

JOURNAL OF AVIAN BIOLOGY

Research

Climate trends and behavior of a model Amazonian terrestrial insectivore, black-faced antthrush, indicate adjustment to hot and dry conditions

Vitek Jirinec, Elisa C. Elizondo, Patricia F. Rodrigues and Philip C Stouffer

V. Jirinec (<https://orcid.org/0000-0001-9856-9681>) ✉ (vjirinec@ierceecology.org), P. F. Rodrigues (<https://orcid.org/0000-0003-3138-6447>) and P. C. Stouffer (<https://orcid.org/0000-0002-0052-0423>), *Biological Dynamics of Forest Fragments Project, Inst. Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.* – VJ, PFR, PCS and E. C. Elizondo (<https://orcid.org/0000-0003-3690-9040>), *School of Renewable Natural Resources, Louisiana State Univ. and LSU AgCenter, Baton Rouge, LA, USA.* VJ also at: *Integral Ecology Research Center, Blue Lake, CA, USA.* ECE also at: *Dept. of Entomology and Wildlife Ecology, Univ. of Delaware, Newark, DE, USA.*

Journal of Avian Biology

2022: e02946

doi: 10.1111/jav.02946

Subject Editor: Andreas Nord

Editor-in-Chief: Jan-Åke Nilsson

Accepted 5 May 2022



Rainforest loss threatens terrestrial insectivorous birds throughout the world's tropics. Recent evidence suggests these birds are declining in undisturbed Amazonian rainforest, possibly due to climate change. Here, we first asked whether Amazonian terrestrial insectivorous birds were exposed to increasingly extreme ambient conditions using 38 years of climate data. We found long-term trends in temperature and precipitation at our study site, especially in the dry season, which was $\sim 1.3^{\circ}\text{C}$ hotter and 21% drier in 2019 than in 1981. Second, to test whether birds actively avoided hot and dry conditions, we used field sensors to identify periodic intervals of ambient extremes and prospective microclimate refugia within undisturbed rainforest from 2017 to 2019. Simultaneously, we examined how tagged black-faced antthrushes *Formicarius analis* used this space. We collected > 1.3 million field measurements quantifying ambient conditions in the forest understory, including along elevation gradients. For 11 birds, we obtained GPS data to test whether birds adjusted their cover usage using variation in GPS fix success ($n=2724$) as a proxy and elevation using successful locations ($n=640$) across seasonal and daily cycles. For four additional birds, we collected > 180 000 light and temperature readings to assess exposure. Field measurements in the modern landscape revealed that temperature was higher in the dry season and highest on plateaus. Thus, low-lying areas were relatively buffered, providing microclimate refugia during hot afternoons in the dry season. At those times, birds apparently entered cover and shifted downslope. Because climate change intensifies the hot, dry conditions that antthrushes seemingly avoid, our results are consistent with the hypothesis that climate change decreases habitat quality for this species. If other terrestrial insectivores are similarly sensitive, climate-induced changes to otherwise intact rainforest may be related to their recent declines.

Keywords: behavioral thermoregulation, climate change, microclimate refugia, seasonality, soil moisture, soil temperature, terrestrial insectivores



www.avianbiology.org

© 2022 The Authors. Journal of Avian Biology published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

Amazonia is the world's largest tropical forest and harbors a substantial portion of global biodiversity. At over 7 million km², nearly equivalent to the continent of Australia, it contains ~10% of described vertebrate species (Silva et al. 2005, IUCN 2020). Rampant deforestation in the region has motivated research on the consequences of clearing and fragmentation for rainforest biota, including the avifauna (Bierregaard and Gascon 2001, Peres et al. 2010, Stouffer 2020). Tropical insectivorous birds are consistently identified as highly vulnerable to anthropogenic disturbance (Powell et al. 2015, Sherry 2021), with ground-foraging species among the most sensitive to landscape alteration. For example, experimental forest isolation led to loss of terrestrial insectivores from fragments in central Amazonia, with extinctions inversely proportional to fragment size (Stouffer and Bierregaard 1995, Stratford and Stouffer 1999). Similar patterns materialized in Ecuador (Canaday 1996, Canaday and Rivadeneyra 2001). Outside of Amazonia, declines of understory insectivores following disturbance were documented particularly in Costa Rica and Panama (Sekercioglu et al. 2002, Sigel et al. 2006, 2010, Visco et al. 2015), but this phenomenon is not restricted to the Neotropics (Powell et al. 2015, Sherry 2021). Strong sensitivity to forest disturbance thus makes terrestrial insectivores indicators of rainforest health.

New studies have uncovered declines of terrestrial insectivores in apparently undisturbed Amazonia. In Ecuador, abundance of these species decreased markedly over a 14-year interval (Blake and Loiselle 2015). Almost 2000 km away, a similar trend was recently described from central Brazil: over four decades, terrestrial insectivores vanished from over half of primary forest sites and their relative abundance dropped substantially (Stouffer et al. 2021). Terrestrial insectivores declined fastest among 12 ecological guilds examined, followed closely by near-ground insectivores. To estimate population trends of rainforest avifauna requires long-term sampling using standardized methods to survey species that are often elusive and rare (Robinson et al. 2018). Within Amazonia, the two studies in Ecuador and Brazil represent the best available information on population trends of rainforest birds in absence of forest disturbance. Both suggest that terrestrial insectivores – already sensitive to landscape processes – are declining.

Why are terrestrial insectivores disappearing from intact forest? Results from studies in disturbed landscapes offer a place to start. Hypothesized explanations range from vulnerability to changing forest structure (Laurance et al. 2002, Stratford and Stouffer 2015), reduction in forest patch area (Stouffer 2007) and several other factors (Powell et al. 2015, Visco et al. 2015, Sherry 2021). Notably, the 'microclimate hypothesis' posits that non-forest areas and forest edges harbor altered microclimates (*sensu* Chen et al. 1999) that are unsuitable for terrestrial insectivores, which are associated with shaded, cool and wet conditions within forest interior. Isolated forest patches gain abnormal microclimate as a consequence of edge effects – they become brighter, hotter, drier

and these conditions become more variable (Laurance et al. 2002, Stratford and Robinson 2005). Several studies concluded birds avoided these microclimates (Karr and Freemark 1983, Laurance 2004, Laurance and Gomez 2005, Patten and Smith-Patten 2012, Ausprey et al. 2021, Jirinec et al. 2021a, but see Pollock et al. 2015), though whether microclimate influences birds directly (via physiology) or indirectly (via resources) remains unclear. Regardless, poor body condition was linked to drier habitat for some species (Wikelski et al. 2000, Busch et al. 2011, Nishikawa et al. 2021), and dry season length was associated with negative population growth (Brawn et al. 2017). With interior forest conditions possibly shifting due to climate change, birds could face these altered, suboptimal microclimates even in undisturbed areas.

Anomalies in ambient conditions are hypothesized to be most detrimental to organisms in stable environments, because ecological theory predicts that physiology is shaped by the conditions under which it evolved (Janzen 1967). Animals that display the narrowest physiological tolerances tend to reside in the tropics (Deutsch et al. 2008, Huey et al. 2009, Porter and Kearney 2009, Diamond et al. 2012, Pollock et al. 2021), where temperature and precipitation are relatively stable throughout the year. This notion is supported both for endotherms, such as birds, and ectotherms – their prey. Within Amazonia, terrestrial insectivores inhabit the most stable of environments – the forest interior floor, removed from both edge effects and the hotter, brighter, drier canopy > 20 m above the ground (Kapos 1989, Walther 2002, Stratford and Robinson 2005, Scheffers et al. 2013, Sheldon et al. 2018). Here, temperature and light intensity near the forest edge and canopy climb, whereas water availability drops. In particular, the hygric niche and its key roles for tropical endotherms are receiving increasing attention (Boyle et al. 2020), and a recent study revealed that terrestrial insectivores in Amazonia selected light microhabitats that were even darker than the shaded forest floor, with treefall gaps > 2200 times brighter than locations birds chose (Jirinec et al. 2022a). In the absence of edge effects, undisturbed forest should provide an optimal environment for terrestrial insectivores and their prey.

Yet even large tracts of primary forest may be experiencing some disturbance. Human activities cause the climate to diverge from historical norms across the globe, including the tropics (Neelin et al. 2006, Mora et al. 2013, Bathiany et al. 2018). In Amazonia, average temperature has climbed ~0.05°C year⁻¹ since 1973 (Almeida et al. 2017). In contrast with consistent warming, precipitation is more spatially variable. Shifts in rainfall regimes are sometimes manifested through wetter wet seasons, but dry seasons are often drier and longer (Fu et al. 2013, Almeida et al. 2017), with droughts predicted in the future (Neelin et al. 2006). Climate change has already been linked to changes in forest structure by increasing tree mortality, abundance of dry-affiliated species and biomass of lianas (Laurance et al. 2014, Esquivel-Muelbert et al. 2019, Aleixo et al. 2019). In central Brazil, climate-linked shifts in body size and shape were detected in an entire community of understory birds, including terrestrial

insectivores (Jirinec et al. 2021a). This mounting evidence shows that today's terrestrial insectivores occupy a hotter and often drier Amazonia than just a few decades ago, with conditions in 'undisturbed' forest increasingly approaching those that result from forest fragmentation. Here, we address two objectives while drawing on extensive research in a landscape of both locally disturbed and undisturbed areas. First, we estimate the exposure of terrestrial insectivores to climate change using 38 years of data from a climate reanalysis focused on our study site, rather than relying on broad regional patterns. Second, to test our hypothesis that hot and dry conditions are unsuitable for birds, we implement field sensors to identify cyclic periods of ambient extremes and prospective microclimate refugia, while simultaneously tracking the behavior of black-faced antthrush *Formicarius analis*, a model terrestrial insectivore.

Methods

Study area

We conducted this study at the Biological Dynamics of Forest Fragments Project (BDFFP), a site that offers a unique opportunity to assess the impacts of environmental change on terrestrial insectivores (Supporting information). Located just north of Manaus, Brazil (Fig. 1), the BDFFP is a nexus of research on the Amazon rainforest (Laurance et al. 2018), including birds (Stouffer 2020), and is one of the sites where terrestrial insectivores declined in primary forest (Stouffer et al. 2021). For more details, see Supporting information.

Ambient conditions

General climate trends since 1966 were recently published for the BDFFP (Jirinec et al. 2021a). Here we replicate that analysis with data from 1981 to 2019 and also use this interval to quantify the timing of the annual seasonal cycle (Supporting information).

We empirically identified prospective microclimate refugia (Supporting information) with field measurements. The buffering effect of physical cover in a rainforest setting was revealed elsewhere (Isaac et al. 2008, Scheffers et al. 2014); here we focused on elevational refugia within small-scale watersheds ('micro-catchments') typical of the region (Tomasella et al. 2008). To determine whether valleys moderated ambient extremes, we measured temperature and soil moisture along three elevational transects with a total of nine datalogging stations (Fig. 1, Supporting information). We selected transects along slopes in primary forest to coincide with LiDAR elevation data and placed stations away from treefall gaps such that each transect held one station at the valley bottom, hillslope and atop a hill or a plateau (Supporting information). The elevation ranges sampled by the three transects were 30, 44 and 46 m (Supporting information). Each station contained one logger (TrueLog100)

and one sensor (SMT100), both manufactured by Truebner (Truebner GmbH, Neustadt, Germany). We inserted sensors fully into the ground; temperature and water content readings thus correspond to the topmost 11 cm of soil – a relevant stratum for birds that seldom leave the forest floor. Loggers were programmed to measure temperature (°C) and soil moisture (% volumetric water content) every 10 min for the duration of sampling. We assigned the sampling periods to be Aug–Nov (dry season; DS) and Feb–May (wet season; WS). We chose these months because they fell within the DS or WS based on historical rainfall data (Fig. 2), contained the most bird observations, and were of equal length for the analysis of microclimate conditions. Aside from automated measurements at these nine locations, we manually sampled stream temperature within valleys across a broader area to investigate the effects of perennial streams on valley microclimate, and to assess opportunities for cooling via bathing (Jullien and Thiollay 1998). These 53 samples were collected evenly throughout daylight hours over 32 days within 21 Jun–13 Sep 2019 in the two study areas (Fig. 1).

Tracking bird behavior

Because vagile animals can exploit heterogeneity within their habitat to maintain optimal body temperature by behavioral thermoregulation (Cowles and Bogert 1944, Porter et al. 1973, Stevenson 1985, Huey et al. 2003), we expected birds to seek areas that buffer hot and dry conditions during the DS. To examine this empirically, we used the WS as the baseline for comparison, and tested our prediction that birds move downslope and into cover during the DS (see Supporting information: Microclimate refugia).

