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Unshaded coffee imposes a heavier load on thermoregulation than shaded coffee for birds in a tropical mountainous region

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ABSTRACT

Distribution shifts and local extinctions in tropical montane birds are expected to result from intolerance to elevated temperatures driven by both climate warming and changes in land use which affect local, microclimatic temperatures ($T_a$mic). However, the physiological basis of this phenomenon is yet insufficiently explored. Here, we experimentally measured the response to heat of four wild-caught bird species and predicted how heat exposure would increase the demand for evaporative cooling in a tropical montane region dominated by coffee farming. For this, we first measured $T_a$mic inside shaded and unshaded coffee farms from March to July 2020. Subsequently, we exposed the birds to a temperature gradient in a controlled laboratory environment and measured body temperature and the rates of resting metabolism and evaporative water loss. Using segmented and linear mixed regression models, we determined the temperatures in which these parameters sharply increased (i.e. inflection points). We then used these values to predict the daily amount of time in which $T_a$mic would demand a cooling response and compared it between farm types with generalised linear regression models. Finally, we estimated the water lost to cooling as a percentage of the species-specific body mass. Maximum $T_a$mic in unshaded coffee was significantly higher than in shaded coffee, while $T_a$mic in shaded farms was similar to $T_a$mic inside forest patches used as a reference. The four tested bird species exhibited different rates of change and inflection points of the metabolic parameters. For all of them, shifting from a shaded to an unshaded coffee farm increased the number of hours of exposure by 2–3 times. Interspecific differences were found in the amount of water predicted to be lost to cooling inside the farms. However, these daily losses, even under the most extreme scenario, represented only a small proportion of body mass lost in the form of water. Taken together, we demonstrate that these four bird species are able to endure the current thermal environment of a tropical montane agricultural landscape, without the risks of chronic or lethal dehydration. Nonetheless, we found that unshaded coffee farms increase the demand for water necessary to maintain water balance over consecutive days, which might become more critical if current scenarios of global warming in the tropics are realised in the future.

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1. Introduction

Global assessments of the effects of climate change on birds predict extinctions, distribution shifts and abundance declines (Şekercioğlu et al., 2008). Tropical montane and high-elevation species are thought to be particularly vulnerable to warming temperatures (Freeman et al., 2018). However, the physiological underpinnings of population-level responses to climatic variation are largely unknown.

In some cases, the species' response to warming is influenced by the climatic disruptions generated by land-use changes (Jetz et al., 2007). For example, alterations of microclimates following deforestation at the lower elevation margins can increase the rate of elevational range shifts (Guo et al., 2018). Likewise, agriculture in tropical dry regions exacerbates the effect of high temperatures and low precipitation, promoting species that are used to hot and dry conditions in detriment of forest-dependent birds (Frishkoff et al., 2016). In general, the clearing of tropical forests leads to simplified landscapes characterised by open areas that are warmer and drier (Sales et al., 2020).

Heterogeneous landscapes can buffer against temperature extremes (Suggitt et al., 2011), with vegetation structure being a key factor for microclimatic regulation in tropical human-dominated environments (Jucker et al., 2018). In forest remnants and agroforestry systems, tree canopies insulate the understory against high temperatures and hence stabilise microclimatic conditions (Barradas and Fanjul, 1986; Lin, 2007). For instance, coffee is a versatile crop which can be cultivated under the canopy of woody vegetation (shaded coffee) or exposed under the sun without shade (unshaded coffee) (Perfecto et al., 1996). The presence of shade regulates the microclimate of coffee farms against fluctuations in temperature, humidity and solar radiation (Lin, 2007; Ehrenbergerová et al., 2017) and can positively influence crop yields (Moreira et al., 2018). However, whether and how the resulting attenuation of microclimatic fluctuations through shade trees benefits thermoregulation in birds that thrive in coffee-dominated landscapes is unknown.

Birds possess a variety of physiological mechanisms that allow them to cope with environmental temperature variations and

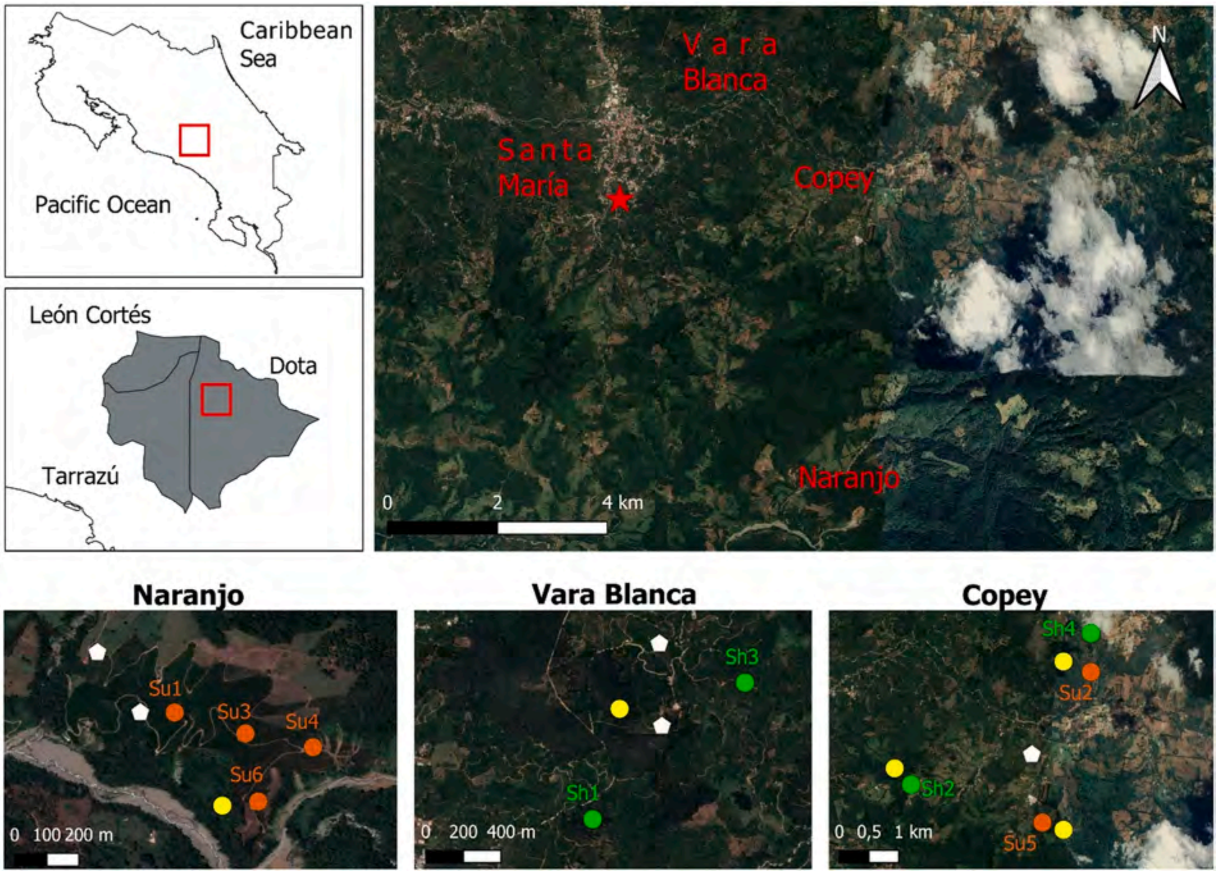

Fig. 1. Map of the study area. The inserts show the location within Costa Rica and within the Zona de los Santos region, composed by the cantons of León Cortés, Tarrazú and Dota. Sampling localities were situated close to the town of Santa María (in Dota), where the laboratory in which metabolic measurements were carried out was established (red star). The three small maps at the bottom show the location of bird mist-netting stations (white pentagons) and of the deployment locations of iButton temperature loggers inside forest patches (yellow circles) and coffee farms (shaded = green; unshaded = orange;) in the sampling localities of Naranjo, Vara Blanca and Copey. Shaded and unshaded farm locations are numbered consecutively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

