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Light and thermal niches of ground-foraging Amazonian insectivorous birds

Vitek Jirinec[1,2,3] | Patricia F. Rodrigues[1,2] | Bruna R. Amaral[1,4] |
Philip C Stouffer[1,2]

[1]Biological Dynamics of Forest Fragments Project, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil

[2]School of Renewable Natural Resources, Louisiana State University and LSU AgCenter, Baton Rouge, Louisiana, USA

[3]Integral Ecology Research Center, Blue Lake, California, USA

[4]Department of Ecosystem Science and Management, Pennsylvania State University, University Park, Pennsylvania, USA

Correspondence
Vitek Jirinec
Email: vjirin1@lsu.edu

Abstract

Insectivores of the tropical rainforest floor are consistently among the most vulnerable birds to forest clearing and fragmentation. Several hypotheses attempt to explain this pattern, including sensitivity to extreme microclimates found near forest borders, particularly brighter and warmer conditions. Importantly, this "microclimate hypothesis" has additional implications for intact forest under global climate change that could be evaluated through direct assessment of the light and temperature environment of terrestrial insectivores. In this study, we harness novel technology to directly quantify the light and thermal niches of 10 species of terrestrial insectivores in undisturbed Amazonian rainforest. Loggers placed on birds ($N = 33$) and their environment ($N = 9$) recorded nearly continuous microclimate data from 2017 to 2019, amassing >5 million measurements. We found that midday light intensity in tree fall gaps (~39,000 lux) was >40 times higher than at the ground level of forest interior (950 lux). Light intensity registered by sensors placed on birds averaged 17.4 (range 3.9–41.5) lux, with species using only 4.3% (0.9%– 10.4%) of available light on the forest floor. Birds therefore selected very dark microhabitats—the light environment was >2200 times brighter in tree fall gaps. Bird thermal niche was a function of ambient temperature as well as body temperature, which averaged >40.5°C but varied among species. Forest floor temperature peaked daily at 27.0°C, whereas bird loggers averaged 35.1°C (34.5–35.7°C) at midday. The antpitta *Myrmothera campanisona* and the antthrush *Formicarius colma* used thermal conditions closest to their body temperatures, whereas leaftossers (*Sclerurus* spp.) and *Myrmornis torquata* occupied relatively cool microclimates. We found no general link between abundance trends and variation in species-specific light and thermal niches. However, all species occupied markedly dim and cool microclimates. Because such conditions are rare outside the interior of primary forest, these results support the microclimate hypothesis in disturbed landscapes. Moreover, strong avoidance of conditions that are becoming more common under climate change highlights the vulnerability of terrestrial insectivores even in the absence of disturbance and may be the reason for enigmatic declines in Amazonia and elsewhere.

INTRODUCTION

The Neotropics are a hotspot of avian diversity, with Amazonia holding the world's highest richness of suboscine passerines (Harvey et al., 2020). These birds largely comprise understory insectivores, a group highly sensitive to disturbance and therefore useful as indicators of change in rainforest ecosystems (Bregman et al., 2014; Powell et al., 2015a; Sherry, 2021). Approximately 20% of the Amazon rainforest had been removed by 2018 (Artaxo, 2019; da Cruz et al., 2021), but the footprint of disturbance is even greater as clearing degrades habitat beyond deforested areas (Bregman et al., 2014). The creation of fragments and edges has led to local declines of understory insectivores in Amazonia (Canaday, 1996; Canaday & Rivadeneyra, 2001; Stouffer & Bierregaard, 1995; Stratford & Stouffer, 1999), and elsewhere in the Neotropics (Sekercioglu et al., 2002; Sigel et al., 2006, 2010). Of understory insectivores, ground-foraging species may be the most sensitive to disturbance—these terrestrial insectivores were the first to leave experimentally isolated forest patches, with extinctions inversely proportional to fragment size (Stouffer & Bierregaard, 1995; Stratford & Stouffer, 1999)—and among the last to recover following forest regrowth in the same landscape (Powell et al., 2013, 2015b). Understory insectivores—especially terrestrial species—therefore often vanish from disturbed areas.

Why are these species lost in degraded rainforest? Several non-mutually exclusive hypotheses have been proposed (refer to Powell et al., 2015a, for review), including large area requirements (Stouffer, 2007), effects of altered forest structure (Stratford & Stouffer, 2015), dispersal limitation (Bates, 2002), and the direct or indirect consequences of novel microclimate due to edge effects (Kapos, 1989). The latter explanation, termed the "microclimate hypothesis," stems from the observation that small forest patches become hotter, drier, and brighter following isolation (Laurance et al., 2002), conditions that may be unsuitable for birds with considerable physiological and sensory specialization (Stratford & Robinson, 2005). The microclimate hypothesis has recently gained additional interest following reports showing that insectivores have not only declined in degraded forest, but also within seemingly intact Amazonia (Blake & Loiselle, 2015; Stouffer et al., 2021). In Brazil, terrestrial insectivores—the same species that first faded in fragments within this landscape—have decreased most strongly among 12 ecological guilds (Stouffer et al., 2021). Importantly, the microclimate hypothesis does not hinge on fragmentation; the driver is change in microclimatic conditions, which at the local scale may be induced by forest disturbance, or at the macro scale by climate change.

Climate models and empirical data show many parts of Amazonia becoming increasingly hotter and drier (Almeida et al., 2017; Fu et al., 2013; Marengo et al., 2018; Neelin et al., 2006), and these changes are in turn linked to shifts in forest structure and composition (Aleixo et al., 2019; Brienen et al., 2015; Duque et al., 2015; Esquivel-Muelbert et al., 2019; Feldpausch et al., 2016). Aside from changes in temperature and precipitation, downward trends in regional cloud cover (Norris et al., 2016) are likely to lead to brighter light environments. Furthermore, as droughts reduce forest leaf area (Nepstad et al., 2004), periodically brighter conditions may be occurring more frequently. Rainforest specialists such as terrestrial insectivores are therefore exposed to shifting conditions in regions generally considered as intact, possibly explaining the abundance changes in forests removed from local disturbance (Stouffer et al., 2021).