We selected *F. analis* as a model terrestrial insectivore. The BDFFP contains 13 species of terrestrial insectivores (Stouffer 2007), but only *F. analis* is both adequately common and sufficiently large to carry GPS tags (Johnson and Wolfe 2017, Rutt et al. 2017, Jirinec et al. 2021b). The species is a permanent resident that maintains a year-round territory defended by a mated pair, but territory stability can fluctuate among years (Stouffer 2007). Five radio-tracked birds revealed a home range size of ~12 ha (Stouffer 2007), though our study suggest average home range over longer time intervals may be about twice this size (Supporting information). Nevertheless, even the smaller estimate indicates home ranges can contain sufficient topographical gradients for elevational refugia in this landscape. As with nearly all terrestrial insectivores, capture rates of *F. analis* displayed a declining trend since the early 1980s in the Bayesian analysis in Stouffer et al. (2021) – i.e. > 50% probability that this species has declined. These results rest on raw captures of 9 and 3 individuals captured in > 26 000 and > 13 000 net hours in two intervals, respectively. Low capture numbers indicate that *F. analis* occurs at low densities and seldom falls in mist nets, leading to wide credible intervals on abundance trends for this and other terrestrial insectivores.

We caught territorial birds using target-netting. First, we located birds by broadcast of conspecific playback to elicit a

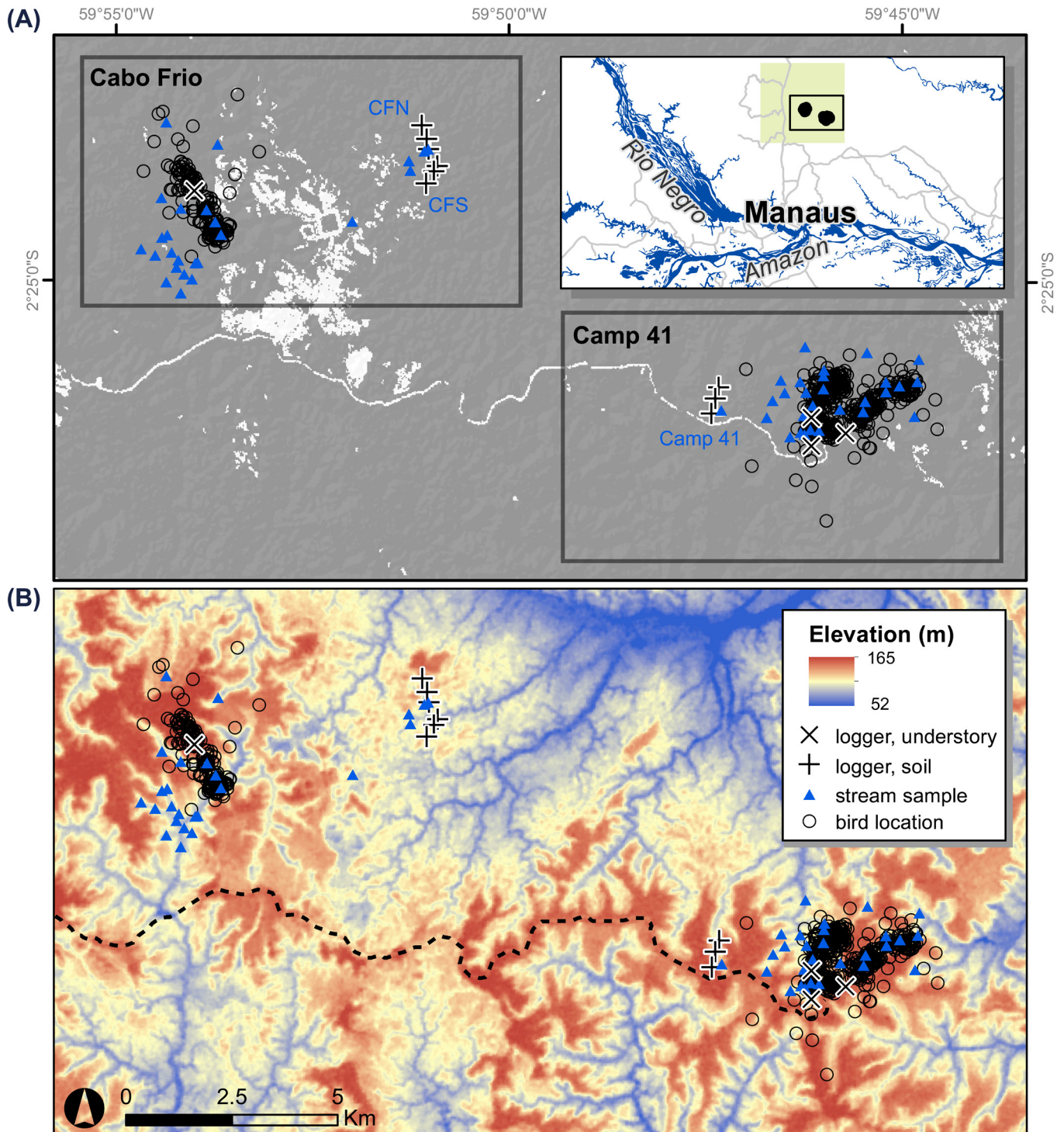


Figure 1. Survey areas at the Biological Dynamics of Forest Fragments Project in the state of Amazonas, Brazil. Panel 'A' depicts the two study areas, Cabo Frio and Camp 41, with Landsat-derived forest cover in 2017 (gray). Panel 'B' shows topographical variation (range ~100 m) in the same scene. Both panels contain the 640 GPS locations of 11 *Formicarius analis* individuals considered in this analysis (2017–2019), as well as the locations of sensors that measured ambient conditions. The green rectangle (inset) shows the region where we summarized ERA5-Land data for the climate change analysis.

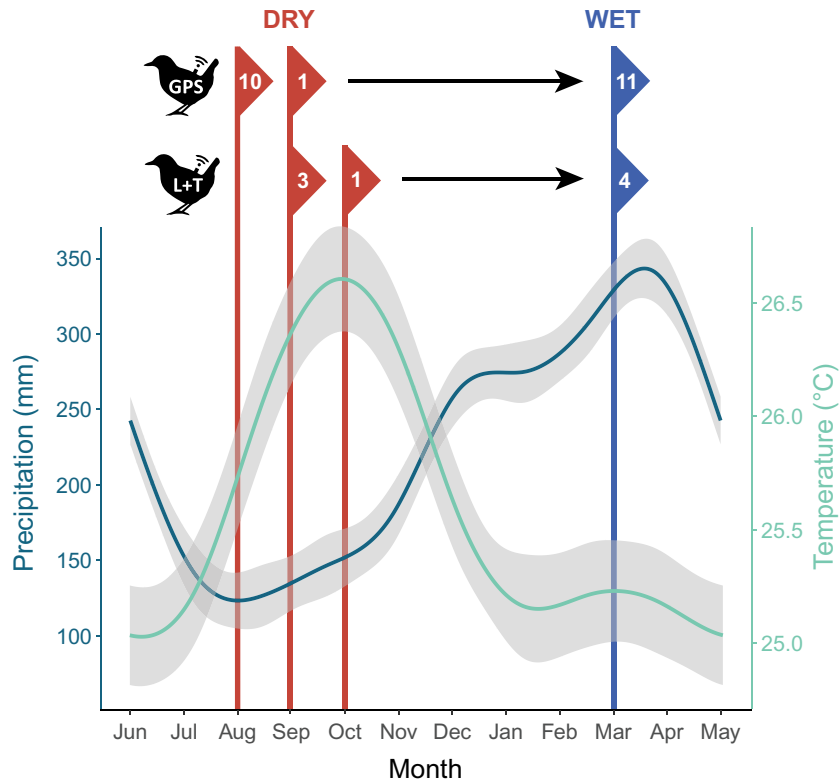


Figure 2. Annual climate and schedule of bird sampling. We first used an autoregressive generalized additive model and local rainfall and temperature data to broadly identify periods of annual climate extremes for comparison of bird behavior. Climate data come from ERA5-Land reanalysis and are a compilation of 38 years for our study area. Lines are model fits with the 95% CI shaded in gray. We then tracked black-faced anthruses *Formicarius analis* over one annual cycle, either with a GPS ($n=11$) or a temperature logger ($n=4$). Flags represent sample sizes and sampling onsets. For birds with GPS tags, individuals were tracked over one month in the dry season (Aug or Sep) and one month the following wet season (Mar), depending on year. Birds with biologgers were tracked over two months in each season, starting either in Sep, Oct or Mar.

vocal response of a local territorial individual. After detection, we set two or more 12-m mist nets (32 mm mesh) arranged in a ‘V’ formation with playback in the center. When a focal bird approached the playback speaker, a concealed operator flushed the bird into the nets. We then repeated the capture process the following year to recover devices. Initial trapping and data recovery required 257 days spread across 12 months in three years: 2017 (Jun–Aug), 2018 (Jun–Oct) and 2019 (Jun–Sep). At each capture occasion, we took standard morphometric measurements, cloacal temperatures and applied (or removed) either GPS or biologging tags. Age and sex is difficult to determine for this species (Johnson and Wolfe 2017), but we only tagged birds that were in their definitive plumage. For details about tag fitting, materials and the lack of detrimental effects of tagging on study birds, see Jirinec et al. (2021b).

We tracked bird positions in space and time with archival GPS tags (PinPoint-50; Lotek, Newmarket, Ontario, Canada). Tags had a 12-second timeout after which they either acquired sufficient GPS signal to determine location (fix=success) or not (fix=fail). We programmed tags to try one fix every three daylight hours over one month in each of the two seasons (07:00, 10:00, 13:00, 16:00 local time). This

schedule ensured tag battery would last the study interval while consistently sampling diel periods without influence of possible commutes to roosting areas (Jirinec et al. 2015), and allowed us to compare a similar number of locations (up to 124 fixes per season) for each bird. In 2017 and 2018, we deployed a total of 18 GPS tags, of which we recovered 11 in subsequent years. Recovered tags contained locations from eight birds in the 2017 DS–2018 WS cycle and three birds in the 2018 DS–2019 WS cycle (Fig. 2). Using successful fixes, we extracted elevation from a 12-m WorldDEM (Riegler et al. 2015) and tested whether elevational use shifted in tandem with ambient conditions (Supporting information).

While we used successful GPS fixes to measure elevation shifts, we applied both successful and failed fixes to track cover use (Supporting information). Because the precision of GPS tags was insufficient to resolve microhabitat directly from x to y coordinates (Supporting information), we employed the inverse probability of GPS fix as a proxy for cover use (i.e. low fix probability reflects more cover use). Dense vegetation and other physical barriers hinder satellite signal, leading to relatively fewer locations within these areas (Di Orio et al. 2003, Jiang et al. 2008, Recio et al. 2011). Although this is usually undesirable, here it allowed us to track cover use indirectly

with standardized intervals over which tags located satellites (12 seconds). Because GPS signal varies little spatially and temporally ('GPS.gov: space segment' 2020), the probability of successful GPS fix is inversely proportional to the level of surrounding obstruction, with probability of fix near '1' in open sky and '0' inside logs, stumps or dense vegetation. To evaluate this assumption, we radio-tracked a single *F. analis* between 19 Jul and 24 Aug 2017, which allowed us to observe behavior directly. If birds sought cover during periods of ambient extremes, those times should coincide with relatively lower average probability of GPS fix even if not all failed fixes represented birds entering cover. It is important to note that this species nests in cavities and breeding may thus be conflated with cover use. But because antthrushes generally nest during the WS at our site (Stouffer et al. 2013), relatively lower GPS fix rate in the DS would indicate that signal-inhibiting factors are stronger outside the breeding season.

To quantify exposure to ambient microclimate, we tracked birds with biologging tags ('geolocators'; Intigeo-P65B1-11T-20deg, Migrate Technology, Cambridge, UK). Tags recorded light intensity (lux) every 5 min and temperature (°C) every 15 min for two months each season. Biologgers sampled both light intensity and temperature atop a stalk to prevent feather shading (Supporting information). Thus, light readings represented direct exposure to light, while temperature was a combination of body and ambient temperature. To better understand the relationship between tag measurements and ambient conditions, we sampled light and temperature with four ambient biologgers that were placed near tagged birds ~10 cm high in the understory of mature forest, at a mean elevation of 136 m (Fig. 1, Supporting information). We also sampled the body temperature of 36 individual birds via cloacal measurements (McCafferty et al. 2015) using a medical thermometer (HM-1255, Highmex Care, China) with an upper temperature limit of 43.0°C. Measurements were taken as soon as possible after capture to lessen its effects on body temperature (Prinzinger et al. 1991). In 2017 and 2018, we deployed 13 biologgers on birds, of which we recovered four in the following years in areas broadly representing habitat where birds were tracked with GPS (three recoveries in Cabo Frio, one in Camp 41). Light and temperature data came from three birds tracked over the 2017–2018 seasonal cycle: Sep–Oct and Mar–Apr, and one bird tracked over the 2018–2019 cycle in Oct–Nov and Mar–Apr (Fig. 2). Ambient loggers collected data in concert with bird tags, providing an approximation of ambient conditions to which birds were exposed. Measurements from identical devices on birds and their environment allowed us to see whether bird behavior changed with ambient conditions.