safeguard their body temperature (T_b) from reaching life-threatening levels (Angilletta et al., 2010). When ambient temperature (T_a) decreases, metabolic heat production helps to maintain a stable T_b (Steiger et al., 2009). In turn, increases in T_a trigger heat dissipation by evaporative cooling (evaporative water loss, EWL) through the body surface or the respiratory tract (McKechnie and Wolf, 2004). Some open-habitat passerines can endure hyperthermia of several degrees above T_a which results in passive heat dissipation from the body to the environment (Weathers, 1997; Nilsson et al., 2016), thus economising water (Gerson et al., 2019). Even though birds may tolerate hyperthermia for a certain amount of time, prolonged exposure to extreme T_a can lead to harmful effects for reproduction and survival (Mitchell et al., 2018; Riddell et al., 2019).

A recent study claimed that changes in microclimate temperatures following the removal of shade trees from coffee farms in East Africa could cause serious losses of insectivorous bird species richness, under current and future climate change scenarios (Schooler et al., 2020). The disappearance of tropical insectivorous birds from natural and disturbed areas has already been related to resource bottlenecks (Lister and Garcia, 2018) and obstacles to dispersal across the countryside (Şekercioğlu et al., 2002). However, very little is known about the thermal sensitivity in this and other bird groups living in agricultural areas. Assessments of stress-related blood parameters (e.g. corticosterone) in North American birds showed that farming intensity can in fact influence their physiological response (Latimer et al., 2020; van Vliet et al., 2020), but the role of temperature was not explicitly defined.

Previous work on the ecophysiology of tropical birds has been focused on the constraints and costs related to elevational distribution in forest-dwelling species, based on the tolerance to cold temperatures (e.g. Jankowski et al., 2013; Freeman, 2015; Londoño et al., 2017). However, no study so far has analysed the influence of microclimatic alterations related to agricultural practices on the thermal tolerance of tropical birds that frequent farmlands. Likewise, the physiological response of tropical montane birds to heat still remains unexplored. Here, we quantified the costs of thermoregulation for four bird species commonly found in Costa Rican montane coffee farms to explore the relationship between microclimatic buffering and the thermal physiology of these species. We predicted that the lack of shade would increase the number of hours of heat exposure, resulting in higher rates of water loss for evaporative cooling in these birds. We, therefore, first looked into differences in microclimatic temperature between shaded and unshaded coffee farms, using adjacent forest patches as a reference. Then, we exposed the birds to a temperature gradient in a controlled environment and measured their response in terms of T_b, metabolic heat production and evaporative cooling. Based on the results, we calculated the thermoregulatory costs arising from exposure to heat in the coffee farms during a 5-month period and estimated the amount of water that the birds could potentially loose from heat exposure as a percentage of their body mass.

2. Materials and methods

Field sampling and data collection took place from March to November 2020 in the central mountains of Costa Rica, specifically in the Zona de los Santos coffee-growing region (N 9º40', W 84º06'). The sampling period comprised the tropical dry and rainy seasons. Roughly, in Costa Rica the dry season occurs from December to April and the wet season from May to November, with some weeks between June and August in which precipitation is reduced or halted. Average precipitation in the study area is ~2000–4000 mm/year. The highest temperatures are reached around March and the lowest around December.

Birds were captured and microclimatic temperatures measured in shaded and unshaded coffee farms at three sites within the study region (Fig. 1): Naranjo (1700 masl), Vara Blanca (1800 masl) and Copey (1900 masl). WorldClim monthly weather data (period 2010–2018) for those sites show that year-round minimum, average and maximum temperatures range between 10 and 12 °C, 16–18 °C and 22–24 °C, respectively (Fick and Hijmans, 2017). The shaded coffee farms of the study sites were characterised by the presence of forest-remnant, crop (e.g. avocado, citrus, banana) and nitrogen-fixing (*Erythrina* sp. and *Inga* sp.) trees. The unshaded farms were either devoid of trees or had a few crop or pruned nitrogen-fixing trees mixed in (see Fig. S1 for pictures of the farm types). In shaded farms, trees had an average maximum height of 20.13 m (sd = 5.51), which produced an estimated average canopy cover of 43.75% (sd = 19.50). In unshaded farms, tree average maximum height was 9.60 m (sd = 8.55) and percent canopy cover was 8.60% (sd = 6.55).

2.1. Thermal environment of coffee farms

Microclimate temperatures ($T_a$mic) in coffee farms and forest patches adjacent to the farms were recorded with Thermochron® iButton® loggers (model DS1921G, accuracy ± 1 °C, Maxim Integrated, USA) between March and July 2020. Four loggers were deployed in shaded coffee farms, six in unshaded farms and five in forest patches and were programmed to collect a temperature read every two hours. We installed the loggers at random locations inside the farms (separated by a minimum of 200 m when in the same farm) and at approximately 55–150 m distance to the nearest forest patch (Fig. 1). Being aware that measurements using iButton loggers may sometimes result in overestimation of $T_a$mic (Maclean et al., 2021), we took several precautions to minimise this source of error. First, to protect them from direct sunlight, the loggers were attached to half-cut white plastic bottles, leaving the bottom uncut to function as a "roof" (Fig. S1). This set-up was nailed to the trunk of woody trees at a height of about 1.5 m above the ground, where they could be exposed to wind flow. Finally, we checked the $T_a$mic databases of all the deployed iButtons and removed measurements in which $T_a$mic increased disproportionally with regards to the previous one – i.e., all increases of more than 10 °C between consecutive 2-hour periods (n = 35, 0.13% of all data points).

2.2. Metabolic trials

Thermal physiology trials were carried out between August and November 2020 on four Neotropical bird species that use different

Table 1
Bird species selected for thermal physiology experiments, their body mass, main diet preference, habitat and elevational distribution in metres above sea level (masl). The number in parenthesis, in the elevation range column, indicates seasonal movements by the species. Data from Stiles and Skutch (1989) and Garrigues and Dean (2014).

Species	N	Body mass (g) ± sd	Dietary guild	Main habitat	Elevation range (masl)
Cabanis's wren	2	19.55 ± 1.34	Insectivore	Shrubland	0–2000
Silver-throated tanager	5	21.49 ± 1.89	Frugivore	Forest	600 (0)–2000
Yellow-faced grassquit	8	9.45 ± 0.55	Granivore	Open areas	0–2200
Lesser goldfinch	10	9.91 ± 0.75	Granivore	Open areas	850–2200 (2750)

habitats but that are commonly found in human-dominated landscapes (Table 1). These were silver-throated tanager (*Tangara icterocephala*, n = 5), yellow-faced grassquit (*Tiaris olivaceus*, n = 8), lesser goldfinch (*Spinus psaltria*, n = 10), and Cabanis's wren (*Cantorchilus modestus*, n = 2). The tanager is mostly frugivorous, forest-dwelling and tends to join mixed-species flocks, the grassquit and the goldfinch live in conspecific groups, feed mostly on seeds and prefer open grassy areas, and the wren is solitary, insectivorous and mainly inhabits the understory of disturbed habitats (Stiles and Skutch, 1989). In our study area, all species were seen moving vertically throughout the coffee bushes in the open parts of coffee farms. In the case of the granivores, they also spent most of their time on the ground or in grassy patches within the farms.

