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*Research*

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

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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 ~1.3°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

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## Introduction

Amazonia is the world's largest tropical forest and harbors a substantial portion of global biodiversity. At over 7 million km$^2$, 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

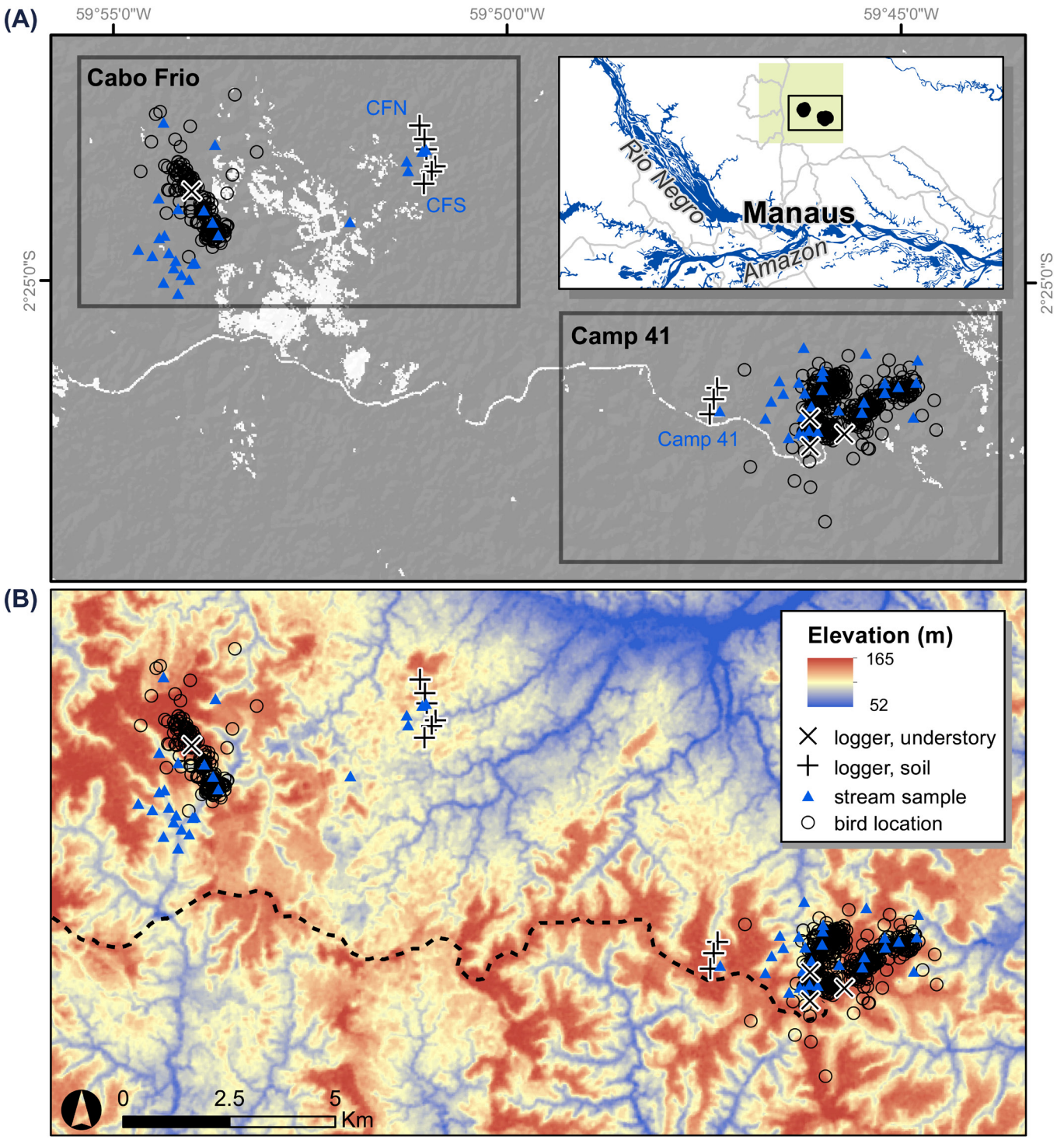


Figure 1. Survey areas at the Biological Dynamics of Forest Fragments Project in the state of Amazonas, Brazil. Panel 'A' depicts the two study areas, Cabo Frio and Camp 41, with Landsat-derived forest cover in 2017 (gray). Panel 'B' shows topographical variation (range ~100 m) in the same scene. Both 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.