Despite the important implications of the microclimate hypothesis, conflicting results have emerged from the few studies to explicitly evaluate microclimate requirements of rainforest birds. In Amazonia, GPS-tagged individuals of the terrestrial insectivore *Formicarius analis* sought shelter and low-lying areas with cooler and wetter microclimate during dry season afternoons, when ambient conditions were at their extreme (Jirinec et al., 2021a). In Panama, an early report of mist net captures concluded that birds tracked microclimate optima for physiological reasons (Karr & Freemark, 1983), but a later study from the same region using radiotracked understory insectivores found no evidence of microclimate selectivity (Pollock et al., 2015), and responses to acute heat stress suggested that birds carried sufficient thermal margins to defend against climate warming (Pollock et al., 2021). Yet, light penetration—a part of microclimate—was the key variable explaining edge avoidance in Belize and Costa Rica (Patten & Smith-Patten, 2012), and larger-eyed species used low-light environments and were more sensitive to landscape disturbance in Peru (Ausprey et al., 2021). In Brazil, species

vulnerable to forest disturbance did not have relatively larger eyes and were not constrained to vocalize in dimly lit crepuscular periods (Rutt et al., 2019b).

The vulnerability of terrestrial insectivores to changing microclimate is therefore unresolved and questions remain particularly about the role of light and temperature in shaping bird occurrence. Stouffer et al. (2021) suggested that abundance trends clustered by vertical foraging stratum in tropical forest birds; terrestrial species decreased whereas midstory species increased in capture rates over time. The forest has a vertical gradient in both light intensity and temperature (Stratford & Robinson, 2005) and because of long-term shifts in these variables, it follows to ask whether light and thermal niches are correlates of vulnerability to climate change. Ausprey et al. (2021) demonstrated light niche partitioning at the coarse scale of the forest vertical profile but, given the intrinsic gradient in microclimate across this space, these results together with Stouffer et al. (2021) reveal little about how birds should respond to climate shifts. For these and similar questions, it is more informative to examine the use of light and temperature environments by birds within a single forest stratum.

Here, we leverage high-resolution data from modern biologging technology to estimate the light and thermal niches of 10 species of terrestrial insectivores within primary forests in Amazonia. We begin with the concept that the interior of primary forest is a dark and cool haven for terrestrial insectivores (*sensu* Patten & Smith-Patten, 2012). Accordingly, we hypothesized that these species avoid bright and warm conditions and occupy correspondingly low-light and low-temperature niches. We further hypothesize that, despite all species inhabiting the forest floor, terrestrial insectivores partition their environment at the fine scale, leading to separation of light and thermal niches among species. Last, we test the hypothesis that more vulnerable species (as identified from long-term abundance trends) use relatively dimmer and cooler microclimates.

METHODS

Study area

The Biological Dynamics of Forest Fragments Project (BDFFP) is ~70 km north of the Brazilian city of Manaus, in central Amazonia (Figure 1). This region lies near the Guiana Shield, leading to reticulated topography with higher elevation plateaus punctuated by shallow microcatchments (Tomasella et al., 2008). Although the BDFFP was originally established to study the effects of forest fragmentation on Amazonian biota, the region remained

>90% covered with humid *terra firme* forest at least until 2017 (Rutt et al., 2019a). In mature forest, the canopy is layered, averaging ~27 m in height with regular emergent trees 40–50 m tall (Almeida et al., 2019), whereas the understory is relatively open and dominated by stemless palms (Almeida et al., 2019; Klein, 1989), with very few herbs and shrubs (Gentry & Emmons, 1987). We worked at two sites, Cabo Frio and Camp 41, both of which were situated completely within primary, continuous forest. The climate at the BDFFP is hot and humid year-round with a single wet–dry cycle. The dry season usually occurs from June through November, when mean air temperature is ~1.3°C higher and precipitation is ~40% of the average wet season (Jirinec et al., 2021a). We tagged birds in the dry season, but data collection generally occurred throughout the entire seasonal cycle.

Species selection and bird capture

We selected 10 species for sampling (Table 1). This group represents the majority of terrestrial insectivores for which abundance trends were estimated (Stouffer et al., 2021); we omitted only *Cyphorhinus arada*, but included one additional species (*Myrmothera campanisona*) for which abundance trends were unknown because it seldom fell into passive monitoring nets. We chose these species for two reasons. First, most of these were previously captured and tracked, offering some confidence they can be recaptured successfully (Stouffer, 2007). Second, variation in abundance trends supplied an indirect test for the microclimate hypothesis outside human disturbance. Although terrestrial insectivores declined strongly as a group, population trends varied by species within the guild (Stouffer et al., 2021). We used this variation to assign species into three groups such that within-group abundance trends of one species were relatively lower ("sensitive" species) compared with the other ("resilient") species, whereas group members were also close phylogenetic relatives (Appendix S1: Figure S1). Sensitivity designations were based on point estimates from the posterior distributions in figure 1a in Stouffer et al. (2021). Although these species comprised a single ecological guild, they were taxonomically and ecologically diverse; they contained three families and included cavity (*Formicarius* spp.), burrow (*Sclerurus* spp.), and cup (all others) nesters. Individual-specific microclimate use was measured by loggers placed on birds for ~1 year (Jirinec et al., 2021b).