The birds were captured with mist nets or baited traps set up inside the coffee farms between 07 and 12 h, transferred to metallic or wooden holding cages (c. 80 × 50 × 80 cm) and offered water and food (fruit, mealworms and a grain mix of millet, sorghum and sunflower seed). By capturing the birds inside the farms we guaranteed that they used the farms as part of their home ranges – further confirmed by field observations of individuals inside coffee shrubs. Only the dimorphic grassquit and goldfinch could be reliably sexed. Juveniles and individuals that showed signs of breeding condition were released immediately. Otherwise, the birds were transported by car to a field lab away from the farms where the experiments were carried out (max. 40 min trip duration; 1600 m elevation). Once in the lab, they were weighted with an electronic pocket scale (Ecotone, Poland) before the start of the trial. A temperature sensitive transponder (PIT) tag (Biotherm13, USA) was injected subcutaneously with a trocar in the intra-scapular area to measure body temperature (T_b) when activated by a reader system (HPR Plus, Biomark, USA) placed outside the metabolic chamber (see below). Individuals that showed signs of distress when being handled were tested without being injected a tag. Cloacal T_b was also measured in all the birds just prior and after the trial with a digital, dual-channel, K-type thermocouple (model TL253, accuracy ± 1.5%, Proster, Hong Kong).

Once prepared, the birds were introduced individually into the metabolic chamber, which consisted of a 1.4 l glass container with a hermetic-seal plastic lid. The bottom of the container was covered with a ~3 mm layer of mineral oil to trap excreta and prevent its evaporation, and in which a wire mesh platform above the oil layer attached with a small dry wood perch was placed (~10 cm height). Chamber T_a was measured by inserting a thermocouple ~5 cm between the container and lid, and sealed with polytetrafluoroethylene Teflon film tape. The metabolic chamber was placed inside an 18 l portable mini incubator (ICT-P Series, Falc Instruments, Italy) which allows inside temperatures to be manipulated in the range of 10–65 °C, with a precision of ± 0.2 °C. The incubator temperature was adjusted to reach the desired chamber T_a, as recorded by the thermocouple.

Trials began immediately after the bird was placed inside the metabolic chamber and all were conducted during day-time hours, ending no later than 17 h. The relative humidity (RH) and O_2 transferred from the chamber by the excurrent air flow were analysed using a flow-through respirometry system (OxBox 2.0, FIWI – University of Veterinary Medicine, Vienna, Austria) powered by a 12 V car battery. The rate of the flow of air that passed through the whole system was controlled with the built-in mass flow controller of the OxBox. The system's integrated relative humidity and O_2 analysers were calibrated just prior to the start of the trials and did not require further calibrations. The incoming air flow was scrubbed of water vapour using Drierite (Hammond, USA) before being divided into reference and chamber measurement flows, which were then directed to the analysers. We used Bev-A-Line® tubing throughout the system. Considering the similar body weights of the bird species (Table 1), the flow rate was fixed at 60 l h^{-1}. Before measurements were taken, however, an initial wash-out step ensured that traces of humidity were removed from the tubing and chamber by forcing dry air to pass through the whole set-up at a flow rate of 200 l h^{-1} for 60 min. This procedure was performed with the bird inside the chamber, allowing it to adjust to the chamber and ensuring that it was in a post-absorptive state before the measurements started. The wash-out step was tested multiple times before the beginning of fieldwork, until the final configuration was good enough to reduce the absolute humidity to an average of 0.04% (range = 0–0.41%) without a bird in the chamber.

We measured RH and O_2 in 30-min periods, partitioned in 5 min for the reference air and 25 min for the chamber air flow. Throughout the trials, individual birds were subjected to a set of three or four different T_a in 5 °C increases or decreases, covering the range from 10 to 45 °C. The selected range of T_a covered the thermal conditions that the birds experience under field conditions at the study site. Because we were unaware of the birds' tolerance of high T_a during trials, we set the limit at 45 °C to avoid any possible lethal stress. Each measurement period was conducted at a given stabilised T_a (± 0.5 °C) which was then increased or decreased to continue with the next period. The birds were exposed to the first T_a of the trial sequence during the wash-out period and the total duration of the trials was never longer than 3 h. For the duration of the trial, the birds' behaviour was monitored with a mini camera located in front of the chamber and connected to an external monitor to detect the onset T_a of panting to dissipate heat or shivering and fluffing of feathers to generate and retain heat. In addition, whenever T_a approached the extreme values of the tested range, if birds were observed to display sustained escaping behaviours (e.g. pecking the lid of the chamber, moving frantically, sudden sharp rise in T_b) the trial was stopped and the birds immediately removed from the chamber and placed in the holding cages. They were constantly checked

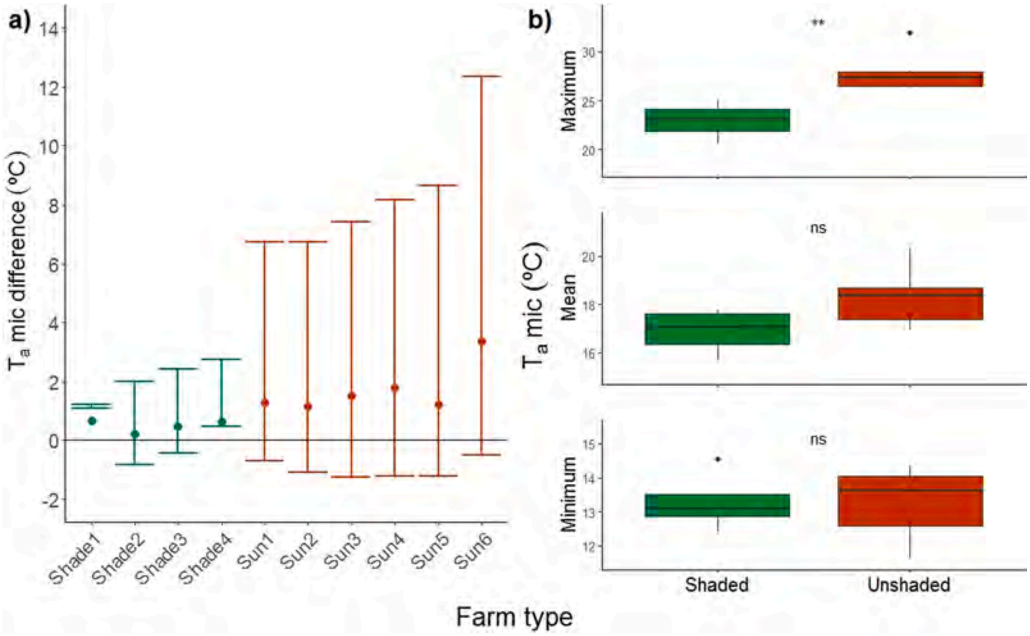

Fig. 2. Differences in averaged microclimate temperatures ($T_a$mic) between shaded coffee farms, unshaded farms and forest patches during a five-month period in the central mountains of Costa Rica. In a), the dependent variable is the difference in $T_a$mic between each farm and its nearest forest patch. Points and whiskers are the monthly-averaged mean and minimum and maximum values, respectively, and farms in the x-axis were ordered from heavily shaded to fully unshaded coffee (see Figs. 1, S1). Panel b), shows the differences in the means of minimum, mean and maximum $T_a$mic between shaded and unshaded coffee farms. ns = not significant, ** = $p < 0.01$.

for their recovery; if unable to do so by themselves, the birds were assisted by manually providing them with water or food and keeping control of their T_b. Data from birds that showed sustained escaping behaviours was not included in the analysis (for the tanager at T_a 15 °C and 44 °C; grassquit at T_a 11 °C, 12 °C, 14 °C, 16 °C, 37 °C, 38 °C, 42 °C, 44 °C, 45 °C; and goldfinch at T_a 11 °C, 16 °C, 17 °C, 43 °C).

