DISSERTATION / DOCTORAL THESIS

Titel der Dissertation /Title of the Doctoral Thesis

„Land use and warming effects on tropical birds: diversity and physiological vulnerability“

verfasst von / submitted by

Otto Monge Solano

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Doctor of Philosophy (PhD)

Wien, 2022 / Vienna 2022

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	UA 794 685 437
Dissertationsgebiet lt. Studienblatt / field of study as it appears on the student record sheet:	Biologie
Betreut von / Supervisor:	Univ.-Prof. Dott. Leonida Fusani, Mphil, PhD Dipl.-Biol. Dr. Christian Schulze Univ.-Prof. Mag. Dr. Stefan Dullinger

Acknowledgements

This work would have never seen the light if it was not for the collaboration of all the coffee producers who decided to allow me to conduct fieldwork inside their farms. Not only was the demanding task of collecting data satisfactorily achieved but some of them granted me the fortune of sharing all of their knowledge about nature, about how coffee production works and how both are intimately related. This knowledge is not acquired in a university class but is the result of years of careful observation from live experience and which, in many cases, is handed down from generation to generation. For this, I am grateful.

I also wish to acknowledge the valuable assistance I received from the Madrigal Ureña family. Their explanations of the coffee fruit cycle, the management of the coffee shrubs and what the birds are doing inside their farms helped me to gain valuable insights in order to understand the results and implications of this work. In addition, they offered their kind help with the mist-netting, cage-keeping and implanting of PIT tags on the birds when the possibility of having assistants became complicated due to the COVID-19 pandemic.

I want to thank the Ministry of the Environment and Energy (MINAE) of the Government of Costa Rica, through the National System of Conservation Areas (SINAC), for the issuing of research permits as well as the Tarrazú Cooperative of Coffee Producers (CoopeTarrazú) for help with logistics during the initial visits to several farms. Funding was granted by the Ministry of Science, Innovation, Technology, and Telecommunications (MICITT) through a doctoral scholarship (N°MICITT-PINN-CON-2-1-4-17-1-008) and fieldwork was supported through an Interdisciplinary Research Grant awarded by the Faculty of Life Sciences of the University of Vienna (UniWie). My best regards go as well to Isolde Prommer at the Vienna Doctoral School of Ecology and Evolution for all of her support when dealing with administrative procedures.

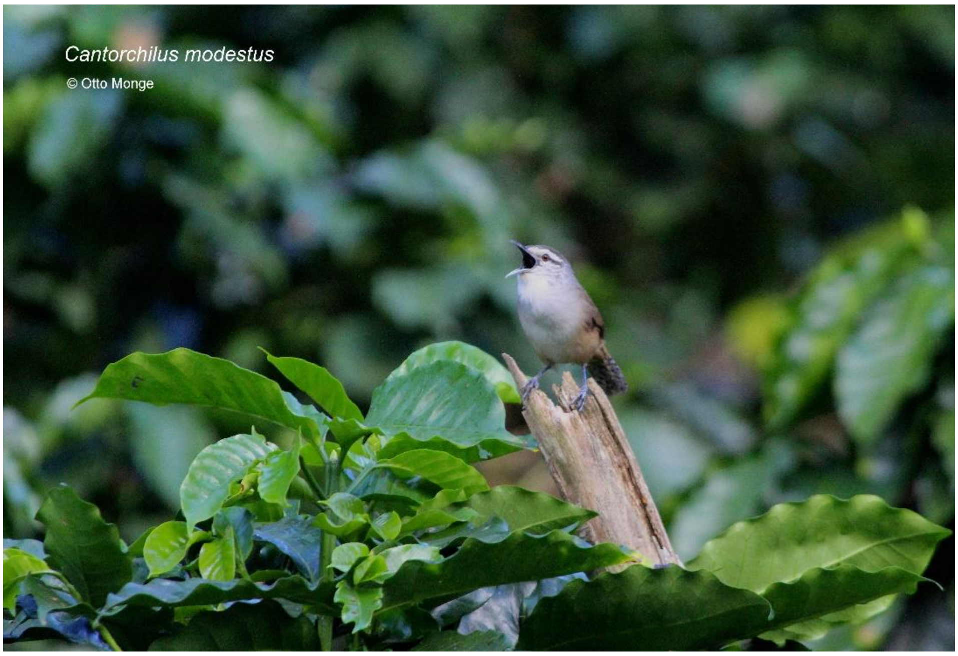
I am most indebted to my thesis committee for accepting to supervise my thesis and for the enormous support they provided me during all the stages of my PhD. Dr. Leonida Fusani gave me so many important advices and also made me a part of his wonderful group at the Konrad Lorenz Institute for Evolution and Cognition Research (KLIVV). Dr. Christian Schulze shared his ample knowledge on birds from all parts of the world and Dr. Stefan Dullinger helped me many times when I most needed it and cleared the multiple statistics doubts that I had. Altogether, they critically reviewed my many drafts and sometimes long list of plots and tables from the analyses (and likewise endured my lengthy PowerPoint presentations!), offering their valuable input in order to improve my written work, and supported my grant applications. But apart from all the academic guidance, they encouraged me to think outside the box, to push myself further and not give up, to be more analytic and patient (e.g. when dealing with responses from manuscript reviewers), and even lent me their hand to help me deal with Austrian immigration procedures. This is something that I truly appreciate.

Many ideas that were ultimately materialized in this thesis were enrichened from the countless conversations held with Dr. Ivan Maggini at the KLIVV. Ivan was always kind enough to even stop his work to help me clear doubts regarding avian thermoregulation and other topics. Moreover, he also gave valuable comments and

corrections and co-authored two manuscripts that emerged from the chapters in this thesis. On top of that, he invited me to several birding trips around Vienna, which I truly enjoyed. Likewise, I gained valuable insights about coffee and wildlife from conversations and trips to coffee farms of my study site with Natalia Aristizábal.

My colleagues at the KLIVV and UniWie offered me their friendship as well as their support when I needed it. More importantly, we shared a few drinks and sometimes “enjoyed” spicy exotic foods. Thanks to Andrea Ferretti, Barbara, Armando, Clementine, Elisa, Filipa, Giovanni, Judith, Julia, Ivan, Sara Lado, and Sara Ricci.

Last, but certainly not least, I wish to thank my family. No one knows better my ups-and-downs than my wife, Ivania. She stands beside me in my endeavors, even accepting the difficult decision to move to a foreign country with a very contrasting culture and withstanding many months of my absence. Our child has given me so many reasons to keep going and concluding this PhD work is one of them; he is the strongest fighter I know and he truly inspires me. I also wish to recognize the time and effort that my parents invested in my education and that have led me to this point. Their support and love are truly important in my life. Finally, my brothers and sisters have been always there for me, cheering me up and being proud of what I do and I whole-heartedly thank them for that.



A Cabanis’s wren (*Cantorchilus modestus*), one of the most common birds found in coffee farms in Costa Rica, sings atop a coffee shrub in the early morning.

Table of contents

Publications associated with this thesis

Published

Chapter 1

Monge O, Dullinger S, Fusani L, Schulze CH. 2022. Taxonomic, functional and phylogenetic bird diversity response to coffee farming intensity along an elevational gradient in Costa Rica. Agriculture, Ecosystems & Environment, 326:107801. doi:10.1016/j.agee.2021.107801

Chapter 2

Monge O, Schulze CH, Dullinger S, Fusani L, Maggini I. 2022. Unshaded coffee imposes a heavier load on thermoregulation than shaded coffee for birds in a tropical mountainous region. Global Ecology and Conservation, 36:e02117. doi:10.1016/j.gecco.2022.e02117

Submitted

Chapter 3

Monge O, Maggini I, Schulze CH, Dullinger S, Fusani L. 2022. Physiologically vulnerable or resilient? Tropical birds, global warming and re-distributions. Submitted to Ecology and Evolution

General introduction

Birds from all over the world have been consistently and systematically declining for the past 4-5 decades; and the cause is us, humans (Lees et al. 2022). Human activities have led to the loss of hundreds of millions of individual birds across North America and Europe since the 1970's and 1980's (Rosenberg et al. 2019; Burns et al. 2021). Although birds are one of the best studied groups of organisms, research efforts are not homogenously spread throughout the globe leading to a substantial unawareness of the human impacts on bird populations in certain regions. The world's Tropics, where the most important hotspots of avian diversity are located, suffer from this lack of information.

Despite recent efforts to fill in the gaps, studies have been particularly localized. For example, more than 10 years of selective logging in Southeast Asia have not been as detrimental to bird species richness as the fragmentation of large forest tracts (Lambert & Collar 2002). Similarly, long-term monitoring of bird populations in an agriculture-dominated and fragmented landscape in Costa Rica revealed that decades of forest loss has resulted in steep declines, especially of understory insectivores (Şekercioğlu et al. 2019). Besides habitat loss, climate change appears to have been involved in abundance declines and population re-arrangements along elevational gradients in the Australian Wet Tropics for almost two decades (Williams & de la Fuente 2021).

Of all the most severe threats to birds worldwide, the one with the least known impact is climate change and extreme weather (Lees et al. 2022). One possible explanation is the lack of clarity when defining the nature of causal factors. This is because climate change can impact birds directly, when higher temperatures exceed species-specific thermal tolerance, or indirectly through variations in resource availability or alterations of habitats (Cahill et al. 2013). Direct effects of warming can occur when either extremely high temperatures over consecutive days (i.e. heat waves) or gradual warming exceed the physiological capacity of birds to cool down the body through evaporative heat loss mechanisms (Conradie et al. 2020). Ultimately, prolonged exposure to such drastic conditions, especially in water-limited environments, can lead to local extinctions and population declines (Albright et al. 2017; Riddell et al. 2019). Potential intervening mechanisms include breeding failure when parents fail to deliver enough food for their offspring because they are forced to dedicate more time and energy in thermoregulating in the heat (Cunningham et al. 2013) and adult survival being directly compromised by this trade-off between thermoregulation and efficient foraging (du Plessis et al. 2012). On the other hand, indirect effects are manifested when climatic variation affects the availability of resources vital for thermoregulation, such as insect prey or water sources (Lister & García 2018; Curtis et al. 2021). In this case, exposure to even moderate heat combined with a lack of such resources would seriously challenge thermoregulation. For instance, insectivores which depend on water contained in their prey would have to increase their food intake whereas granivores which depend on water sources would need to follow these or risk dehydration (Riddell et al. 2019). Naturally, indirect effects can occur in the absence of extreme warming, as suggested in undisturbed tropical rainforests (Blake & Loiselle 2015; Stouffer et al. 2021), and this can further confound the nature of avian responses to climate change.

Another source of uncertainty regarding the avian response to climate change is how this threat interacts with other pervasive stressors, such as land-use change. While deforestation decreases the extent of suitable habitat, it can also alter the wet-dry climatic balance that bird experience in tropical environments (Loiselle et al. 2010). This way, climate appears to affect tropical birds indirectly because by eliminating natural habitat, human activities, such as intensive agriculture, can convert wet ecosystems into drier ones which attracts birds from dry habitats and pushes wet-affiliated birds towards forest remnants (Frishkoff et al. 2016). Birds who find refuge in scantily disturbed forests might be able to escape these unfavorable conditions, e.g. by shifting towards higher elevation habitats (Srinivasan & Wilcove 2021). In contrast, birds that persist in dried, converted lands would directly face the negative effects of warming. Heat waves combined with drought in areas devoid of forest cover may exceed the thermal tolerance limits for many of those species (Senior et al. 2017). Forest lost to agriculture might also mean that resources vital for breeding success might become scarcer for tropical birds whose reproductive timing is also sensitive to seasonal shifts in climatic conditions (Cartwright et al. 2014). Thus, land-use change is a major amplifier of the direct and indirect effects of climate change.

Although studies have evaluated how land-use change modulates the effects of climate, the direct response of tropical birds to warming when facing habitat loss or degradation remains poorly known. A reason is that heat tolerance of many species has not been properly quantified. This can be addressed by linking changing microclimatic conditions and the species' physiological response to warming across gradients of land-use change. This is truly a novel avenue of research, as the absence of empirical data on this issue demonstrates.

Tropical understory birds seem to show a preference for cool and humid microhabitats inside forests (Patten & Smith-Patten 2012), perhaps because these sites show a low degree of temperature variation (Pollock et al. 2015). In fact, forest-interior birds might be protected against warming because tropical forests are crucial buffers of microclimatic temperature variation and extremes (De Frenne et al. 2019). However, the seemingly stable thermal conditions inside tropical forests may be disrupted by land-use change. Forest loss and fragmentation create novel microclimatic conditions at forest edges and in open areas (Patten & Smith-Patten 2012), which forest-interior birds may not have previously experienced. Birds which suddenly find themselves exposed to such conditions may need to resort to strategies to lessen detrimental effects. One option is to reduce locomotion and remain inactive for long periods during the day, but this could be counter-productive as the time dedicated to vital functions, such as foraging and reproduction, would be consequently reduced (Bosque et al. 1999; Steiger et al. 2009). More likely, topical birds may rely on microhabitat features within disturbed landscapes to deal with elevated levels of heat. For instance, the body temperature of the lethargic rainforest-dwelling marbled frogmouth (*Podargus ocellatus*, Podargidae) exposed to full sun rose sharply in absence of convective wind, but cooled down at a rate of 1ºC/10 minutes when the species switched to a shaded place with convective wind (Lasiewski et al. 1970). Thus, at least for this species, securing microsites characterized by shade and air movement might ease the thermoregulatory costs associated with warming.

Studies from sub-tropical regions are more numerous than those from the wet tropics and show the capacity of birds from these latitudes to use microsite features to deal with high heat. For example, birds might switch from hunting using sun-exposed perches to shaded ones during the hottest hours of the day, despite this change reducing foraging success (Cunningham et al. 2015). Even ground-foraging species that avoid trees change foraging locations to densely foliated trees to benefit from the buffering of microsite temperatures during the hottest hours of days (Martin et al. 2015). Ground-nesting birds can safeguard their broods against excessive heat by selecting nesting microsites that moderate temperatures up to 10ºC and are characterized by tall or dense vegetation and minimal bare-ground (Carroll et al. 2015; Raynor et al. 2018). These previous studies show how vital microhabitat features are in providing opportunities for birds to overcome and deal with increased levels of warming. Nevertheless, land-use change has the potential to deplete or completely eliminate these habitat features, depending on the level of intensity of the usage.

A decline of important avian groups has long been predicted to result in the loss of the ecosystem processes promoted by birds in their natural habitats (Şekercioğlu et al. 2004). Through its effects on tropical bird community assembly, climate change has the potential to alter the distribution of key ecological functions that birds provide, such as seed dispersal, across spatial gradients (Bender et al. 2019). Negative effects on richness of tropical bird species (i.e. taxonomic diversity), ecological roles (i.e. functional diversity), and evolutionary distinct lineages (i.e. phylogenetic diversity) also arise from the loss and degradation of natural habitats (Şekercioğlu et al. 2004). Indeed, resource availability and the variety of habitats can influence avian functional and phylogenetic diversity along tropical mountains (Boyce et al. 2019). For instance, a decrease in resource availability can reduce functional diversity and a simplification of the vegetation structure can negatively impact phylogenetic diversity (Hanz et al. 2018).

