussian distribution. We specified generalized additive mixed models

270   with autoregressive moving average (ARMA) error structure for each climate variable, modeled

271   as the smooth of the numeric month in annual seasonality models and as the smooth of year in

272   climate change models. We set ARMA within each year and selected the AR order by first

273   plotting residual autocorrelation functions of non-ARMA models, followed by iterative

274   likelihood ratio tests among models with plausible AR orders to select the appropriate model

275   structure.

276   Last, to analyze biologger data, we used different GAM structures for light and

277   temperature with separate seasonal analyses. For light exposure, we modeled light intensity as

278   the smooth of numeric time of day (0 – 23.99) using the cyclic cubic regression spline (bs = 'cc',

279   k = 50), the smooth of the successive observation rank per group (bird or logger) with the

280   Gaussian process basis (bs = 'gp', k = 50), and group as the random effect (bs = 're', k = 50).

281   Light exposure models were fit with restricted maximum likelihood and Gamma distribution

282   with a log link function. Temperature model structure was identical, although we used Gaussian

283   distribution in place of Gamma.

284   To test whether valleys buffered ambient extremes, we calculated seasonal profiles by

285   elevation using locally estimated scatterplot smoothing (LOESS). Prior to smoothing, we

286   averaged timeseries by elevation (e.g., mean of the three valley transects per 10-min interval)—

287   this resolved data gaps and created a single timeseries group per elevation. Each LOESS line

288   represents the estimate of R function loess(), with $\alpha = 0.5$ on the group average. For temperature

289   and soil moisture, these were averages of the raw measurements. For daily temperature

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290   summaries, we first extracted the minimum, maximum, and range in temperature per day in the

291   group average, and then estimated the LOESS lines of the summary timeseries.

292   Prior to modeling of bird GPS data, we quantified tag location error and incorporated it

293   into our analyses. Vegetation and topography reduce not only the probability of fix but also the

294   accuracy of acquired locations (Jiang et al., 2008), which was of particular concern for birds with

295   SWIFT-enabled tags that often used valleys in mature rainforest. We therefore placed two

296   calibration sensors (identical to bird tags) to represent stationary birds—they were positioned

297   ~10 cm high in the understory of mature forest, near study birds, and were stratified by elevation

298   (lower tag: 91 m, upper tag: 140 m; Appendix 2). Although calibration tags sampled a somewhat

299   different time of year, we programmed them with the same daily fix schedule as study birds,

300   from 17 Jun – 31 Aug 2019. Out of 608 fix attempts, this yielded 411 successful locations, which

301   we then used in R package 'ctmm' (Fleming et al., 2020) to estimate location error. Because

302   satellite-based screening methods such as HDOP can be misleading and eliminate accurate

303   locations (Recio et al., 2011), we instead identified spatial outliers for our calibration tags based

304   on relative distance to other locations. For each tag, we first we used the outlie() function in

305   'ctmm' to calculate the distance from the median longitude and latitude to each point, which

306   highlighted one obvious outlier for the lower tag (2,200 km deviation from core cluster) and

307   another for the upper tag (1.2 km). We removed both of these outliers before estimating location

308   error by running the uere.fit() function in 'ctmm' for each remaining calibration dataset. After

309   generating an error radius of 52 m (95% CI: 49 – 56 m) and 41 m (38 – 44 m) for the lower and

310   upper tag, respectively, we conservatively estimated that each valid bird fix was on average 52 m

311   away from the true location. This horizonal error is relatively small, given the typical home

312   range size (Appendix 2). We similarly removed outliers from the location dataset for each of the

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313   11 GPS tags recovered from birds. As with the calibration data, we used outlie() to calculate core

314   deviation for each bird and removed all locations that were farther than 1.5-times the

315   interquartile range in core deviation. We believe that this vetting process constituted an objective

316   way to remove outliers and quantify spatial error from small GPS tags deployed in this

317   challenging environment.

318   To model bird GPS data, we used linear mixed models (LMMs) and generalized linear

319   mixed models (GLMMs) in R package 'lme4' (Bates et al., 2020). First, to determine whether

320   GPS fix probability varied temporally, we used GLMMs to model fix attempt as a binary

321   response (success = 1, fail = 0) with season (dry, wet) and time of fix (hour: 07:00, 10:00, 13:00,

322   16:00) as explanatory variables and bird as a random effect. We applied the binomial error

323   distribution with the logit link function (logistic regression) and fit these models by maximum

324   likelihood with adaptive Gauss-Hermite quadrature using 25 sample points. This dataset

325   involved all 2,724 fix attempts for the 11 recovered GPS tags, including failed fix attempts and

326   successful fixes that were later removed as outliers. Second, we used the final valid location

327   dataset (filtered via 'ctmm') to test whether birds shifted elevations during ambient extremes. To

328   attach elevation to GPS data, we averaged DEM values with ArcGIS (ArcMAP 10.7.1, ESRI,

329   Redlands, California, USA) within 52 m of each valid fix to account for estimated horizontal

330   error. We then used LMMs to model elevation as the response with season and time of fix as

331   explanatory variables and bird as the random effect. To compare the relative importance of each

332   covariate, we built the same four models for elevation and the probability of GPS fix and

333   compared competing models using AIC_c (Burnham & Anderson, 2002). The models were (a) a

334   null (intercept-only), (b) hour, (c) season, and (d) an hour*season interaction. All models were fit

335   using maximum likelihood, but we refit top LMMs with restricted maximum likelihood for

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336   interpretation of coefficients (Zuur et al., 2009). Finally, for each top model, we examined model

337   diagnostics in R package 'DHARMa' (Hartig, 2020) using 10,000 simulations, as well as the

338   model fit with conditional coefficients of determination (r^2_c) calculated with r.squaredGLMM()

339   in R package 'MuMIn' (Bartoń, 2020). Analyses were conducted using R version 3.6.3 (R Core

340   Team, 2020).

341

342   RESULTS

343   *Ambient conditions*

344   Climate has changed at the BDFFP over the last four decades. Within- and among-year

345   variation in both temperature and precipitation was considerable, but three of the four models

346   revealed significant climate trends over time (Figure 3). DS temperature had the strongest

347   positive relationship with year—in 2019, DS temperature was ~1.3°C higher than in 1981.

348   Temperature in the WS also rose—in 2019, WS temperature was ~0.6°C higher than in 1981. DS

349   rainfall declined over time, with 2019 precipitation totaling ~34 mm (21%) less than in 1981.

350   WS rainfall indicated an increasing, but insignificant trend. Hence, terrestrial insectivores at the

351   BDFFP are currently exposed to significantly hotter and drier conditions than in the early

352   1980s—especially during the DS.

353   In modern forest, microclimate differed by time of day, season, and elevation (Table 1,

354   Figure 4). The nine microclimate stations, operational Jun 2017 – Sep 2019, acquired 594,119

355   readings of both temperature and soil moisture over the four seasonal intervals. Only two gaps in

356   the timeseries occurred, when rodents severed sensor cables, resulting in no data between 6 Nov

357   2018 – 21 Jun 2019 at CFN-3 and 11 Mar 2019 – 21 Jun 2019 at CFN-2. Although we originally

358   placed all stations away from forest gaps, single trees fell within 10 m of both Camp 41-1 and

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359   CFS-1 during the WS of 2018. Soil moisture was lowest overall in the DS, but elevation created

360   the strongest contrasts, with driest conditions at uppermost sites while valleys remained much

361   wetter. Temperature varied by season, with higher mean, daily minimum, maximum, and range

362   in DS. Extremes intensified at upper elevations. Daily peaks in temperature emerged most often

363   between 14:00 and 15:00, regardless of season, although they tended to occur ~30 min later in

364   the DS and were more variable during the WS (Table 1). Stream temperature during the DS was

365   relatively cool and varied little across space and time (mean ± SD = 24.6 ± 0.4°C, range = 23.6 –

366   25.7, n = 53). In short, afternoons in the dry season produced the hottest and driest periods of the

367   year, but valleys offered microclimate refugia where conditions were milder.