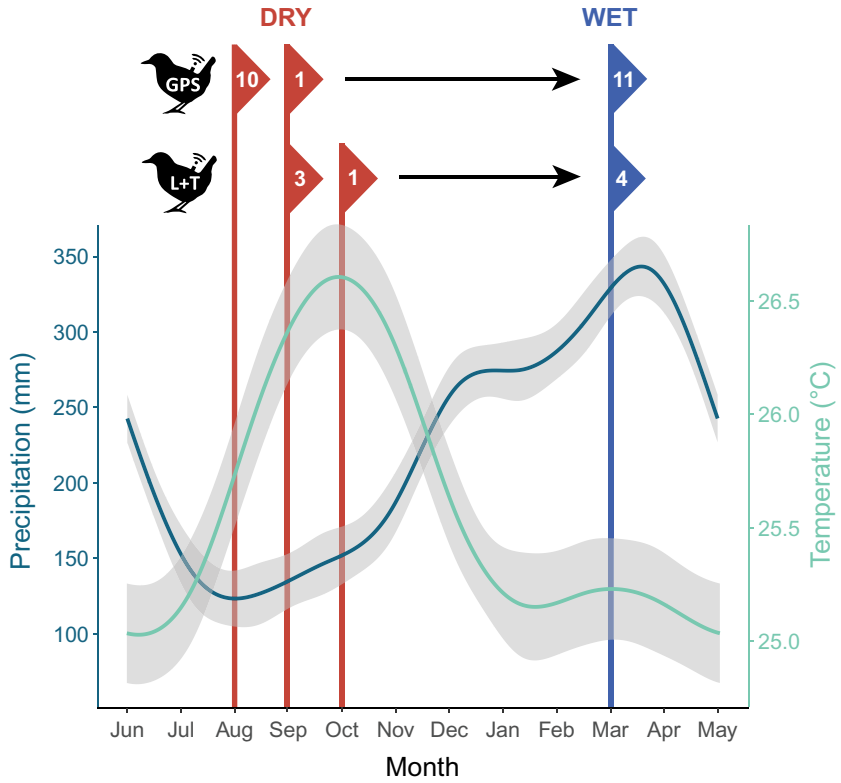


Figure 2. Annual climate and schedule of bird sampling. We first used an autoregressive generalized additive model and local rainfall and temperature data to broadly identify periods of annual climate extremes for comparison of bird behavior. Climate data come from ERA5-Land reanalysis and are a compilation of 38 years for our study area. Lines are model fits with the 95% CI shaded in gray. We then tracked black-faced antthrushes *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