In this context, the intensity of the human impacts could modulate the loss of the different dimensions of avian diversity in tropical landscapes. At a low intensity of land-use change, bird species composition and richness can decline but functional and phylogenetic diversity might just be weakly altered (Rurangwa et al. 2021). As land uses intensifies, the diversity of functional traits represented by the bird community begins to decline and shifts in composition (Bregman et al. 2016). At the other end of the intensification spectrum, landscapes dominated by monocultures are characterized by homogeneity of functional roles (Velásquez-Trujillo et al. 2021) and the erosion of phylogenetic diversity (Frishkoff et al., 2014), even if taxonomic diversity does not drastically decline. This idiosyncratic response of the dimensions of avian diversity warrant more examination across different systems of land-use intensification in tropical landscapes.

The relevance of jointly assessing different dimensions of bird diversity lies on its usefulness to determine the cascading effects of the variation in bird species richness on ecological function and evolutionary history. It is expected that climate change and land-use intensification alter tropical bird species numbers and composition in different ways, but both may result in homogenization of functional and phylogenetic diversity (Borges et al. 2021). However, there is a pressing need for more empirical studies that explore different manifestations of land-use intensity (Dullinger et al. 2021) and how this can impact the different dimensions of birds in tropical landscapes. The aforementioned gaps in knowledge highlight the necessity for more holistic research in order to improve our understanding of human-driven threats to tropical avian populations. To this end, this work set out to make a contribution.

My thesis is centered around the question of how tropical birds can be affected by changes in land use and warming, with a particular interest on the interaction between both threats. My general objective was to study the community- and species-level responses of tropical birds to the environmental stress brought upon by land-use changes and warming and understand the role of the interplay between both stressors in modulating the responses. As study system, I selected the avian communities that thrive in landscapes dominated by coffee farms, following an elevational gradient that covered the entire range of cultivation of this crop in the central mountains of Costa Rica (~300 – 2100 m). I chose this crop because it is one of the best studied examples of how cultivation intensification can affect the biodiversity of tropical agro-ecosytems and the ecosystem services it provides (Jha et al. 2014). Following common practice, the levels of cultivation intensity are defined by the structure and composition of vegetation planted alongside coffee shrubs (Figure 1; Perfecto et al. 1996). At the same time, these same vegetation elements not only characterize the extent of intensification but may provide microclimatic buffering and may hence shield bird populations from future warming (Siles et al. 2010, Schooler et al. 2020).

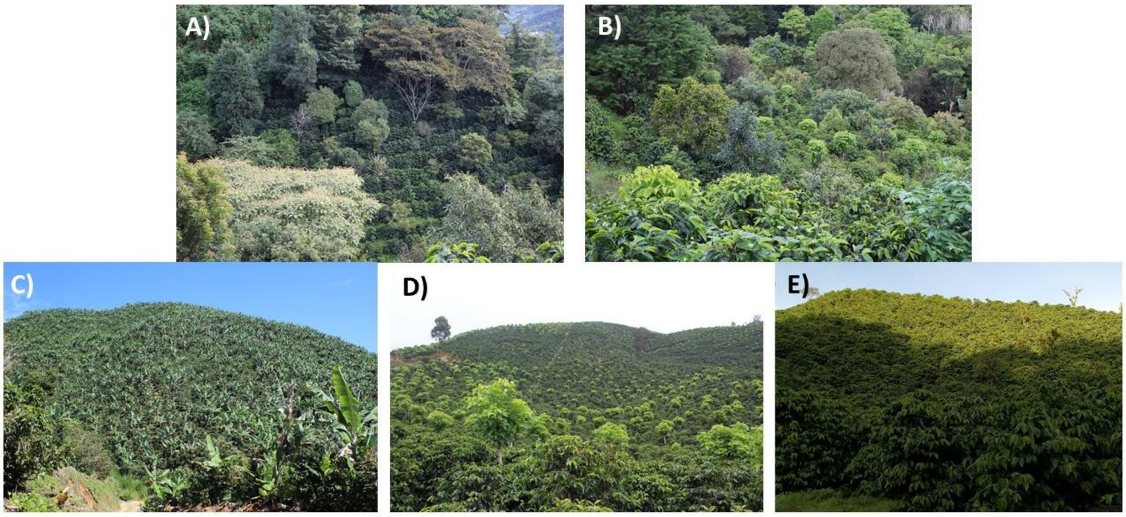


Figure 1. Progression of coffee cultivation intensification, from low- to high-intensity systems (**A** to **E**). (**A)** Coffee grows shaded by native forest trees. (**B**) Native trees and crops, such as avocado, mango or pine, are intermixed with coffee shrubs. Crop monocultures consist of coffee grown along with only one other crop plant: e.g. (**C**) *Musa* sp. or (**D**) *Erythrina poeppigiana*. (**E)** Full sun-grown coffee without any shade trees.

To understand the effects of land use and climate on bird populations that use coffee plantations, I visited farms to collect data during 2019 and 2020. I conducted field observations and laboratory measurements of birds in farms that span the full coffee cultivation intensity gradient. To complement the results from the fieldwork, I conducted a literature review in order to scrutinize empirical data regarding the thermal physiology of tropical birds that would help to understand the degree of their vulnerability to climate change.

In **Chapter 1**, my aim was to analyze the relationship between avian diversity and different sets of vegetation features that represented the intensity gradient in coffee farms across an elevational gradient. In other words, which vegetation features modified which dimensions of avian diversity in coffee farms and how do these effects vary across elevations. The inclusion of a gradient instead of discrete categories (e.g. shaded coffee vs. sun coffee) helped to overcome the limitation of assigning farms to either category because the structure and composition of the vegetation present at almost all farms was not homogeneous across local sites. For example, at a given farm, one sampling site could be characterized by a crop monoculture while the next would include a mixture of native and crop plants. In very few cases, the dimensions of avian diversity have been jointly assessed in tropical agricultural landscapes (e.g. Jayathilake et al., 2021), as previous work has mostly focused on the taxonomic dimension. In the case of coffee plantations, no study has yet concertedly analyzed the three dimensions of avian diversity. In addition, because differences in bird species composition result in varied responses of avian diversity dimensions along elevational gradients (Montaño-Centellas et al., 2019), it became imperative to assess how community characteristics at different elevational zones related to the response of avian diversity to coffee intensification. For this, a representative sample of farms with different levels of intensification were selected across the elevational gradient to determine how elevation modulated the effect of cultivation intensity on the taxonomic, functional and phylogenetic dimensions of bird diversity. Recent work has analyzed how these dimensions match between tropical agriculture and forest land use types at different elevation zones (Sreekar et al. 2021), but the question remains of how gradients of agriculture intensification across elevations modify these dimensions.

Subsequently, I assessed the physiological response of agriculture-associated tropical birds to the thermal environment of microhabitat in fully shaded and sun-grown coffee farms in **Chapter 2**. Here, I chose six farms that were either fully shaded by trees or completely grown under full sun so as to represent both extremes of the coffee cultivation intensity gradient. In these farms, temperature loggers were installed to collect microclimatic temperature measurements ($T_a$mic) for five months and these measurements were compared to those collected in parallel under the canopy of nearby forest patches. I linked the measurements of $T_a$mic with experimental estimations of heat tolerance of four bird species known to occur inside coffee farms of the study area. These birds were captured in three of the study farms and transported to a field laboratory in which their thermal tolerance was experimentally quantified through respirometry. The purpose of this approach was to determine the experimental temperatures that demanded a strong thermoregulatory response and compare these to the $T_a$mic that the birds experience in either shaded or sun-grown coffee farms. Thus, **Chapter 2** tested the hypothesis that when $T_a$mic in farms devoid of tree cover is significantly different from that of shaded farms then the birds would need to thermoregulate more often and more intensely in sun-grown coffee farms.

Finally, in **Chapter 3** I collated and analyzed publications related to tropical bird thermoregulation, the effects of climate change and its interaction with anthropogenic land-use changes. The purpose was to review existing literature that dealt with the physiological characteristics of tropical birds that confer vulnerability or resilience to the effects of climate change. The rationale for conducting this review was to understand if tropical birds are inherently physiologically vulnerable to thermal variation as it has been traditionally assumed for tropical biotas in general. Moreover, this synthetic review was performed to underscore the need to tackle the many knowledge gaps that exist in the literature regarding the nature of the responses of tropical birds to warming and suggest ways to advance research forward.

References

Albright TP, Mutiibwa D, Gerson AR, Smith EK, Talbot WA, O'Neill JJ, et al. 2017. Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. Proc. Natl. Acad. Sci. 114:2283–2288.

Bender IMA, Kissling WD, Böhning-Gaese K, Hensen I, Kühn I, Nowak L, et al. 2019. Projected impacts of climate change on functional diversity of frugivorous birds along a tropical elevational gradient. Sci. Rep. 9:17708.

Blake JG, Loiselle BA. 2015. Enigmatic declines in bird numbers in lowland forest of eastern Ecuador may be a consequence of climate change. PeerJ 3:e1177. doi:10.7717/peerj.1177.

Borges FJA, Fortunato DDS, Loyola R. 2021. Critical areas for retaining multiple dimensions of bird diversity in the Cerrado. Journal for Nature Conservation 64:126079.

Bosque C, Pacheco MA, Siegel RB. 1999. Maintenance energy costs of two partially folivorous tropical passerines. Auk 116:246–252.

Boyce AJ, Shakya S, Sheldon FH, Moyle RG, Martin TE. 2019. Biotic interactions are the dominant drivers of phylogenetic and functional structure in bird communities along a tropical elevational gradient. Auk 136:ukz054.

Bregman TP, Lees AC, MacGregor HE, Darski B, de Moura NG, Aleixo A, et al. 2016. Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. Proc. R. Soc. B: Biol. Sci. 283:20161289.

Burns F, Eaton MA, Burfield IJ, Klvaňová A, Šilarová E, Staneva A, et al. 2021. Abundance decline in the avifauna of the European Union reveals cross-continental similarities in biodiversity change. Ecol. Evol. 11:16647–16660.

Cahill AE, Aiello-Lammens ME, Fisher-Reid MC, Hua X, Karanewsky CJ, Yeong Ryu H, et al.. 2013. How does climate change cause extinction? Proc. R. Soc. B 280:20121890.

Carroll JM, Davis CA, Elmore RD, Fuhlendorf SD, Thacker ET. 2015. Thermal patterns constrain diurnal behavior of a ground-dwelling bird. Ecosphere 6:222.

Cartwright S, Nicoll MAC, Jones CG, Tatayah V, Norris K. 2014. Agriculture modifies the seasonal decline of breeding success in a tropical wild bird population. J. Appl. Ecol. 51:1387–1395.

Conradie SR, Woodborne SM, Wolf BO, Pessato A, Mariette MM, McKechnie AE. 2020. Avian mortality risk during heat waves will increase greatly in arid Australia during the 21st century. Conserv. Physiol. 8:coaa048.

Cunningham SJ, Martin RO, Hojem CL, Hockey PA. 2013. Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly-warming arid savanna: a study of common fiscals. PLoS One 8: e74613.

Cunningham SJ, Martin RO, Hockey PA. 2015. Can behaviour buffer the impacts of climate change on an arid-zone bird? Ostrich 86:119–126.

Curtis JR, Robinson WD, Rompré G, Moore RP, McCune B. 2021. Erosion of tropical bird diversity over a century is influenced by abundance, diet and subtle climatic tolerances. Sci. Rep. 11:10045.

De Frenne P, Zellwegger F, Rodríguez-Sánchez F, Scheffers BR, Hylander K, Luoto M, et al. 2019. Global buffering of temperatures under forest canopies. Nat. Ecol. Evol. 3:744–749.

du Plessis KL, Martin RO, Hockey PA, Cunningham SJ, Ridley AR. 2012. The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. Glob. Chang. Biol. 18:3063–3070.

Dullinger I, Essl F, Moser D, Erb KH, Haberl H, Dullinger S. 2021. Biodiversity models need to represent land use-intensity more comprehensively. Glob. Ecol. Biogeogr. 30:924–932.

Frishkoff LO, Karp DS, Flanders J, Zook JR, Hadly EA, Daily GC, et al. 2016. Climate change and habitat conversion favour the same species. Ecol. Lett. 19:1081-1090.

Hanz DM, Böhning-Gaese K, Ferger SW, Fritz SA. Neuschulz EL, Quitián M, et al. 2019. Functional and phylogenetic diversity of bird assemblages are filtered by different biotic factors on tropical mountains. J. Biogeogr. 46:291– 303.

Jayathilake HM, Warren-Thomas E, Nelson L, Dolman P, Bumrungsri S, Juthong W, Carrasco LR, Edwards DP. 2021. Fruit trees and herbaceous plants increase functional and phylogenetic diversity of birds in smallholder rubber plantations. Biol. Conserv. 257:109140.

Jha S, Bacon CM, Philpott SM. Méndez VE, Läderach P, Rice RA. 2014. Shade Coffee: Update on a Disappearing Refuge for Biodiversity. BioScience 64:416–428.

Lambert FR, Collar NJ. 2002. The future for Sundaic lowland forest birds: long-term effects of commercial logging and fragmentation. Forktail 18:127-146.

Lasiewski RC, Dawson WR, Bartholomew GA. 1970. Temperature regulation in the little Papuan frogmouth, *Podargus ocellatus*. Condor 72:332–338.

Lees AC, Haskell L, Allinson T, Bezeng SB, Burfield IJ, Renjifo L.M., et al. 2022. State of the World's Birds. Ann. Rev. Env. Res. 47:1.

Lister BC, Garcia A. 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. Proc. Natl. Acad. Sci. 115:E10397–E10406.

Loiselle BA, Graham CH, Goerck JM, Ribeiro MC. 2010. Assessing the impact of deforestation and climate change on the range size and environmental niche of bird species in the Atlantic forests, Brazil. J. Biogeogr. 37:1288-1301.

Martin RO, Cunningham SJ, Hockey PA. 2015. Elevated temperatures drive fine-scale patterns of habitat use in a savanna bird community. Ostrich 86:127–135.

Montaño-Centellas FA, McCain C, Loiselle B. 2019. Using functional and phylogenetic diversity to infer avian community assembly along elevational gradients. Global Ecol. Biogeogr. 29:232–245.

Patten MA, Smith-Patten BD. 2012. Testing the microclimate hypothesis: light environment and population trends of Neotropical birds. Biol. Conserv. 155:85–93.

Perfecto I, Rice RA, Greenberg R, Van der Voort ME. 1996. Shade coffee: A disappearing refuge for biodiversity. BioScience 46:598–608.

Pollock HS, Cheviron ZA, Agin TJ, Brawn JD. 2015. Absence of microclimate selectivity in insectivorous birds of the Neotropical forest understory. Biol. Conserv. 188:116–125.

Raynor EJ, Powell LA, Schacht WH. 2018. Present and future thermal environments available to Sharp-tailed Grouse in an intact grassland. PloS ONE 13:e0191233.

Riddell EA, Iknayan KJ, Wolf BO, Sinervo B, Beissinger SR. 2019. Cooling requirements fueled the collapse of a desert bird community from climate change. Proc. Natl. Acad. Sci. 116:21609–21615.

Rosenberg KV, Dokter AM, Blancher PJ, Sauer JR, Smith AC, Smith PA, et al. 2019. Decline of the North American avifauna Science 366:120–124.