368

369   *Bird behavior*

370   The 11 GPS tags attempted a total of 2,724 locations, with 688 (25%) successful fixes

371   (640 [23%] after outlier removal). The four bird biologgers returned a total of 140,245 light and

372   46,748 temperature readings, whereas the four ambient loggers returned 125,232 and 41,744

373   readings, respectively.

374   We detected significant temporal patterns in the probability of GPS fix—our proxy for

375   shelter use. The top model, by ΔAIC_c > 53, was the interaction model that contained both hour

376   and season (Table 2). Using 07:00 in the WS as the baseline, the probability of GPS fix (inverse

377   of shelter use) was significantly higher at 13:00 and 16:00 in the WS but dropped substantially at

378   13:00 and 16:00 in the DS (Figure 5A). In the seasonal model, probability of a successful fix was

379   27% in the WS and 22% in the DS (β_{dry} = -0.29, SE = 0.09, P = 0.001).

380   Birds shifted downslope during ambient extremes. In model selection, the seasonal model

381   was better than models that contained both hour and season covariates (Table 3). According to

382   this seasonal model, birds were ~4 m lower in the DS than the WS (β_{dry} = -4.35, SE = 0.90, t = -

383   4.85, P < 0.001, r^2_c = 0.56). As individuals ranged across, on average, 41.2 m of vertical space in

384   a given season (Appendix 3), 4 m constitutes an ~10% proportional shift in vertical space use. In

385   the second model (interaction between hour and season), bird elevation varied significantly by

386   time of day within season (Figure 5B). Using 07:00 in the WS as the baseline, birds were ~4 m

387   higher at 16:00 in the WS ($\beta_{16:00,\ wet}$ = 3.77, SE = 1.84, t = 2.05, P = 0.04) and ~7 m lower at

388   16:00 in the DS ($\beta_{16:00,\ dry}$ = -6.54, SE = 2.57, t = -2.54, P = 0.01, r^2_c = 0.56). For the single bird

389   tagged with a VHF radio tag, we collected 68 locations that were concentrated in the DS

390   afternoon, but we saw the bird only once (1%) and triangulation suggested it often hid in a large,

391   streamside log.

392   Biologgers showed that birds altered their behavior by season (Figure 6). Light intensity

393   varied considerably through time in both bird and ambient datasets—model r^2 were relatively

394   low, especially in the WS. Birds experienced a much darker environments than ambient

395   biologgers indicated, with light exposure in the DS lower, even though light environment in the

396   DS was far brighter. Temperature recorded by both bird and ambient loggers was higher in the

397   DS, but the seasonal difference in peak temperature was about 50% lower for birds. Body

398   temperatures of birds were high (41.7 ± 0.7°C, range 40.3 – 43.0°C, n = 36), with tags showing

399   birds were exposed to higher ambient temperatures in the DS—tags recorded peaks at ~36.3°C in

400   the DS and ~35.5°C in the WS. The timing of birds' daily temperature peaks was similar in both

401   seasons (14:16 and 14:21 in the DS and the WS, respectively). However, in contrast to ambient

402   conditions, the variation in timing was usually smaller and similar across seasons for birds

403   (Table 1).

404

18

405   DISCUSSION

406   We analyzed several high-resolution datasets for birds and their environment within

407   Amazonian rainforest. We found that *F. analis*—a member of the sensitive terrestrial insectivore

408   guild—attempted to sidestep extremes in ambient conditions within primary *terra firme* forest.

409   Valleys and shelters offered microclimate refugia, and birds sought these during the afternoons

410   of the dry season—the hottest and driest period of the year. Importantly, over the last four

411   decades, climate change has made the dry season more extreme: we found that the modern dry

412   season at the BDFFP is ~21% drier and ~1.3°C hotter than in the early 1980s—and these trends

413   are only intensifying. Even if birds were not thermally stressed per se, periodic reductions in

414   habitat and mobility constrain foraging opportunities; warming climate thus shortens the interval

415   over which birds can meet their energetic needs (Bennett et al., 1984; Chappell & Bartholomew,

416   1981). Our study was motivated by alarming declines of terrestrial insectivores at both

417   Amazonian sites with long-term data on primary forest avifauna, including the BDFFP (Blake &

418   Loiselle, 2015; Stouffer et al., 2020). The ultimate goal of this study was to evaluate whether

419   climate change is a possible mechanism. We found that climate is increasingly shifting towards

420   conditions birds attempt to avoid, and despite evidence that birds actively influenced their

421   thermal exposure, they managed to do so by only ~50%. Our results are thus consistent with the

422   hypothesis that climate change lowers habitat quality for terrestrial insectivores.

423   In lowland tropical rainforest, terrestrial insectivores inhabit the coolest and most stable

424   of a warm environment, with a limited palette of options to behaviorally thermoregulate during

425   hot and dry periods (Janzen, 1967). For these birds, we hypothesized that valleys and shelter may

426   function as refugia and predicted that these would be used preferentially during ambient

427   extremes. We then identified these periods empirically at two scales—daily and seasonal—and

19

428   compared bird behavior at opposite ends of this ambient gradient. The top layer of soil, upon

429   which terrestrial insectivores live and forage, experienced the highest temperatures between

430   14:00 and 15:00 in the DS (Table 1), but temperatures were lower in valleys (Figure 4). As

431   expected, soil water content was related to rainfall—soils were drier in the DS and substantially

432   drier at upper elevations than in valleys (Figure 4). Accordingly, we found that *F. analis* shifted

433   its average elevation downslope during the DS—by up to 10 m (Figure 5B). Our proxy for

434   shelter use (inverse probability of obtaining a GPS location) also revealed strong daily patterns

435   within season (Figure 5A). Compared to a WS morning baseline, these results suggest that

436   shelter use was 12x higher at 13:00 and 3x higher at 16:00 in the DS. Data from biologgers

437   supported these results—although ambient light conditions were far brighter in the DS, birds at

438   that time occupied darker areas (Figure 6). Still, birds experienced temperatures ~1°C higher in

439   the DS than the WS, though the ambient increase in DS temperature was ~2°C.

440   A similar study from Panama did not find that nine understory insectivores selected

441   buffered microclimates, or that microclimate varied appreciably over time (Pollock et al., 2015).