We used target-netting to capture birds. Because terrestrial insectivores have become less common in recent years (Stouffer et al., 2021), we devoted extensive effort to locating birds using conspecific playback, then repeated
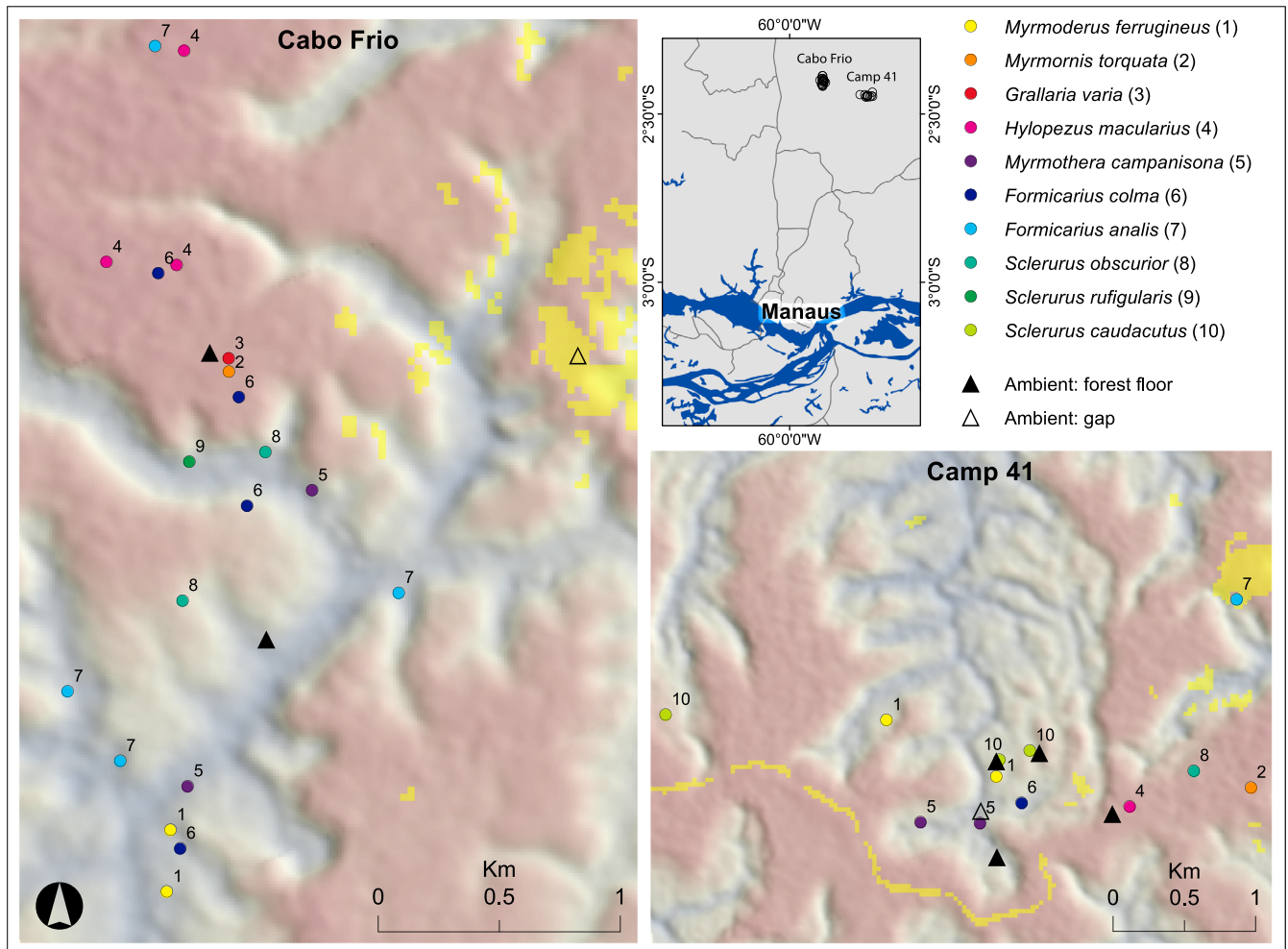
FIGURE 1 Sampling sites at the Biological Dynamics of Forest Fragments Project in central Amazonia. Working at two study areas (Cabo Frio, Camp 41), we deployed 71 loggers on 10 species of ground-foraging insectivores (indexed by numerals), 33 of which we recaptured for data recovery (circles denote tagging locations). Triangles indicate identical loggers placed on the forest floor (filled) and within tree fall gaps (empty) to quantify ambient conditions. The map color gradient represents elevation ranging from 55 m (blue) to 150 m (red) asl. Yellow pixels signify gaps and areas outside mature *terra firme* forest derived by classification of Landsat 8 imagery acquired in 2020

TABLE 1 Study species and sample sizes

Species	Code	Deployed	Recovered	Duration (total days)[a]	Light (*N*)	Temp (*N*)
Myrmoderus ferrugineus	MYFE	9	4 (44%)	1393	400,459	133,486
Myrmornis torquata	MYTO	9	3 (33%)	1111	319,369	106,457
Grallaria varia	GRVA	1	1 (100%)	449	129,101	0
Hylopezus macularius	HYMA	4	4 (100%)	1351	388,148	129,379
Myrmothera campanisona	MYCA	4	4 (100%)	1270	365,034	121,679
Formicarius colma	FOCO	12	5 (42%)	1259	361,952	120,651
Formicarius analis	FOAN	13	5 (38%)	1466	420,901	140,300
Sclerurus obscurior	SCOB	8	3 (38%)	791	227,105	75,703
Sclerurus rufigularis	SCRU	6	1 (17%)	310	88,862	29,620
Sclerurus caudacutus	SCCA	5	3 (60%)	1087	312,301	104,096
Total		71	33 (46%)	10,487	3,013,232	961,371

[a]Sum of days over which tags recorded data (i.e., tag days).

the process in the general area to recapture birds in subsequent years for data recovery. We captured and recaptured birds over three dry seasons, with logger deployment in June–August 2017, recovery and deployment June–October 2018, and recovery June–October 2019. This effort required a total of 257 field days over the three seasons, during which time field teams walked >3500 km, particularly when locating individuals for logger recovery. Once we located a target species, we set several mist nets around an audio lure with observers wearing ghillie camouflage suits monitoring the area for incoming birds. Birds usually approached from the ground rather than by flying; when a bird was near a net, observers flushed it in. Capture opportunities were few, especially during recapture because birds were vigilant, approached infrequently, and moved up to several kilometers from tagging locations (Jirinec et al., 2021a, 2021b). Although we aimed to tag adult (definitive molt cycle) males to increase chances of territoriality and site fidelity, seven of the study species are sexually monochromatic (Johnson & Wolfe, 2017) and so we cannot rule out that some individuals were females. The only *Grallaria varia* we managed to tag was a gravid female. Overall, we deployed 71 loggers and recovered 33 (46%), reaching a final sample size of 10,487 tag days with 1–5 individuals per species (Table 1). In all but five cases, loggers recorded bird microclimate over the entire seasonal cycle (Appendix S1: Table S1).