Rurangwa ML, Aguirre-Gutiérrez J, Matthews TJ, Niyigaba P, Wayman JP, Tobias JA, et al. 2021. Effects of land-use change on avian taxonomic, functional and phylogenetic diversity in a tropical montane rainforest. Divers Distrib. 27:1732–1746.

Schooler SL, Johnson MD, Njoroge P, Bean WT. 2020. Shade trees preserve avian insectivore biodiversity on coffee farms in a warming climate. Ecol. Evol. 10:12960–12972.

Şekercioğlu CH, Daily GC, Ehrlich PR. 2004. Ecosystem consequences of bird declines. Proc. Natl. Acad. Sci. 101:18042–18047.

Şekercioğlu ÇH, Mendenhall CD, Oviedo-Brenes F, Horns JJ, Ehrlich PR, Daily GC. 2019. Long-term declines in bird populations in tropical agricultural countryside. Proc. Natl. Acad. Sci. 116:9903–9912.

Senior RA, Hill JK, González Del Pliego P, Goode LK, Edwards DP. 2017. A pantropical analysis of the impacts of forest degradation and conversion on local temperature. Ecol. Evol. 7:7897–7908.

Siles P, Harmand JM, Vaast P. 2010. Effects of *Inga densiflora* on the microclimate of coffee (*Coffea arabica* L.) and overall biomass under optimal growing conditions in Costa Rica. Agroforest. Syst. 78:269–286.

Sreekar R, Si X, Sam K, Liu J, Dayananda S, Goodale U, et al. 2021. Land use and elevation interact to shape bird functional and phylogenetic diversity and structure: Implications for designing optimal agriculture landscapes. J. Appl. Ecol. 58:1738–1748.

Srinivasan U, Wilcove DS. 2021. Interactive impacts of climate change and land-use change on the demography of montane birds. Ecology 102:e03223.

Steiger SS, Kelley JP, Cochran WW, Wikelski M., 2009. Low metabolism and inactive lifestyle of a tropical rain forest bird investigated via heart-rate telemetry. Physiol. Biochem. Zool. 82:580–589.

Stouffer PC, Jirinec V, Rutt CL, Bierregaard ROJ, Hernández-Palma A, Johnson EI, et al. 2021. Long-term change in the avifauna of undisturbed Amazonian rainforest: ground-foraging birds disappear and the baseline shifts. Ecol. Lett. 24:186–195.

Velásquez-Trujillo V, Betancurt-Grisales JF, Vargas-Daza AM, Lara CE, Rivera-Páez FA, Fontúrbel FE, et al. 2021. Bird Functional Diversity in Agroecosystems and Secondary Forests of the Tropical Andes. Diversity 13:493.

Williams SE, de la Fuente A. 2021. Long-term changes in populations of rainforest birds in the Australia Wet Tropics bioregion: A climate-driven biodiversity emergency. PLoS ONE 16:e0254307.

Chapter 1. Taxonomic, functional and phylogenetic bird diversity response to coffee farming intensity along an elevational gradient in Costa Rica

Otto Monge, Stefan Dullinger, Leonida Fusani, Christian H Schulze

Abstract

The expansion of the agricultural frontier in the species-rich tropical regions of the world has generated conflicts between the need to secure food production and local income on the one hand, and the conservation of biodiversity on the other one. As natural areas give way to farmlands, the future of sensitive taxa may depend on how intensively the crops are cultivated. In this study, we use several features of non-crop vegetation composition and structure as indicators of cultivation intensity and evaluate their correlation with taxonomic, functional and phylogenetic facets of the avian community. Our study system consisted of coffee farms in Costa Rica spread across a ~2000 m elevational span. Using regression modelling and multi-model inference we related six vegetation features to five biodiversity metrics in this system and evaluated whether the results differed among elevational zones. The most influential variable was the number of trees with a dbh larger than 30 cm, promoting higher species richness, functional redundancy and phylogenetic structure. Shade cover and the number of non-coffee crops increased species and phylogenetic richness, respectively. The effect of individual vegetation features on particular biodiversity metrics varied across elevation, possibly due to the idiosyncratic response of each facet to the elevation gradient or to local ecological processes. We conclude that vegetation features related to cultivation intensity have effects on avian diversity, but that these effects differ among biodiversity metrics and are sensitive to the environmental context. Consequently, targeted conservation management should be based on more comprehensive studies that include all relevant biodiversity facets and consider the larger-scale perspective. In general, our results suggest that when designing bird-friendly strategies (e.g. certifications) there is likely no “one-size-fits-all” strategy.

Keywords: agricultural landscape, agroforestry, bird ecology, conservation

Introduction

The ever-rising demand for land allocated to growing crops strengthens the conflict between the conservation of natural resources and food production and results in the large-scale conversion of natural areas and proliferation of human-dominated landscapes (Laurence et al., 2013). These landscapes are often patchy mosaics of forests and cultivated lands under different management practices (Laurence et al., 2013, Aerts et al., 2016). This situation is particularly problematic for conservation in the world’s tropics, where forest disturbance can drastically reduce the number of species of many different taxa (Alroy, 2017).

Assessing biodiversity in agricultural landscapes contributes to a general understanding of how much of it is preserved, or lost, by changes of broad land-use types, but also of management practices within particular land use types (Erb et al., 2017). For example, long-term studies of bird populations in tropical agricultural landscapes highlight their sensitivity to the intensification of cultivation practices and document population declines of forest-affiliated (Maas et al., 2009, Şekercioğlu et al., 2019), ecosystem service-delivering (Hendershot et al., 2020), and evolutionarily distinct species (Frishkoff et al., 2014). Thus, gaining knowledge about the impacts of not only the conversion of natural ecosystems but also of the intensification of used ones is a key step towards adapting farmlands and lessening the detrimental effects on the various dimensions of biodiversity (Dullinger et al., 2021).

Assessments that include the taxonomic dimension of biodiversity (i.e. species richness) can become more meaningful when considering additional information, such as the functional roles of species in the ecosystem or their evolutionary histories. For instance, avian functional traits can be lost non-randomly in tropical habitats subjected to degradation, affecting ecosystem-service provision and ecosystem stability (Bregman et al., 2016). Additionally, in fragmented landscapes, the risk of extinction can vary according to the phylogenetic relatedness of bird species (Luther et al., 2020), a situation that can lead to losses of phylogenetic diversity in forest birds since they can be more closely related in highly forested landscapes (Morante-Filho et al., 2017). Indeed, the relevance of considering these three facets of biodiversity is underscored by the varied results obtained when coupling them. In some cases, the taxonomic, functional and phylogenetic diversity can concertedly decrease in agricultural landscapes (Prescott et al., 2016), show the opposite trend (García-Navas and Thuiller, 2020), or vary haphazardly along gradients of landscape disturbance (Jeliazkov et al., 2016). Because the congruence between these facet measurements might ease (Pool et al., 2014) and the incongruence challenge (Martín-Regalado et al., 2019) conservation planning, there is an obvious urgency for multi-faceted biodiversity assessments in order to develop targeted and effective conservation strategies (Ke et al., 2018).

Agroforestry is a way of compensating the loss of natural habitat by integrating non-crop vegetation elements into farmlands. The aim is to preserve biodiversity without compromising economic yields (Clough et al., 2011). For crops like coffee, these elements can generate a highly heterogeneous system, when compared to a monoculture (Perfecto et al., 1996), and reduce the difference in bird community composition between farmlands and neighbouring forests (Karp et al., 2012). In general, even slightly increasing tree cover within tropical farmlands can bolster bird taxonomic diversity (Şekercioğlu et al., 2019). Increased canopy closure can especially benefit insectivorous birds (Pérez-Cabral et al., 2021), for example by regulating local microclimates via enhanced shade cover (Schooler et al., 2020). Non-crop elements embedded in tropical farmlands can thus be pivotal in maintaining avian diversity.

Past studies have highlighted the relevance of non-crop vegetation to taxonomic bird diversity in coffee agro-ecosystems. For example, the height of non-coffee trees, their taxonomic diversity and the canopy cover they offer have been identified as major elements that increase bird richness and abundance (Greenberg et al., 1997a; Waltert et al., 2005; Gordon et al., 2007). Detailed studies have also shown that these vegetation elements can influence certain groups of birds differently. For instance, the diversity of forest- and canopy-associated birds can depend on large trunk trees, tree height and tree diversity, whereas understory- and ground-dwellers can be affected by the amount of small, thin trees and shade cover (Bakermans et al., 2012; Rodrigues et al., 2018). Also, non-crop tree density can relate positively to particular groups, such as insectivores and range-restricted species, and negatively to others, such as migrants and nectarivores (Waltert et al., 2005). In contrast to the work focused on taxonomic diversity, the response of functional and phylogenetic bird diversity to intensity gradients in tropical agroforestry is scantily represented in the literature, apart from a recent study in rubber agroforests from tropical Asia (Jayathilake et al., 2021).

In montane environments, tropical bird communities experience an important species turnover along elevational gradients (Sreekar et al., 2017). In consequence, the effects of different agroforestry management strategies on bird diversity may also vary along the elevational gradient. For example, Araneda et al. (2018) demonstrated that Chilean traditional indigenous farmlands at middle-elevations have modified the landscape by creating high vegetation heterogeneity, thus bolstering bird taxonomic diversity there more than at any other elevational band. On the other hand, low-intensity heterogeneous agriculture was consistently richer in bird species during the winter than highly-intensified areas throughout a ~2000 m elevational span in the Himalayas (Elsen et al., 2016). However, the response of tropical avian populations to land-use gradients across elevations remains poorly understood.

Here, we undertook a multi-faceted approach to assess the bird diversity present at coffee farms in Costa Rica along gradients of cultivation intensity across a ~2000 m elevational span. We used structural and compositional features of the vegetation on the coffee farms to evaluate the response of taxonomic, functional and phylogenetic diversity to the intensification gradient and analysed whether this response varied among these three facets. We also aimed to determine the relative contribution of these features to the modulation of bird taxonomic, functional and phylogenetic diversity. Finally, we asked whether the contributions of these features were consistent along the full elevational gradient of the coffee growing region or if they were present only at certain elevations.

Materials and methods

Study area

Data collection took place in south-central Costa Rica (09º26’N, 83º55’W; Fig. 1) in 2019 and 2020. Within the c. 311 km^2 study area, coffee farms were selected to represent the full elevational extent of cultivation for this crop in Costa Rica (i.e. from 300 to 2150 m above sea level). This altitudinal gradient encompasses different natural habitats, such as the tropical lowland, premontane and lower montane forest zone. All of the coffee plantations followed management practices that fell somewhere in the continuum that ranges from less to more intensified (Perfecto et al., 1996). Some of the farms represented both extremes (i.e. total elimination of non-coffee plants versus coffee shaded by native tree canopy), while others had a mixture of native plants and edible, nitrogen-fixing or timber-producing cultivates (henceforth “crops”).

Surveys of the avian communities and measurements of vegetation

Throughout the study area, 120 sampling points were established inside 51 coffee farms. At each farm, one or several points (mean = 2.3 points per farm, range = 1 – 10) were located and georeferenced with a Garmin eTrex 30x GPS unit, which also measured their elevation. At these sampling points, birds were surveyed from June 2019 to August

2020 in imaginary circles of 25 m radius, separated by at least 200 m, in which all bird species seen or heard were counted. Upon reaching a point, an initial 5 min period allowed the birds to get used to the observer, who then proceeded with the survey for 10 min before moving on to the next one. Surveys started at sunrise and ended one or two hours before noon and every census point was visited seven times.

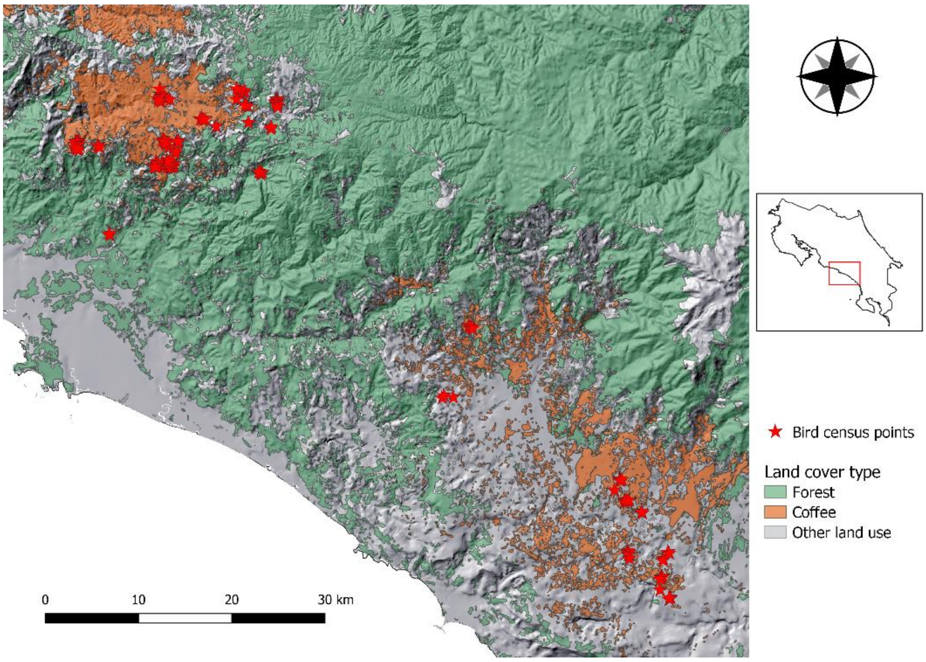


Figure 1. Relief map of the study area showing the location of the bird census points in coffee plantations. The inset shows the location of the study area (red rectangle) within Costa Rica.

One of the main features of agricultural intensification in coffee plantations is the loss of natural vegetation and the suppression of other cultivated plants. Therefore, in order to characterize the gradient of intensification inside the surveyed farms, several structural and composition features of the vegetation (henceforth abbreviated as vegetation features) were measured (Table 1). The measurements captured the number of individual native and cultivated plants, the diameter-at-breast-height (dbh) of the tree trunks, the maximum height of those plants with dbh greater than 10 cm, and the percentage of canopy cover. All plants that were not coffee shrubs were counted and measured inside the same points used to survey birds. The percentage of shade cover was estimated using the Gap Light Analysis Mobile Application (GLAMA; Tichý, 2015) in a Huawei P Smart 2019 smartphone. This approach has been validated and suggested as an alternative for canopy photography in ecological studies, faster and more accessible than conventional digital cameras (Bianchi et al., 2017). Pictures were taken using the front lens of the device levelled at breast height and, using the suggested cut-level of black and white pixels to define light gaps, the Canopy Cover Index was computed. Because we did not employ a fish-eye lens, pictures were corrected using the built-in procedure for recalibrating the real view angle of the camera. We took one measurement at each of the four cardinal directions, looking towards the centre of the census point, and one more at the centre.

Table 1. Structural and compositional vegetation features measured at the 120 bird survey points and their definition. The mean of the measurements and their respective standard deviation are shown.