442   However, that study was conducted in older secondary forest and utilized observers following

443   radio-tagged individuals. We benefited from novel technology that let us sample on-bird

444   conditions without observer disturbance and monitor the same individuals across seasons within

445   primary forest. At our study site, we found stream temperature—within valleys in the DS—to be

446   relatively constant and cool (24.6°C), which was 17.1°C lower than the average body

447   temperature of *Formicarius analis* (41.7°C). Thus, even if only through bathing (Jullien &

448   Thiollay, 1998), valley bottoms offer opportunities for rapid cooling.

449   Our data indicated that thermal and hydrological dynamics behaved as expected at the

450   BDFFP, generating microclimate refugia at the valley bottoms. For instance, katabatic flow of

451   colder air to low-lying areas (Pypker et al., 2007) lowers temperature in valleys, which tend to be

452   already shaded. Hydrology within Amazonian micro-catchments is dominated by baseflow—rain

453   infiltrates to groundwater and is slowly released into streams, which consequently have a

454   relatively steady flow throughout the year (Tomasella et al., 2008), buffering temperature

455   extremes (Davis et al., 2019; Elsenbeer, 2001; Fridley, 2009). More water within valleys may

456   also allow cooling by enabling higher evapotranspiration when forest may be water-limited in

457   drier areas and periods (Aleixo et al., 2019; Berg & Sheffield, 2019). Thus, in the DS, the

458   demarcation between the dry upper slopes and wet lower slopes is not gradual (Figure 4). This

459   threshold means that even a relatively small downslope shift can abruptly result in wet and cool

460   conditions. In our data, the second DS was the only exception to this pattern—valleys showed

461   higher maxima and range values, but we attributed this to treefalls that had occurred at two of the

462   three low-elevation sites, likely leading to higher solar input. Otherwise, temperature average,

463   minimum, maximum, and range were all higher in the DS and amplified on plateaus. Notably,

464   the effect of elevation on temperature (but not water content) was erased in the WS. This is likely

465   because cloud cover (Graham et al., 2003), air humidity (Aleixo et al., 2019), and environmental

466   water content are all higher during the WS, mediating temperature fluctuations across the

467   landscape. Passing clouds and precipitation possibly led to the inconsistent times of daily

468   temperature peaks in the WS (Table 1).

469   Compared with downslope shifts, shelter use appears to be an additional but separate

470   form of behavioral thermoregulation. Low rates of successful GPS fixes implied that birds

471   sought cover in the afternoons of the DS—tags were nearly unable to acquire signal at 13:00 (3%

472   success) and 16:00 (9% success), whereas the highest success rates occurred at 13:00 and 16:00

473   in the wet season (30 and 36%; Figure 5A). Elevation at bird locations suggested that birds

21

474   shifted downslope between 13:00 and 16:00 in the DS, where GPS signal could be harder to

475   acquire, but birds were not significantly lower when fix probability was lowest at 13:00. Our

476   calibration data demonstrate that elevation alone cannot account for fix probability; both

477   calibration tags obtained much higher success rates than bird tags, with the lower device

478   attaining a slightly higher success rate than the upper device (69% vs 66%). This suggests that

479   physical cover, in addition to valleys possibly blocking signal, drove the reductions in GPS fix

480   rates. This notion was corroborated by our manually tracked bird—although observations

481   concentrated in the afternoon, we only saw the bird once (1%) and triangulation suggested it

482   often hid in a large, streamside log. Our results are thus consistent with the hypothesis that,

483   during periods of ambient extremes, birds sought physical cover where ambient conditions were

484   buffered (Scheffers et al., 2014).

485   We believe that our results are most compatible with birds responding directly to ambient

486   extremes, but we cannot rule out indirect effects. Biomass of arthropod prey in the leaf litter

487   drops with soil moisture (Jirinec et al., 2016; Levings & Windsor, 1984), including seasonal

488   reductions in the DS (McKinnon et al., 2015; Pearson & Derr, 1986; Willis, 1976), and vertical

489   movements that track moisture within the leaf litter (Usher, 1970). Mestre et al. (2010)

490   quantified prey in regurgitated samples of *Formicarius analis* at the BDFFP, predominantly

491   finding ants (Formicidae; ~55%). In Panama, ant activity dropped by 25% in the DS and was

492   >200% higher in ravines than exposed plateaus (Kaspari & Weiser, 2000). Capture rates of

493   terrestrial insectivores as a guild—and *Formicarius analis* in particular—correlated with litter

494   arthropod abundance, suggesting that these birds track resource availability within their home

495   ranges (Karr & Brawn, 1990). Another terrestrial insectivore—the Song Wren (*Cyphorhinus*

496   *phaeocephalus*)—was in the poorest body condition at the dry end of the rainfall gradient in

22

497 Panama (Busch et al., 2011). Likewise, Spotted Antbirds (*Hylophylax naevioides*)—which, like

498 *F. analis*, breed during the WS—were found to be ~8-15% lighter during the late DS (Wikelski

499 et al., 2000). Regardless of whether we detected a direct or indirect response to ambient

500 extremes, the conclusion is likely the same—hot and dry periods are undesirable for terrestrial

501 insectivores.

502   Future studies can augment this research in several ways. Although the variation in GPS

503 fix success allowed us to estimate shelter use, the challenging environment for GPS tags resulted

504 in a loss of ~75% of locations with elevation data. This introduced two issues. First, the

505 markedly smaller size of the elevation dataset may have reduced our ability to resolve the effect

506 of season and daytime as AIC_c substantially penalized the interaction model due to its

507 complexity (Table 2). Second, areas and times where tags received relatively few fixes may have

508 been underrepresented—an issue raised in previous studies on habitat selection (D'Eon, 2003).

509 However, GPS tags recorded substantially higher number of fixes in the WS when GPS signal

510 should have been hindered by cloud cover (Graham et al., 2003; Figure 6). To obtain these

511 results, birds must have moved higher up and to more open locations during the WS. Researchers

512 could avoid the above issues with direct observations of radio-tagged birds, though that raises

513 concerns about logistics and observer effects on birds—both potentially insurmountable. Overall,

514 our conclusions stand on relatively high-resolution and diverse datasets, but we only considered

515 a single species and two seasonal cycles. Nevertheless, the ultimate cause of biological

516 seasonality is climate over evolutionary time. We propose two studies that could provide further

517 evidence for negative influence of climate change: 1) testing if less sensitive ground-foraging

518 species do not respond to ambient extremes, and 2) a decadal study showing that annual

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519   elevational shifts and shelter use are a function of the seasonal severity for a given year (e.g.,

520   more extreme response during hot and dry El Niño years).

521

522   CONCLUSIONS

523   This study highlights that heterogeneity in the 'stable' lowland rainforest exists in three

524   domains—daily, seasonal, and topographical. *Formicarius analis*, a member of the terrestrial

525   insectivore guild, which should be among the most buffered from periodic fluctuations in

526   temperature and water availability, nonetheless seeks shelter and moves to areas where

527   conditions are milder during ambient extremes. Regardless of whether our study revealed that

528   these birds behaviorally thermoregulate or that they instead track a shifting food base (or both),

529   climate change exacerbates the very conditions that lead to such behavior and thus likely shrinks

530   suitable habitat for this species at the BDFFP. *Formicarius analis* and other terrestrial

531   insectivores may thus be especially vulnerable to climate change. In fact, the impetus for this

532   study was the substantial decline of terrestrial insectivores reported recently within primary

533   forests at the BDFFP (Stouffer et al., 2020). Previous decades of tracing avian responses to forest

534   fragmentation raise the possibility that hotter and drier conditions may be at least partially

535   responsible for disappearances in fragments. Our results are consistent with the predictions of

536   this microclimate hypothesis for birds in continuous primary forest. Furthermore, we underscore

537   that climate change will increasingly produce such conditions in lowland Amazonia, which

538   mostly lacks topographical variation and associated refugia. If these sensitive specialists act as a

539   barometer within the vast and biodiverse forests of Amazonia, their behavior raises cause for

540   concern.