Results

Ambient conditions

Temperature and precipitation trends indicated climate change at the BDFFP over the last four decades, matching

earlier results (Jirinec et al. 2021a). Within- and among-year variation in both climate variables was considerable, but three of the four models revealed significant trends over time (Fig. 3). DS temperature had the strongest positive relationship with year – in 2019, mean DS temperature was ~1.3°C higher than in 1981. Temperature in the WS also rose – in 2019, mean WS temperature was ~0.6°C higher than in 1981. DS rainfall declined over time, with mean 2019 precipitation totaling ~34 mm (21%) less than in 1981. Mean WS rainfall indicated an increasing, but insignificant trend. These trends indicate that terrestrial insectivores at the BDFFP are

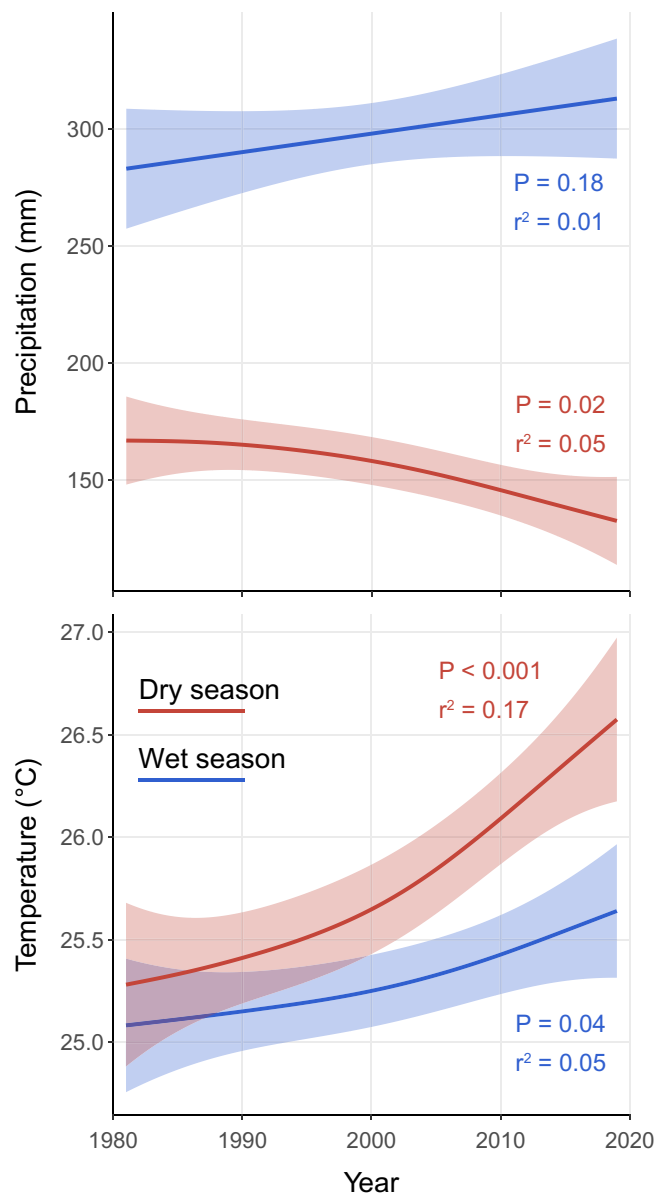


Figure 3. Climate change at the Biological Dynamics of Forest Fragments Project (BDFFP) within Amazonian Brazil. Lines are fitted generalized additive models with ARMA errors, with shading representing 95% CI. Climate data are monthly summaries compiled for the BDFFP area from ERA5-Land reanalysis.

currently exposed to significantly hotter and drier conditions than in the early 1980s – especially during the DS.

Microclimate differed by time of day, season and elevation (Supporting information, Fig. 4). The nine microclimate stations, operational Jun 2017–Sep 2019, acquired 594 119 readings of both temperature and soil moisture over the four seasonal intervals. Soil moisture was lowest overall in the DS, but elevation created the strongest contrasts, with driest conditions at uppermost sites while valleys remained much wetter. Temperature varied by season, with higher mean, daily minimum, maximum and range in the DS. Temperature extremes intensified at upper elevations (Fig. 4). Daily peaks in temperature emerged most often between 14:00 and 15:00, regardless of season, although they tended to occur ~30 min later in the DS and were more variable during the WS (Supporting information). Stream temperature during the DS was relatively cool and varied little across space and time (mean \pm SD = 24.6 \pm 0.4°C, range = 23.6–25.7, n = 53). In summary, afternoons in the dry season produced the hottest and driest periods of the year, but valleys offered microclimate refugia where conditions were milder.

Bird behavior

The 11 GPS tags attempted a total of 2724 fixes, but only 688 (25%) were successful (640 after outlier removal; Supporting information). The four bird biologgers returned a total of 140 245 light and 46 748 temperature measurements, whereas the four ambient loggers returned 125 232 and 41 744 measurements, respectively.

We detected significant temporal patterns in the probability of GPS fix – our proxy for cover use. The top model, by $\Delta AIC_c > 53$, was the interaction model that contained both time of day (hour) and season (Supporting information). Using 07:00 in the WS as the baseline, cover use (inverse of GPS fix success) was significantly lower at 13:00 and 16:00 in the WS but increased substantially at 13:00 and 16:00 in the DS (Fig. 5A). In the seasonal model, probability of a successful fix was 27% in the WS and 22% in the DS ($\beta_{\text{dry}} = -0.29$, SE = 0.09, $p = 0.001$).

Birds shifted downslope during ambient extremes. In model selection using AIC_c , the seasonal model was better than models that contained both hour and season covariates (Supporting information). According to this seasonal model, birds were ~4 m lower in the DS than the WS ($\beta_{\text{dry}} = -4.35$, SE = 0.90, $t = -4.85$, $p < 0.001$, $r^2_c = 0.56$). In the second model (interaction between hour and season), bird elevation varied significantly by time of day within season (Fig. 5B). Using 07:00 in the WS as the baseline, birds were ~4 m higher at 16:00 in the WS ($\beta_{16:00, \text{wet}} = 3.77$, SE = 1.84, $t = 2.05$, $p = 0.04$) and ~7 m lower at 16:00 in the DS ($\beta_{16:00, \text{dry}} = -6.54$, SE = 2.57, $t = -2.54$, $p = 0.01$, $r^2_c = 0.56$). For the single bird tagged with a radio tag, we collected 68 locations that were concentrated in the DS afternoon, but we saw the bird only once (1%) and triangulation suggested it often hid in a large, streamside log.

Biologgers showed that birds altered their behavior by season (Fig. 6). Light intensity varied considerably through time in both bird and ambient datasets – model r^2 were relatively low, especially in the WS. Birds selected much darker environments (by one or more orders of magnitude) than shown by ambient biologgers, and occupied darker microhabitats in the DS even though the light environment was far brighter at that time. Temperature recorded by both bird and ambient loggers was higher in the DS, but the seasonal difference in peak temperature was about ~1°C lower for birds. Body temperature of birds obtained via cloacal measurements was high (41.7 \pm 0.7°C, range 40.3–43.0°C, n = 36), with tags showing birds were exposed to higher ambient temperatures in the DS – tags recorded peaks at ~36.3°C in the DS and ~35.5°C in the WS. The timing of birds' daily temperature peaks was similar in both seasons (14:16 and 14:21 in the DS and the WS, respectively). However, in contrast to ambient conditions, the variation in timing was usually smaller and similar across seasons for birds (Supporting information).

Discussion

We collected > 1.3 million measurements of environmental conditions and bird behavior across three years in the Amazonian forest understory. We found that the black-faced antthrush – a member of the sensitive terrestrial insectivore guild – behaved in a manner consistent with avoidance to extremes in ambient conditions. Valleys and cover offered microclimate refugia, and bird behavior suggested they moved to such locations during the afternoons of the dry season – the hottest and driest periods of the year. Importantly, over the last four decades, trends in temperature and precipitation at our study site suggest directional climate change that matches large-scale estimates from climate models for the region (Pachauri et al. 2014). Our analysis indicated that the dry season has become more severe at the BDFFP – averaging ~21% drier and ~1.3°C hotter than in the early 1980s, results that align with a recent study which also linked these changes to shifts in bird body size and shape (Jirinec et al. 2021a). Although there are other possible explanations for the observed bird behavior (discussed below), our a priori expectations were based on the mounting evidence that terrestrial insectivores are sensitive to shifts in ambient conditions (Powell et al. 2015, Sherry 2021). Our results were consistent with these expectations and suggest that birds are subjected to increasingly unfavorable conditions. Even if birds can effectively buffer their exposure with such behavior, periodic reductions in habitat and mobility constrain foraging opportunities; warming climate thus shortens the interval over which birds can meet their energetic needs (Chappell and Bartholomew 1981, Bennett et al. 1984). This study was designed in response to declines of terrestrial insectivores at both Amazonian sites with long-term data on primary forest avifauna, including the BDFFP (Blake and Loiselle 2015, Stouffer et al. 2021), with the goal to evaluate whether climate change was a possible mechanism. We conclude that

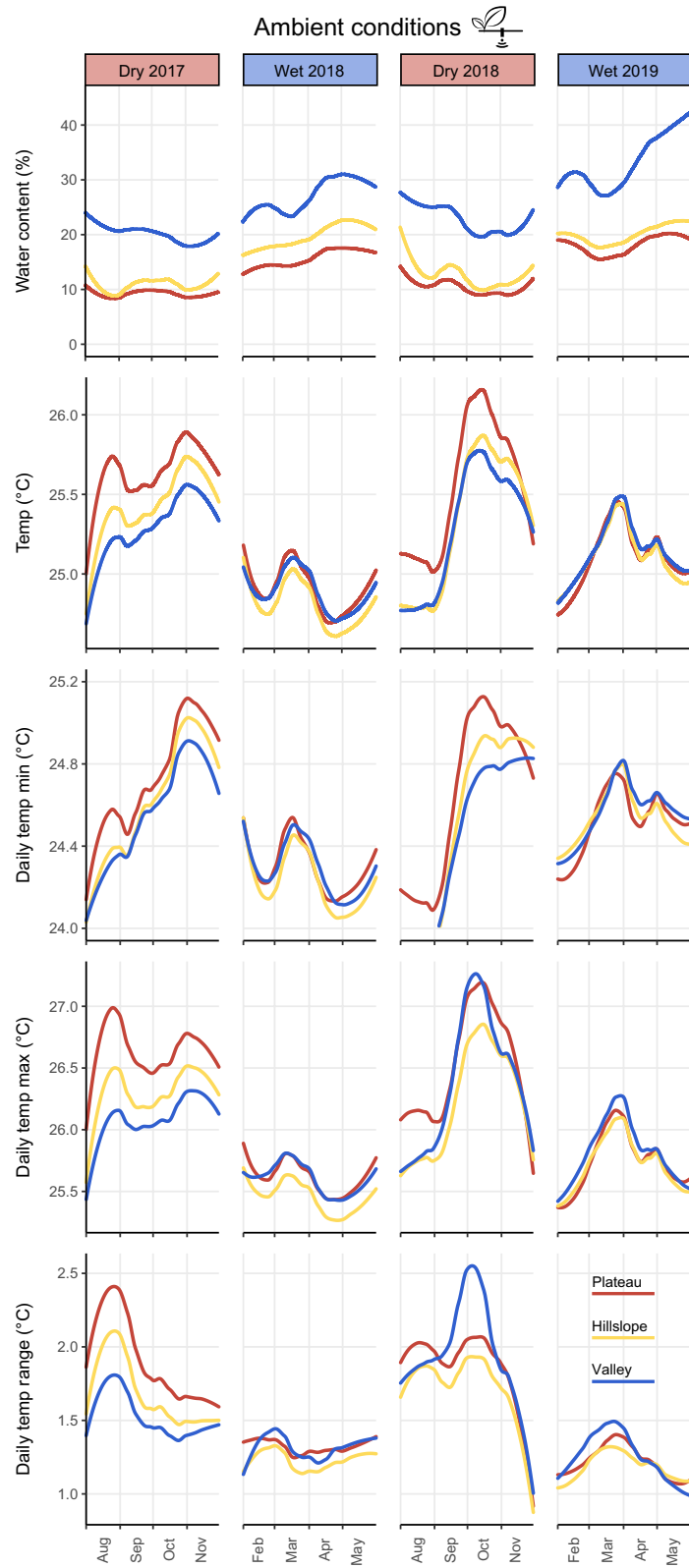


Figure 4. Forest floor microclimate within Amazonian micro-catchments in primary *terra firme* forest. Plots depict water content and temperature measurements from the top 11 cm of soil at nine microclimate stations arranged along three elevational transects, each with a station placed in a valley (blue), hillslope (yellow) and atop a plateau (red). Stations obtained a reading every 10 min during each four-month season; here we show the locally estimated scatterplot smoothing of the average for each elevational group (i.e. each line smooths the mean of the three timeseries).