Vegetation feature	Definition	Mean (sd)
Crop plants	Number of cultivated plant species other than coffee	2.4 (1.4)
Native plants	Number of native plant species	3.1 (3.4)
dbh < 30 cm	Number of plants with dbh less than 30 cm	70.7 (40.4)
dbh ≥ 30 cm	Number of plants with dbh greater than or equal to 30 cm	2.5 (4.5)
Max height	Maximum height of trees (m) with dbh greater than or equal to 10 cm	15.3 (7.9)
Shade cover	Average percentage of canopy shade cover	21.4 (14.8)

Measures of bird taxonomic, functional and phylogenetic diversity

The identity of the bird species and their abundance was recorded at each census point, but for further analysis, some data that was originally taken were removed. This applied to raptors and scavengers seen soaring high up in the sky but not using the farm resources in any way (e.g. hunting prey or perching). Likewise, parrots and other large frugivores that flew over without stopping to perch or forage were also discarded. Species heard or seen moving through river or forest corridors, live fences or forest patches adjacent to the coffee farms were not considered if the species did not enter the farm during the survey period. Nocturnal or crepuscular species were not included but North and South American migrant species were because of their known prevalence inside coffee plantations (Perfecto et al., 1996). The final pruned dataset was then used for all further analyses, considering the observed number of species (i.e. richness) as the measure of taxonomic diversity (TD).

Several avian functional traits that are directly related to resource use were compiled to estimate functional diversity (FD). Traits associated with diet and use of the vertical space were extracted from the EltonTraits database (Wilman et al., 2014) which partitions the percentage of the total diet into different food items and habitat use into several vertical strata. Morphological traits can also be linked to the degree of farming intensity because they reflect the ability of birds to exploit available resources differently (e.g. large birds consume more and bigger food items than small ones). For this, beak measurements for most passerines were collected from Ricklefs (2017) and body mass for all species from Wilman et al. (2014). Because beak data for some species was not available, we imputed missing values using the regularized iterative PCA algorithm implemented in the *imputePCA* function of the ‘missMDA’ package (Josse and Husson, 2016) in R. Traits and their definition are summed in Table 2.

Table 2. List of functional traits for birds and their definition. The mean of the measured traits and their respective standard deviation are included.

Functional trait	Definition	Mean (sd)
Fruit	Percentage of fruit in diet	24.2 (28)
Seeds	Percentage of seeds in diet	9.4 (19.9)
Nectar	Percentage of nectar in diet	11 (27.8)
Other plant	Percentage of other plant material in diet	2.9 (8.4)
Invertebrates	Percentage of invertebrate prey in diet	45.9 (34.3)
Vertebrates	Percentage of vertebrate prey in diet	6.6 (20.7)
N Items	Number of different food items in diet	2.3 (0.9)
Ground	Percentage time spent on the ground stratum	19 (31.6)

Functional trait	Definition	Mean (sd)
Understory	Percentage time spent in the understory stratum	23.7 (25)
Mid-high	Percentage time spent in the mid-high stratum	34.9 (27)
Canopy	Percentage time spent in the canopy stratum	20.4 (25.3)
N strata	Number of strata utilized by the species	2.3 (0.8)
Bill depth	Bill depth at the base in millimetres	7.8 (4.9)
Bill length	Bill length from the base in millimetres	21.6 (16.2)
Body mass	Body mass in grams	96.4 (223.2)

With the set of traits, we computed two metrics of functional diversity to describe the functionality and ecological importance of the avian assemblages in the coffee agro-ecosystem. Considering a multi-trait space, functional evenness (FEve) is the regularity and functional divergence (FDiv) the variation in the abundance distribution of traits within that space, with the two measures being orthogonal to each other (Mason et al., 2005). FEve is maximized when functional traits are equally abundant and evenly distributed within the community niche space whereas FDiv values are higher when traits are more abundant at the extreme ends of trait space (Villéger et al., 2008). The imputed trait dataset was first transformed, centered and z-score standardized before computing these metrics in the R package ‘FD’ (Laliberté et al., 2014). The percentage variables were transformed with arcsine square root and the rest with log10; all traits were given the same weights, species abundance was used for the calculation of the metrics, and the *cailliez* correction was applied.

Finally, the amount of phylogenetic variation retained by each bird community was assessed through the phylogenetic diversity (PD) and the mean pairwise distance (MPD) estimators. PD measures the total number of branch lengths within a tree visualizing the phylogenetic relatedness between species in the community and MPD is the average nodal distance between species for a given community (Webb, 2008). For this, we downloaded a subset of the avian phylogenetic tree of Jetz et al. (2012), with the Hackett et al. (2008) backbone tree, composed of all species in our pruned dataset. Because we chose to create 10000 trees from the phylogeny subset, a consensus phylogenetic tree was first built before calculating the branch lengths used to compute PD and MPD. Analyses were conducted with the R package ‘picante’ (Kembel et al., 2010).

Null models

Intuitively, PD is related to species richness because the more species are added to a particular pool, the higher the chances that they represent distant lineages. Although the relationship between species richness and the other metrics is less clear, we generally wanted to make sure to evaluate their response independent of species richness effects. We therefore created null communities by randomizing the species dataset and calculated a standardized effect size for the parameters (sesFDiv, sesFEve, sesPD, and sesMPD) under a “richness” null model, in which randomizations were based on the species’ abundance within communities. For the FD metrics, the randomization of the bird species matrix was performed with the function *randomizeMatrix* while for the phylogenetic metrics we used the *ses.pd* and *ses.mpd* functions, respectively, in ‘picante’.

Statistical analysis

The effect of the agriculture intensity gradient on the three facets of bird biodiversity in coffee farms was evaluated through mixed-effects regression models. The vegetation variables served as fixed effects while the farms were kept as random effects. Before running the analyses, multi-collinearity among the predictors was checked considering a variance inflation factor ≤ 5 (Zuur et al., 2009). Then, predictors were centered and z-score standardized after transforming those highly skewed: Crop plants, Native plants and dbh ≥ 30 cm with log10+1, shade cover with arcsine square root and dbh < 30 cm with square root. TD models were analysed with a Poisson generalized linear mixed model with a log-link, while the FD and PD response metrics were fitted to a Gaussian distribution with an identity-link in a linear mixed model.

We followed a model-averaging approach to determine the relative contributions of the elements of the intensification gradient in explaining the variation of the biodiversity facets. We first tested a full model for each facet and evaluated it to control for overdispersion and normality of the residuals. This global model was then decomposed into alternative models containing all possible combinations of predictors and these alternative models were then compared based on their Akaike Information Criterion (AIC) values. As a condition for model selection, those with a deltaAIC (i.e. the difference in AIC values resulting when comparing a given model against the one with the lowest AIC) ≤ 4 had their parameter estimates averaged (cf. Burnham and Anderson 2004). The relative contribution of each vegetation variable in explaining TD, sesFEve, sesFDiv, sesPD, and sesMPD was then calculated based on the sum of AIC weights from all the models in which the variable appeared. Models were built, evaluated and averaged in the packages ‘lme4’ (Bates et al., 2015) and ‘nlme’ (Pinheiro et al., 2021), ‘DHARMA’ (Hartig, 2018) and ‘car’ (Fox and Weisberg, 2019) and ‘MuMIn’ (Barton, 2020), respectively. We also executed univariate regressions between each facet metric and its corresponding most contributing variable and graphically presented these relationships. For these latter models, we used a Poisson generalized linear model for species richness and Gaussian regression models for the rest.

Elevation categories

In mountainous areas, tropical avian communities are strongly shaped by the elevational gradient (Montaño-Centellas et al., 2021). For this reason, we assessed whether farming intensification affected birds differently across elevations. We first tested for a significant effect of elevation on bird community composition and then performed an ordination of the species dataset, with the package ‘vegan’ (Oksanen et al., 2015). The hypothesis testing for an effect of elevation was conducted with a permutational multivariate analysis of variance (PERMANOVA) using the function *adonis* and the ordination with a non-metric multidimensional scaling (NMDS) with *metaMDS*. As expected, elevation significantly affected bird community composition (F= 26.09, p=0.001). The NMDS, based on a Bray-Curtis species distance matrix, allowed us to visually identify points of compositional turnover along the elevation gradient of our study area, by adding elevation contour lines to the NMDS with the function *ordisurf*. This way, the data was sub-set to include sampling points located in the lowlands (300 – 800 m; n = 28 sampling points), mid-elevations (800 – 1600 m; n = 57) and highlands (1600 – 2150 m; n = 35). Although some of the sampling points overlapped, an analysis of similarities (ANOSIM) showed that the defined zones differed significantly in bird species composition (R=0.56; p=0.001). This classification allowed us to determine which vegetation elements contributed the most to the variation in the metrics at each zone and compare the response of the bird biodiversity facets between zones. The statistical analysis followed the same model averaging as above, but because of singularity problems owing to lower sample sizes linear regressions were used instead of linear mixed effects models.

Results

Across the 120 sampling points, visited seven times, we recorded 8304 individuals of 201 species from 35 families (Table S2). The most abundant species was the scarlet-rumped tanager (*Ramphocelus passerinii*, n=498 individuals) and the most frequent the clay-coloured thrush (*Turdus grayi*) which appeared on 85% of all sampling points. We detected four species under the IUCN Near Threatened conservation status (www.iucnredlist.org): the residents yellow-throated toucan (*Ramphastos ambiguus*) and resplendent quetzal (*Pharomachrus mocinno*) and the migratory olive-sided flycatcher (*Contopus cooperi*) and golden-winged warbler (*Vermivora chrysoptera*). Two additional species are currently listed as Vulnerable, the ruddy pigeon (*Patagioenas subvinacea*) and the turquoise cotinga (*Cotinga ridgwayi*). Twenty-five species were obligate insectivores (diet composed exclusively of invertebrates) while obligate frugivorous (100% fruits) and nectarivorous (90% nectar) birds were represented by six and 20 species, respectively. The three most species-rich families encountered during field observations were Thraupidae (tanagers, n=27 species), Tyrannidae (flycatchers, n=24) and Trochilidae (hummingbirds, n=20). Six species were removed in the final dataset used for analysis, including the quetzal.

Taxonomic, functional and phylogenetic responses to the elements of the agricultural intensification gradient

Overall, structural (i.e. shade, tree dbh and height) and compositional (i.e. amount of crop and native plant species) features of the vegetation inside coffee farms modified all facets of avian biodiversity. Increasing structural and compositional complexity fostered species richness, phylogenetic diversity and evolutionary structure (sesMPD) (Fig. 2), although relationships with individual vegetation features were statistically insignificant in part. By contrast, vegetation features were uncorrelated with functional evenness and negatively associated with functional divergence (Table 2).

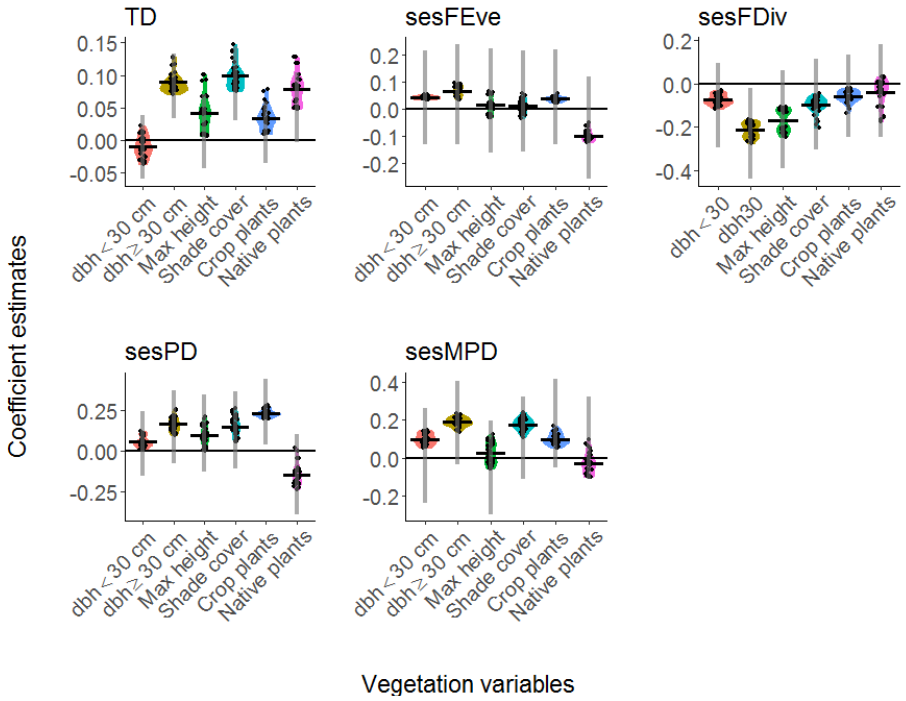


Figure 2. Effects of structural and compositional vegetation features on metrics of bird biodiversity across an agricultural intensification gradient in coffee farms. Coefficient estimates were averaged from all mixed-effects regression models that contained the respective variable out of a set of models with all possible predictor combinations. The black bar traversing each violin is the coefficient mean for each predictor from all models in which it appeared, the black dots represent the estimates in each individual model, and the grey bars represent the 95% confidence intervals around the overall average. The number of models considered for each metric was n=64.

The individual vegetation features studied varied in their effect on the different biodiversity facets and none of the facets was determined by the same combination of features (Table 2). The number of large trees (dbh ≥ 30) was the most influential variable. Its mean effect (across all models) had a .95-confidence interval not including 0 in the case of TD and sesFDiv (Fig. 2). Consistently, its coefficient was statistically significant in the subset of best models for the same metrics (Table 2). Moreover, the number of large trees was the only feature among the three most important ones in models of all five biodiversity metrics. Shade cover, native plants and crop plants were among the three most important variables for two or three metrics and (marginally) significantly correlated to one of the metrics each. Tree height and the number of thin trees (dbh < 30 cm) were statistically uncorrelated to all facets.

Table 3. Marginal coefficient estimates of mixed-effects regression models averaged over all models with a deltaAIC ≤ 4, the statistical significance of these averaged effects as evaluated by a z-test, and the relative contribution of the three most important predictor variables assessed by the mean AIC weights of all the models that contain these variables.

Parameter	**Estimate (SE)**	**z-value**	**P(>z)**	**Relative contribution**
Species richness				
dbh ≥ 30 cm	0.083 (0.025)	3.280	<0.01	1.00
Shade cover	0.087 (0.029)	3.005	<0.01	1.00
Native plants	0.050 (0.027)	1.824	0.068	0.67
sesFEve				

Parameter	**Estimate (SE)**	**z-value**	**P(>z)**	**Relative contribution**
Native plants	-0.071 (0.098)	0.721	0.471	0.28
dbh ≥ 30 cm	0.055 (0.096)	0.579	0.562	0.20
Crop plants	0.044 (0.091)	0.480	0.631	0.18
sesFDiv				
dbh ≥ 30 cm	-0.214 (0.099)	2.152	<0.05	0.83
Max height	-0.152 (0.107)	1.424	0.154	0.47
dbh < 30 cm	-0.094 (0.093)	1.013	0.311	0.30
sesPD				
Crop plants	0.241 (0.102)	2.371	<0.05	0.98
Native plants	-0.143 (0.124)	1.153	0.249	0.43
dbh ≥ 30 cm	0.149 (0.114)	1.308	0.191	0.43
sesMPD				
dbh ≥ 30 cm	0.182 (0.112)	1.632	0.103	0.60
Shade cover	0.183 (0.118)	1.550	0.121	0.57
dbh < 30 cm	0.107 (0.110)	0.973	0.330	0.32

In univariate regressions, all but the sesFEve metric showed statistically significant correlation with the feature identified as most influential for them by the multi-model inference approach (Fig. 3). Significant trends from the metrics calculated under the null models show that increasing the number of large trunked trees inside the farms relates to under-dispersion in functional divergence as well as phylogenetic clustering, as shown by sesMPD. At the same time, over-dispersion of sesPD increased with the number of different crop plants, but this variable was not a significant contributor to any of the FD metrics (Fig. 2).