541

558

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827

TABLES

Table 1. Timing of daily temperature extremes (mean ± SD in min) by season for ground microclimate stations and bird biologgers.

category[a]	season[b]	time	n^c
ground: plateau	dry	14:46 ± 149	259
	wet	14:11 ± 269	265
ground: mid-slope	dry	14:40 ± 128	257
	wet	14:08 ± 245	252
ground: valley	dry	14:13 ± 89	259
	wet	13:49 ± 183	251
birds	dry	14:16 ± 89	331
	wet	14:21 ± 100	319

[a] For ground soil stations, each elevation category is a mean of three stations. The bird category is a mean of four individuals

[b] dry (Aug – Nov) and wet (Feb – Mar)

[c] Sample size in days

Table 2. Model selection for probability of GPS fix, including the number of model parameters (K), AIC_c weight (w), and log likelihood (LL).

model	covariates	K	AIC_c	ΔAIC_c	w	LL
interaction	hour*season	9	2988.1	0	1.00	-1485.0
season	season	3	3041.9	53.8	0.00	-1518.0
diel and season	hour + season	6	3044.6	56.4	0.00	-1516.3
null		2	3050.5	62.4	0.00	-1523.3
diel	hour	5	3053.2	65.0	0.00	-1521.6

Table 3. Model selection for bird elevation, including the number of model parameters (K),

AIC$_c$ weight (w), and log likelihood (LL).

model	covariates	K	AIC$_c$	ΔAIC$_c$	w	LL
season	season	4	4965.3	0	0.87	-2478.6
interaction	hour*season	10	4970.1	4.8	0.08	-2474.9
diel and season	hour + season	7	4971.0	5.7	0.05	-2478.4
null		3	4986.3	21.0	0.00	-2490.1
diel	hour	6	4990.6	25.3	0.00	-2489.3

828   FIGURE LEGENDS

829   Figure 1. Survey areas at the Biological Dynamics of Forest Fragments Project in the state of

830   Amazonas, Brazil. Panel 'A' depicts the two study areas, Cabo Frio and Camp 41, with Landsat-

831   derived forest cover in 2017 (gray). Panel 'B' shows topographical variation (range ~100 m) in

832   the same scene. Both panels contain the 640 GPS locations of 11 *Formicarius analis* individuals

833   considered in this analysis (2017 – 2019), as well as the locations of sensors that measured

834   ambient conditions. The green rectangle (inset) shows the region where we summarized ERA5-

835   Land data for the climate change analysis.

836

837   Figure 2. Annual climate and schedule of bird sampling. We first used an autoregressive

838   generalized additive model and local rainfall and temperature data to broadly identify periods of

839   annual climate extremes for comparison of bird behavior. Climate data come from ERA5-Land

840   reanalysis and are a compilation of 38 years for our study area. Lines are model fits with the 95%

841   CI shaded in gray. We then tracked Black-faced Antthrushes (*Formicarius analis*) over one

842   annual cycle, either with a GPS ($n = 11$) or temperature logger ($n = 4$). For birds with GPS tags,

843   individuals were tracked over one month in the dry season (Aug or Sep) and one month the

844   following wet season (Mar), depending on year. Birds with biologgers were tracked over two

845   months in each season, starting either in Sep, Oct, or Mar.

846

847   Figure 3. Climate change at the Biological Dynamics of Forest Fragments Project within

848   Amazonian Brazil. Lines are fitted generalized additive models with ARMA errors, with shading

849   representing 95% CI. Climate data are monthly summaries compiled for the BDFFP area from

850   ERA5-Land reanalysis.

851

852   Figure 4. Forest floor microclimate within Amazonian micro-catchments in primary *terra firme*

853   forest. Plots depict water content and temperature measurements from the top 11 cm of soil at

854   nine microclimate stations arranged along three elevational transects, each with a station placed

855   in a valley (1, blue), midway up a hillside (2, gray), and atop a plateau (3, red). Stations obtained

856   a reading every 10 minutes during each four-month season; here we here show the locally

857   estimated scatterplot smoothing of the average for each elevational group (i.e. each line smooths

858   the mean of the three timeseries).

859

860   Figure 5. Probability of GPS fix (A) and elevation (B) by time of day and season for tags on 11

861   *Formicarius analis* in primary, continuous *terra firme* forest. Each bird was tracked four times

862   daily over one month in the dry season (red) and one month in the wet season (blue) in 2017 –

863   2019. Error bars represent 95% confidence intervals and P-values test the difference against a

864   baseline (dashed line: 07:00 in the wet season).

865

866   Figure 6. Light and temperature environment by day and season for birds and ambient

867   conditions. Lines and 95% CIs are fits from generalized additive models with birds ($n = 4$) and