2.3. Data analysis

All statistical computations were conducted in the R environment (version 4.0.4, R Core Team, 2021). First, we tested for differences in minimum, mean and maximum $T_a$mic between shaded and unshaded coffee farms with two-sample Welch's t-tests. The reliability of the t-tests was confirmed by visually examining the diagnostic plots.

We then proceeded to estimate and analyse the physiological parameters. Gas and humidity traces measured by the respirometry system were converted to rates of oxygen consumption (VO_2, mlO_2 hr^{-1}) and water vapour production (VH_2O, mlH_2O hr^{-1}), using equations 10.2 and 10.9 from Lighton (2008) respectively. The lowest 10 min mean values for each T_a period were selected to filter out data taken when the birds became agitated during measurements. VH_2O was converted to EWL considering a conversion factor of 0.803 mgH_2O, and VO_2 (mlO_2 hr^{-1}) to resting metabolic rate (RMR, W) considering 20.1 J mlO_2^{-1}. VH_2O was also used to compute the evaporative heat loss (EHL, W), using a latent heat vaporisation factor of 2.43 J mg^{-1}, and the evaporative cooling capacity (ECC) was calculated as EHL/RMR. The rate of change in T_b (°C min^{-1}) and the average, minimum ($T_b$min) and maximum T_b ($T_b$max) were calculated for the last 10 min of each T_a period. $T_b$min was calculated for T_a only below 20 °C and $T_b$max for T_a only above 35 °C. If a bird was not injected with a PIT tag during a trial, its cloacal T_b measured right before introducing or after extracting the bird from the chamber was considered instead. The changes of RMR, EWL, ECC, and T_b were modelled as a function of T_a using segmented regressions, to determine inflection points in their linear relationships, in the package segmented (Muggeo, 2008). Following this, linear mixed-effects models (LMM) were used to compute the slopes before and after the inflection T_a, using trial T_a as fixed effect and individual identity as a random effect in the package lme4 (Bates et al., 2015). The 95% confidence intervals around the inflection points and slopes from the regressions were estimated.

Finally, we modelled the impact on water balance of exposure to high temperatures inside the coffee farms. We began by assessing the amount of time per day, from March to July, in which $T_a$mic surpassed the EWL T_a inflection point detected in the metabolic trials for each bird species. For this, we summed the number of hours above the inflection T_a for each day of the month, as a measure of heat exposure. Then, to test if the presence of shade inside the farms modified each species' water balance, we compared the accumulated number of hours per month above the EWL inflection between shaded and unshaded farms using a generalised linear model (GLM) with a Poisson distribution and a log-link. Month was also included as a predictor in the models to test for significant temporal differences as the dry season transitioned into the wet season. Over-dispersion and model assumptions were checked with the package

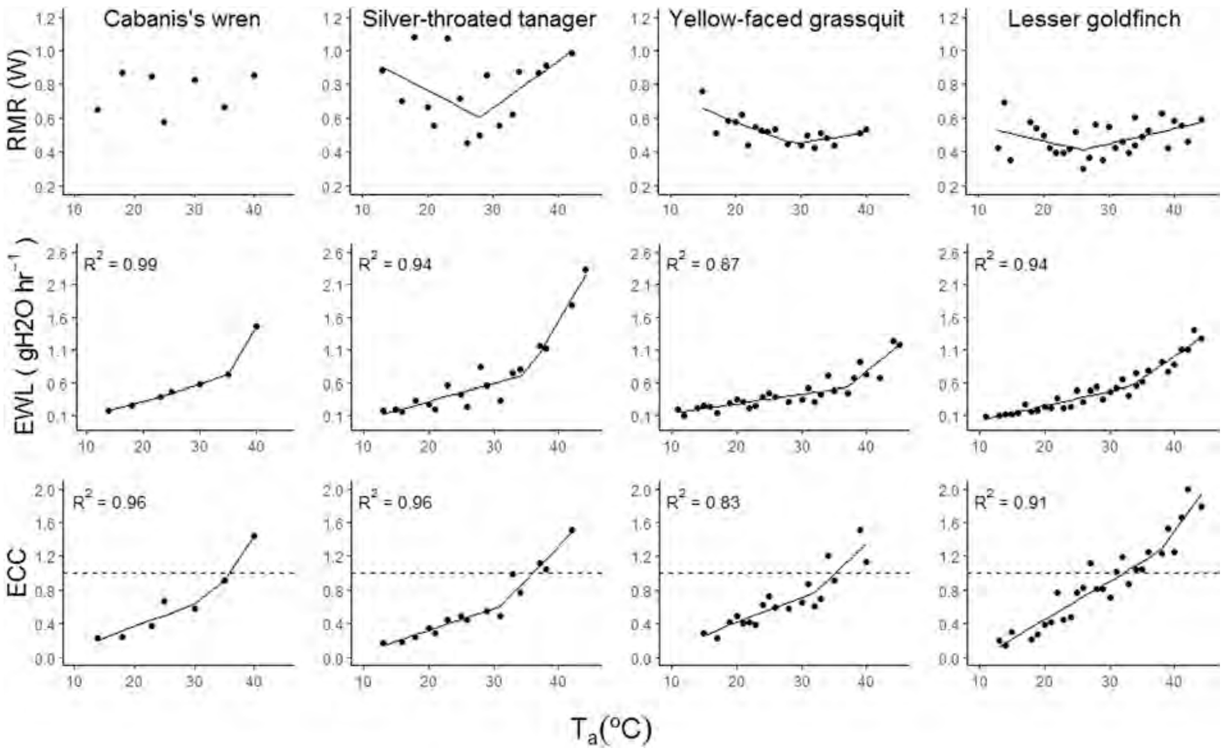

Fig. 3. Relationship between resting metabolic rate (RMR), evaporative water loss (EWL) and evaporative cooling capacity (ECC) and ambient temperature (T_a) inside the metabolic chamber. The black lines were obtained from segmented regression models used to detect inflection points where the response of parameters to further increase of T_a changed sharply. The dashed line in the ECC plots shows where the ratio of metabolic heat dissipation/production is 1. The R^2 coefficients were estimated from the segmented regressions; in the case of RMR, because of its typical "U-shaped" relationship with T_a, no coefficient is included.

DHARMa (Hartig, 2021). Lastly, we computed the percentage of body mass lost to evaporative cooling in the form of water, considering that a threshold of $\geq$ 15% has been deemed as a conservative dehydration tolerance mark for desert passerines (Albright et al., 2017). Using the slopes from the segmented (for the wren only) and LMM regressions, we estimated the change in EWL for each °C of change in T_a – i.e., how much water the birds lost per hour. Based on the species-specific daily amount of time spent above the EWL inflection point, the rate of water lost to evaporative cooling was multiplied by the amount of hours to get the daily water loss. Finally, the water lost was recalculated as a percentage of the birds' total body mass.