Birds were measured, marked, and outfitted with microclimate loggers. We took standard morphometric measurements and banded each bird with a metal alphanumeric band and one to two color bands. In 2019, we also measured bird body temperature (T_b) in the cloaca (McCafferty et al., 2015; Prinzinger et al., 1991) using a medical thermometer (HM-1255, Highmex Care, China). Because the capture process may affect T_b due to stress (Lewden et al., 2017; Maggini et al., 2018), we sampled T_b quickly (<5 min) after birds fell into nets. During first capture we attached a light-level geolocator to serve as a microclimate logger (Intigeo-P65B1-11T-20deg, Migrate Technology Ltd, Cambridge, UK). Tags (logger + harness) weighed ≤1 g, representing ~0.8%–4.7% of bird body mass, depending on species and individual. Loggers measured light intensity and temperature at the top of a stalk positioned 9 mm above the logger base to minimize the influence of feather shading and body heat. Light sensors calculated illuminance (here "light intensity") as lux (lumens/m²) at quasilogarithmic resolution with 249 discrete levels and range 1–74,000 lux, whereas temperature sensors calculated temperature at 0.125°C resolution and 0.5°C accuracy. The light sensor spectral response corresponded well with the spectral response of avian vision (Ausprey et al., 2021). We fixed tags with a leg-loop harness (Jirinec et al., 2021b); light readings therefore reflected direct exposure to light striking the bird's dorsal region (between the back and rump), whereas temperature was a mix of air temperature (T_a) and T_b. Loggers were programmed to sample light and temperature every 5 and 15 min, respectively, for final sample sizes of >3 million light and >900,000 temperature readings (Table 1). For more details about bird capture, harness, and the lack of harmful tag effects, please refer to Jirinec et al. (2021b).

We quantified ambient conditions with identical loggers placed on the forest floor and within tree fall gaps to characterize the diversity of light environments available to birds (Endler, 1993). We systematically selected general locations for forest loggers to be away from tree falls and to represent a range of elevations and areas in which we captured birds (Figure 1), then we determined final locations by shifting 3 m at a random bearing. We placed forest loggers (N = 6) on top of PVC pipes ~10 cm away from the forest floor such that sensors faced upward. To represent the two major bright light environments (Endler, 1993), gap loggers (N = 2) were placed in an open field and a large tree fall gap such that they faced the open sky for most diurnal hours and were above the herbaceous layer (i.e., >10 cm high). Ambient loggers sometimes succumbed to elements and wildlife and therefore functioned for various intervals, but at least one forest logger operated throughout the entire study period. Overall, we obtained 562,743 and 283,436 light readings (1956 and 985 tag-days) from forest floor and gap loggers, respectively. We used temperature measurements (N = 187,120) from forest floor loggers to represent T_a.

Covariates

We produced two variables to represent the light niche. First, we used the raw light intensity measurements ("absolute light") from bird sensors. Second, we calculated the proportion of available light ("proportional light") used by birds (Ausprey et al., 2021) as the time-specific fraction of light intensity recorded by bird and forest floor loggers, respectively. To account for asynchrony between bird and ambient loggers, this proportion was derived from hourly averages. For bird loggers, we averaged light intensity readings per individual by hour (N ≤ 12) whereas, for ambient light, we averaged readings from any ambient forest logger recording at the same time as the bird logger (N ≤ 72). Because *Formicarius* spp. and *Sclerurus* spp. nest in cavities that reduce light exposure during breeding, we ignored daytime readings with lux = 1 (minimum sensor threshold) for both absolute and proportional light in these species. However, because most terrestrial insectivores frequently registered 1 lux even outside incubation periods of cavity nesters, we only ignored diurnal darkness intervals
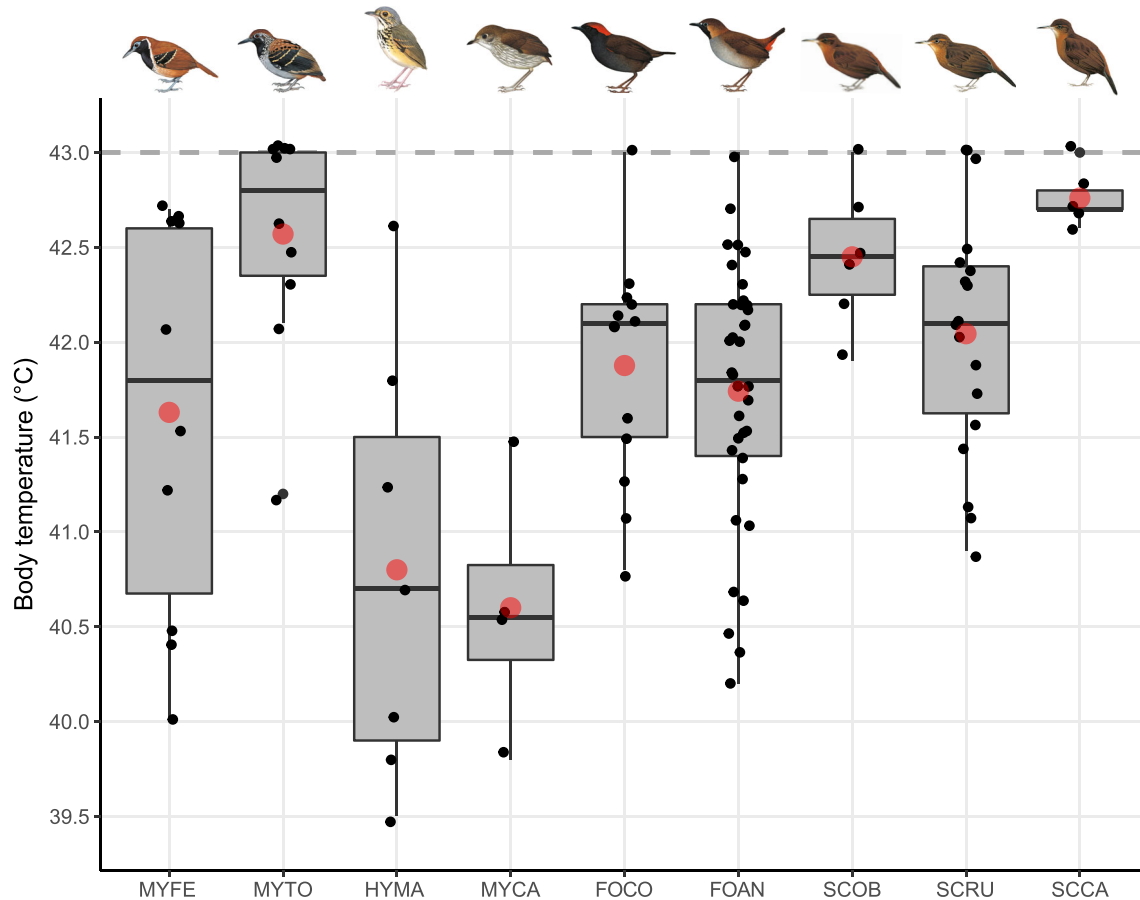
FIGURE 2 Internal body temperature of birds. Histogram bars are medians and red dots means; species codes from Table 1. We used mean body temperature (T_b) to calculate species-specific thermal margin in Figure 5. T_b measurements (points) come from unique individuals, except for two SCCA records taken 38 days apart. The dashed line indicates the upper limit for our thermometer

≥15 min (i.e., at least three consecutive measurements). For all birds, we discarded logger data before midnight on tag day and 3 h before recapture to reflect normal bird activity.