868   ambient loggers ($n = 4$) as random effects. Note that y-axis on the ambient light plot is 2 orders
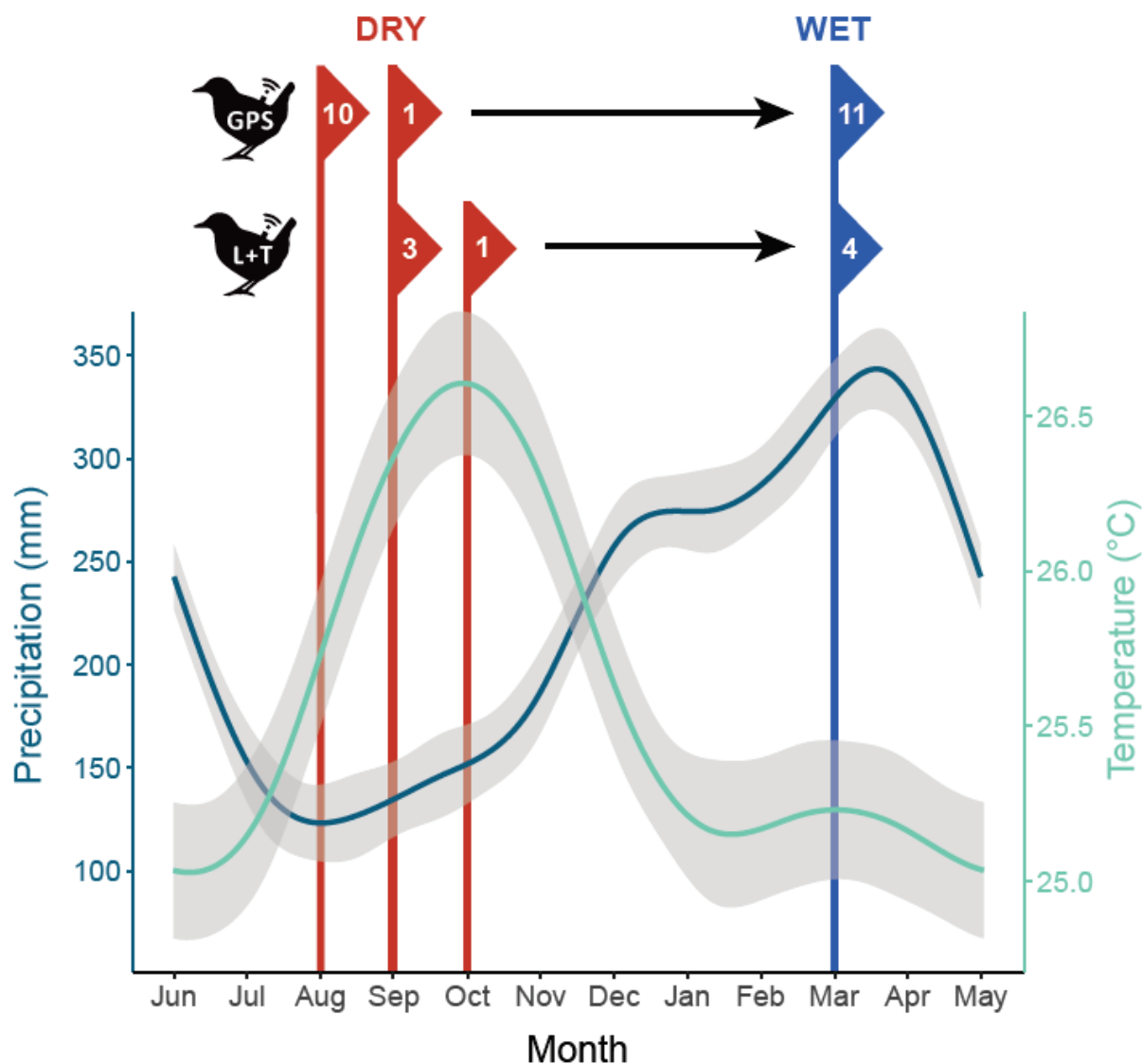
869   of magnitude higher.
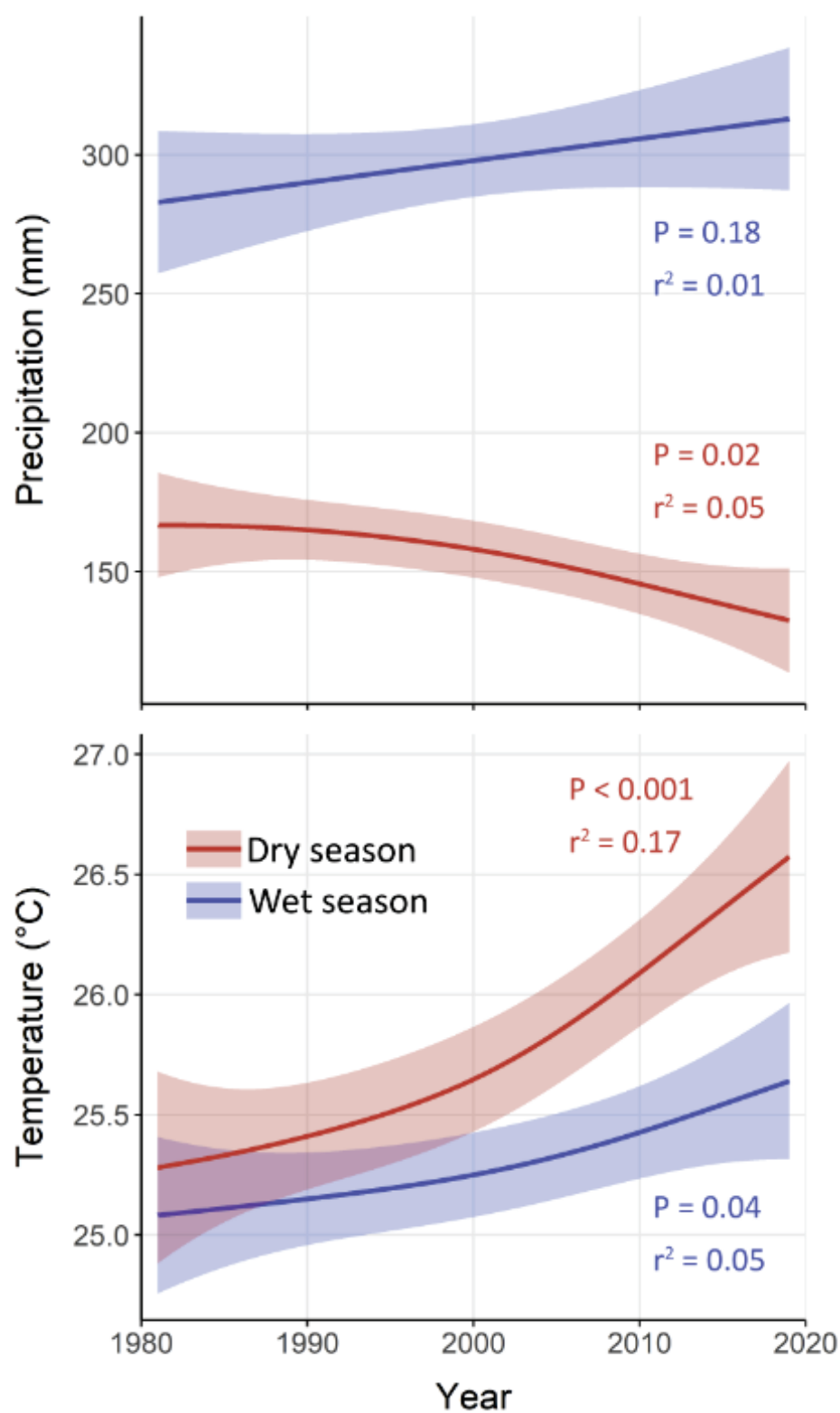
870

Figure 1.