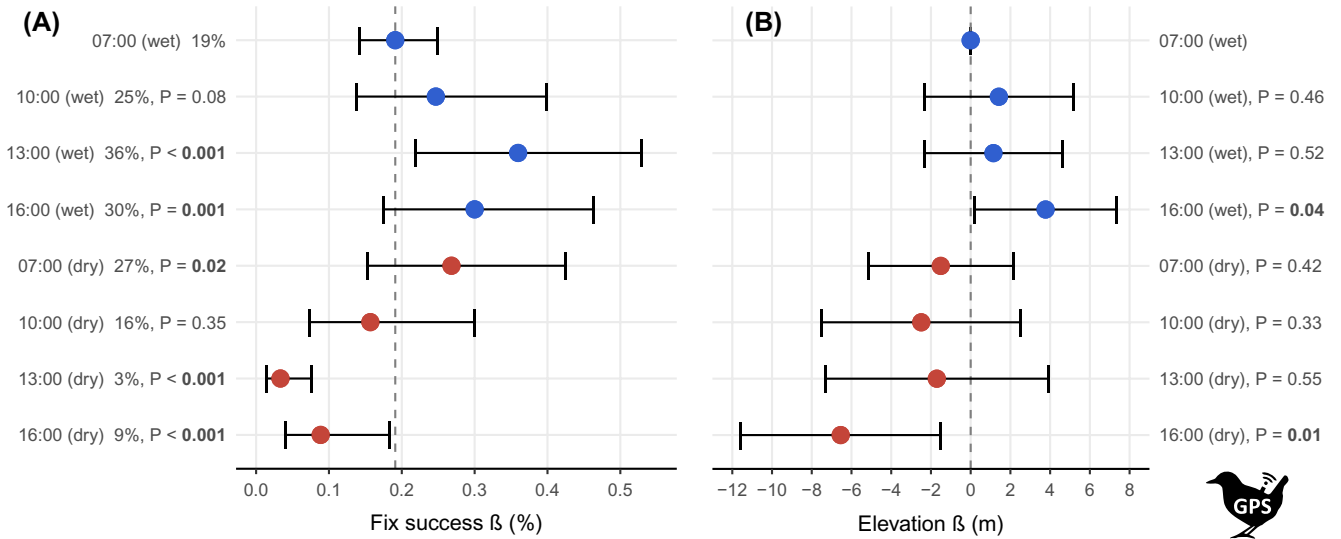


Figure 5. Probability of GPS fix (A) and elevation (B) by time of day and season for tags on 11 *Formicarius analis* in primary, continuous *terra firme* forest. Each bird was tracked four times daily over one month in the dry season (red) and one month in the wet season (blue) in 2017–2019. Error bars represent 95% confidence intervals and p-values test the difference against a baseline (dashed line: 07:00 in the wet season).

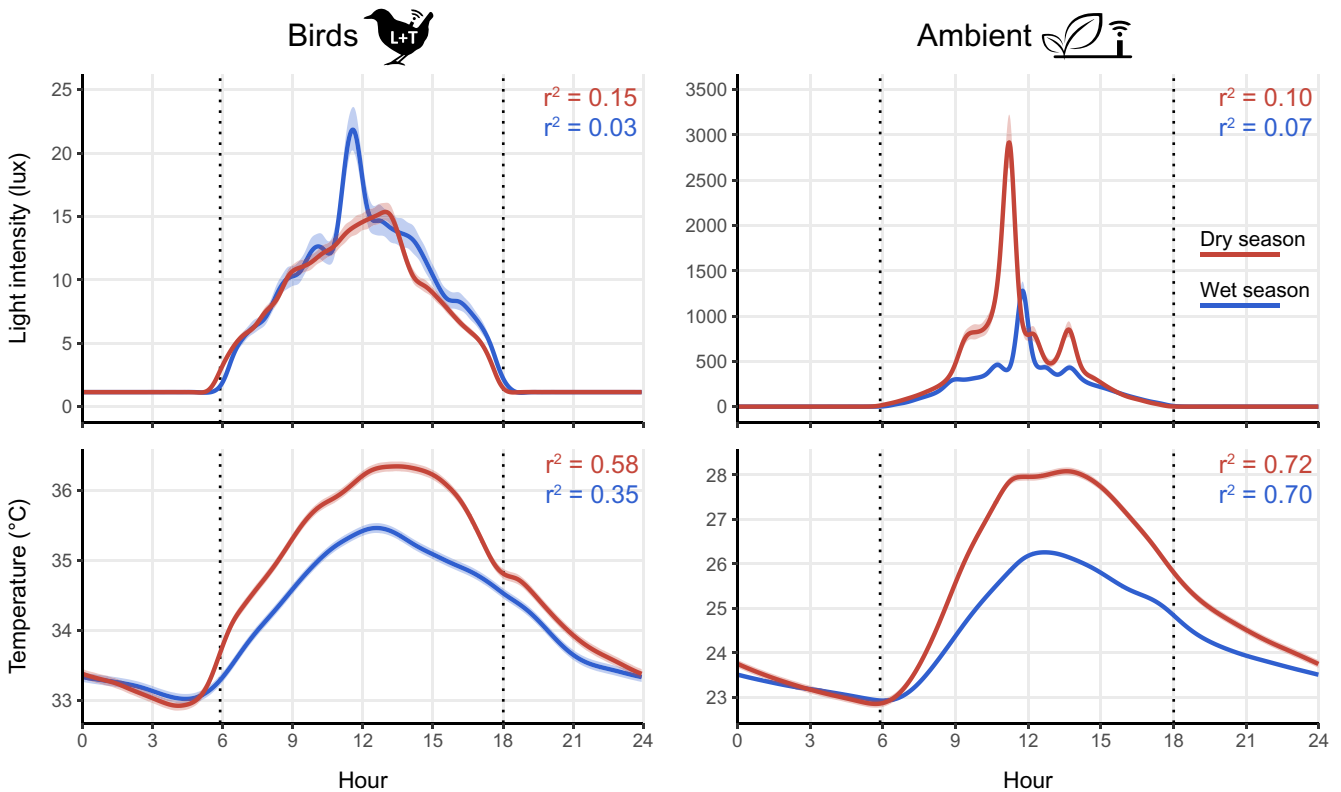


Figure 6. Light and temperature environment by day and season for birds and ambient conditions. Lines and 95% CIs are fits from generalized additive models with birds ($n = 4$) and ambient loggers ($n = 4$) as random effects. Note that y-axis on the ambient light plot is 2 orders of magnitude higher.

the current trends in temperature and precipitation likely do lower habitat quality for *F. analis* and similar species.

In lowland tropical rainforest, terrestrial insectivores inhabit the coolest and most stable of a warm environment (Janzen 1967), with a limited palette of options to behaviorally thermoregulate during hot and dry periods (Huey et al. 2012). For these birds, we hypothesized that valleys and cover may function as refugia and predicted that these would be used preferentially during ambient extremes (Karr and Freemark 1983). Accordingly, we found that *F. analis* shifted its average elevation downslope during the DS – by up to 10 m (Fig. 5B). Our proxy for cover use (low probability of GPS fix) also revealed strong daily patterns within season (Fig. 5A). Compared to a WS morning baseline, these results suggest that cover use was 12× higher at 13:00 and 3× higher at 16:00 in the DS. Data from biologgers supported these results – although ambient light conditions were far brighter in the DS likely owing to lower cloud cover and foliage density (Graham et al. 2003, Nepstad et al. 2004), birds at that time occupied darker areas (Fig. 6). If birds attempted to behaviorally thermoregulate, they still experienced average temperatures ~1°C higher in the DS than the WS, though the DS ambient temperature was ~2°C higher (Fig. 6). The scope of this study did not include determining whether birds experienced heat stress, or that they would in absence of the behavior we documented. Heat stress is a function of temperature, water availability and activity (Huey et al. 2012), and thus challenging to determine for free-living individuals. Rather, we monitored temperature and water availability at various temporal scales to reveal the best opportunity for heat stress to arise – the afternoons during the modern dry season – and demonstrated that bird activity was consistent with seeking cooler and wetter areas at that time. We acknowledge that other explanations exist for these periodic movements, including birds tracking invertebrate prey itself responding to environmental change (below). Regardless of the root cause of observed behavior, the ultimate reason for biological seasonality is climate. Directional climate change together with our results suggest *F. analis* and similar species may occupy increasingly suboptimal environment.

Our data indicated that thermal and hydrological dynamics behaved as expected at the BDFFP, generating microclimate refugia at the valley bottoms. We found stream temperature – within valleys in the DS – to be relatively constant and cool (24.6°C), which was 17.1°C lower than the average body temperature of *F. analis* (41.7°C). Thus, even if only through bathing (Jullien and Thiollay 1998), streams within valleys offered opportunities for rapid cooling. Aside from direct access to streams, valley moisture likely supplied indirect cooling benefits. Hydrology within Amazonian micro-catchments is dominated by baseflow – rain infiltrates to groundwater and is slowly released into streams, which consequently have a relatively steady flow throughout the year (Tomasella et al. 2008), buffering temperature extremes (Fridley 2009, Davis et al. 2019). More water within valleys may also allow cooling by enabling higher evapotranspiration when forest may be water-limited in drier areas and periods

(Aleixo et al. 2019, Berg and Sheffield 2019). Thus, in the DS, the demarcation between the dry upper slopes and wet lower slopes is not gradual (Fig. 4). This threshold means that even a relatively small downslope shift can result in markedly wetter and cooler conditions. In our data, the second DS was the only exception to this pattern – valleys showed higher maximum and range (but not average) in temperature, but we attributed this to treefalls that had occurred at two of the three valleys sites, likely causing higher solar input. Otherwise, temperature average, minimum, maximum and range were all higher in the DS and amplified on plateaus. Notably, the effect of elevation on temperature (but not water content) was erased in the WS. This may be because cloud cover (Graham et al. 2003), air humidity (Aleixo et al. 2019) and environmental water content are all higher during the WS, mediating temperature fluctuations across the landscape. Passing clouds and precipitation possibly led to the inconsistent times of daily temperature peaks in the WS (Supporting information).

Aside from downslope shifts, cover use is another potential type of behavioral thermoregulation. Low rates of successful GPS fix implied that birds sought cover in the afternoons of the DS – tags were nearly unable to acquire signal at 13:00 (3% success) and 16:00 (9% success), whereas the highest success rates occurred at 13:00 and 16:00 in the wet season (30 and 36%; Fig. 5A). Elevation at bird locations suggested that *F. analis* shifted downslope between 13:00 and 16:00 in the DS, where GPS signal could be harder to acquire, but birds were not significantly lower when fix probability was lowest at 13:00. Our calibration data (Supporting information) demonstrate that elevation alone cannot account for fix probability; both calibration tags obtained much higher success rates than bird tags, with the lower device attaining a slightly higher success rate than the upper device (69% versus 66%). This suggests that physical cover, in addition to valleys possibly blocking signal, drove the reductions in GPS fix rates. This notion was corroborated by our manually tracked bird – although observations concentrated in the afternoon, we only saw the bird once (1%) and triangulation suggested it often hid in a large, streamside log. Our results are thus consistent with the hypothesis that, during periods of ambient extremes, birds sought physical cover where ambient conditions were buffered (Scheffers et al. 2014).