To put the results for PD and FD in perspective, we followed the behaviour of the two sites in which the lowest and the highest number of bird species were recorded during fieldwork (Fig. 3). For both PD metrics, these two sites appeared not to differ from what would be expected for a random community. For FD metrics, however, both sites showed over-dispersion of functional evenness and the site with the lowest species richness had higher functional divergence than expected by chance while the one with the highest richness approached random values.

Elevation-dependent responses to the environmental gradient

As expected, the effects of vegetation features on the biodiversity facets were not consistent along elevation (Fig. 4). The vegetation features contributing most to the across-elevation analysis (Figs. 2, 3; Table 2) proved statistically significant predictors of biodiversity facets only in certain elevational belts. In the case of species richness, trees with dbh ≥ 30 cm was significant only in the lowlands, shade cover in the middle-elevations and native plants in the highlands. By contrast, crop plants related positively to species richness in the lowlands, a result not captured when analysing the whole elevation gradient. The same was true for sesMPD and shade cover in the highland zone. For sesFDiv and sesPD the most important variables according to the across-elevation analysis (Table 2) had strongest effects at middle-elevations.

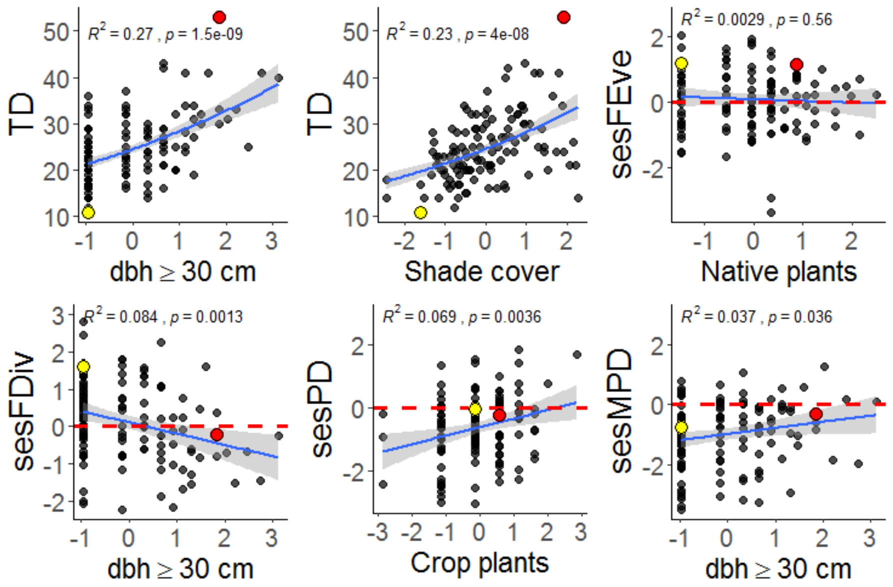


Figure 3. Univariate regression plots between the five biodiversity metrics and the variable that had the largest impact on them according to multi-model inference. For the ses metrics, the red dotted line separates over- (above) and under- (below) dispersed values. The grey shading corresponds to the standard errors of the regressions. The red and yellow points represent the sampling sites with the highest and lowest species richness, respectively.

Discussion

In this study, we found that structural and compositional features of the vegetation associated with the gradient of agricultural intensification modulate the facets of bird diversity in tropical farmlands. Our results are in line with other studies reporting increasing bird species richness with vegetation complexity in tropical agro-ecosystems. Indeed, particularly in coffee farms, bird taxonomic diversity increases in a “step-by-step” fashion as vegetation structure and composition changes from monoculture to floristically diverse systems (Gordon et al., 2007). This increase can then reach a plateau with little differences between different classes of agroforestry systems (Van Der Wal et al., 2012). However, a central question in the assessment of bird diversity in agriculture is if the trend set by taxonomic diversity transposes to functional and phylogenetic diversity as well. That is, if these two other facets also correlate with vegetation complexity and if their response is linked to changes in species richness. What we found is that, independent of the species richness gradient, some of the functional and phylogenetic metrics respond to an intensification gradient while others do not, and those that are responsive, may be associated with different features of the vegetation. With respect to phylogenetic diversity, prior studies also reported mixed effects of land use on PD (Frishkoff et al., 2014, Jayathilake et al., 2021). Regarding functional diversity, our results complement recent observations that declines in functional diversity of dietary guilds can happen in tropical agroforests that show high bird species richness (Rocha et al., 2019; Jarrett et al., 2020).

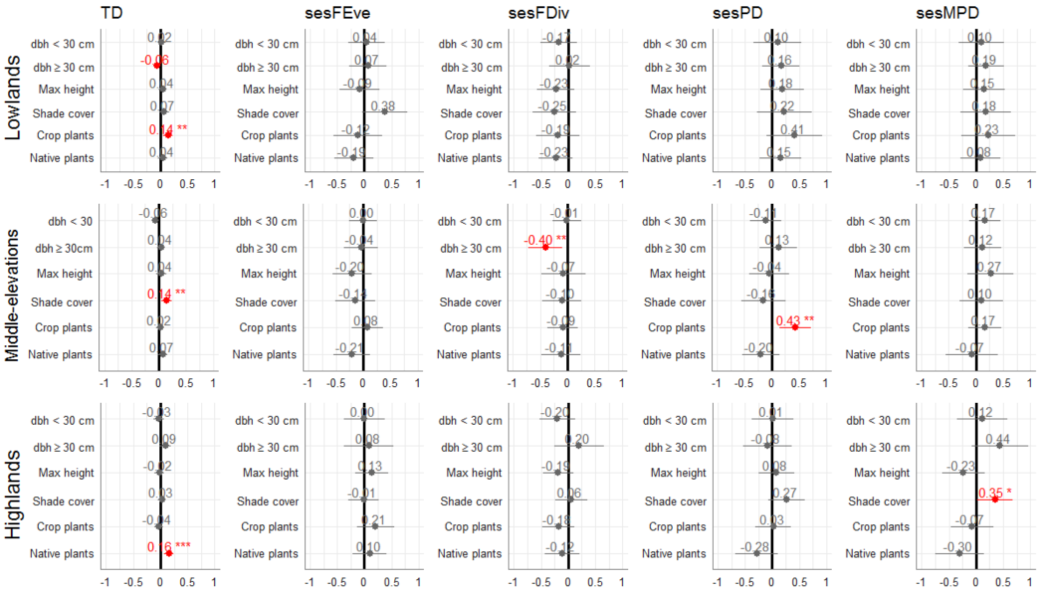


Figure 4. Estimated coefficients and their 95% confidence intervals (generated from averaged regression models with deltaAIC ≤ 4) for predictors of five measures of avian biodiversity at three elevational zones. Statistically significant effects (i.e. different from zero) are colored red and asterisks display the level of significance: *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$.

Agricultural intensification gradients and avian biodiversity in coffee agro-ecosystems
Avian TD, FD and PD responded to the variation of specific vegetation features inside the coffee farms of our study area. Overall, trees with a dbh larger than 30 cm most strongly affected avian biodiversity. Even though this vegetation feature has been previously associated with high bird taxonomic diversity (Bakermans et al., 2012; Rodrigues et al., 2018), its relevance for FD and PD remained yet unexplored. Large trees attract a variety of bird groups to coffee farms, including upper canopy migratory foragers (Bakermans et al., 2012), mid-high canopy foragers, forest-dependent species, insectivores and frugivores (Rodrigues et al., 2018). Besides offering fruit and arthropod resources, known to be exploited by many bird species (Carlo et al., 2004; Narango et al., 2018), large trees can also host communities of epiphytic plants which can become richer with increasing tree dbh (Flores-Palacios and García-Franco, 2006). Epiphytic plants in coffee farms can be used by a wide variety of bird species for foraging, as nesting sites, as a source of nesting materials and they can even regulate microclimatic conditions (Cruz-Angón et al., 2005). Although we did not measure the diversity of epiphytes, this could indeed be an influential element for avian functional and phylogenetic diversity in tropical farmlands.

Taxonomic and (marginally) phylogenetic diversity were also influenced by the percentage of shade cover in our study. The maintenance of shade inside coffee farms can boost bird species richness (Gordon et al., 2007; Bakermans et al., 2012; Rodrigues et al., 2018), possibly by generating cool microclimatic conditions (Schooler et al., 2020). In contrast, tree height had no influence on any facet in our study even though it can promote bird richness not only in coffee (Gordon et al., 2007), but also in in cacao plantations (Clough et al., 2011; Jarrett et al., 2020; Pérez-Cabral et al., 2021). In tree-crop agro-ecosystems, vertical structure is a relevant factor. For example, herbaceous and understory vegetation height in oil palm and rubber plantations increases avian TD (Nájera and Simonetti, 2010; Warren-Thomas et al., 2019), FD and PD (Jayathilake et al., 2021). Thus, it is surprising that tree height was largely insignificant in our study. In conjunction, thin trees also did not have a significant influence. One possible explanation is that the effect of these variables is restricted to particular groups of birds, masking the overall effect when considering the entire avian community. For instance, while certain upper canopy migratory birds can be attracted to tall trees, some ground foraging species can in turn be associated to trees with thin and medium size trunks (e.g. dbh 8 – 38cm; Bakermans et al.; 2012).

Among the compositional vegetation features, the number of different crop plants had an effect on the phylogenetic richness, while the native plants contributed to increase of TD. Throughout the study area, the most prominent and prevalent non-coffee crops were the nitrogen-fixing *Inga* sp. and *Erythrina* sp., followed by banana and its relatives (*Musa* spp.). Of these, *Inga* is known to positively affect bird communities in coffee farms, mainly because it acts as a foraging hub for birds looking to prey on invertebrates (Wunderle Jr. and Latta, 1998). The leaves of *Inga* trees are commonly attacked by canopy arthropods (e.g. Homoptera) and their flowers represent an important source of nectar; hence, *Inga* trees provide valuable resources for many insectivorous, nectarivorous (Johnson, 2000), and omnivorous birds (Greenberg et al., 1997b). At our study sites, *Inga* trees attracted many phylogenetically distant birds such as hummingbirds, woodpeckers, tityras, vireos, New World warblers, tanagers, bush-tanagers, and goldfinches consuming either invertebrates or nectar. The native plants inside the coffee farms correlated positively to TD, probably because birds take advantage of native plants inside coffee farms to forage fruits (Carlo et al., 2004; Bakermans et al., 2012) or invertebrate prey (Narango et al., 2018).

Moreover, whereas TD and PD was fostered by at least one of the vegetation features considered here, FD was either independent of (sesFEve) or negatively associated to (sesFDiv) the structural and compositional features inside the coffee farms. For sesFDiv, multi-model inference showed that under-dispersion was associated with higher numbers of large trees, in particular. Considering the univariate relationship between sesFDiv and large trees, the abundance of species representing extreme trait values was higher in farms with lower numbers of large trees. This means that more intensified coffee farms, poorer in species, may promote lesser degrees of overlap in functional niche space (Mason et al., 2005), maybe because of more intense competition for fewer resources. These latter results support the idea of higher functional redundancy in more structurally complex farms.

Elevation and the facets of avian diversity in tropical agricultural landscapes

Effects of the components of agricultural intensification on the facets of avian biodiversity were concentrated at particular elevations. A similar result has been reported in one of the few studies on this issue where tree height and the number of plants with small stems were the vegetation features that correlated positively with bird species richness, but only at lower elevations (Wunderle Jr., 1999). Here, we disentangled these relationships by conducting separate analyses for all facets at three different elevation zones. Our results show that the vegetation features most important for a particular metric vary across elevation. Moreover, TD was the only facet significantly related to at least one feature at each elevation zone whereas sesFEve did not relate to any variable at any zone.

The spatial scale at which the biodiversity facets are measured is important to understand their response to environmental gradients. Local and large-scale processes can be linked and jointly affect the relationship of taxonomic, functional and phylogenetic diversity with environmental factors (Pavoine and Bonsall, 2011). We hypothesize that two larger-scale trends modify the response of avian biodiversity facets to individual vegetation features associated with agroforestry intensity. First, the facets do not change in parallel along the elevation gradient. In our study system, TD declined while sesFEve, sesPD and sesMPD remained constant and FDiv increased with elevation (Fig. S2). That biodiversity facets are not consistent across elevational gradients has already been shown in tropical avifaunas (Montaño-Centellas et al., 2019). Bird communities at higher elevations commonly have less species but not necessarily lower phylogenetic diversity and often even higher functional diversity. For instance, FD of Andean birds was found being over-dispersed at high elevations most likely in reaction to resource-scarce environments (Montaño-Centellas et al., 2020). It is plausible that the incongruent changes in the biodiversity facets along elevation also affect their sensitivity to land use intensification and the associated vegetation features. Secondly, certain processes might act locally and not translate into a larger-scale effect. The most relevant vegetation features did not differ in magnitude across the three elevational zones [crop plants (Pearson's r=0.08, df=118, p=0.38), shade cover (r=0.07, df=118, p=0.46) and large dbh (r=-0.17, df=118, p=0.06)]. Hence, elevation-dependent variation in their effects on bird diversity cannot be explained by differences in their distribution. We rather assume that the change in taxonomic richness at the large-scale level plays a role for this variation. For example, crop plants related positively to species richness in the lowlands only. Since TD is higher in that elevation zone, it is possible that species richness was related to crop plants because this element diversified the available resources inside the farms. This way, birds benefitted from and were attracted to highly diversified farms presumably because increased competition and niche overlap in the lowlands can be attenuated in resource-rich environments (Graham et al., 2012), allowing more different species to co-exist (Pavoine et al., 2011) inside farms with higher numbers of crop plants. Thus, local processes at each of the elevation zones might explain differences in the response of the metrics used to measure bird diversity to the vegetation elements inside the coffee farms.

Conclusions

The results of this study underpin the so far scarce evidence of incongruent responses of the facets of avian diversity to farming intensity in tropical agricultural landscapes. It was evident that, at the plot-level, sites with the highest species richness did not necessarily exhibit high FD or PD. We conclude that evaluations of bird diversity within tropical farmlands would most likely be strengthened and deliver more comprehensive results when the functional and phylogenetic facets are included as well.

At the same time, we emphasize that wherever management decisions are designed in order to boost bird diversity inside tropical farmlands (e.g. certification processes), it is not enough just to keep trees inside the farms. Different vegetation structural and compositional features present along intensification gradients modify different facets of avian diversity differently, and at different elevations. Comprehensive assessments will thus have to consider carefully selected sets of vegetation features and their effects on all biodiversity facets at different elevation zones. Ideally, such studies would identify the specific combination of features that maximize particular aspects of bird diversity inside cultivated lands under particular conditions. They would thus deliver a scientific basis for farmers, certification agencies and decision-makers that want to maximize all biodiversity facets simultaneously as well as to those that want to focus on particular facets (e.g. functional diversity) independent of others (e.g. species richness). These management choices should match the reality of bird diversity at the plot and wider-scale (e.g. elevation zone) levels.