Two variables were produced to represent the thermal niche. First, we used the raw logger temperature (T_L) measurements. Second, because body heat elevated T_L, we subtracted mean species-specific T_b (Figure 2) from T_L. We considered this value the "thermal margin" between T_a and T_b, but we caution that this was a simplistic approach as T_L is a function of bird size, activity, and thermoregulatory behavior.

Analysis

We analyzed light and temperature data using generalized additive models (GAMs) implemented in *mgcv* package version 1.8-34 (Wood, 2020) within R version 4.0.5. For light environment and absolute light, we modeled light intensity for each group or species as the sum of three smooths: numeric time of day (0–23.99) using the
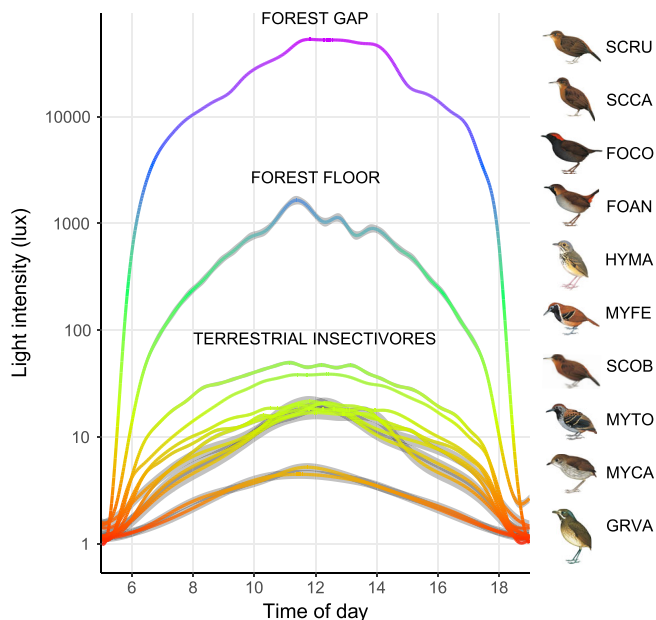
cyclic cubic regression spline basis function (bs = "cc," k = 50), index of sequential observation number per logger (1 to N) with the Gaussian process basis (bs = "gp," k = 50), and logger as the random effect (bs = "re") in cases with more than one logger per group. Model structure for proportional light was identical except for a lower basis number threshold for the circadian smooth (k = 20). Absolute light models assumed Gamma distribution with a log link function, whereas proportional light models assumed quasibinomial distribution with a logit link; both model sets were fit with restricted maximum likelihood. Thermal models were identical to light models, but we assumed Gaussian distribution. In all cases, we executed GAMs with *mgcv*'s bam() function and considered the circadian smooth to reflect light and thermal environments and associated niches.

RESULTS

Terrestrial insectivores used markedly dim light niches. Model output of ambient light environment, averaged

between 9:00 AM and 3:00 PM (midday), revealed light conditions in tree fall gaps and forest floor to be ~39,000 lux and ~950 lux, respectively. All species experienced lower midday light intensity than representative fixed

FIGURE 3 Light environments and bird exposure. Curves (color) and confidence intervals (gray ribbons) are generalized additive models of light intensity clipped to the diurnal period. Data come from identical sensors placed in forest gaps representing near-open sky levels, forest floor representing general bird habitat, as well as the birds themselves, indicated on the right *y-axis* in the same sequence as the curves (according to the 9:00 AM to 3:00 PM average). Time of day on the *x-axis* is given in 24 h format

points on the forest floor, with a mean of 17.4 lux and in the range 3.9–41.5 lux (Figure 3 and Table 2). Absolute and proportional light estimates were highest for SCRU, but even this species used only ~10% of available forest floor light (Figure 4). GRVA and MYCA used the darkest niches, with both exposed to <5 lux of absolute and <1% of proportional light, respectively (Figure 4). Proportional light use of all species averaged ~4% of midday light intensity on the forest floor (Table 2).

The thermal niche was a function of ambient temperature as well as species-specific T_b. Mean and median T_b was >40.5°C for all species (Figure 2). SCCA and MYTO were held among the highest T_b, approaching 43°C, whereas MYCA and HYMA had the lowest at near 40.5°C. GAM of T_a peaked at 27.0°C, whereas average midday T_L from GAMs were 35.1°C (Figure 5 and Table 2). Midday T_L ranged across 1.2°C from 34.5°C (HYMA) to 35.7°C (FOCO). The thermal margin varied substantially more than T_L (across 2.6°C), from 5.3°C (MYCA) to 7.9°C (SCCA). Except for HYMA and FOCO, all species registered a momentary dip in T_L between 5:00 PM and 6:00 PM that in some cases surpassed the nighttime minimum (Figure 6), and was likely to reflect a consistent bathing schedule. This phenomenon was especially pronounced in *Sclerurus* spp. as T_L in all three species dropped >3°C at ~6:00 PM, although T_L returned to the expected level within ~1 h. SCRU appeared to have an additional but smaller dip at ~6:00 PM.

We found little support for the hypothesis that variation in light and thermal niches followed abundance trends of terrestrial insectivores (Figure 6). Out of the four groups of closely related species, only *Formicarius*

**TABLE 2** Light and temperature environment of terrestrial insectivores

Species	Absolute light (lux)	Proportional light (%)[a]	T_L (°C)	Thermal margin (°C)[b]
Myrmoderus ferrugineus	14.18	3.02	34.93	6.7
Myrmornis torquata	13.56	2.49	35.08	7.49
Grallaria varia[c]	3.9	0.9	...	...
Hylopezus macularius	15.7	3.59	34.51	6.29
Myrmothera campanisona	4.08	0.95	35.26	5.34
Formicarius colma	18.28	5.75	35.72	6.15
Formicarius analis	15.76	4.74	35.48	6.26
Sclerurus obscurior	14.16	4.05	35.16	7.29
Sclerurus rufigularis	41.45	10.41	34.67	7.37
Sclerurus caudacutus	33.02	7.07	34.89	7.87
Mean	17.41	4.3	35.08	6.75

Note: Values represent averages of model output between 9:00 AM and 3:00 PM.