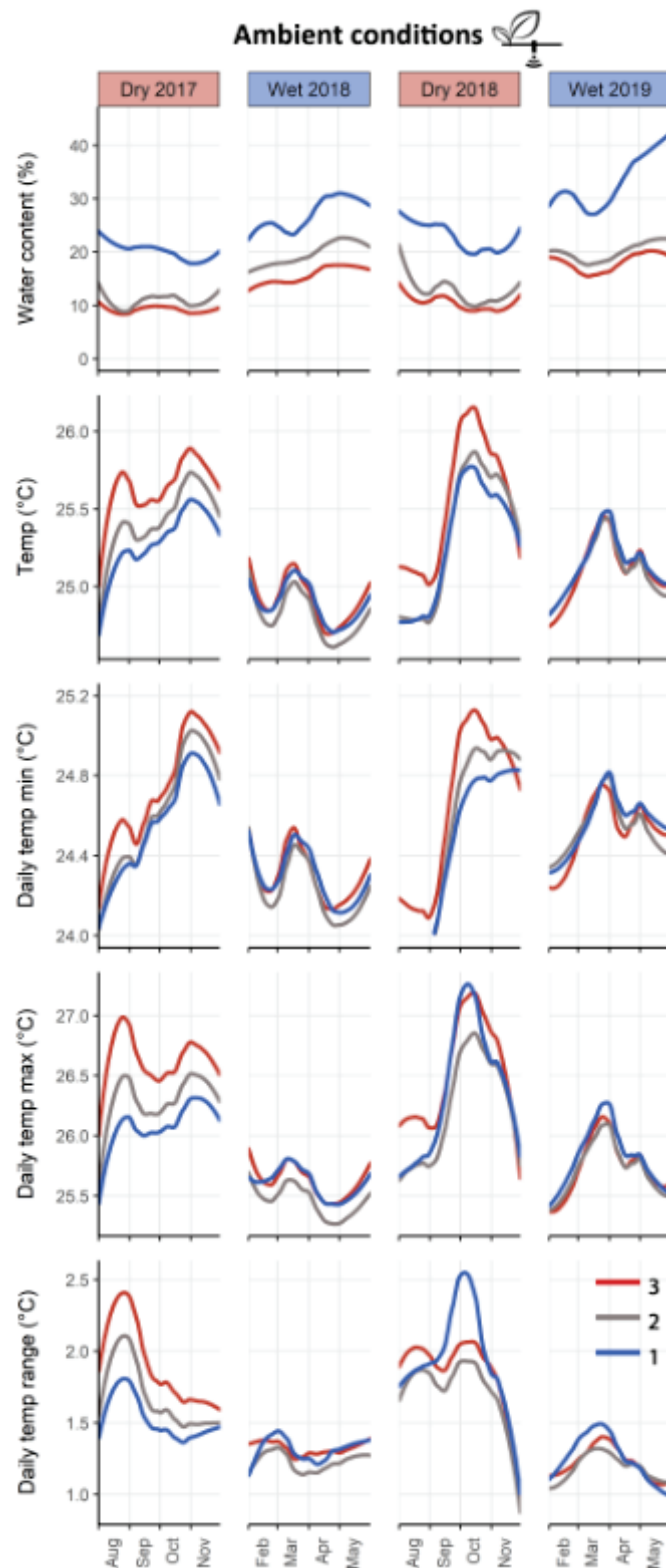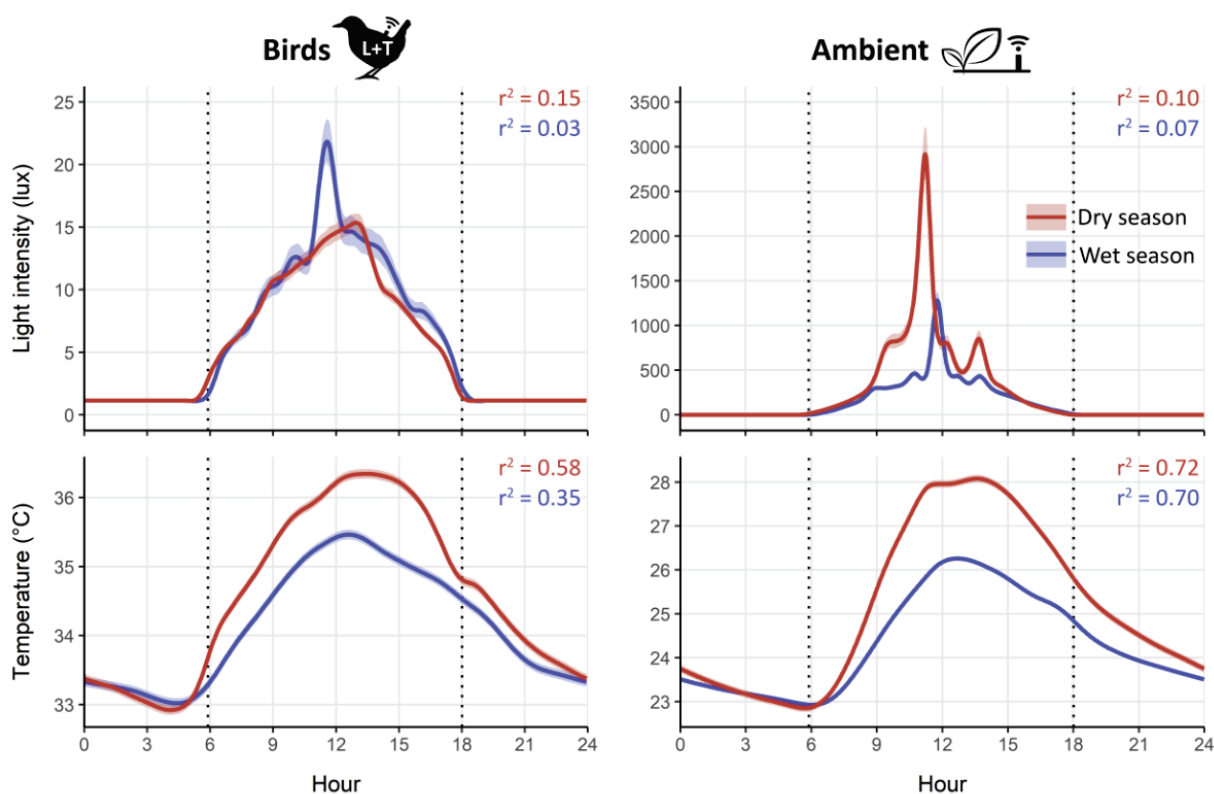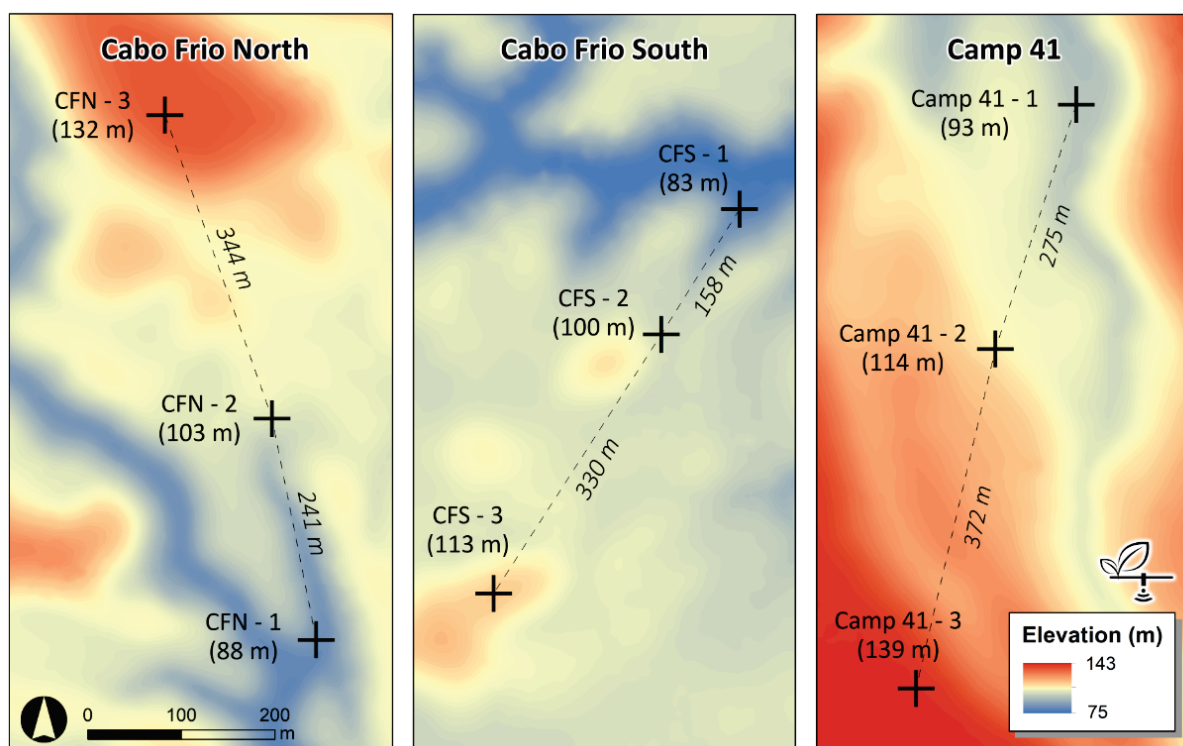