Acknowledgements

We would like to thank all the farm owners who granted us permission to conduct fieldwork inside their properties. Research permits were authorized by the Costa Rican Ministry of Energy and the Environment. This work was funded by a scholarship grant awarded by the Costa Rican Ministry of Science and Technology (N°MICITT-PINN-CON-2-1-4-17-1-008). Additional resources were obtained thanks to an Interdisciplinary Research Networks funding grant from the Faculty of Life Sciences of the University of Vienna.

References

Aerts, R., Spranghers, S., & Şekercioğlu, Ç.H., 2016. Conservation of ecosystem services does not secure the conservation of birds in a Peruvian shade coffee landscape. Bird Conserv. Int. 27, 71–82. https://doi.org/10.1017/S0959270916000149.

Alroy, J., 2017. Effects of habitat disturbance on tropical forest biodiversity. Proc. Natl Acad. Sci. USA 114, 6056–6061. https://doi.org/10.1073/pnas.1611855114.

Araneda, P., Sielfeld, W., Bonacic, C., Ibarra, J.T., 2018. Bird diversity along elevational gradients in the Dry Tropical Andes of northern Chile: The potential role of Aymara indigenous traditional agriculture. PLoS ONE 13, e0207544. https://doi.org/10.1371/journal.pone.0207544.

Bakermans, M. H., Rodewald, A. D., Vitz, A. C., Rengifo, C., 2012. Migratory bird use of shade coffee: the role of structural and floristic features. Agroforest. Syst. 85, 85–94. https://doi.org/10.1007/s10457-011-9389-0.

Barton, K., 2020. Mu-MIn: Multi-model inference. R Package Version 1.43.17 (http://R-Forge.R-project.org/projects/mumin/).

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67, 1–48. http://dx.doi.org/10.18637/jss.v067.i01.

Bianchi, S., Cahalan, C., Hale, S., Gibbons, J. M., 2017. Rapid assessment of forest canopy and light regime using smartphone hemispherical photography. Ecol. Evol. 7, 10556–10566. https://doi.org/10.1002/ece3.3567.

Bregman, T.P., Lees, A.C., MacGregor, H.E.A., Darski, B., de Moura, N.G., Aleixo, A., Barlow, J., Tobias, J.A., 2016. Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. Proc. R. Soc. B 283, 20161289. http://dx.doi.org/10.1098/rspb.2016.1289.

Burnham, K.P., Anderson, D.R. 2004. Multi-model inference. Understanding AIC and BIC in multi-model selection. Sociol. Method. Res. 33, 261–304. http://doi.org.0.1177/0049124104268644.

Carlo, T.A., Collazo, J., Groom, M., 2004. Influences of fruit diversity and abundance on bird use of two shaded coffee plantations. Biotropica 36, 602–614. https://doi.org/10.1111/j.1744-7429.2004.tb00354.x.

Clough, Y., Barkmann, J., Juhrbandt, J., Kessler, M., Wanger, T.C., Anshary, A., Buchori, D., Cicuzza, D., Darras, K., Putra, D.D., 2011. Combining high biodiversity with high yields in tropical agroforests. Proc. Natl. Acad. Sci. 108, 8311–8316. https://doi.org/10.1073/pnas.1016799108.

Cruz-Angón, A., Greenberg, R., 2005. Are epiphytes important for birds in coffee plantations? An experimental assessment. J. Appl. Ecol. 42, 150–159. https://doi.org/10.1111/j.1365-2664.2004.00983.x.

Dullinger, I., Essl, F., Moser, D., Erb, K., Haberl, H., & Dullinger, S., 2021. Biodiversity models need to represent land-use intensity more comprehensively. Global Ecol. Biogeogr 30, 924–932. https://doi.org/10.1111/geb.13289.

Elsen, P.R., Kalyanaraman, R., Ramesh, K., Wilcove, D.S., 2017. The importance of agricultural lands for Himalayan birds in winter. Conserv. Biol. 31, 416–426. https://doi.org/10.1111/cobi.12812.

Erb, K.H., Luyssaert, S., Meyfroidt, P., Pongratz, J., Don, A., Kloster, S., Kuemmerle, T., Fetzel, T., Fuchs, R., Herold, M., Haberl, H., Jones, C.D., Marín-Spiotta, E., McCallum, I., Robertson, E., Seufert, V., Fritz, S., Valade, A., Wiltshire, A., Dolman, A.J. 2017. Land management: data availability and process understanding for global change studies. Global Change Biol. 23, 512–533.

Flores-Palacios, A., García-Franco, J., 2006. The relationship between tree size and epiphyte species richness: testing four different hypotheses. J. Biogeogr. 33, 323–330. https://doi.org/10.1111/j.1365-2699.2005.01382.x.

Fox, J., Weisberg, S., 2019. An R Companion to Applied Regression, third ed. Sage, California.

Frishkoff, L.O., Karp, D.S., M'Gonigle, L.K., Mendenhall, C.D., Zook, J., Kremen, C., Hadly, E.A., & Daily, G.C., 2014. Loss of avian phylogenetic diversity in neotropical agricultural systems. Science 345, 1343–1346. https://doi.org/10.1126/science.1254610.

García-Navas, V., Thuiller, W., 2020. Farmland bird assemblages exhibit higher functional and phylogenetic diversity than forest assemblages in France. J Biogeogr. 47, 2392–2404. https://doi.org/10.1111/jbi.13950.

Gordon, C., Manson, R., Sundberg, J., Cruz-Angón, A., 2007. Biodiversity, profitability, and vegetation structure in a Mexican coffee agroecosystem. Agric. Ecosyst. Environ.
118, 256–266. https://doi.org/10.1016/j.agee.2006.05.023.

Graham, C., Parra, J.L., Tinoco, B.A., Stiles, F.G., McGuire, J., 2012. Untangling the influence of ecological and evolutionary factors on trait variation across hummingbird assemblages. Ecology 93, S99–S111. https://doi.org/10.1890/11-0493.1.

Greenberg, R., Bichier, P., Angon, A. C., Reitsma, R., 1997a. Bird populations in shade and sun coffee plantations in central Guatemala. Conserv. Biol. 11, 448–459. https://doi.org/10.1046/j.1523-1739.1997.95464.x.

Greenberg, R., Bichier, P., Sterling, J., 1997b. Bird populations in rustic and planted shade coffee plantations of eastern Chiapas, Mexico. Biotropica 29, 501–514. https://doi.org/10.1111/j.1744-7429.1997.tb00044.x.

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox, W.A., Han, K.-L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W., Witt, C.C., Yuri, T., 2008. A phylogenomic study of birds reveals their evolutionary history. Science 320, 1763–1768. https ://doi.org/10.1126/science.1157704.

Hartig, F., 2018. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.1 (https://CRAN.R-project.org/package=DHARMa).

Hendershot, J.N., Smith, J.R., Anderson, C.B., Letten, A.D, Frishkoff, L.O., Zook, J.R., Fukami, T., Daily, G.C., 2020. Intensive farming drives long-term shifts in avian community composition. Nature 579, 393–396. https://doi.org/10.1038/s41586-020-2090-6.

Jarrett, C., Smith, T., Claire, T., Ferreira, D., Tchoumbou, M., Elikwo, M., Wolfe, J. D., Brzeski, K., Welch, A., Hanna, R., Powell, L., 2021. Bird communities in African cocoa agroforestry are diverse but lack specialized insectivores. J Appl. Ecol. 58, 1237–1247. http://doi.org/10.1111/1365-2664.13864

Jayathilake, H.M., Warren-Thomas, E., Nelson, L., Dolman, P., Bumrungsri, S., Juthong, W., Carrasco, L.R., Edwards, D.P., 2021. Fruit trees and herbaceous plants increase functional and phylogenetic diversity of birds in smallholder rubber plantations. Biol. Conserv. 257, e109140. https://doi.org/10.1016/j.biocon.2021.109140.

Jeliazkov, A., Mimet, A., Chargé, R., Jiguet, F., Devictor, V., Chiron, F., 2016. Impacts of agricultural intensification on bird communities: New insights from a multi-level and multi-facet approach of biodiversity. Agr. Ecosyst. Environ. 216, 9–22. http://doi.org/10.1016/j.agee.2015.09.017.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Mooers, A.O., 2012. The global diversity of birds in space and time. Nature 491, 444–448. https://doi.org/10.1038/nature11631.

Johnson, M.D., 2000. Effects of shade-tree species and crop structure on the winter arthropod and bird communities in a Jamaican shade coffee plantation. Biotropica 32, 133–145. https://doi.org/10.1111/j.1744-7429.2000.tb00456.x.

Josse, J., Husson, F., 2016. missMDA: A Package for Handling Missing Values in Multivariate Data Analysis. J. Stat. Softw. 70, 1–31. http://doi:10.18637/jss.v070.i01.

Karp, D.S., Rominger, A.J., Zook, J., Ranganathan, J., Ehrlich, P.R., Daily, G.C., 2012. Intensive agriculture erodes β-diversity at large scales. Ecol. Lett. 15, 963–970. http://doi.org/10.1111/j.1461-0248.2012.01815.x.

Ke, A., Sibiya, M.D., Reynolds, C., McCleery, R.A., Monadjem, A., Fletcher Jr., R.J., 2018. Landscape heterogeneity shapes taxonomic diversity of non-breeding birds across fragmented savanna landscapes. Biodivers. Conserv. 27, 2681–2698. https://doi.org/10.1007/s10531-018-1561-7

Kembel, S., Cowan, P., Helmus, M., Cornwell, W., Morlon, H., Ackerly, D., Blomberg, S., Webb, C., 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26, 1463–1464.

Laliberté, E., Legendre, P., Shipley, B., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Laurance, W.F., Sayer, J., Cassman, K.G., 2014. Agricultural expansion and its impacts on tropical nature. Trends Ecol. Evol. 29, 107–116. http://doi:10.1016/j.tree.2013.12.001.

Luther, D.A., Cooper, W., Wolfe, J.D., Bierregaard, R., Gonzalez, A., Lovejoy, T., 2020. Tropical forest fragmentation and isolation: Is community decay a random process? Global Ecol. Conserv. 23, e01168. https://doi.org/10.1016/j.gecco.2020.e01168.

Maas, B., Dwi Putra, D., Waltert, M., Clough, Y., Tscharntke, T. Schulze, C.H., 2009. Six years of habitat modification in a tropical rainforest margin of Indonesia do not affect bird diversity but endemic forest species. Biol. Conserv. 142, 2665–2671. https://doi.org/10.1016/j.biocon.2009.06.018.

Martín-Regalado, C.N., Briones-Salas, M., Lavariega, M.C., Moreno, C.E., 2019. Spatial incongruence in the species richness and functional diversity of cricetid rodents. PLoS ONE 14, e0217154. https://doi.org/10.1371/journal.pone.0217154.

Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111, 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x.

Montaño-Centellas, F.A., McCain, C., Loiselle, B., 2019. Using functional and phylogenetic diversity to infer avian community assembly along elevational gradients. Global Ecol. Biogeogr. 29, 232–245. https://doi.org/10.1111/geb.13021.

Montaño-Centellas, F.A., Loiselle, B.A., Tingley, M.W., 2021. Ecological drivers of avian community assembly along a tropical elevation gradient. Ecography 44, 574–588. https://doi.org/10.1111/ecog.05379.

Morante-Filho, J.C., Arroyo-Rodríguez, V., de Andrade, E.R., Santos, B.A., Cazetta, E., Faria, D., 2017. Compensatory dynamics maintain bird phylogenetic diversity in fragmented tropical landscapes. J. Appl. Ecol. 55, 256–266. https://doi.org/10.1111/1365-2664.12962.

Nájera, A., Simonetti, J.A., 2010. Can oil palm plantations become bird friendly? Agroforest Syst 80, 203–209. https://doi.org/10.1007/s10457-010-9278-y.

Narango, D.L., Tallamy, D., Snyder, K.J., Rice, R., 2019. Canopy tree preference by insectivorous birds in shade-coffee farms: Implications for migratory bird conservation. Biotropica 51, 387–398. https://doi.org/10.1111/btp.12642.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R.B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H. (2015). Vegan: Community ecology package. R package version 2.3-1 (http://CRAN.R-project.org/package=vegan).

Pavoine, S., & Bonsall, M., 2011. Measuring biodiversity to explain community assembly: a unified approach. Biol. Rev. 86, 792–812. https://doi.org/10.1111/j.1469-185X.2010.00171.x.

Pavoine, S., Véla, E., Gachet, S., Bélair, G.D., Bonsall, M., 2011. Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. J. Ecol. 99, 165–175. https://doi.org/10.1111/j.1365-2745.2010.01743.x.

Pérez-Cabral, J., Faria, D., Morante-Filho, J.C., 2021. Landscape composition is more important than local vegetation structure for understory birds in cocoa agroforestry systems.
Forest Ecol. Manag. 481, 118704. https://doi.org/10.1016/j.foreco.2020.118704.

Perfecto, I., Rice, R. A., Greenberg, R., Voort, M. E., Van, D. E. R., 1996. Shade Coffee: A Disappearing Refuge for Biodiversity. BioScience 46, 598–608. https://doi.org/10.2307/1312989

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2021. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-152 (https://CRAN.R-project.org/package=nlme).

Pool, T.K., Grenouillet, G., Villéger, S., 2014. Species contribute differently to the taxonomic, functional, and phylogenetic alpha and beta diversity of freshwater fish communities. Divers. Distrib. 20, 1235–1244. https://doi.org/10.1111/ddi.12231.

Prescott, G.W., Gilroy, J.J., Haugaasen, T., Medina-Uribe, C.A., Foster, W.A., Edwards, D.P., 2016. Reducing the impacts of Neotropical oil palm development on functional diversity. Biol. Conserv. 197, 139–145. https://doi.org/10.1016/j.biocon.2016.02.013.

Ricklefs, R.R., 2017. Passerine morphology: external measurements of ca. one-quarter of passerine bird species. Ecology 98, 1472–1472. https://doi.org/10.1002/ecy.1783.

Rocha, J.D.S., Laps, R.R., Machado, C.G., Campiolo, S., 2019. The conservation value of cacao agroforestry for bird functional diversity in tropical agricultural landscapes. Ecol. Evol. 9, 7903–7913. https://doi.org/10.1002/ece3.5021.

Rodrigues, P., Dugo, G.S., Dorresteijn, I., Schultner, J., Hanspach, J., Hylander, K., Senbeta, F., Fischer, J., 2018. Coffee management and the conservation of forest bird diversity in southwestern Ethiopia. Biol. Conserv. 217, 131–139. https://doi.org/10.1016/j.biocon.2017.10.036.

Schooler, S.L., Johnson, M.D., Njoroge, P., Bean, W.T., 2020. Shade trees preserve avian insectivore biodiversity on coffee farms in a warming climate. Ecol. Evol. 23, 12960–12972. http://doi.org/10.1002/ece3.6879.

Şekercioğlu, Ç.H., Mendenhall, C.D., Oviedo-Brenes, F., Horns, J.J., Ehrlich, P.R., Daily, G.C., 2019. Long-term declines in bird populations in tropical agricultural countryside. Proc. Natl Acad. Sci. USA 116, 9903–9912. https://doi.org/10.1073/pnas.1802732116.

Sreekar, R., Corlett, R.T., Dayananda, S., Goodale, U.M., Kilpatrick, A., Kotagama, S.W., Koh, L.P., Goodale, E., 2017. Horizontal and vertical species turnover in tropical birds in habitats with differing land use. Biol. Lett. 13, 20170186. http://dx.doi.org/10.1098/rsbl.2017.0186.