3. Results

3.1. Microclimate inside coffee farms

The thermal environment inside the coffee farms was characterised by highly variable $T_a$mic. The average daily range in shaded farms was 9.66 °C (sd = 1.65) while for unshaded farms it was 14.60 °C (sd = 1.91). Maximum $T_a$mic occurred between 10 and 12 h, while minimum $T_a$mic was recorded between 04 and 06 h. Overall, maximum $T_a$mic was higher inside the farms than in adjacent forest patches, especially in unshaded farms, while mean and minimum $T_a$mic differed little between farms and forests (Fig. 2a). The averaged reference $T_a$mic inside the forest was 13.56 °C (sd = 0.80) for the minimum, 16.25 °C (sd = 0.74) for the mean, 19.96 °C (sd = 1.54) for the maximum, and 6.39 °C (sd = 1.74) for the daily range of $T_a$mic.

When analysing minimum, mean and maximum $T_a$mic, we found that the farm types differed only in their maximum $T_a$mic (ΔT_amic 4.93, 95% CI: 1.90 – 7.97, $t_{df=7.05} = -3.84$, $p < 0.01$). On the contrary, the differences in the means of the minimum and mean $T_a$mic were not statistically significant (Fig. 2b).

3.2. Thermoregulation under experimental and semi-natural conditions

RMR. There was insufficient data to estimate parameters for the wren. The T_a in which RMR reached its lowest value were 26 °C for the tanager, 32 °C for the grassquit and 26 °C for the goldfinch. According to the LMM analysis, the slope estimate for the grassquit was only significantly different from zero before the inflection T_a, while neither slopes were for the tanager and the goldfinch (Table A1). The highest thermoregulatory energetic expenditure in wrens was 0.87 W at 18 °C, in tanagers 1.08 W at 18 °C, in grassquits 0.76 W at

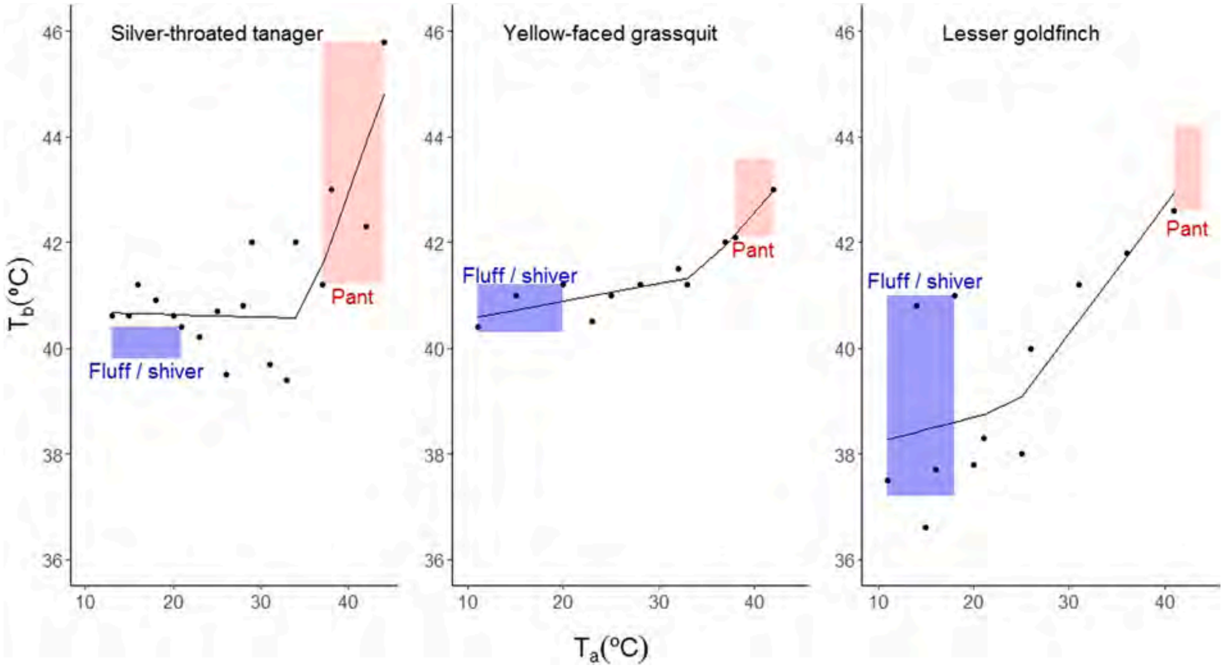

Fig. 4. Change in body temperature (T_b) in response to the ambient temperature (T_a) inside the metabolic chamber. The black lines were obtained from segmented regression models fitted to T_b and T_a, used to detect inflection points in which changes in T_a resulted in sharp changes in T_b. Shaded areas represent the range of T_a in which birds displayed thermoregulatory behaviours: panting to dissipate heat (red) and fluffing of feathers and/or shivering to generate heat (blue). Vertically, they span from the average T_b down to the minimum ($T_b$min) or up to the maximum T_b ($T_b$max) in which the behaviours were observed. Note: the maximum panting temperature for the goldfinch corresponds to its cloacal T_b measurement because that individual was not injected a PIT tag. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

15 °C, and in goldfinches 0.70 W at 14 °C (Fig. 3).

EWL. For all species, the segmented linear relationship between EWL and T_a was highly significant ($p < 0.001$). The species with the lowest and highest inflection T_a were the goldfinch and the grassquit, respectively (Table A1). The tanager and the wren had comparably lower rate of change in EWL before the inflection, followed by the grassquit, while the goldfinch had the highest rate. However, after the inflection T_a, the rate of change was 5.0 times higher for the wren, as estimated from the segmented regression. The rate was 5.7 times higher for the tanager, and 3.5 times for the grassquit and goldfinch, according to the estimated LMM slopes (Fig. 3).

ECC. The segmented linear relationship between ECC and T_a was significant for the grassquit ($p < 0.001$), tanager and goldfinch ($p < 0.01$) and marginally significant for the wren ($p = 0.06$). In the goldfinch, the rate of change in ECC increased by a factor of 2.5 after reaching the inflection T_a. For the wren, according to the segmented regression slopes, the rate of change increased by a factor of 4. In tanagers and grassquits, the rate of change increased by 2- and 1.25-fold, respectively. Goldfinches were able to dissipate all metabolic heat produced earlier than the other species, at around T_a 30 °C. In turn, tanagers achieved parity between metabolic heat dissipation and production at around T_a 33 °C, while wrens and grassquits did so at 35 °C.

T_b. Because both wren individuals became uneasy during handling, we did not inject a PIT tag in them and were thus unable to measure T_b for this species during the metabolic trials. The inflection points for the tanager and the grassquit were similar, around 34 °C. In the case of the goldfinch, T_b inflection was low, 24 °C, and T_b was highly variable throughout the trials (Table A1; Fig. 4). The average T_b for this species was 39.4 °C and ranged between 36.3 and 42.6 °C. Variation in tanagers was also high (range 39.2–45.8 °C; average = 41.2 °C), but this was due to one individual who suffered a dramatic increase in T_b and died, despite ending the trial five minutes after beginning the measurements at $T_a = 44$ °C. In contrast, the variation in T_b was lower for the grassquit (40 °C–43.6 °C; average = 41.4 °C). The tanager T_b changed at a rate of 9.5 times after reaching the inflection T_a. For the grassquit and goldfinch, the rate changed by 5- and 0.7-fold, respectively. The almost unmodified rate of change in T_b before and after the inflection in the goldfinch results from high individual variation in thermoregulation during cold T_a, in which some individuals experienced a decrease in T_b to 36–37 °C while others remained at 40–41 °C. Grassquits and goldfinches were first observed shivering at T_a 16 °C. In turn, only one tanager shivered and it occurred at T_a 13 °C. During panting, T_b changed from 41.2 °C to $T_b$max 45.8 °C in tanagers, from T_b 42.1 °C to $T_b$max 43.6 °C in grassquits and from T_b 42.9 °C to $T_b$max 44.2 °C (both cloacal T_b) in goldfinches (Fig. 4).