We suggest our results are most compatible with birds responding directly to ambient extremes, but we cannot rule out other explanations. A recent comparison of heat tolerances of tropical and temperate birds that included *F. analis* indicate that tropical birds have lower tolerances but appear to be sufficiently buffered from climate change (Pollock et al. 2021). Their study measured responses to acute heat stress of stationary birds, highlighting the need to examine the role of chronic exposure to increasing temperatures or access to water – a critical component of endothermic thermoregulation and ecology (Huey et al. 2012, Boyle et al. 2020). Downslope shifts towards perennial streams in the water-limited DS could explain elevational movements in this study, though variation in cover use (GPS success) would

remain to be justified. Another potential mechanism for elevational shifts is tracking prey availability – biomass of arthropods in the leaf litter drops with soil moisture (Levings and Windsor 1984, Jirinec et al. 2016), including seasonal reductions in the DS (Willis 1976, Pearson and Derr 1986, McKinnon et al. 2015), and vertical movements within the leaf litter (Usher 1970). Mestre et al. (2010) quantified prey in regurgitated samples of *F. analis* at the BDFFP, predominantly finding ants (Formicidae; ~55%). In Panama, ant activity dropped by 25% in the DS and was > 200% higher in ravines than exposed plateaus (Kaspari and Weiser 2000). Capture rates of terrestrial insectivores as a guild – and *F. analis* in particular – correlated with litter arthropod abundance, suggesting that these birds track resource availability within their home ranges (Karr and Brawn 1990). A critical question is whether sufficient resources are accessible to birds at all times of year under current and future climate scenarios. However, that is a challenging question to answer and our data offer no such resolution.

Future studies can augment this research in several ways. Although the variation in GPS fix success allowed us to estimate cover use, the challenging environment for GPS tags resulted in a loss of ~75% of locations with elevation data. This introduced two concerns. First, the markedly smaller size of the elevation dataset may have reduced our ability to resolve the effect of season and daytime as AIC_c substantially penalized the interaction model due to its complexity (Supporting information). Second, areas and times where tags received relatively few fixes may have been underrepresented – a concern raised in previous studies on habitat selection (D'Eon 2003). However, GPS tags recorded substantially higher number of fixes in the WS when GPS signal should have been hindered by cloud cover and higher foliage density (Graham et al. 2003, Nepstad et al. 2004, Fig. 6). To obtain these results, birds must have moved higher up and to more open locations during the WS. Researchers could avoid the above complications with direct observations of radio-tagged birds, though that raises complications in logistics, observer effects on birds and standardization of location times. Although our conclusions stand on relatively high-resolution and diverse datasets, we only considered a single species, two seasonal cycles and a single site. We propose two studies that could further evaluate the effects of changing conditions for terrestrial insectivores: 1) testing whether less sensitive ground-foraging species do not respond to ambient extremes, and 2) a long-term study of whether annual elevational shifts and cover use are a function of the seasonal severity in a given year.

Conclusion

Our results are consistent with the predictions of this microclimate hypothesis for birds in continuous primary forest. Furthermore, we underscore that climate change will increasingly produce such conditions in lowland Amazonia, which mostly lacks topographical variation and associated refugia.

If these sensitive specialists act as a barometer within the vast and biodiverse forests of Amazonia, their behavior raises cause for concern.

Acknowledgements – We thank Bruna Amaral, Flamarion Assunção and Jairo Lopes for tireless assistance in the field. Cameron Rutt conceptualized geolocator use to study microclimate and supplied critical feedback. Erik Johnson, Richard Keim, Michael Kaller, Michael Dance and Stephen Midway provided constructive comments in analysis and interpretation of data. Ryan Burner compiled climate data. Field logistics were facilitated by the BDFFP. This is publication no. 840 of the BDFFP Technical Series and no. 64 of the Amazonian Ornithology Technical Series of the INPA Collections Program. The manuscript was approved by the Director of the Louisiana State Univ. Agricultural Center as manuscript number 2022-241-37078.

Funding – US National Science Foundation (LTREB grant no. 0545491 and 1257340), the National Institute of Food and Agriculture, US Department of Agriculture, McIntire Stennis projects no. 94098 and 94327, Smithsonian Tropical Research Inst., Neotropical Bird Club, American Philosophical Society, American Ornithological Society, Animal Behavior Society and the Wilson Ornithological Society.

Conflicts of interest – The authors declare no conflict of interests.

Author contributions

Vitek Jirinec: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (lead); Methodology (lead); Project administration (supporting); Resources (supporting); Supervision (supporting); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Elisa C. Elizondo:** Funding acquisition (supporting); Writing – review and editing (supporting). **Patricia F. Rodrigues:** Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Philip C Stouffer:** Conceptualization (supporting); Data curation (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (lead); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

Transparent peer review

The peer review history for this article is available at <<https://publons.com/publon/10.1111/jav.02946>>.

Data availability statement

Data is available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.5qfttdz7z>> (Jirinec et al. 2022b).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Aleixo, I., Norris, D., Hemerik, L., Barbosa, A., Prata, E., Costa, F. and Poorter, L. 2019. Amazonian rainforest tree mortality driven by climate and functional traits. – *Nat. Clim. Change* 9: 384–388.
- Almeida, C. T., Oliveira-Júnior, J. F., Delgado, R. C., Cubo, P. and Ramos, M. C. 2017. Spatiotemporal rainfall and temperature trends throughout the Brazilian Legal Amazon, 1973–2013. – *Int. J. Climatol.* 37: 2013–2026.
- Ausprey, I. J., Newell, F. L. and Robinson, S. K. 2021. Adaptations to light predict the foraging niche and disassembly of avian communities in tropical countrysides. – *Ecology* 102: e03213.
- Bathiany, S., Dakos, V., Scheffer, M. and Lenton, T. M. 2018. Climate models predict increasing temperature variability in poor countries. – *Sci. Adv.* 4: eaar5809.
- Bennett, A. F., Huey, R. B., John-Alder, H. and Nagy, K. A. 1984. The parasol tail and thermoregulatory behavior of the cape ground squirrel *Xerus inauris*. – *Physiol. Zool.* 57: 57–62.
- Berg, A. and Sheffield, J. 2019. Historic and projected changes in coupling between soil moisture and evapotranspiration (ET) in CMIP5 models confounded by the role of different ET components. – *J. Geophys. Res. Atmos.* 124: 5791–5806.
- Bierregaard Jr., R. O. and Gascon, C. 2001. The Biological Dynamics of Forest Fragments Project: overview and history of a long-term conservation project. – In: Bierregaard Jr., R. O., Gascon, C., Lovejoy, T. E. and Mesquita, R. (eds), *Lessons from Amazonia*. Yale Univ. Press, pp. 5–12.
- Blake, J. G. and Loiselle, B. A. 2015. Enigmatic declines in bird numbers in lowland forest of eastern Ecuador may be a consequence of climate change. – *PeerJ* 3: e1177.
- Boyle, W. A., Shogren, E. H. and Brawn, J. D. 2020. Hygric niches for tropical endotherms. – *Trends Ecol. Evol.* 35: 938–952.
- Brawn, J. D., Benson, T. J., Stager, M., Sly, N. D. and Tarwater, C. E. 2017. Impacts of changing rainfall regime on the demography of tropical birds. – *Nat. Clim. Change* 7: 133–136.
- Busch, D. S., Robinson, W. D., Robinson, T. R. and Wingfield, J. C. 2011. Influence of proximity to a geographical range limit on the physiology of a tropical bird. – *J. Anim. Ecol.* 80: 640–649.
- Canaday, C. 1996. Loss of insectivorous birds along a gradient of human impact in Amazonia. – *Biol. Conserv.* 77: 63–77.
- Canaday, C. and Rivasdeyera, J. 2001. Initial effects of a petroleum operation on Amazonian birds: terrestrial insectivores retreat. – *Biodivers. Conserv.* 10: 567–595.
- Chappell, M. A. and Bartholomew, G. A. 1981. Activity and thermoregulation of the antelope ground squirrel *Ammospermophilus leucurus* in winter and summer. – *Physiol. Zool.* 54: 215–223.
- Chen, J., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosnoff, K. D., Mroz, G. D., Brookshire, B. L. and Franklin, J. F. 1999. Microclimate in forest ecosystem and landscape ecology. – *BioScience* 49: 288–297.
- Cowles, R. B. and Bogert, C. M. 1944. A preliminary study of the thermal requirements of desert reptiles. – *Bulletin of the AMNH.* 83: 261–296.
- D'Eon, R. G. 2003. Effects of a stationary GPS fix-rate bias on habitat-selection analyses. – *J. Wildl. Manage.* 67: 858–863.
- Davis, K. T., Dobrowski, S. Z., Holden, Z. A., Higuera, P. E. and Abatzoglou, J. T. 2019. Microclimatic buffering in forests of the future: the role of local water balance. – *Ecography* 42: 1–11.
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C. and Martin, P. R. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. – *Proc. Natl Acad. Sci. USA* 105: 6668–6672.
- Di Orio, A. P., Callas, R. and Schaefer, R. J. 2003. Performance of two GPS telemetry collars under different habitat conditions. – *Wildl. Soc. Bull.* 31: 372–379.
- Diamond, S. E., Sorger, D. M., Hulcr, J., Pelini, S. L., Toro, I. D., Hirsch, C., Oberg, E. and Dunn, R. R. 2012. Who likes it hot? A global analysis of the climatic, ecological and evolutionary determinants of warming tolerance in ants. – *Global Change Biol.* 18: 448–456.
- Esquivel-Muelbert, A., Baker, T. R., Dexter, K. G., Lewis, S. L., Brienen, R. J. W., Feldpausch, T. R., Lloyd, J., Monteagudo-Mendoza, A., Arroyo, L., Álvarez-Dávila, E., Higuchi, N., Marimon, B. S., Marimon-Junior, B. H., Silveira, M., Vilanova, E., Gloor, E., Malhi, Y., Chave, J., Barlow, J., Bonal, D., Cardozo, N. D., Erwin, T., Fauset, S., Hérault, B., Laurance, S., Poorter, L., Qie, L., Stahl, C., Sullivan, M. J. P., ter Steege, H., Vos, V. A., Zuidema, P. A., Almeida, E., de Oliveira, E. A., Andrade, A., Vieira, S. A., Aragão, L., Araujo-Murakami, A., Arets, E., Aymard, C. G. A., Baraloto, C., Camargo, P. B., Barroso, J. G., Bongers, F., Boot, R., Camargo, J. L., Castro, W., Moscoso, V. C., Comiskey, J., Valverde, F. C., da Costa, A. C. L., Pasquel, J. del A., Fiore, A. D., Duque, L. F., Elias, F., Engel, J., Llampazo, G. F., Galbraith, D., Fernández, R. H., Coronado, E. H., Hubau, W., Jimenez-Rojas, E., Lima, A. J. N., Umetsu, R. K., Laurance, W., Lopez-Gonzalez, G., Lovejoy, T., Cruz, O. A. M., Morandi, P. S., Neill, D., Vargas, P. N., Camacho, N. C. P., Gutierrez, A. P., Pardo, G., Peacock, J., Peña-Claros, M., Peñuela-Mora, M. C., Petronelli, P., Pickavance, G. C., Pitman, N., Prieto, A., Quesada, C., Ramírez-Angulo, H., Réjou-Méchain, M., Correa, Z. R., Roopsind, A., Rudas, A., Salomão, R., Silva, N., Espejo, J. S., Singh, J., Stropp, J., Terborgh, J., Thomas, R., Toledo, M., Torres-Lezama, A., Gamarra, L. V., van de Meer, P. J., van der Heijden, G., van der Hout, P., Martinez, R. V., Vela, C., Guimarães Vieira, I. C. and Phillips, O. L. 2019. Compositional response of Amazon forests to climate change. – *Global Change Biol.* 25: 39–56.
- Fridley, J. D. 2009. Downscaling climate over complex terrain: high finescale (< 1000 m) spatial variation of near-ground temperatures in a montane forested landscape (Great Smoky Mountains). – *J. Appl. Meteor. Climatol.* 48: 1033–1049.
- Fu, R., Yin, L., Li, W., Arias, P. A., Dickinson, R. E., Huang, L., Chakraborty, S., Fernandes, K., Liebmann, B., Fisher, R. and Myneni, R. B. 2013. Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. – *Proc. Natl Acad. Sci. USA* 110: 18110–18115.
- Graham, E. A., Mulkey, S. S., Kitajima, K., Phillips, N. G. and Wright, S. J. 2003. Cloud cover limits net CO₂ uptake and growth of a rainforest tree during tropical rainy seasons. – *Proc. Natl Acad. Sci. USA* 100: 572–576.
- Huey, R. B., Deutsch, C. A., Tewksbury, J. J., Vitt, L. J., Hertz, P. E., Álvarez Pérez, H. J. and Garland, T. 2009. Why tropical forest lizards are vulnerable to climate warming. – *Proc. R. Soc. B* 276: 1939–1948.
- Huey, R. B., Hertz, P. E. and Sinervo, B. 2003. Behavioral drive versus behavioral inertia in evolution: a null model approach. – *Am. Nat.* 161: 357–366.
- Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A. M., Jess, M. and Williams, S. E. 2012. Predicting organismal vul-