Tichý, L., 2015. Field test of canopy cover estimation by hemispherical photographs taken with a smartphone. J. Veg. Sci. 27, 427–435. https://doi.org/10.1111/jvs.12350.

Van Der Wal, H., Peña-Álvarez, B., Arriaga-Weiss, S.L., Hernández-Daumás, S., 2012. Species, Functional Groups, and Habitat Preferences of Birds in Five Agroforestry Classes in Tabasco, Mexico. Wilson J. Ornithol. 124, 558–571. https://doi.org/10.1676/10-111.1.

Villéger, S., Mason, N. W., & Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301. https://doi.org/10.1890/07-1206.1.

Waltert, M., Bobo, K.S., Sainge, N.M., Fermon, H., & Mühlenberg, M. (2005). From forest to farmland: habitat effects on afrotropical forest bird diversity. Ecol. Appl. 15, 1351–1366. https://doi.org/10.1890/04-1002.

Warren-Thomas, E., Nelson, L., Juthong, W., Bumrungsri, S., Brattström, O., Stroesser, L., Chambon, B., Penot, É., Tongkaemkaew, U., Edwards, D.P., Dolman, P.M., 2019. Rubber agroforestry in Thailand provides some biodiversity benefits without reducing yields. J. Appl. Ecol. 57, 17–30. https://doi.org/10.1111/1365-2664.13530.

Webb C.O., 2000. Exploring the Phylogenetic Structure of Ecological Communities: An Example for Rain Forest Trees. Am. Nat. 156, 145–155. https://doi.org/10.1086/303378.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M., Jetz, W., 2014. EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals: ecological Archives E095-178. Ecology 95, 2027. https://doi.org/10.1890/13- 1917.1

Wunderle J. 1999. Avian distribution in Dominican shade coffee plantations: area and habitat relationships. J. Field Ornithol. 70, 58–70.

Wunderle, J., Latta, S., 1998. Avian resource use in Dominican shade coffee plantations. Wilson J. Ornithol. 110, 271–281.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. Smith, G., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.

Figure captions

Chapter 2. Unshaded coffee imposes a heavier load on thermoregulation than shaded coffee for birds in a tropical mountainous region

Otto Monge, Christian H. Schulze, Stefan Dullinger, Leonida Fusani, Ivan Maggini

Abstract

Distribution shifts and local extinctions in tropical montane birds are supposed 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 physiological response of four bird species to heat and predicted the amount of days that heat exposure would increase the demand for evaporative cooling, based on $T_a$mic recorded inside mountainous shaded and sun-grown coffee farms. Maximum $T_a$mic in sun coffee was significantly higher than in shade coffee. On the other hand, $T_a$mic in shaded farms was similar to $T_a$mic inside forest patches used as a reference. In response to increasing experimental ambient temperature (T_a), the four tested bird species exhibited different rates of change and onset T_a of the evaporative cooling response and of the increase in body temperature. Accordingly, the amount of time that the birds were predicted to be exposed to heat inside the farms also varied across species. Yet, for all of them, shifting from a shaded to an unshaded coffee farm could increase the number of hours exposed to heat by 2-3 times. Inter-specific differences were also found in the amount of water predicted to be lost to evaporative cooling inside the farms. However, these daily loses, even under the harshest scenario, represented only a small proportion of their body mass lost in the form of water. Moreover, our predictions also show that heat exposure to $T_a$mic within the farms dilutes as the dry season transitions into the wet season. Taken together, we demonstrate that these four bird species are able to endure the current thermal environment of a tropical mountainous agricultural landscape, as it currently does not pose a risk of chronic or lethal dehydration. Nonetheless, we found the more intensified, sun coffee farms to elevate the risk of exposure to $T_a$mic that increases the demand for water in order to maintain water balance over consecutive days. If sun coffee farms become devoid of vital resources needed to support adequate evaporative cooling responses in birds, they might become thermal filters in the future.

Keywords: avian, biodiversity, climate change, thermal physiology

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 because their narrow vertical ranges might make them more 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 characterized 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 stabilize microclimatic conditions (Barradas & 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 (sun 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 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), while increases in T_a triggers heat dissipation by evaporative cooling (evaporative water loss, EWL) through the body surface or the respiratory tract (McKechnie & 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 economizing 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 & 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 in North American birds showed that farming intensity can in fact modulate their physiological response (Latimer et al. 2020; Van Vliet et al. 2020), but the role of temperature was not explicitly defined.

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. First, we looked into differences in microclimatic temperature between sun and shaded 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 lose from heat exposure as a percentage of their body mass. We predicted that the lack of shade in sun farms would increase the exposure to heat, and that more hours of exposure would result in higher water losses destined for evaporative cooling in these birds.

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 a few weeks towards the end of June in which precipitation is reduced or halted. Highest temperatures are reached around March, the lowest around December.

Birds were captured and microclimatic temperatures measured in sun and shaded 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 – 12 ºC, 16 – 18 ºC and 22 – 24 ºC, respectively (Fick & Hijmans 2017). The shaded coffee farms of the study sites were characterized by the presence of native, crop (e.g. avocado, citrus, banana), nitrogen-fixing (*Erythrina* sp. and *Inga* sp.) and timber trees. The sun farms were either devoid of trees or had a few native, crop or pruned nitrogen-fixing trees mixed in. 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 sun farms, tree average maximum height was 9.60 m (sd = 8.55) and percent canopy cover was 8.60 % (sd = 6.55).

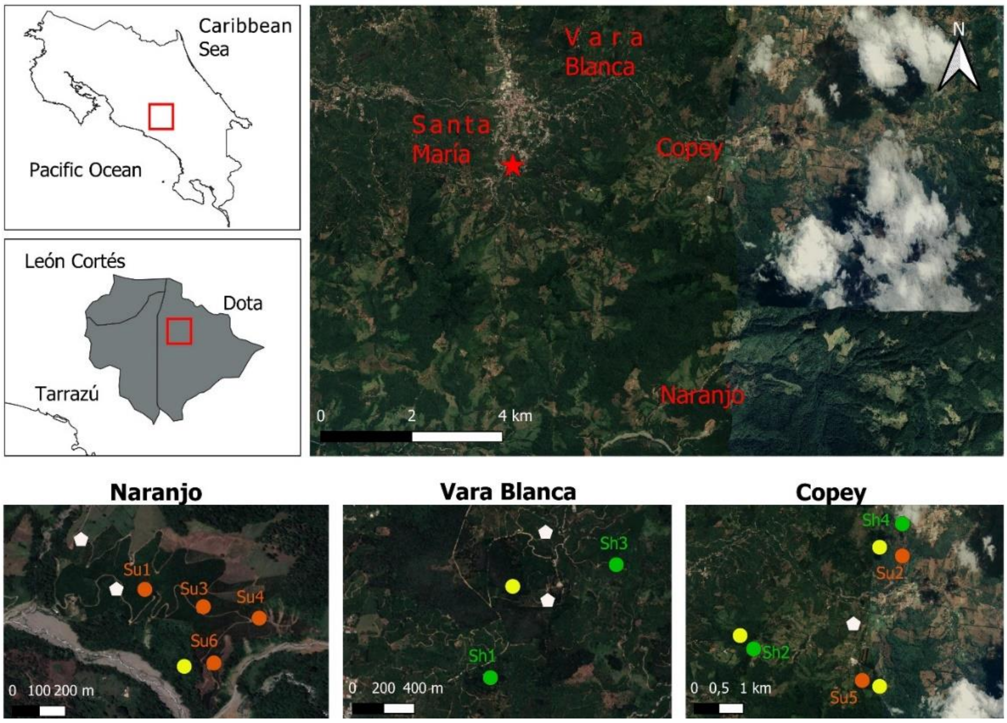


Figure 1. Map of the study area. The inserts show the location within Costa Rica and within the Zona de los Santos region, composed by the cantons of León Cortés, Tarrazú and Dota. Sampling localities were situated close to the town of Santa María (in Dota), where the laboratory in which metabolic measurements 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 (sun = orange; shaded = green) in the sampling localities of Naranjo, Vara Blanca and Copey. Shaded and sun farm locations are numbered consecutively.

Thermal environment of coffee farms

Microclimate temperatures ($T_a$mic) at coffee farms and forest patches adjacent to the farms were recorded with Thermochron® iButton® loggers (model DS1921G, accuracy ± 1ºC, Maxim Integrated, USA) between March and July 2020. Four loggers were deployed in shaded coffee farms, six in sun 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). We were aware of the possibility that measurements using iButton loggers may sometimes result in overestimation of $T_a$mic (Maclean et al. 2021), therefore we took several precautions to minimize 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". 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 ºC between consecutive 2-hour periods (n = 35, 0.13% of all data points).

Metabolic trials

Thermal physiology trials were carried out between August and November 2020 on four ecologically diverse bird species commonly found in human-dominated landscapes

(Table 1). These were silver-throated tanager (*Tangara icterocephala*), yellow-faced grassquit (*Tiaris olivaceus*), lesser goldfinch (*Spinus psaltria*), and Cabanis's wren (*Cantorchilus modestus*). 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 & Skutch 1989).

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

The birds were captured with mist nets or baited traps set up inside the coffee farms between 07 – 12 hr, transferred to metallic or wooden holding cages (c. 80 x 50 x 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. 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 minutes 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 inside, 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 ºC, with a precision of ±0.2 ºC. 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 hr. 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 12V 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 gas 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 hr^{-1}. Before measurements were taken, however, an initial wash-out step ensured that traces of water vapour 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 hr^{-1} for 60 minutes. 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-minute 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 ºC increases or decreases, covering the range from 10 to 45 ºC. Thus, each measurement period was conducted at a given stabilized T_a (± 0.5 ºC) which was then increased or decreased to continue with the next period. The total duration of the trials was never longer than 3 hr. The birds were exposed to the first T_a of the trial sequence during the wash-out period. 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 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 ºC and 44 ºC; grassquit at T_a 11 ºC, 12 ºC, 14 ºC, 16 ºC, 37 ºC, 38ºC, 42 ºC, 44 ºC, 45 ºC; and goldfinch at T_a 11 ºC, 16 ºC, 17 ºC, 43 ºC).

Data analysis

All statistical computations were conducted in the R environment (version 4.0.4, R Core Team 2021). We tested for differences in $T_a$mic at the coffee farms with a two-way analysis of variance (ANOVA), which included an interaction term between the factorized predictors, farm type (sun – shaded) and temperature class (minimum – average – maximum). The reliability of the ANOVA was confirmed by visually examining the residuals and by checking normality with the Shapiro-Wilk test (W = 0.95, p = 0.22) and the homogeneity of variance with the Levene's test (F = 0.62, p =

0.69). The ANOVA simultaneously tested for significant differences in overall $T_a$mic between farm types and for differences associated with the temperature classes. Specific significant associations between each level of farm type and temperature class, were detected by performing a Tukey HSD post-hoc test on the results of the ANOVA. The difference in means at each temperature class was calculated considering a 95% confidence level.

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 the trial. 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 vaporization 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 (ºC 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 ºC and $T_b$max for T_a only above 35ºC. 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 during the sampling period inside the coffee farms. We began by assessing the amount of time per day, for the five months of the study, in which $T_a$mic surpassed the EWL T_a inflection point that was 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. Then, to test if the presence of shade inside the farms modified the species' water balance, we compared the accumulated number of hours per month above the EWL inflection between shaded and sun farms using a generalized linear model (GLM) with a Poisson distribution. 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 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 ºC 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.

Results

Microclimate inside coffee farms

The thermal environment inside the coffee farms was characterized by highly variable $T_a$mic. The average daily range in shaded farms was 9.66 ºC (sd = 1.65) while for sun farms it was 14.60 ºC (sd = 1.91). Maximum $T_a$mic occurred between 10 – 12 hr, while minimum $T_a$mic was recorded between 04 – 06 hr. Overall, maximum $T_a$mic was higher inside the farms than in adjacent forest patches, especially in sun farms, while average and minimum $T_a$mic did not differ between farms and forests (Fig. 2a). The averaged reference $T_a$mic inside the forest was 13.56 ºC (sd = 0.80) for the minimum, 16.25 ºC (sd = 0.74) for the mean, 19.96 ºC (sd = 1.54) for the maximum, and 6.39 ºC (sd = 1.74) for the daily range of $T_a$mic.

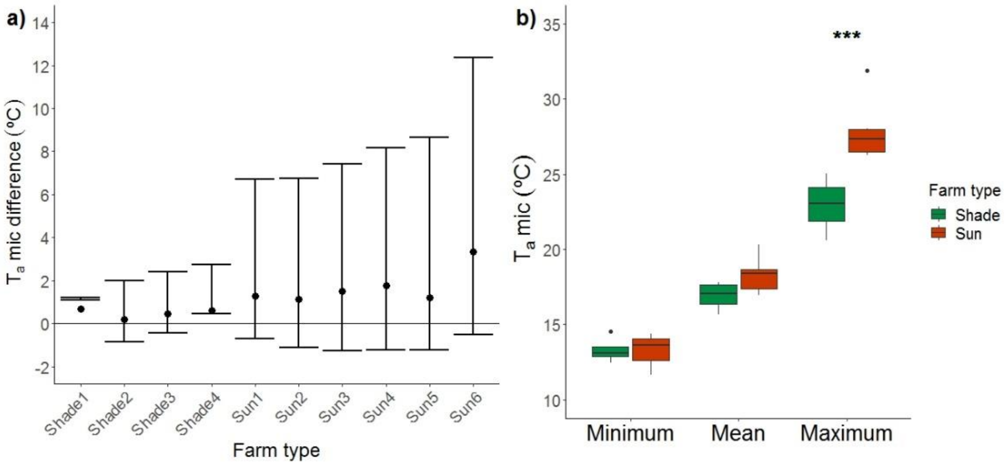


Figure 2. Differences in averaged microclimate temperatures ($T_a$mic) between shaded coffee farms, sun farms and forest patches during a five-month period in the central mountains of Costa Rica. In **a)**, the dependent variable is the difference in $T_a$mic between each farm and its nearest forest patch. Points are the average and whiskers the minimum and maximum values, and farms in the x-axis were ordered from heavily shaded to full-sun coffee (see Fig. 1). In **b)**, asterisks show the significance of average $T_a$mic differences between the farm types, according to the three temperature classes, resulting from a Tukey HSD post-hoc test performed on a two-way ANOVA. *** = $p < 0.001$.

$T_a$mic inside sun and shaded coffee farms were significantly different (F = 14.79, $p < 0.001$). The interaction between the farm type and the temperature classes was also significant (F = 7.17, $p < 0.01$). Applying a post-hoc test to these results revealed that the thermal differences inside the coffee farm types were driven solely by the maximum $T_a$mic (Fig. 2b). The magnitude of the average difference in maximum $T_a$mic between sun and shade farms was 4.93 (1.99 – 7.87 95% CI; $p < 0.001$), whereas for the average and minimum $T_a$mic it was 1.41 (-1.53 – 4.35 95% CI; p = 0.68) and -0.01 (-2.95 – 2.93 95% CI; p = 0.99), respectively.