3.3. Predicted physiological response to the thermal environment of the coffee farms

The number of hours in which $T_a$mic surpassed EWL inflection points significantly declined from March through July, regardless of

Table 2

Model results from the Poisson GLM regression of hours of exposure to $T_a$mic that surpassed the inflection points of EWL recorded in metabolic trials against farm type and month. Shaded farms and the month of March were taken as reference categories in the models. Note: there were 0 h of exposure during the months of June and July for the yellow-faced grassquit.

Species		Estimate	SE	z-value	p-value
Cabanis's wren					
	Intercept	1.90	0.28	6.70	$p < 0.001$
	April	-0.41	0.20	-1.99	$p < 0.05$
	May	-1.46	0.30	-4.90	$p < 0.001$
	June	-2.02	0.38	-5.35	$p < 0.001$
	July	-2.71	0.52	-5.24	$p < 0.001$
	Unshaded coffee	2.08	0.28	7.34	$p < 0.001$
Silver-throated tanager					
	Intercept	1.42	0.36	3.90	$p < 0.001$
	April	-0.45	0.19	-2.37	$p < 0.05$
	May	-1.79	0.31	-5.75	$p < 0.001$
	June	-2.20	0.37	-5.90	$p < 0.001$
	July	-3.58	0.72	-5.00	$p < 0.001$
	Unshaded coffee	2.80	0.36	7.70	$p < 0.001$
Yellow-faced grassquit					
	Intercept	0.15	0.71	0.21	$p = 0.84$
	April	-0.61	0.25	-2.39	$p < 0.05$
	May	-1.71	0.38	-4.44	$p < 0.001$
	Unshaded coffee	3.61	0.72	5.04	$p < 0.001$
Lesser goldfinch					
	Intercept	2.22	0.23	9.60	$p < 0.001$
	April	-0.34	0.13	-2.64	$p < 0.01$
	May	-1.35	0.18	-7.39	$p < 0.001$
	June	-2.21	0.26	-8.40	$p < 0.001$
	July	-2.50	0.30	-8.32	$p < 0.001$
	Unshaded coffee	2.70	0.23	11.66	$p < 0.001$

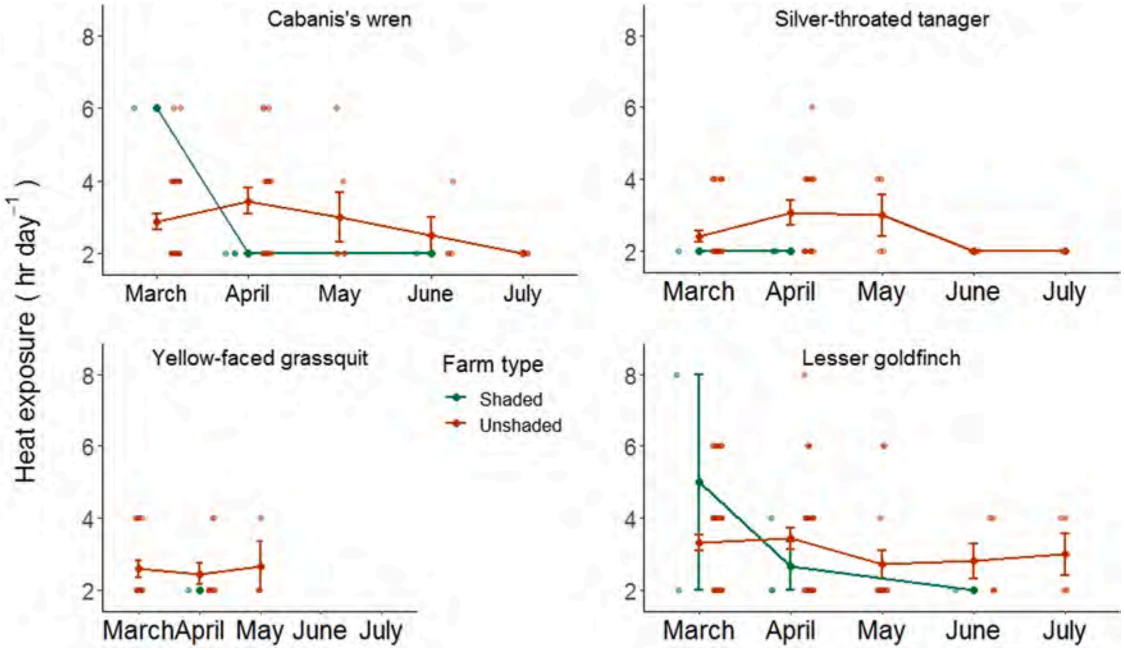

Fig. 5. Daily heat exposure for four bird species inside coffee farms in the central mountains of Costa Rica. Shown is the mean number of hours per day (> 0), enclosed by standard error bars, for five months in which the species experienced $T_a$mic that surpassed the inflection points of EWL recorded in metabolic trials. The points are the individual daily $T_a$mic values.

the farm type (Table 2). The difference between March and April was marginally significant whereas during July the number of hours declined around 3-fold for all species. On average, and during the five months of the study, the wren was exposed to 2.99 h (sd = 1.36) per day to $T_a$mic above EWL inflection for 69 days, the tanager to 2.56 h (sd = 0.98) for 57 days, the grassquit to 2.53 h (sd = 0.90) for 30 days, and the goldfinch to 3.23 h (sd = 1.54) for 98 days. Heat exposure within shaded farms occurred only during March, April and

Table 3
Predictions of water lost to evaporation (EWL) from exposure to heat in coffee farms. The slopes were estimated when regressing EWL to T_a during respirometry trials in linear mixed-effects and segmented models. The maximum amount of hours above the EWL inflection is the species-specific value during the period from March to July 2020, according to the $T_a$mic recorded inside the farms. The percentage of water lost to evaporative cooling was calculated relative to average body mass.

Species	Slope above EWL inflection	Maximum hours of $T_a$mic above EWL inflection point in a given day	Amount of water lost (gH_2O)	Percentage of water lost
Cabanis's wren	0.15[a]	6	0.90	4.6%
Silver-throated tanager	0.17	6	1.02	4.8%
Yellow-faced grassquit	0.07	4	0.28	3.0%
Lesser goldfinch	0.07	8	0.56	5.7%

[a] estimated from a segmented regression.

June for the wren [average 2.80 h (sd = 0.64) per day for 5 days], during March and April for the tanager [average 2.00 h (sd = 0.62) for 4 days], during April for the grassquit (2 h in one day), and during March, April and June for the goldfinch [average 3.33 h (sd = 0.81) in 6 days]. In contrast, heat exposure inside unshaded farms occurred during the five months for all species, except the grassquit for which heat exposure stopped in June (Fig. 5). For comparison, there were zero hours of heat exposure above EWL inflection inside the forest patches, for any of the species and months.

Our predictions of water loss during heat exposure in coffee farms show that during a typical day in which the birds face the maximum amount of hours above EWL inflection, none of the species would lose more than 10% of their body weight to evaporative cooling (Table 3). The two heavier species, tanagers and wrens, lost water at a higher rate than the smaller grassquits and goldfinches. However, the higher T_a inflection of EWL in the grassquit resulted in less predicted hours of exposure and, in consequence, the lowest amount of water lost to evaporative cooling in a single day among all species. In contrast, the goldfinch lost more water in proportion to body mass due to exposure to more hours of heat than the other species. According to our predictions, it would take 6.7 consecutive days under four hours of daily heat exposure for a grassquit to lose 20% of water relative to body weight. For wrens, tanagers and goldfinches, the predicted amount of days would be 4.4, 4.2 and 3.5, exposed to six, six and eight hours daily, respectively.