[a]Time-specific usage of forest floor light calculated from ambient loggers.

[b]Absolute difference between logger temperature (T_L) and bird body temperature (T_b) (at zero, $T_L = T_b$).

[c]Logger did not record temperature.
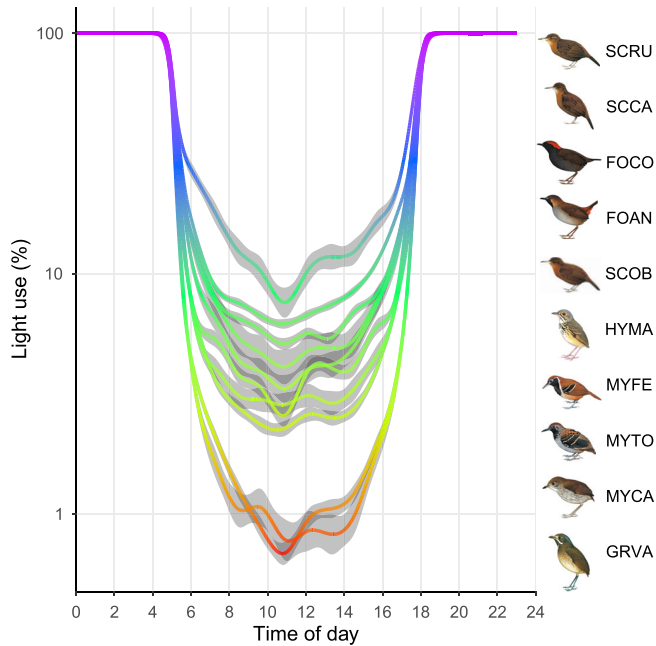
FIGURE 4 Proportional use of available light. Curves (model fit) and ribbons (confidence intervals) are generalized additive models of percentage use of concurrent light conditions, represented by the quotient of bird light exposure and time-specific ambient conditions on the forest floor. Time of day on the *x-axis* is given in 24 h format

spp. matched our prediction that birds with more a negative population change used darker and cooler microclimate.