- nerability to climate warming: roles of behaviour, physiology and adaptation. – *Phil. Trans. R. Soc. B* 367: 1665–1679.
- Isaac, J. L., De Gabriel, J. L. and Goodman, B. A. 2008. Microclimate of daytime den sites in a tropical possum: implications for the conservation of tropical arboreal marsupials. – *Anim. Conserv.* 11: 281–287.
- IUCN 2020. The IUCN Red List of threatened species. – <www.iucnredlist.org>.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. – *Am. Nat.* 101: 233–249.
- Jiang, Z., Sugita, M., Kitahara, M., Takatsuki, S., Goto, T. and Yoshida, Y. 2008. Effects of habitat feature, antenna position, movement and fix interval on GPS radio collar performance in Mount Fuji, central Japan. – *Ecol. Res.* 23: 581–588.
- Jirinec, V., Burner, R. C., Amaral, B. R., Bierregaard, R. O., Fernández-Arellano, G., Hernández-Palma, A., Johnson, E. I., Lovejoy, T. E., Powell, L. L., Rutt, C. L., Wolfe, J. D. and Stouffer, P. C. 2021a. Morphological consequences of climate change for resident birds in intact Amazonian rainforest. – *Sci. Adv.* 7: eabk1743.
- Jirinec, V., Elizondo, E. C., Rodrigues, P. F. and Stouffer, P. C. 2022b. Data from: Climate trends and behavior of a model Amazonian terrestrial insectivore, black-faced antthrush, indicate adjustment to hot and dry conditions. – Dryad Digital Repository, <<https://doi.org/10.5061/dryad.5qfttdz7z>>.
- Jirinec, V., Isdell, R. E. and Leu, M. 2016. Prey availability and habitat structure explain breeding space use of a migratory songbird. – *Condor* 118: 309–328.
- Jirinec, V., Rodrigues, P. F. and Amaral, B. 2021b. Adjustable leg harness for attaching tags to small and medium-sized birds. – *J. Field Ornithol.* 92: 77–87.
- Jirinec, V., Rodrigues, P. F., Amaral, B. R. and Stouffer, P. C. 2022a. Light and temperature niches of ground-foraging Amazonian insectivorous birds. – *Ecology* 103: e3645.
- Jirinec, V., Varian, C. P., Smith, C. J. and Leu, M. 2015. Mismatch between diurnal home ranges and roosting areas in the wood thrush *Hylocichla mustelina*: possible role of habitat and breeding stage. – *Auk* 133: 1–12.
- Johnson, E. I. and Wolfe, J. D. 2017. Molt in neotropical birds: life history and aging criteria. – CRC Press.
- Jullien, M. and Thiollay, J. M. 1998. Multi-species territoriality and dynamic of neotropical forest understory bird flocks. – *J. Anim. Ecol.* 67: 227–252.
- Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. – *J. Trop. Ecol.* 5: 173–185.
- Karr, J. R. and Brawn, J. D. 1990. Food resources of understory birds in central Panama: quantification and effects on avian populations. – *Stud. Avian Biol.* 13: 58–64.
- Karr, J. R. and Freemark, K. E. 1983. Habitat selection and environmental gradients: dynamics in the ‘stable’ tropics. – *Ecology* 64: 1481–1494.
- Kaspari, M. and Weiser, M. D. 2000. Ant activity along moisture gradients in a neotropical forest. – *Biotropica* 32: 703–711.
- Laurance, S. and Gomez, M. 2005. Clearing width and movements of understory rainforest birds. – *Biotropica* 37: 149–152.
- Laurance, S. G. W. 2004. Responses of understory rain forest birds to road edges in central Amazonia. – *Ecol. Appl.* 14: 1344–1357.
- Laurance, W. F., Andrade, A. S., Magrach, A., Camargo, J. L. C., Valsko, J. J., Campbell, M., Fearnside, P. M., Edwards, W., Lovejoy, T. E. and Laurance, S. G. 2014. Long-term changes in liana abundance and forest dynamics in undisturbed Amazonian forests. – *Ecology* 95: 1604–1611.
- Laurance, W. F., Camargo, J. L. C., Fearnside, P. M., Lovejoy, T. E., Williamson, G. B., Mesquita, R. C. G., Meyer, C. F. J., Bobrowiec, P. E. D. and Laurance, S. G. W. 2018. An Amazonian rainforest and its fragments as a laboratory of global change. – *Biol. Rev.* 93: 223–247.
- Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., Gascon, C., Bierregaard, R. O., Laurance, S. G. and Sampaio, E. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. – *Conserv. Biol.* 16: 605–618.
- Levings, S. C. and Windsor, D. M. 1984. Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry season on Barro Colorado Island, Panama. – *Biotropica* 16: 125–131.
- McCafferty, D. J., Gallon, S. and Nord, A. 2015. Challenges of measuring body temperatures of free-ranging birds and mammals. – *Anim. Biotelemet.* 3: 33.
- McKinnon, E. A., Rotenberg, J. A. and Stutchbury, B. J. M. 2015. Seasonal change in tropical habitat quality and body condition for a declining migratory songbird. – *Oecologia* 179: 363–375.
- Mestre, L. A. M., Cohn-Haft, M. and Dias, M. M. 2010. Diet and prey availability of terrestrial insectivorous birds prone to extinction in Amazonian forest fragments. – *Braz. Arch. Biol. Technol.* 53: 1371–1381.
- Mora, C., Frazier, A. G., Longman, R. J., Dacks, R. S., Walton, M. M., Tong, E. J., Sanchez, J. J., Kaiser, L. R., Stender, Y. O., Anderson, J. M., Ambrosino, C. M., Fernandez-Silva, I., Giuseffi, L. M. and Giambelluca, T. W. 2013. The projected timing of climate departure from recent variability. – *Nature* 502: 183–187.
- National Coordination Office for Space-Based Positioning, Navigation, and Timing 2020. – <<https://www.gps.gov/systems/gps/space/>>.
- Neelin, J. D., Münnich, M., Su, H., Meyerson, J. E. and Holloway, C. E. 2006. Tropical drying trends in global warming models and observations. – *Proc. Natl Acad. Sci. USA* 103: 6110–6115.
- Nepstad, D., Lefebvre, P., Lopes da Silva, U., Tomasella, J., Schlesinger, P., Solórzano, L., Moutinho, P., Ray, D. and Guerreira Benito, J. 2004. Amazon drought and its implications for forest flammability and tree growth: a basin-wide analysis. – *Global Change Biol.* 10: 704–717.
- Nishikawa, E. T., Pollock, H. S. and Brawn, J. D. 2021. Dry season intensity has equivocal effects on the nutritional condition of understory birds in a neotropical forest. – *Ornithology* 138: 1–13.
- Pachauri, R. K., Allen, M. R., Barros, V. R., Broome, J., Cramer, W., Christ, R., Church, J. A., Clarke, L., Dahe, Q. and Dasgupta, P. 2014. Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change.
- Patten, M. A. and Smith-Patten, B. D. 2012. Testing the microclimate hypothesis: light environment and population trends of neotropical birds. – *Biol. Conserv.* 155: 85–93.
- Pearson, D. L. and Derr, J. A. 1986. Seasonal patterns of lowland forest floor arthropod abundance in southeastern Peru. – *Biotropica* 18: 244–256.
- Peres, C. A., Gardner, T. A., Barlow, J., Zuanon, J., Michalski, F., Lees, A. C., Vieira, I. C. G., Moreira, F. M. S. and Feeley, K. J. 2010. Biodiversity conservation in human-modified Amazonian forest landscapes. – *Biol. Conserv.* 143: 2314–2327.
- Pollock, H. S., Brawn, J. D. and Cheviron, Z. A. 2021. Heat tolerances of temperate and tropical birds and their implications for susceptibility to climate warming. – *Funct. Ecol.* 35: 93–104.

- Pollock, H. S., Cheviron, Z. A., Agin, T. J. and Brawn, J. D. 2015. Absence of microclimate selectivity in insectivorous birds of the Neotropical forest understory. – *Biol. Conserv.* 188: 116–125.
- Porter, W. P. and Kearney, M. 2009. Size, shape and the thermal niche of endotherms. – *Proc. Natl Acad. Sci. USA* 106: 19666–19672.
- Porter, W. P., Mitchell, J. W., Beckman, W. A. and DeWitt, C. B. 1973. Behavioral implications of mechanistic ecology. – *Oecologia* 13: 1–54.
- Powell, L. L., Cordeiro, N. J. and Stratford, J. A. 2015. Ecology and conservation of avian insectivores of the rainforest understory: a pantropical perspective. – *Biol. Conserv.* 188: 1–10.
- Prinzinger, R., Preßmar, A. and Schleucher, E. 1991. Body temperature in birds. – *Comp. Biochem. Physiol. A Physiol.* 99: 499–506.
- Recio, M. R., Mathieu, R., Denys, P., Sirguy, P. and Seddon, P. J. 2011. Lightweight GPS-tags, one giant leap for wildlife tracking? An assessment approach. – *PLoS One* 6: e28225.
- Riegler, G., Hennig, S. D. and Weber, M. 2015. WorldDEM – a novel global foundation layer. – *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences*.
- Robinson, W. D., Lees, A. C. and Blake, J. G. 2018. Surveying tropical birds is much harder than you think: a primer of best practices. – *Biotropica* 50: 846–849.
- Rutt, C. L., Jirinec, V., Johnson, E. I., Cohn-Haft, M., Vargas, C. F. and Stouffer, P. C. 2017. Twenty years later: an update to the birds of the Biological Dynamics of Forest Fragments Project, Amazonas, Brazil. – *Rev. Bras. Ornitol.* 25: 277–296.
- Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E. and Evans, T. A. 2014. Microhabitats reduce animal's exposure to climate extremes. – *Global Change Biol.* 20: 495–503.
- Scheffers, B. R., Phillips, B. L., Laurance, W. F., Sodhi, N. S., Diesmos, A. and Williams, S. E. 2013. Increasing arboreality with altitude: a novel biogeographic dimension. – *Proc. R. Soc. B* 280: 20131581.
- Sekercioglu, C. H., Ehrlich, P. R., Daily, G. C., Aygen, D., Goehring, D. and Sandí, R. F. 2002. Disappearance of insectivorous birds from tropical forest fragments. – *Proc. Natl Acad. Sci. USA* 99: 263–267.
- Sheldon, K. S., Huey, R. B., Kaspari, M. and Sanders, N. J. 2018. Fifty years of mountain passes: a perspective on Dan Janzen's classic article. – *Am. Nat.* 191: 553–565.
- Sherry, T. W. 2021. Sensitivity of tropical insectivorous birds to the Anthropocene: a review of multiple mechanisms and conservation implications. – *Front. Ecol. Evol.* 9: 662873.
- Sigel, B. J., Douglas Robinson, W. and Sherry, T. W. 2010. Comparing bird community responses to forest fragmentation in two lowland Central American reserves. – *Biol. Conserv.* 143: 340–350.
- Sigel, B. J., Sherry, T. W. and Young, B. E. 2006. Avian community response to lowland tropical rainforest isolation: 40 years of change at La Selva Biological Station, Costa Rica. – *Conserv. Biol.* 20: 111–121.
- Silva, J. M. C. D., Rylands, A. B. and Fonseca, G. A. B. D. 2005. The fate of the Amazonian areas of endemism. – *Conserv. Biol.* 19: 689–694.
- Stevenson, R. D. 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. – *Am. Nat.* 126: 362–386.
- Stouffer, P. C. 2007. Density, territory size and long-term spatial dynamics of a guild of terrestrial insectivorous birds near Manaus, Brazil. – *Auk* 124: 291–306.
- Stouffer, P. C. 2020. Birds in fragmented Amazonian rainforest: lessons from 40 years at the Biological Dynamics of Forest Fragments Project. – *Condor* 122: duaa005.
- Stouffer, P. C. and Bierregaard, R. O. 1995. Use of Amazonian forest fragments by understory insectivorous birds. – *Ecology* 76: 2429–2445.
- Stouffer, P. C., Jirinec, V., Rutt, C. L., Bierregaard, R. O., Hernández-Palma, A., Johnson, E. I., Midway, S. R., Powell, L. L., Wolfe, J. D. and Lovejoy, T. E. 2021. Long-term change in the avifauna of undisturbed Amazonian rainforest: ground-foraging birds disappear and the baseline shifts. – *Ecol. Lett.* 24: 186–195.
- Stouffer, P. C., Johnson, E. I. and Bierregaard, R. O. 2013. Breeding seasonality in central Amazonian rainforest birds. – *Auk* 130: 529–540.
- Stratford, J. A. and Robinson, W. D. 2005. Gulliver travels to the fragmented tropics: geographic variation in mechanisms of avian extinction. – *Front. Ecol. Environ.* 3: 85–92.
- Stratford, J. A. and Stouffer, P. C. 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. – *Conserv. Biol.* 13: 1416–1423.
- Stratford, J. A. and Stouffer, P. C. 2015. Forest fragmentation alters microhabitat availability for neotropical terrestrial insectivorous birds. – *Biol. Conserv.* 188: 109–115.
- Tomasella, J., Hodnett, M. G., Cuartas, L. A., Nobre, A. D., Waterloo, M. J. and Oliveira, S. M. 2008. The water balance of an Amazonian micro-catchment: the effect of interannual variability of rainfall on hydrological behaviour. – *Hydrol. Process.* 22: 2133–2147.
- Usher, M. B. 1970. Seasonal and vertical distribution of a population of soil arthropods: Collembola. – *Pedobiologia* 10: 224–236.
- Visco, D. M., Michel, N. L., Boyle, W. A., Sigel, B. J., Woltmann, S. and Sherry, T. W. 2015. Patterns and causes of understory bird declines in human-disturbed tropical forest landscapes: a case study from Central America. – *Biol. Conserv.* 191: 117–129.
- Walther, B. A. 2002. Vertical stratification and use of vegetation and light habitats by neotropical forest birds. – *J. Ornithol.* 143: 64–81.
- Wikelski, M., Hau, M. and Wingfield, J. C. 2000. Seasonality of reproduction in a neotropical rain forest bird. – *Ecology* 81: 2458–2472.
- Willis, E. O. 1976. Seasonal changes in the invertebrate litter fauna on Barro Colorado Island, Panama. – *Rev. Bras. Biol.* 36: 643–657.