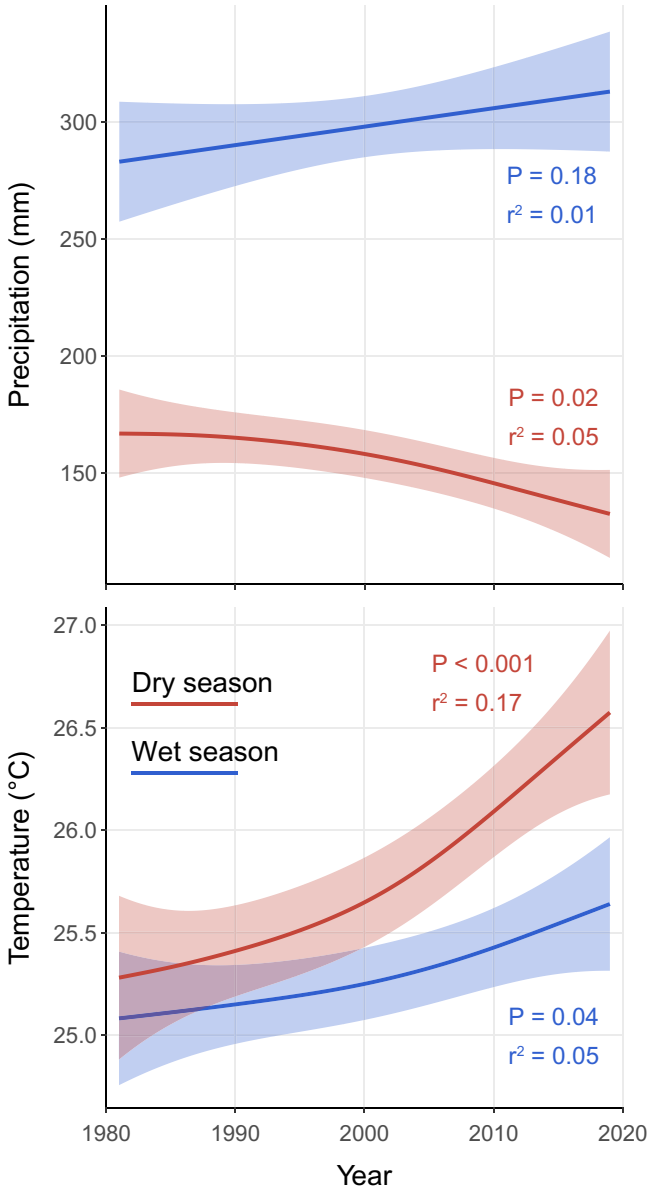


Figure 3. Climate change at the Biological Dynamics of Forest Fragments Project (BDFFP) within Amazonian Brazil. Lines are fitted generalized additive models with ARMA errors, with shading representing 95% CI. Climate data are monthly summaries compiled for the BDFFP area from ERA5-Land reanalysis.

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 ± SD = 24.6 ± 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 ($\beta_{dry} = -0.29$, 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 ($\beta_{dry} = -4.35$, 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 ($\beta_{16:00, wet} = 3.77$, SE = 1.84, t = 2.05, p = 0.04) and ~7 m lower at 16:00 in the DS ($\beta_{16:00, dry} = -6.54$, 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 ± 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