DISCUSSION

Our results support the notion that terrestrial insectivores select markedly dim conditions on the already shaded rainforest floor. Midday light intensity in this lowest forest stratum averaged 2.4% of light levels within open forest gaps, a result closely matching levels (1.2%) found in the region previously (Shuttleworth, 1984). Yet, the absolute light experienced by birds was much lower, averaging 0.04% of gap levels for the entire guild. This makes gap light intensity >40 times higher than that on the forest floor and >2200 times higher than the average exposure of terrestrial insectivores. GRVA and MYCA, the two antpitta species that used the darkest microhabitats (Table 2), registered 0.01% of gap light levels. The proportion of available light used—a more robust measure of exposure that incorporated concurrent weather—agreed that birds used an exceptionally shaded microclimate: as a guild, terrestrial insectivores used ~4% of midday light in their habitat on the forest floor, with the GRVA and MYCA exposed to ~1% of ambient levels. Although we
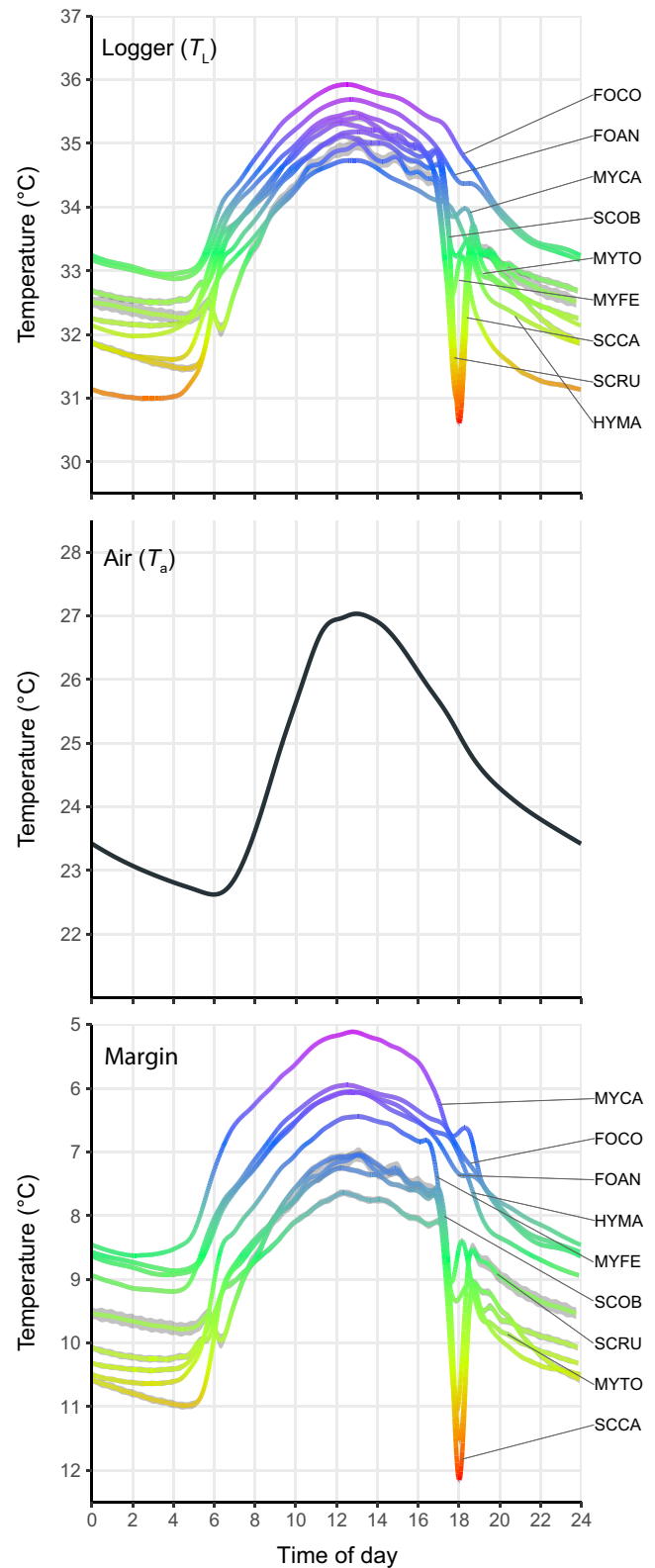
FIGURE 5 Circadian thermal environment of terrestrial insectivores. Panels show raw logger temperature readings (T_L), air temperature on the forest floor (T_a), and thermal margin where T_L was adjusted for species-specific body temperature (T_b; bottom). Curves and confidence intervals are outputs from generalized additive models. Time of day on the *x-axis* is given in 24 h format
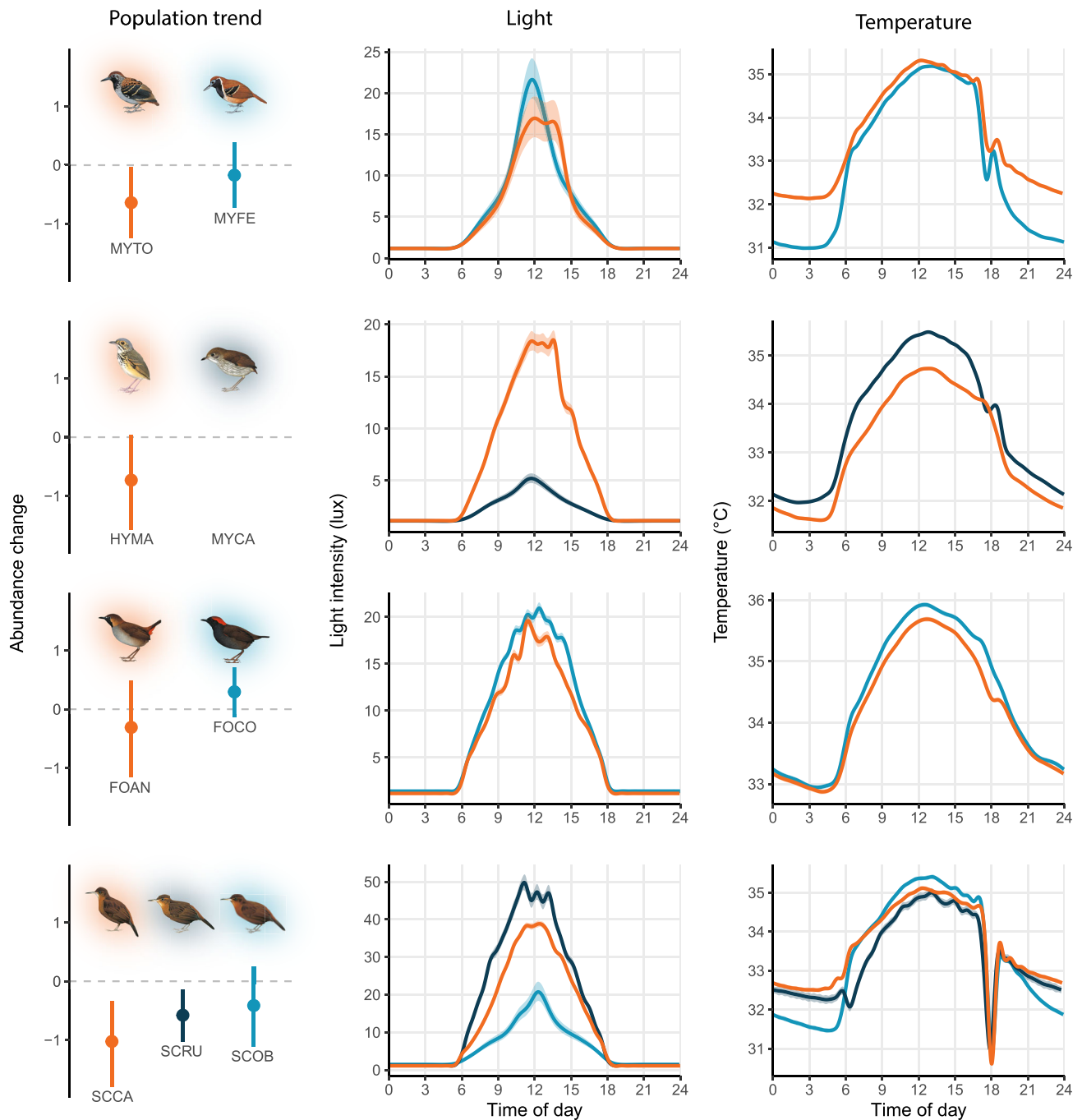
FIGURE 6 Abundance trends and microclimate use of terrestrial insectivores. We grouped these nine species such that group members represented their closest phylogenetic relatives and displayed dissimilar abundance trends. Abundance trends (left column) are summaries of posterior distributions estimated by Stouffer et al. (2021), except MYCA, which was not included in that analysis. Species whose point trend estimates were relatively lower were categorized as "sensitive" (orange) and were expected to occupy dimmer and cooler niches than "resilient" species (blue). Time of day on the *x-axis* is given in 24 h format

cannot rule out some level of feather shading, sensors perched ~1 cm above the skin, most species were relatively small (Jirinec et al., 2021b), and the warm conditions birds occupied were unlikely to induce feather ruffling for thermoregulation. Therefore, we interpret these results as active selection of low-light microhabitat.

This pattern—derived in a novel way through high-resolution sensors placed directly on birds—is consistent with more indirect studies documenting an aversion to bright edges in these and similar species (Laurance, 2004; Laurance & Gomez, 2005; Patten & Smith-Patten, 2012), but does not align with the lack of microclimate

selectivity found by Pollock et al.'s (2015) analysis of radiotagged birds within large forest tracts in Panama. This may possibly be because microclimate on the rainforest floor varies over very small scales (Scheffers et al., 2017), and the scale of selection may therefore be correspondingly small (Suggitt et al., 2011). Because we did not pick atypical locations for non-bird sensors, the conditions we report here should be representative of the average environment available to birds. However, less common microhabitats such as cavities and dense vegetation may supply substantially different microclimates for birds to select (Scheffers et al., 2014).