SUPPORTING INFORMATION

Climate trends and behavior of a model Amazonian terrestrial insectivore, Black-faced Antthrush, indicate adjustment to hot and dry conditions during the dry season

Vitek Jirinec, Elisa C. Elizondo, Patricia F. Rodrigues, Philip C Stouffer

Journal of Avian Biology

SUPPLEMENTARY METHODS

Study area, seasonality, and climate

The BDFFP typifies forests of lowland Amazonia. The project spans approximately 1,200 km² of which ~95% in 2017 was covered with *terra firme* forest (Rutt et al. 2019), growing on nutrient-poor soils of the Guiana Shield (Gascon and Bierregaard 2001). We collected data within continuous primary forest at the Cabo Frio and Camp 41 camps (Figure 1). Both areas have topography characterized by moderate relief where stream valleys dissect upper-elevation plateaus often located ~100 m higher, creating a highly reticulated landscape (Figure 1B).

Temperature and precipitation are high throughout the year but vary seasonally. The region experiences an annual cycle of predictable rainfall fluctuation (Fu et al. 2013). The main goal of this study was to assess whether birds are sensitive to hot and dry conditions; we delineated the seasonal cycle at the BDFFP to understand when birds are expected to respond. To do so, we compiled climate data for 38 years from the ERA5-Land reanalysis (Copernicus Climate Change Service 2017) for the area where birds were historically sampled (Stouffer et al. 2020). ERA5-Land uses satellite and land-based records with a climate model to estimate several

climate values at 9 km resolution. We summarized precipitation and temperature at 2 m above ground level within ~3,300 km² surrounding the study sites (Figure 1), yielding monthly summaries from 1981 to 2019, and then used generalized additive models (GAMs; see *Statistical analyses*) to quantify the annual climate cycle. Our models revealed August to be generally the middle of the dry season, when precipitation is about a third of the total rainfall in March and April, the wettest months (Figure 2). Temperatures peak slightly after the driest period—they are ~1.5 °C higher around October than in the middle of the wet season (Figure 2).

Is the BDFFP experiencing climate change? To answer this question, we grouped the ERA5-Land monthly summaries by season: Jun–Nov (dry) and Dec–May (wet). These seasonal classifications were based on our within-year analysis (Figure 2) and follow past designations for the BDFFP (Stouffer et al. 2020). Climate covariates were modeled with GAMs to determine whether climate change occurred at our site and if climate extremes varied by season. Note that the beginning and terminal years of the timeseries do not coincide with El Niño-Southern Oscillation (ENSO) events.

Microclimate refugia

Ambient extremes can manifest in time and space. Seasonal climate suggests that extremes generally occur during the dry season at the BDFFP. Ambient conditions thus often differ the most between about August and March—intervals that define the trough and crest of the annual rainfall and temperature cycles (Figure 2). Dry season, and especially dry season afternoons, are generally the hottest and driest periods in Amazonia. However, these extremes may be reduced in microclimate refugia—localized areas that remain relatively cool and wet. Here we consider a potential microclimate refugium any site where air temperature may be lower than average at the

scale of the bird home range, regardless of whether outside conditions are truly unfavorable to birds—a diagnosis that is very difficult to make. For example, in primary rainforest in the Philippines, the rate of temperature change in dense vegetation and tree cavity microhabitats was substantially lower relative to ambient temperature, where exposure to extreme temperatures occurred over intervals that were >20 times longer (Scheffers et al. 2014). In addition to this physical cover, topography may also buffer ambient extremes. Temperature generally drops with increasing elevation at large scales—a fact of little consequence in most of low-elevation Amazonia, including our study site. In contrast, at the BDFFP landscape, valleys likely remain wetter and cooler. The bottoms of these “micro-catchments” typically contain streams that are maintained by groundwater throughout the year (Epron et al. 2006, Tomasella et al. 2008). Aside from direct cooling, water buffers against temperature change (Elsenbeer 2001, Fridley 2009, Davis et al. 2019), and wetter soils allow evapotranspiration to occur when drier areas may lead to stomatal closure (Aleixo et al. 2019). Hence, we expected ambient extremes to rise in the afternoons of the dry season, with physical cover and valley bottoms offering buffered microclimates.

Quantifying location error for GPS tags

Prior to modeling of bird GPS data, we quantified tag location error and incorporated it into our analyses. Vegetation and topography reduce not only the probability of fix but also the accuracy of acquired locations (Jiang et al. 2008), which was of particular concern for birds that often used valleys in mature rainforest and our tags with “SWIFT” feature designed to maximize battery life. We therefore placed two calibration tags (identical to bird devices) to represent stationary birds—they were positioned ~10 cm high in the understory of mature forest, within the home

ranges of two study birds, and were stratified by elevation (lower tag: 91 m, upper tag: 140 m; Figure S2D). Although calibration tags sampled a somewhat different time of year, we programmed them with the same daily fix schedule as study birds, from 17 Jun–31 Aug 2019. Out of 608 fix attempts, this yielded 411 successful locations, which we then used in R package “ctmm” (Fleming et al. 2020) to estimate location error. Because satellite-based screening methods such as HDOP can be misleading and eliminate accurate locations (Recio et al. 2011), we instead identified spatial outliers for our calibration tags based on relative distance to other locations. For each tag, we first we used the `outlie()` function in “ctmm” to calculate the distance from the median longitude and latitude to each point, which highlighted one obvious outlier for the lower tag (2,200 m deviation from core cluster) and another for the upper tag (1.2 km). We removed both outliers before estimating location error by running the `uere.fit()` function in “ctmm” for each remaining calibration dataset. After generating an error radius of 52 m (95% CI: 49–56 m) and 41 m (38–44 m) for the lower and upper tag, respectively, we conservatively estimated that each valid bird fix was on average 52 m away from the true location. This horizontal error is relatively small given the typical home range size and topographic variability (Figure S2C). We similarly removed outliers from the location dataset for each of the 11 GPS tags recovered from birds. As with the calibration data, we used `outlie()` to calculate core deviation for each bird and removed all locations that were farther than 1.5-times the interquartile range in core deviation. This vetting process constituted an objective way to remove outliers and quantify spatial error from small GPS tags deployed in this challenging environment.

Statistical analyses

To analyze climate and biologist data, we employed generalized additive models (GAMs) implemented in R package “mgcv” (Wood 2020). GAMs are similar to linear models, but allow for modeling of non-linear relationships in the response using smooth functions of explanatory variables (Wood 2017). Package “mgcv” calculates an approximate p-value for the smooth term; a low p-value constitutes evidence for a significant slope—either positive or negative—somewhere along the range of the covariate, and the GAM plot should be examined for more details (Wood 2017).

To quantify annual seasonality and to test for climate change with ERA5-Land at the BDFFP, we used GAMs that accounted for autocorrelated observations. For all GAM covariates, we chose the basis function both according to its design (e.g., cyclic cubic regression spline starts and ends at identical values, which is appropriate for diel or annual cycles), as well the model diagnostics it produced. Data distribution choice was based on similar criteria as well as presumed data generating processes. We selected the cyclic cubic regression spline basis (bs = “cc”, k = 10) for annual seasonality models and the thin plate regression spline basis (bs = “tp”, k = 10) for climate change models; all were fit with restricted maximum likelihood and Gaussian distribution. We specified generalized additive mixed models with autoregressive moving average (ARMA) error structure for each climate variable, modeled as the smooth of the numeric month in annual seasonality models and as the smooth of year in climate change models. We set ARMA within each year and selected the AR order by first plotting residual autocorrelation functions of non-ARMA models, followed by iterative likelihood ratio tests among models with plausible AR orders to select the appropriate model structure.

Lastly, to analyze bilogger data, we used different GAM structures for light and temperature with separate seasonal analyses. For light exposure, we modeled light intensity as the smooth of numeric time of day (0 – 23.99) using the cyclic cubic regression spline (bs = “cc”, k = 50), the smooth of the successive observation rank per group (bird or logger) with the Gaussian process basis (bs = “gp”, k = 50), and group as the random effect (bs = “re”). Light exposure models were fit with restricted maximum likelihood and Gamma distribution with a log link function. Temperature model structure was identical, although we used Gaussian distribution in place of Gamma.

To test whether valleys buffered ambient extremes, we calculated seasonal profiles by elevation using locally estimated scatterplot smoothing (LOESS). Prior to smoothing, we averaged timeseries by elevation (e.g., mean of the three valley transects per 10-min interval)—this resolved data gaps and created a single timeseries group per elevation. Each LOESS line represents the estimate of R function `loess()`, with $\alpha = 0.5$ (parameter controlling degree of smoothing) on the group average. For temperature and soil moisture, these were averages of the raw measurements. For daily temperature summaries, we first extracted the minimum, maximum, and range in temperature per day in the group average, and then estimated the LOESS lines of the summary timeseries.

To analyze bird GPS data, we used linear mixed models (LMMs) and generalized linear mixed models (GLMMs) in R package “lme4” (Bates et al. 2020). First, to determine whether GPS fix probability varied temporally, we used GLMMs to model fix attempt as a binary response (success = 1, fail = 0) with season (dry, wet) and time of fix (hour: 07:00, 10:00, 13:00, 16:00) as explanatory categorical variables and bird as a random effect (i.e., a varying intercept model). We applied the binomial error distribution with the logit link function (logistic

regression) and fit these models by maximum likelihood with adaptive Gauss-Hermite quadrature using 25 sample points. This dataset involved all 2,724 fix attempts for the 11 recovered GPS tags, including failed fix attempts and successful fixes that were later removed as outliers. Second, we used the final valid location dataset (filtered via “ctmm”) to test whether birds shifted elevations during ambient extremes. To attach elevation to GPS data, we averaged DEM values with ArcGIS (ArcMAP 10.7.1, ESRI, Redlands, California, USA) within 52 m of each valid fix to account for estimated horizontal error. We then used LMMs to model elevation as the response with season and time of fix as explanatory variables and bird as the random effect. To compare the relative importance of each covariate, we built the same four models for elevation and the probability of GPS fix and compared competing models using AIC_c (Burnham and Anderson 2002). The models were (a) a null (intercept-only), (b) hour, (c) season, and (d) an hour*season interaction. All models were fit using maximum likelihood, but we refit top LMMs with restricted maximum likelihood for interpretation of coefficients (Zuur et al. 2009). Finally, for each top model, we examined model diagnostics in R package “DHARMA” (Hartig 2020) using 10,000 simulations, as well as the model fit with conditional coefficients of determination (r^2_c) calculated with `r.squaredGLMM()` in R package “MuMIn” (Bartoń 2020). Analyses were conducted using R version 3.6.3 (R Core Team 2020).

Data gaps

Gaps in the timeseries occurred at two stations, when rodents severed sensor cables, resulting in no data between 6 Nov 2018–21 Jun 2019 at CFN-3 and 11 Mar 2019–21 Jun 2019 at CFN-2 (averaging by the elevation category led to continuous data during the study). Although we

originally placed all stations away from forest gaps, single trees fell within 10 m of both Camp 41-1 and CFS-1 during the WS of 2018. See Figure S1 for transect configuration.