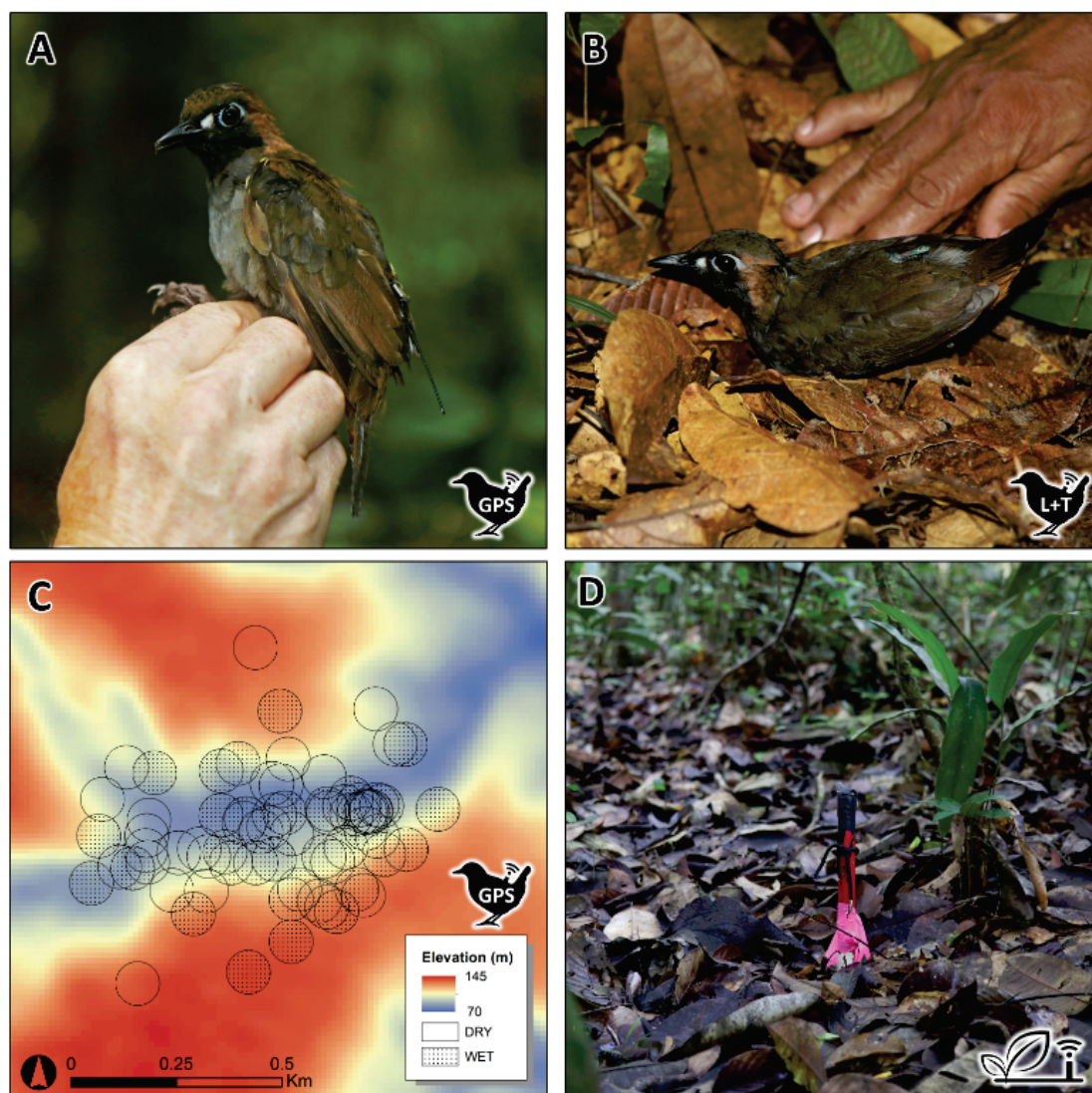43
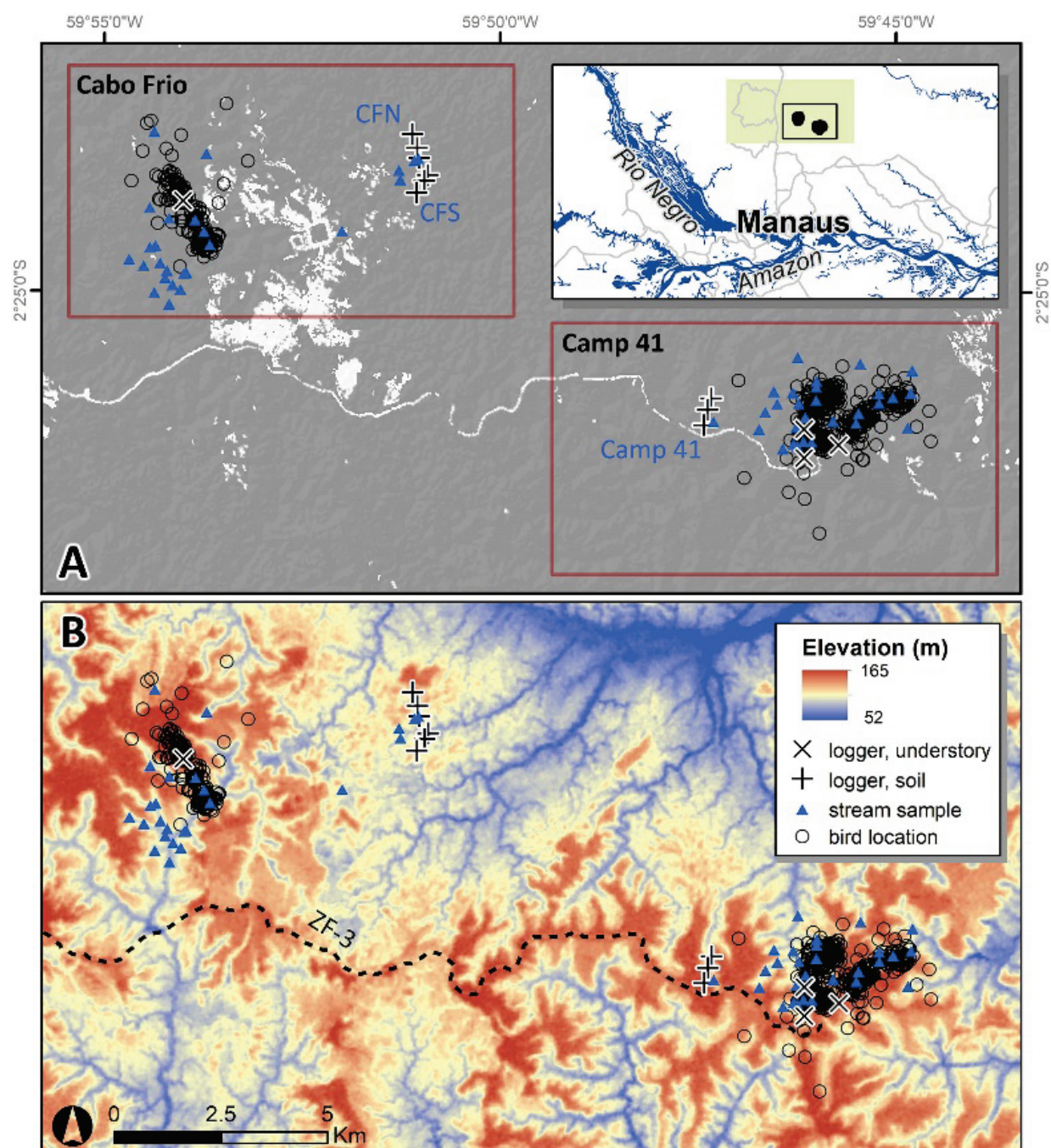
Figure 2.