4. Discussion

The results of this study show that farm management practices in the tropics can influence thermoregulation in agriculture-associated birds, by creating different thermal microclimates that become more challenging when cultivation is intensified. Specifically, we evidenced that maximum daily temperatures are significantly higher in coffee farms with a reduced or absent shade tree canopy, particularly during the dry season. Our four focal species showed diverse heat dissipation responses when exposed to high temperatures. In consequence, the predicted exposure to heat that elevated the demand for evaporative cooling inside the coffee farms varied between species.

4.1. Thermal microclimatic environment of coffee farms

When compared with local temperatures of cleared areas, the understory of tropical lowland and montane forests not only remains cooler during the day but also warmer during the night (De Frenne et al., 2019; Montejo-Kovacevich et al., 2020). The differences in $T_a$mic daily range, minimum, mean, and maximum between forest and farmland found in our study provide further evidence that forest patches are vital thermal buffers in agriculture-dominated landscapes. Even if tropical forests remnants are intervened – e.g. for selective logging – they still provide microclimate buffering and harbour temperature-sensitive species (Senior et al., 2018) if extractive activities are kept at a low level of intensity (Jucker et al., 2018). Under this scenario, farmlands that maintain a vegetation structure similar to intervened forests might contribute in reducing local maxima. This was exemplified in our study by the small differences in maximum temperatures (1.2 °C) between the most heavily shaded farm and its nearest forest patch. The non-coffee vegetation composition in this farm (the first in Fig. 2a) was ~96% forest plants, highlighting the vital role of remnant forest trees in attenuating $T_a$mic increases in agricultural landscapes.

Other studies have already demonstrated that daily temperature variation can decrease by almost 2-fold when shade trees are incorporated within the coffee plantation (Barradas and Fanjul, 1986) while unshaded coffee farms can, on average, be considerably hotter than forest – e.g. by ~6 °C in a Brazilian study area (de Souza et al., 2012). Forest remnant trees as well as tall, unpruned nitrogen-fixing trees in shaded coffee farms can keep daily maxima lower and nightly minima warmer than in unshaded farms (Siles et al., 2010). In contrast, the unshaded farms of our study site were characterised by rows of small (< 2 m) and pruned nitrogen-fixing *Erythrina poeppigiana* trees, thus resulting in reduced $T_a$mic buffering when compared to the shaded farms.

4.2. Thermoregulation and heat exposure in coffee farms

Our analysis of metabolic traits shows that the four study species are able to tolerate daily $T_a$mic and that, as a consequence, they are not threatened by the thermal environment they experience inside the coffee farms. In particular, minimum $T_a$mic of the study area do not appear challenging for the birds since the same temperature range was not energetically demanding for them during the experiments. Also, the T_b of tanagers and grassquits was stable when exposed to cold T_a and, despite T_b being more variable and its rate of change more pronounced in the goldfinch, no individual showed any sign of distress for the range of cold T_a tested.

However, the results evidenced inter-specific differences in heat dissipation and T_b regulation that might be relevant to understand the birds' response if their thermal load increases as a consequence of global warming. In dealing with heat, not only did the tanager's EWL rate start increasing earlier but the rate of change in EWL above the inflection point was almost six times higher than below it. Moreover, shortly after achieving parity between metabolic heat loss and production, T_b spiked and hyperthermia could not be avoided despite initiating a panting response at $T_a = 37$ °C. A similar ECC (~1.5 at $T_a > 40$ °C), aided by low energy-cost panting, is an effective thermoregulatory mechanism to deal with elevated T_a in a large tropical rainforest species (Lasiewski et al., 1970). However, the elevated increase in T_b observed in tanagers after reaching the heat dissipation/production parity (0.4 °C per 1 °C T_a) seem to suggest otherwise for this species. The tanager's response to heat might therefore underscore the sensibility of some tropical forest birds to fragmentation and habitat loss and the ensuing microclimatic changes, as a thermally stressful environment can have a negative impact on their physical condition (Busch et al., 2011).

On the other hand, open-habitat grassquits and goldfinches demonstrated their capacity to endure thermal variation at high T_a. For instance, despite both species showing a similar EWL rate of change as in tanagers and wrens, after the inflection T_a the rate was lower in the former species. Grassquits and goldfinches, however, followed different physiological pathways in response to thermal variation that are worth considering. First, the grassquit had the most delayed onset T_a of increased water loss, which resulted in a much more attenuated hyperthermia at the hottest T_a during the trials. This seems to suggest that grassquits conserve their water until when it is most needed. In turn, goldfinches experienced the highest water expenditure to cool down and dissipated at a maximum twice the metabolic heat produced. The ability to expand the limits of EWL and sustain maximum T_a before entering hyperthermia during heat exposure has been linked to regular water-drinking in arid zone birds (Czenze et al., 2020). While it is possible that the goldfinch is more water-dependent than the grassquit, this has to be confirmed with field observations. Detecting interspecific variation in thermoregulatory water management is crucial to understand population-level responses to episodes of high heat exposure when water is present or absent (Riddell et al., 2019). We suspect that the water economy observed in grassquits could help them cope better with future climate change in agricultural landscapes than goldfinches, who are already suffering from the extremely dry and hot conditions in the arid parts of their range (Albright et al., 2017).

We have shown that, despite differences in sensitivity to heat, all of the tested species are able to withstand current $T_a$mic inside coffee farms of the study area. Yet, since management practices can strongly alter $T_a$mic, especially during the hottest months of the year, thermoregulation becomes more demanding as coffee cultivation intensifies. This was further evidenced from the difference in the amount of heat exposure days between farm types. Thus, in order to tolerate daily exposure to maximum $T_a$mic, the water lost to cooling down the body needs to be replenished more frequently inside unshaded coffee farms. The availability of resources then becomes vital because cooling costs are associated to dietary preference in thermally challenging environments (Riddell et al., 2019). For example, insectivores acquire water from their prey but granivorous birds obtain little water from seeds, leaving them generally dependent on water sources (Albright et al., 2017). Tropical rainforest frugivorous birds access water in relatively high amounts from the fruits in their diets (Worthington, 1989), which means that they might be deterred from entering and remaining in coffee farms devoid of forest or even crop trees. In fact, telemetry data show that silver-throated tanagers persist in coffee-dominated landscapes only with a forest tree cover of at least 10% (Şekercioğlu et al., 2007). However, we observed this and other similar frugivores (e.g. *Piranga bidentata*) inside coffee bushes, even in unshaded farms, and we interpret this as individuals looking for arthropod prey. In arid environments, birds face the challenge of either consuming a high amount of small, low water-content arthropods or increasing foraging activity – and heat exposure in consequence – to catch large, elusive and high water-content prey (Riddell et al., 2019). Our findings show that our focal species would benefit from consuming arthropods to help them maintain water balance over consecutive days, especially in places where coffee farms are rapidly replacing their natural habitats. However, although coffee farms harbour diverse arthropod communities, their abundance is lower in coffee bushes exposed under the sun than in those under shade (Johnson, 2000). Thus, frugivores, insectivores and even granivores, living in unshaded coffee-dominated landscapes may face difficulties in obtaining the resources needed to fulfil daily cooling costs if arthropod communities are depauperate.