SUPPLEMENTARY TABLES

Table S1. Timing of daily temperature extremes (mean \pm SD in min) by season for ground microclimate stations and bird biologgers.

category ^a	season ^b	time	<i>n</i> ^c
ground: plateau	dry	14:46 \pm 149	259
	wet	14:11 \pm 269	265
ground: mid-slope	dry	14:40 \pm 128	257
	wet	14:08 \pm 245	252
ground: valley	dry	14:13 \pm 89	259
	wet	13:49 \pm 183	251
birds	dry	14:16 \pm 89	331
	wet	14:21 \pm 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 S2. 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	<i>w</i>	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 S3. 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	<i>w</i>	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

SUPPLEMENTARY FIGURES

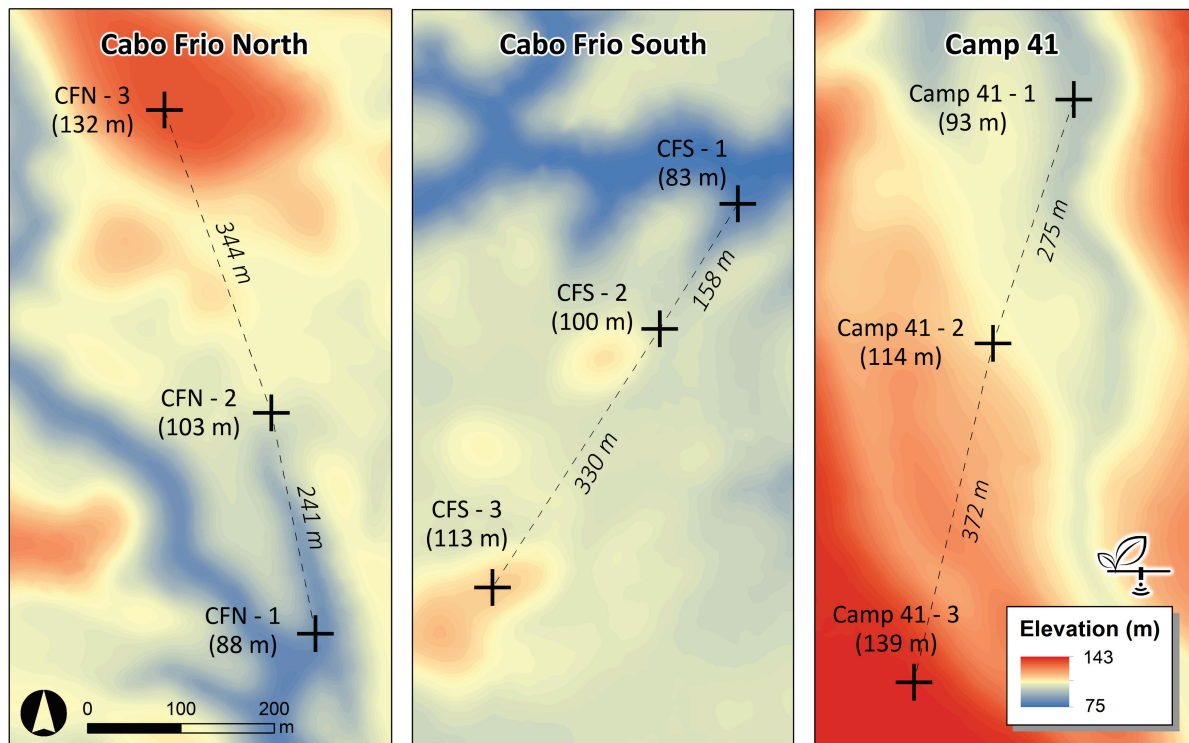


Figure S1. Microclimate datalogging transects within Amazonian micro-catchments. We placed nine stations (black crosses) along three transects, each logging soil temperature and moisture data every 10 min from June 2017 to September 2019.

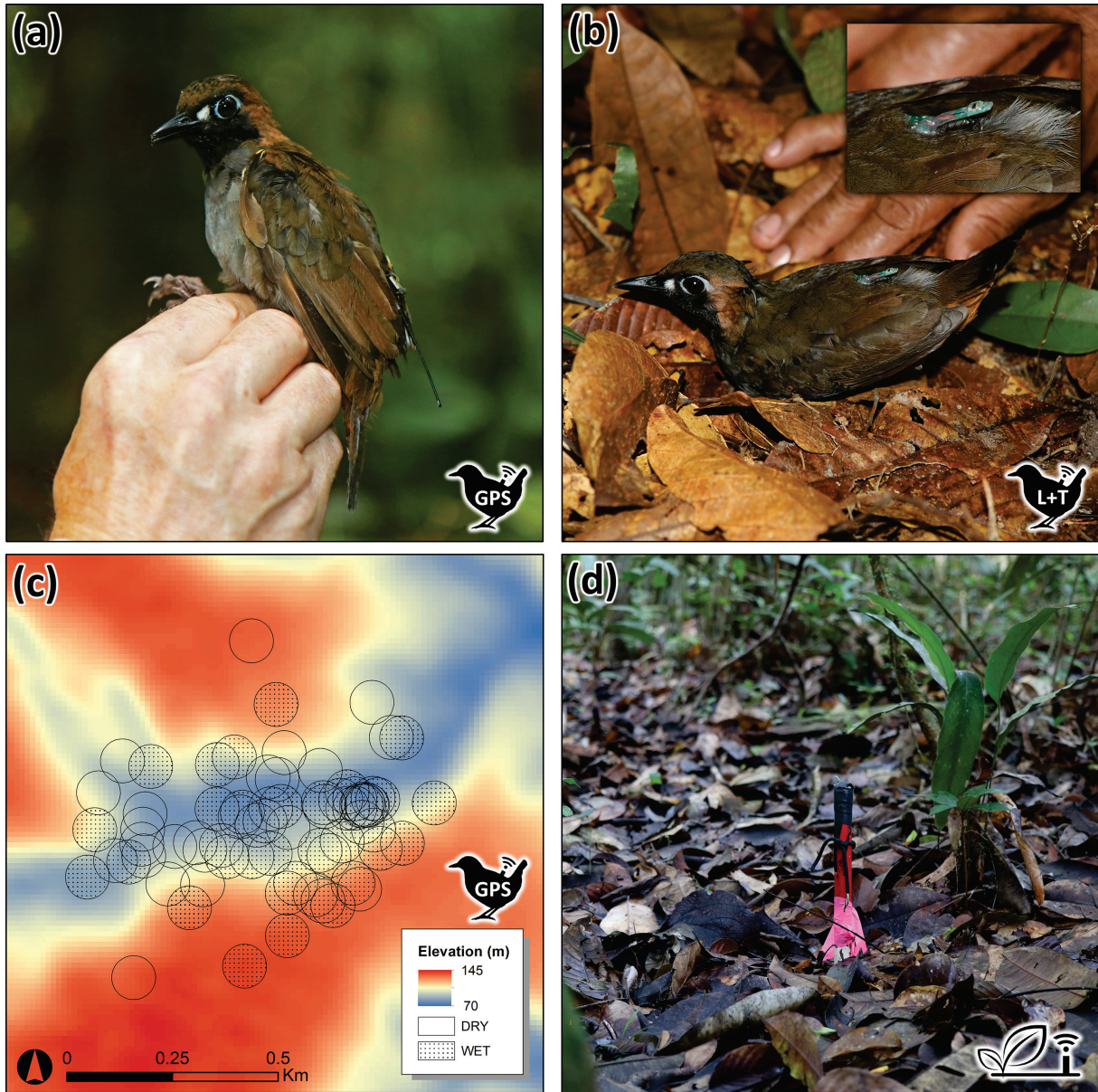


Figure S2. Tracking *Formicarius analis*. Birds were outfitted with either a GPS tag that recorded locations (A), or a bilogger that recorded light intensity and temperature (B). Panel (C) shows locations for one bird categorized by season (dry, wet), where we averaged elevation values within 52 m buffers to account for location error estimated by calibration tags. Calibration tags (both GPS and bi-loggers) were placed atop short stakes within the forest understory to sample ambient conditions (D).

SUPPLEMENTARY REFERENCES

- Aleixo, I., Norris, D., Hemerik, L., Barbosa, A., Prata, E., Costa, F. and Poorter, L. 2019. Amazonian rainforest tree mortality driven by climate and functional traits. - *Nat. Clim. Chang.* 9: 384–388.
- Bartoń, K. 2020. MuMIn: Multi-Model Inference.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P. and Fox, J. 2020. lme4: Linear Mixed-Effects Models using “Eigen” and S4.
2002. Model selection and multimodel inference (KP Burnham and DR Anderson, Eds.). - Springer New York.
- Copernicus Climate Change Service 2017. ERA5: Fifth generation of ECMWF atmospheric reanalyses of the global climate.
- Davis, K. T., Dobrowski, S. Z., Holden, Z. A., Higuera, P. E. and Abatzoglou, J. T. 2019. Microclimatic buffering in forests of the future: the role of local water balance. - *Ecography* 42: 1–11.
- Elsenbeer, H. 2001. Hydrologic flowpaths in tropical rainforest soils— a review. - *Hydrological Processes* 15: 1751–1759.
- Epron, D., Bosc, A., Bonal, D. and Freycon, V. 2006. Spatial variation of soil respiration across a topographic gradient in a tropical rain forest in French Guiana. - *Journal of Tropical Ecology* 22: 565–574.
- Fleming, C. H., Calabrese, J. M., Dong, X., Winner, K., Péron, G., Noonan, M. J., Kranstauber, B., Gurarie, E., Safi, K., Cross, P. C., Mueller, T., Paula, R. C. de, Akre, T., Drescher-Lehman, J., Harrison, A.-L. and Morato, R. G. 2020. ctmm: Continuous-Time Movement Modeling.
- Fridley, J. D. 2009. Downscaling climate over complex terrain: High finescale (<1000 m) spatial variation of near-ground temperatures in a montane forested landscape (Great Smoky Mountains). - *J. Appl. Meteor. Climatol.* 48: 1033–1049.
- Fu, R., Yin, L., Li, W., Arias, P. A., Dickinson, R. E., Huang, L., Chakraborty, S., Fernandes, K., Liebmann, B., Fisher, R. and Myneni, R. B. 2013. Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. - *PNAS* 110: 18110–18115.
- Gascon, C. and Bierregaard, R. O., Jr 2001. The Biological Dynamics of Forest Fragments Project. - In: Bierregaard, R. O., Jr et al. (eds), *Lessons from Amazonia*. Yale University Press, pp. 31–42.

- Hartig, F. 2020. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.
- Jiang, Z., Sugita, M., Kitahara, M., Takatsuki, S., Goto, T. and Yoshida, Y. 2008. Effects of habitat feature, antenna position, movement, and fix interval on GPS radio collar performance in Mount Fuji, central Japan. - *Ecol. Res.* 23: 581–588.
- R Core Team 2020. R: A language and environment for statistical computing. - R Foundation for Statistical Computing, Vienna, Austria.
- Recio, M. R., Mathieu, R., Denys, P., Sirguy, P. and Seddon, P. J. 2011. Lightweight GPS-tags, one giant leap for wildlife tracking? An assessment approach. - *PLoS One* in press.
- Rutt, C. L., Jirinec, V., Cohn-Haft, M., Laurance, W. F. and Stouffer, P. C. 2019. Avian ecological succession in the Amazon: A long-term case study following experimental deforestation. - *Ecology and Evolution* in press.
- Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E. and Evans, T. A. 2014. Microhabitats reduce animal's exposure to climate extremes. - *Global Change Biology* 20: 495–503.
- Stouffer, P. C., Jirinec, V., Rutt, C. L., Bierregaard, R. O., Hernández-Palma, A., Johnson, E. I., Midway, S. R., Powell, L. L., Wolfe, J. D. and Lovejoy, T. E. 2020. Long-term change in the avifauna of undisturbed Amazonian rainforest: Ground-foraging birds disappear and the baseline shifts. - *Ecology Letters* in press.
- Tomasella, J., Hodnett, M. G., Cuartas, L. A., Nobre, A. D., Waterloo, M. J. and Oliveira, S. M. 2008. The water balance of an Amazonian micro-catchment: the effect of interannual variability of rainfall on hydrological behaviour. - *Hydrological Processes* 22: 2133–2147.
- Wood, S. 2017. Generalized additive models: An introduction with R.
- Wood, S. 2020. mgcv: Mixed GAM Computation Vehicle with Automatic Smoothness Estimation.
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. and Smith, G. M. 2009. Mixed effects models and extensions in ecology with R. - Springer-Verlag.