We saw evidence of small-scale partitioning of light niches. Birds ranged across ~39 lux of absolute intensity and ~10% of proportional light at midday (Table 2) and, although most species overlapped over some intervals within the diurnal cycle for absolute light (Figure 3), proportional light curves differed more strongly with non-overlapping confidence intervals (Figure 4). Ausprey et al. (2021) documented clear partitioning of the light environment among 15 species across the ground-to-canopy gradient in a Peruvian cloud forest community, with the terrestrial insectivore *Grallaria przewalskii* using the lowest light levels. Our study suggests that light niche separation occurs even within a single guild of ground insectivores. This finding is consistent with the concept outlined by Endler (1993): despite seeming uniformly dim to a human walking through the forest, the forest floor furnishes very heterogeneous light conditions over time and space, leading to diverse light environments that can be exploited by ground-dwelling species. Our results therefore agree with the notion that light is an important factor in structuring avian ecological niches (Ausprey, 2021).

As found for light, birds appeared to have used diverse thermal niches, but endogenous body heat played a prominent role. The circadian T_a curve on the forest floor peaked at 27°C (Figure 5) but, because birds are endothermic, T_L was near 35°C (Figure 5 and Table 2). To better understand this interaction, we measured T_b and found that it averaged 41.8°C. Although this appeared to be high, it almost perfectly matched the T_b value found for Passeriformes (41.6 ± 1.13°C, mean ± SD) engaged in normal activity (Prinzinger et al., 1991). However, although we sampled T_b quickly after capture to reflect this active phase T_b, several individuals of six species surpassed the maximum temperature (43.0°C) recordable by our thermometer designed for human medical needs (Figure 2), and mean T_b of these species is therefore likely to be even higher. Recorded mean T_b differed by 2.2°C across the guild but appeared to be phylogenetically correlated as congeners were similar (Figure 2). Antpittas (HYMA, MYCA) were the

coolest, whereas leaftossers (*Sclerurus* spp.) and *Myrmornis torquata* were the hottest species. However, T_b and T_L examined together suggested quite distinct thermal niches: mean midday T_L ranged across 1.2°C, but the thermal margin (absolute difference of T_L and T_b) ranged across 2.5°C. For example, MYCA had low T_b but also relatively high T_L, leading to the smallest thermal margin, whereas SCCA had high T_b and average T_L, leading to the largest thermal margin (Figure 5). This difference suggests that SCCA uses relatively cool microclimates, whereas MYCA occupies microclimates with T_a much closer to its T_b. This result matches the previous characterization of the MYCA preferred microhabitat as young tree fall gaps (Stouffer, 2007; Stratford & Stouffer, 2013) where dense understory vegetation provides ample shade, but edge-like environments produce higher T_a (Stratford & Robinson, 2005). If thermal margins reflect thermal niches, MYCA's use of microhabitats with high T_a may explain its tolerance of forest fragmentation. Stratford and Stouffer (2013) designated MYCA as the only species of nine terrestrial and near-ground insectivores to be insensitive to forest fragmentation, partly due to MYCA's colonization of fragments after they were isolated (Stratford & Stouffer, 1999).

One unexpected, but relevant, result was active cooling by birds by apparent bathing, especially in the late afternoon (Figure 5). Although we were unable to observe birds directly at these times due to their secretive habits, we interpreted these T_L drops as the consequence of a regular bathing schedule. In a study of mixed-species flocks of similar avifauna in French Guiana's primary forests, Jullien and Thiollay (1998) observed that birds bathed regularly, including *Thamnomanes* antshrikes using streams every day at ~5:53 PM. Although it is unclear whether birds bathed for thermoregulatory purposes, the temperature of BDFFP streams averaged 24.6°C (Jirinec et al., 2021a) and bathing therefore certainly cools birds. Regardless, the role of bathing as a mechanism of behavioral thermoregulation deserves more attention in future research, especially if increasingly hotter and drier conditions in central Amazonia (Jirinec et al., 2021a, 2021c) reduce bathing opportunities during the dry season when rainfall may be absent for several days.

Species with a higher probability of decline did not necessarily occupy darker and cooler niches. We formulated this expectation according to the microclimate hypothesis applied to continuous forest under climate change. However, these associations were equivocal (Figure 6), and only one group followed this expectation for both light and temperature (FOAN vs. FOCO). The light and thermal niches varied across the guild, but the variation may have been insufficient to link abundance

changes with microclimate use as a mechanism. Credible intervals for abundance shifts overlapped in all groups and, although the Bayesian statistical framework enabled us to state that sensitive species were more likely to have declined compared with resilient species, in no case were abundance trends starkly divergent (Figure 6). Terrestrial insectivores declined as a guild, and therefore perhaps a better benchmark is midstory frugivores, which have increased in capture rate over recent years (Stouffer et al., 2021). Yet we already know that species in higher forest strata occupy brighter and warmer conditions (Ausprey et al., 2021; Stratford & Robinson, 2005; Walther, 2002), and testing for correlation between vulnerability and light and thermal niches across strata may therefore be uninformative. Regrettably, we did not have abundance trends for MYCA, but this species was expected to be quite resilient given its response to landscape disturbance. But, as noted previously, only its thermal niche would conform to our expectations. HYMA—another antpitta and a close relative—used absolute light conditions that were ~4× brighter, with T_L ~1°C cooler. This result aligns with how these species partition the rainforest floor: MYCA in dense, regenerating treefalls with low light but higher T_a, whereas HYMA occupies more open and cooler understory of mature forest. For these species and others, we posit that the variation in light and thermal use we documented here reflect niche partitioning within their guild of ground-foraging insectivores.

In summary, our results endorse the concept that terrestrial insectivores inhabit exceptionally dark and relatively cool environments. These conditions are rare outside the core of mature rainforest (Endler, 1993; Stratford & Robinson, 2005), and we therefore consider our results to be evidence for the microclimate hypothesis as a plausible explanation for the loss of terrestrial insectivores in disturbed landscapes. Moreover, strong avoidance to conditions that are becoming more common under climate change (Jirinec et al., 2021a, 2021c) highlights the vulnerability of terrestrial insectivores even in the absence of disturbance and may be the reason for declines in Amazonia and elsewhere.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data (Jirinec et al., 2021d) are available in Dryad at https://doi.org/10.5061/dryad.c866t1g84.

ORCID
Vitek Jirinec https://orcid.org/0000-0001-9856-9681
Patricia F. Rodrigues https://orcid.org/0000-0003-3138-6447
Bruna R. Amaral https://orcid.org/0000-0002-7555-3780
Philip C Stouffer https://orcid.org/0000-0002-0052-0423

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