Birds that frequent coffee plantations may also curtail heat loads and reduce EWL by shifting to cooler microsites during the hottest hours of the day. For instance, goldfinches constantly move between open grassy patches, where they forage, and tall tree branches (Stiles and Skutch, 1989). Even other small tropical open-habitat granivores that can endure hyperthermic T_b above 44 °C normally stop foraging and shelter in the shade when it gets overly hot (Weathers, 1997). This suggests that the amount of time that coffee-associated birds could dedicate to foraging and other activities is reduced in unshaded farms and extended in shaded farms. However, more research is certainly needed to substantiate the possible relationship between avian temperature-dependent activity and microclimate in tropical agricultural landscapes.

While we have shed some light on the thermal physiology of tropical birds associated with agricultural landscapes based on temperature patterns alone, we acknowledge the relevance of jointly analysing the variations in rainfall and the consequences for thermoregulation and resource availability known for tropical endotherms (Boyle et al., 2020). Evaporative cooling is the avenue for heat dissipation at high T_a (Weathers, 1997), but its efficiency is hampered by high humidity; for example, when relative humidity surpasses 90% (Weathers, 1977) which is the normal condition during the wet season in our study area (Granados-Montero et al., 2020). Because we kept a low level of humidity inside the metabolic chamber during trials, we cannot be certain that the cooling response that the birds showed while tested could be directly transposed into the response while in the field. However, Weathers (1997) argued that even the 1.27 ECC observed in variable seedeaters (*Sporophila corvina*) during trials overestimated the "real" value experienced in the hot and humid lowlands of Panama, most likely a result of the seedeaters' reduced EWL rate at high T_a. As a

Table A1

Points of inflection and the rate of change (i.e. slope) of the relation between RMR, EWL, ECC, and T_b and the T_a during metabolic trials. The inflection T_a were estimated by segmented regressions and slopes in linear-mixed effects model regressions conducted on data below (β_{below}) and above (β_{above}) the inflection T_a. For both parameters, the 95% confidence intervals are provided in parenthesis. The dashes indicate when the estimates could not be computed.

Species		RMR (W)	EWL (gH2O hr^{-1})	ECC	T_b (°C)
Cabanis's wren	Inflection T_a (°C)	–	34.72 (33.98–35.45)	33.00 (24.62–41.39)	–
	β_{below} (°C^{-1})	–	0.03 (0.02–0.03)	0.01 (−0.00 to 0.04)	–
	β_{above} (°C^{-1})	–	0.15 (0.13–0.17)	–	–
Silver-throated tanager	Inflection T_a (°C)	28.00 (19.91–36.09)	35.11 (32.33–37.89)	31.00 (27.06–34.94)	34.80 (29.58–40.03)
	β_{below} (°C^{-1})	-0.02 (−0.05 to 0.01)	0.03 (0.02–0.04)	0.03 (0.02–0.03)	-0.04 (−0.08 to 0.01)
	β_{above} (°C^{-1})	0.02 (0.01–0.05)	0.17 (0.13–0.22)	0.06 (0.05–0.10)	0.38 (0.13–0.75)
Yellow-faced grassquit	Inflection T_a (°C)	28.94 (23.78–34.10)	36.87 (34.13–39.60)	32.00 (24.88–39.12)	34.12 (28.35–39.89)
	β_{below} (°C^{-1})	-0.02 (−0.03 to −0.01)	0.02 (0.01– 0.02)	0.04 (0.04–0.05)	0.04 (0.01–0.07)
	β_{above} (°C^{-1})	0.01 (−0.01–0.02)	0.07 (0.05–0.10)	0.05 (0.04–0.07)	0.21 (0.17–0.24)
Lesser goldfinch	Inflection T_a (°C)	26.00 (18.57–33.43)	33.07 (30.15–36)	37.69 (33.33–42.06)	24.22 (1.84–46.59
	β_{below} (°C^{-1})	-0.01 (−0.02–0.01)	0.02 (0.01–0.03)	0.04 (0.04–0.05)	0.28 (−0.23–0.56)
	β_{above} (°C^{-1})	0.01 (−0.00–0.02)	0.07 (0.05–0.09)	0.10 (0.03–0.15)	0.20 (0.11–0.32)

consequence, tropical birds of humid regions, especially those continually exposed to direct sun radiation, are expected to show EWL rates that hardly increase at high T_a (Weathers, 1977). Indeed, this was the pattern we observed in the open-habitat species. The impairment of evaporative cooling at high T_a and humidity may be widespread and become a potential mechanism of thermal sensitivity in tropical passerines (Gardner et al., 2016). Given that changes in rainfall patterns in the tropics have been observed and are predicted to continue (Zhang and Fueglistaler, 2019), assessing the physiological response of tropical birds to concomitant gradients of humidity and temperature demands urgent attention.

5. Conservation implications

The preservation of forest areas immersed in tropical agricultural landscapes plays a fundamental role, not only in harbouring bird diversity but also for providing an oasis of stable thermal conditions against the synergetic effects of agricultural intensification and climate change. The role of forests as thermal buffers is becoming increasingly relevant in the face of global warming (Ewers and Banks-Leite, 2013) because their capacity to reduce local temperature variation is stronger during extreme events (De Frenne et al., 2019). Even though the lack of microclimatic heterogeneity in tropical forests has been perceived as disadvantageous for the resilience of forest birds against climate warming (Pollock et al., 2015), these habitats are crucial for thermoregulation in birds that thrive in agricultural landscapes and we posit that they will continue to do so in the face of climate warming.

Microclimate buffering as a regulating ecosystem service should be considered in climate change adaptation and mitigation strategies by policymakers (De Frenne et al., 2019) for natural and agricultural areas alike. Agroforestry systems have the potential to reduce air temperatures and thus guarantee the future production and suitability of arable lands for crops of global importance such as coffee (Gomes et al., 2020). Unfortunately, in many parts of Latin America, East Africa and Southeast Asia the trends in coffee cultivation since the 1990s show that shade coffee is being progressively replaced by scantly shaded or unshaded farms (Jha et al., 2014). Because the mitigation of microclimates depends on the amount of shade cover and the inability of intensified farms to regulate temperature extremes can extend across seasons (Lin, 2007), we believe that the expansion of unshaded coffee has the potential to increase the thermal hostility of entire landscape matrices across many tropical regions.

Understanding the underlying physiological mechanisms related to bird survival or extirpation in disturbed environments is fundamental for the development of adaptation strategies aimed at lessening the impacts of human activity on bird diversity (Cooke et al., 2013). This way, agricultural areas could become less hostile to biodiversity in the face of ongoing warming and continue to host recognised and potential ecosystem-service providers. For example, in farmlands of the United States the largely granivorous American goldfinch (*Spinus tristis*) – related to the lesser goldfinch – was found to consume arthropod prey more commonly than previously thought, including pest species (Garfinkel et al., 2021).

In conclusion, the four studied bird species can tolerate current thermal conditions in coffee farms of the study area. If the water lost to cooling is refilled, the amount of days exposed to heat do not seem to pose an immediate life-threatening danger to the study species. However, with the increase in the number of hot days that is predicted in the world's tropics from 1.5 °C warming above current levels (Hoegh-Guldberg et al., 2018), birds will most likely be exposed to higher water losses, which would need to be replenished more constantly. The birds' tolerance of thermal maxima in coffee farms may ultimately depend on the availability of resources. Shaded coffee offers not only buffered $T_a$mic, but also potentially higher amount of resources useful for thermoregulation (e.g. fruiting trees and invertebrate prey). On the other hand, whenever these resources are reduced or absent, intensified unshaded farms might become even more hostile for birds in the future.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

See Table A1.

Appendix B. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02117.

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