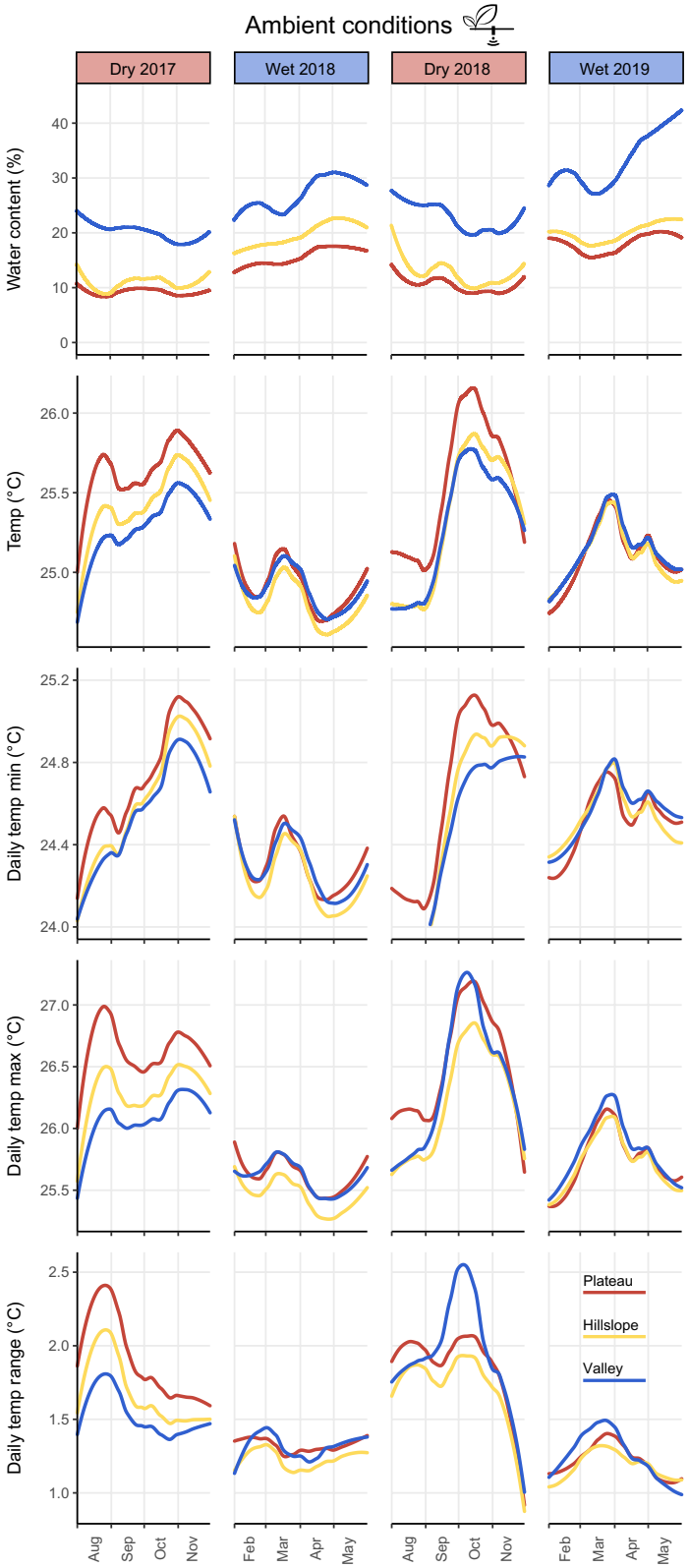


Figure 4. Forest floor microclimate within Amazonian micro-catchments in primary *terra firme* forest. Plots depict water content and temperature measurements from the top 11 cm of soil at nine microclimate stations arranged along three elevational transects, each with a station placed in a valley (blue), 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).

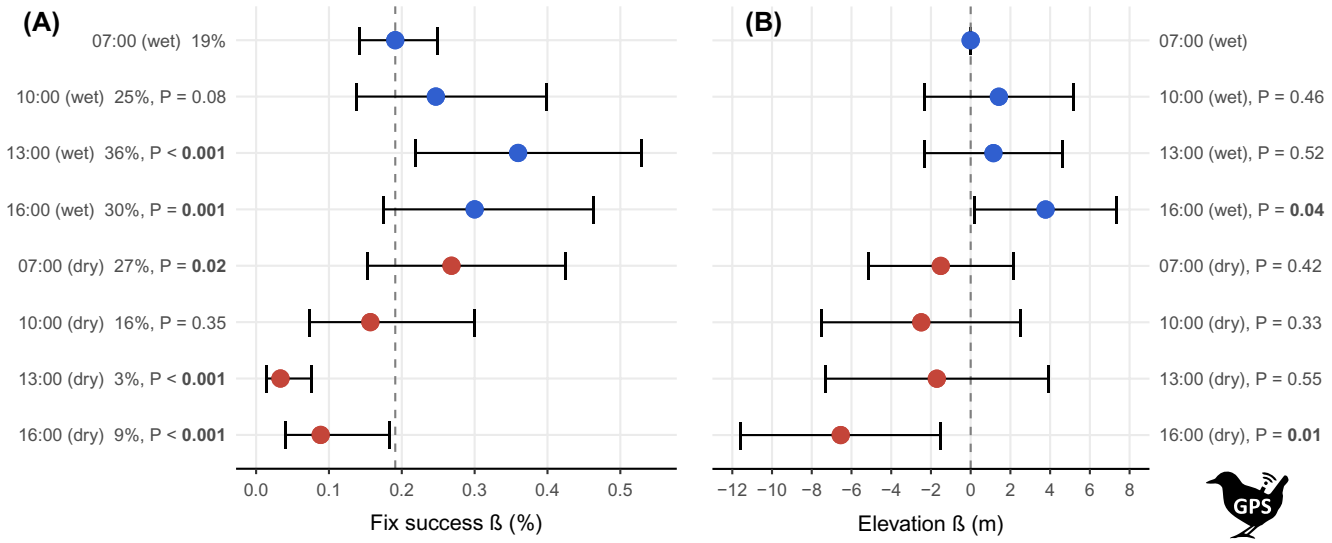


Figure 5. Probability of GPS fix (A) and elevation (B) by time of day and season for tags on 11 *Formicarius analis* in primary, continuous *terra firme* forest. Each bird was tracked four times daily over one month in the dry season (red) and one month in the wet season (blue) in 2017–2019. Error bars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