Figure 3.

Figure 4.

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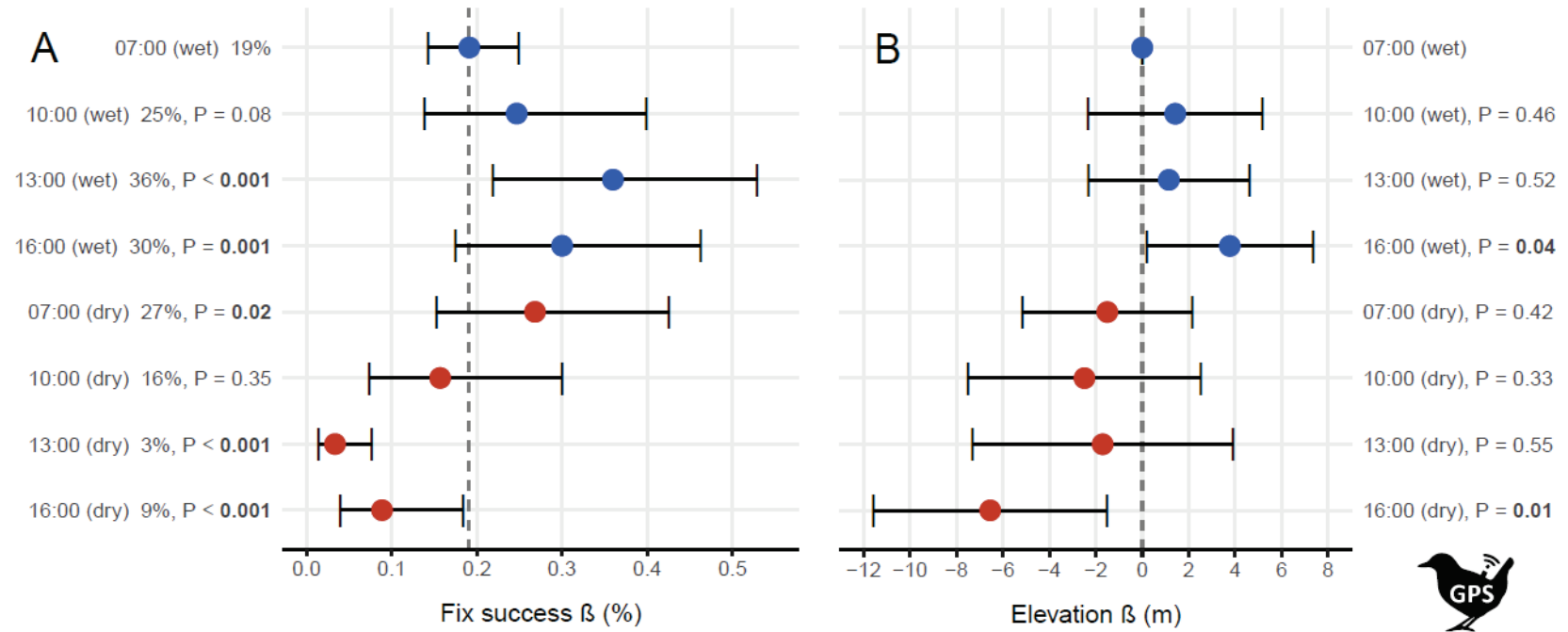
Figure 6.

APPENDIX 1

Appendix 1. Microclimate datalogging transects within Amazonian micro-catchments. We placed nine stations (black crosses) along three transects, each logging soil temperature and moisture data every 10 min from June 2017 to September 2019.

APPENDIX 2

Appendix 2. Tracking *Formicarius analis*. Birds were outfitted with either a GPS tag that recorded locations (A), or a biologger that recorded light intensity and temperature (B). Panel (C) shows locations for one bird categorized by season (dry, wet), where we averaged elevation values within 52 m buffers to account for location error estimated by calibration tags. Calibration tags (both GPS and biologgers) were placed atop short stakes within the forest understory to sample ambient conditions (D).

APPENDIX 3
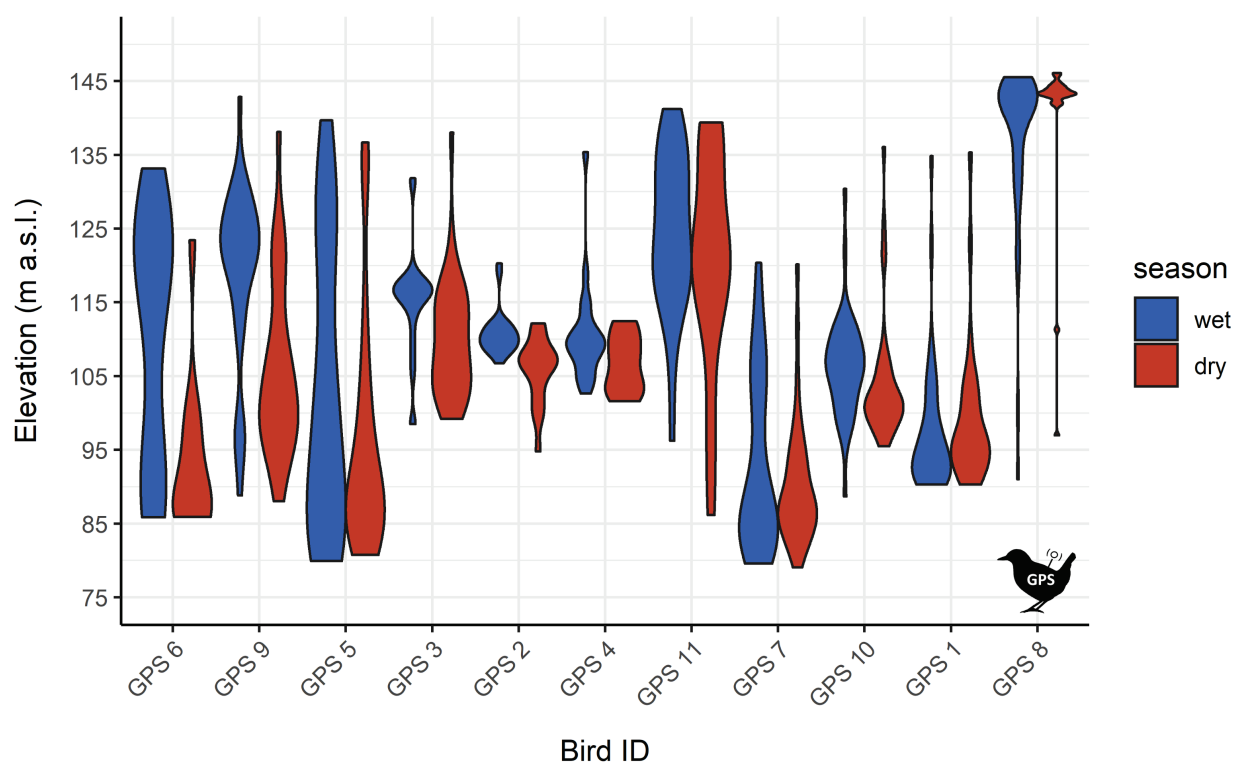
Appendix 3. Violin plots of individual bird elevations by season. Birds are ordered by the mean elevation reduction in the dry season.