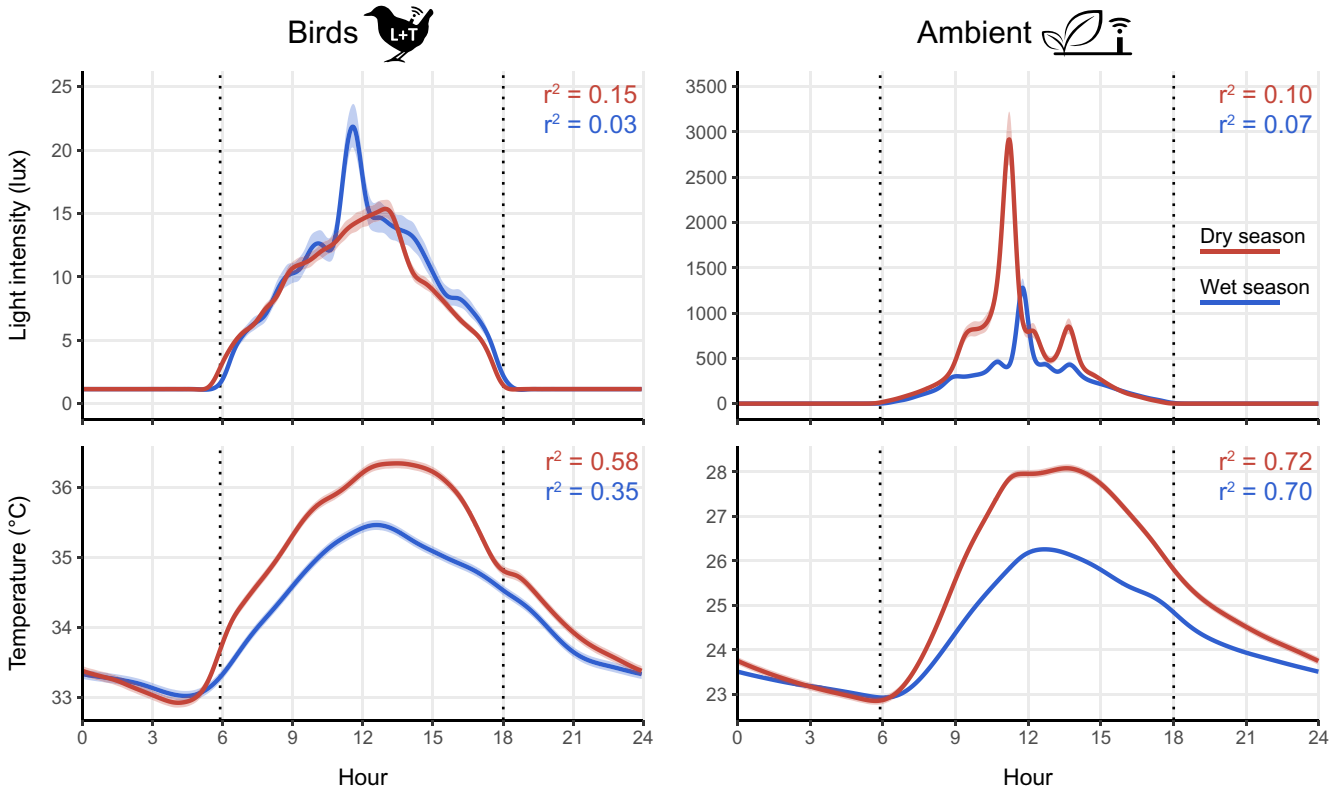


Figure 6. Light and temperature environment by day and season for birds and ambient conditions. Lines and 95% CIs are fits from generalized additive models with birds (n = 4) and ambient loggers (n = 4) as random effects. Note that y-axis on the ambient light plot is 2 orders of magnitude higher.

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.

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### 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).

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### 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.

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