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 ºC for the tanager, 32 ºC for the grassquit and 26 ºC 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 A.1). The highest thermoregulatory energetic expenditure in wrens was 0.87 W at 18 ºC, in tanagers 1.08 W at 18 ºC, in grassquits 0.76 W at 15 ºC, and in goldfinches 0.70 W at 14 ºC (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 A.1). 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 ºC. In turn, tanagers achieved parity between metabolic heat dissipation and production at around T_a 33 ºC, while wrens and grassquits did so at 35 ºC.

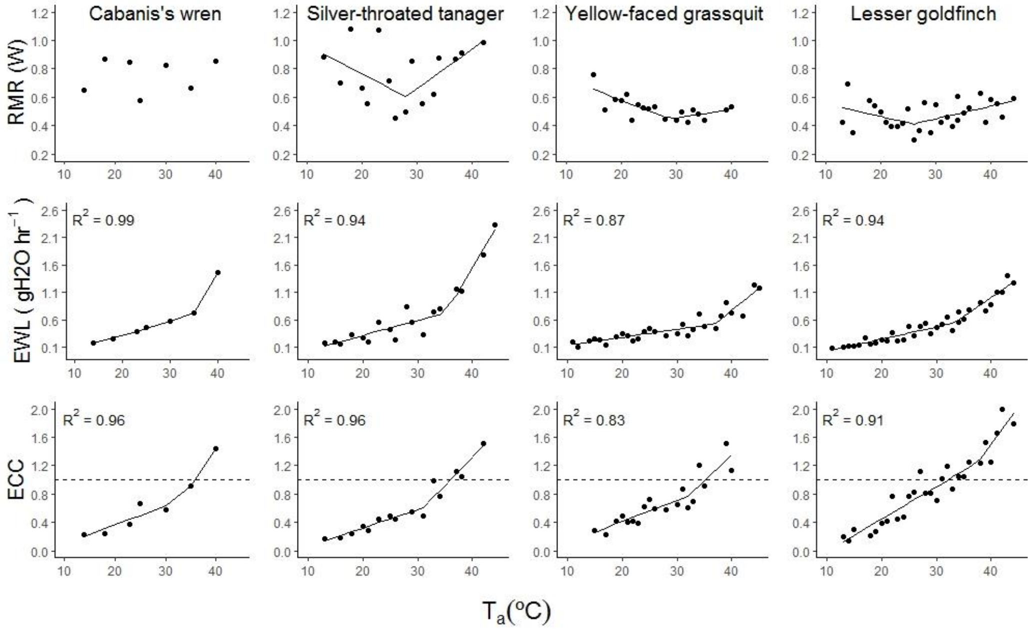


Figure 3. Relationship between resting metabolic rate (RMR), evaporative water loss (EWL) and evaporative cooling capacity (ECC) and ambient temperature (T_a) inside the metabolic chamber. The black lines were obtained from segmented regression models used to detect inflection points where the response 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.

T_b. No data from PIT tags during the metabolic trials was obtained for the wren. The inflection points for the tanager and the grassquit were similar, around 34 ºC. In the case of the goldfinch, T_b inflection was low, 24 ºC, and T_b was highly variable throughout the trials (Table A.1; Fig. 4). The average T_b for this species was 39.4 ºC and ranged between 36.3 – 42.6 ºC. Variation in tanagers was also high (range 39.2 – 45.8 ºC; average = 41.2 ºC), 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 ºC. In contrast, the variation in T_b was lower for the grassquit (40 ºC – 43.6 ºC; average = 41.4 ºC). 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 ºC while others remained at 40 – 41 ºC. Grassquits and goldfinches were first observed shivering at T_a 16 ºC whereas only one tanager individual shivered and it occurred at T_a 13 ºC. For all of them, fluffing of feathers started at higher T_a: at 21 ºC in tanagers, 20 ºC in grassquits and 18 ºC in goldfinches. Below these T_a, T_b in tanagers dropped from 40.4 ºC to $T_b$min 39.8 ºC, at T_a 13ºC. In grassquits, T_b dropped from 41.2 ºC to $T_b$min 40.3 ºC at 11 ºC T_a. In goldfinches, T_b decreased from 41 ºC to $T_b$min 37.2 ºC at 11 ºC T_a. Tanagers and grassquits started panting earlier, at T_a 37 ºC and 38 ºC, respectively, than goldfinches at 41 ºC. During panting, T_b changed from 41.2 ºC to $T_b$max 45.8 ºC in tanagers, from T_b 42.1 ºC to $T_b$max 43.6 ºC in grassquits and from T_b 42.9 ºC to $T_b$max 44.2 ºC (both cloacal T_b) in goldfinches (Fig. 4).

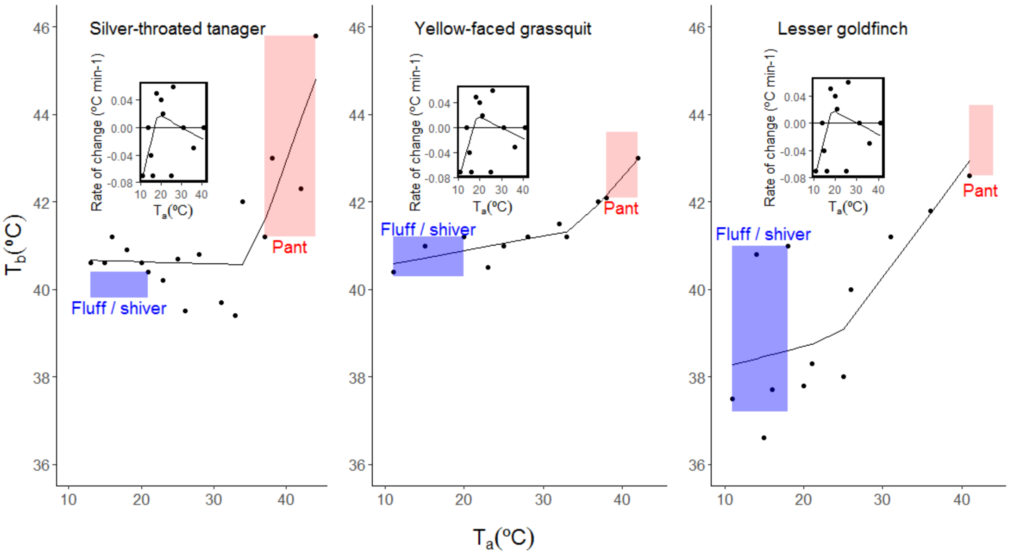


Figure 4. Change in body temperature (T_b) and the rate of change in T_b (inset) in response to the ambient temperature (T_a) inside the metabolic chamber. The black lines were obtained from segmented regression models fitted to T_b and T_a, used to detect inflection points in which changes in T_a resulted 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.

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 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 hr (sd = 1.36) per day to $T_a$mic above EWL inflection for 69 days, the tanager to 2.56 hr (sd = 0.98) for 57 days, the grassquit to 2.53 hr (sd = 0.90) for 30 days, and the goldfinch to 3.23 hr (sd = 1.54) for 98 days. Heat exposure within shaded farms occurred only during March, April and June for the wren [average 2.80 hr (sd = 0.64) per day for 5 days], during March and April for the tanager [average 2.00 hr (sd = 0.62) for 4 days], during April for the grassquit (2 hr in one day), and during March, April and June for the goldfinch [average 3.33 hr (sd = 0.81) in 6 days]. In contrast, heat exposure inside sun farms occurred during the five months for all species, except the grassquit for which heat exposure stopped in June (Fig. 6). For comparison, there were zero hours of heat exposure above EWL inflection inside the forest patches, for any of the species and months.

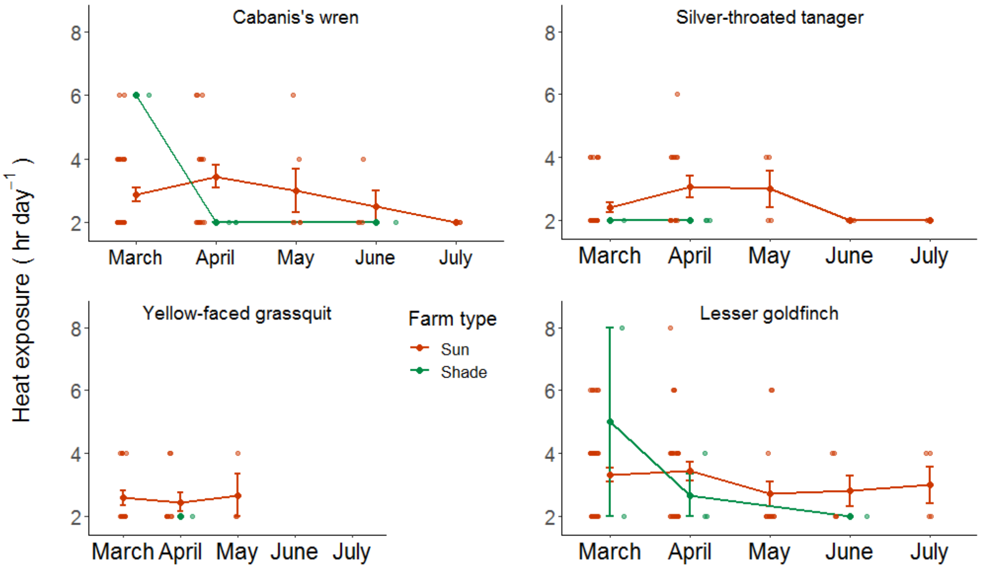


Figure 5. Daily heat exposure for four bird species inside coffee farms in the central mountains of Costa Rica. Shown is the mean number of hours per day (> 0), enclosed by standard error bars, for five months in which the species experienced $T_a$mic that surpassed the inflection points of EWL recorded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

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.

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	$p < 0.001$
	Sun 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	$p < 0.001$

Species		Estimate	SE	z-value	p-value
	Sun 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
	Sun 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
	Sun coffee	2.70	0.23	11.66	p < 0.001

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.

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 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 *	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%

*= estimated from a segmented regression.

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 tree canopy, particularly during the dry season. Our four focal species showed a variety of heat dissipation responses during exposure to high temperatures. In consequence, the predicted exposure to heat that elevated the demand for evaporative cooling inside the coffee farms varied between species.

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, average, 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 suitable microclimates and harbour temperature-sensitive species (Senior et al. 2018) if 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 benefit from reduced local maxima as exemplified by the small differences in maximum temperatures (1.2 ºC) between the most heavily shaded farm in our study and its nearest forest patch. The non-coffee vegetation composition in this farm (the first in Fig. 2a) was ~96% native 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 & Fanjul 1986) while sun coffee farms can, on average, be considerably hotter than forest – e.g. by ~6 ºC in a Brazilian study area (de Souza et al. 2012). However not only native remnant trees but also tall nitrogen-fixing trees in shaded coffee farms can keep daily maxima lower and nightly minima warmer than in sun farms (Siles et al. 2010). In our study site, sun farms were characterized by rows of small nitrogen-fixing *Erythrina* sp. trees (< 2 m), which were also maintained pruned, thus resulting in a reduced $T_a$mic buffering capacity when compared to the shaded farms.

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 when 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 ºC. A similar ECC (~1.5 at T_a > 40 ºC), aided by low energy-cost panting, is an effective thermoregulatory mechanism to deal with elevated T_a in a lethargic 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 ºC per 1 ºC 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 sun 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 sun coffee farms devoid of native or even crop trees. In fact, telemetry data show that silver-throated tanagers persist in coffee-dominated landscapes only with a native 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 sun 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). Coffee farms harbour diverse arthropod communities, but their abundance is lower in coffee bushes exposed under the sun than in those under shade (Johnson 2000). Thus, frugivores, but also insectivores and granivores, living in sun coffee-dominated landscapes may face difficulties in obtaining the resources needed to fulfill 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 & Skutch 1989). Even other small tropical open-habitat granivores that can endure hyperthermic T_b above 44 ºC 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 sun 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 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 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 predicted to continue (Zhang & Fueglistaler 2019), assessing the physiological response of tropical birds to concomitant gradients of humidity and temperature demands urgent attention.

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 & 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 sun 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 sun 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 recognized and potential ecosystem-service providers. For example, in farmlands of the United States the largely granivorous *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 ºC 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 sun farms might become thermal filters in the future.

Acknowledgements

We would like to express our gratitude to the families Madrigal Ureña, Ureña Retana and Leiva Ureña as well as the owners of the Hacienda Copey coffee farm for allowing us to conduct fieldwork on their properties and to M. E. Ureña, G. Madrigal, I.

Madrigal, E. Madrigal, and M. Rivera for their valuable help during field and lab work. Research permits, license to handle animals and all procedures were approved by the Costa Rican Ministry of the Environment and Energy under permit number SINAC-ACC-PI-R-028-2019. Funding was granted by the Costa Rican Ministry of Science and Technology (Nº MICITT-PINN-CON-2-1-4-17-1-008) and by the Faculty of Life Sciences of the University of Vienna, Austria.

References

Albright, T.P., Mutiibwa, D., Gerson, A.R., Smith, E.K., Talbot, W.A., O'Neill, J.J., McKechnie, A.E., Wolf, B.O., 2017. Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. P. Natl. Acad. Sci. 114. 2283–2288. https://doi.org/10.1073/pnas.1613625114.

Angilletta, M.J.,Jr, Cooper, B.S., Schuler, M.S., Boyles, J.G., 2010. The evolution of thermal physiology in endotherms. Front. Biosci. 2, 861–881. https://doi.org/10.2741/e148.

Barradas, V.L., Fanjul, L., 1986. Microclimatic characterization of shaded and open-grown coffee (*Coffea arabica* L.) plantations in Mexico. Agr. Forest Meteorol. 38, 101–112.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67, 1–48. http://dx.doi.org/10.18637/jss.v067.i01.

Boyle, W.A., Shogren, E.H., Brawn, J.D., 2020. Hygric Niches for Tropical Endotherms. Trends Ecol. Evol. 35, 938-952. https://doi.org/10.1016/j.tree.2020.06.011

Busch, D.S., Robinson, W.D., Robinson, T.R., Wingfield, J.C., 2011. Influence of proximity to a geographical range limit on the physiology of a tropical bird. J. Anim. Ecol. 80, 640–649. https://doi.org/10.1111/j.1365-2656.2010.01791.x.

Cooke, S.J., Sack, L., Franklin, C.E., Farrell, A.P., Beardall, J., Wikelski, M., Chown, S.L., 2013. What is conservation physiology? Perspectives on an increasingly integrated and essential science. Conserv. Physiol. 1, cot001. https://doi.org/10.1093/conphys/cot001.

Czenze, Z.J., Kemp, R., van Jaarsveld, B., Freeman, M.T., Smit, B., Wolf, B.O., McKechnie, A.E., 2020. Regularly drinking desert birds have greater evaporative cooling capacity and higher heat tolerance limits than non-drinking species. Funct. Ecol. 34, 1589–1600. https://doi.org/10.1111/1365-2435.13573.

De Frenne, P., Zellwegger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., Lenoir, J., 2019. Global buffering of temperatures under forest canopies. Nat. Ecol. Evol. 3, 744–749. https://doi.org/10.1038/s41559-019-0842-1.

de Souza, H.N., Goede, R.G., Brussaard, L., Cardoso, I.M., Duarte, E.M., Fernandes, R.B., Gomes, L.C., Pulleman, M.M., 2012. Protective shade, tree diversity and soil properties in coffee agroforestry systems in the Atlantic Rainforest biome. Agr. Ecosyst. Environ. 146, 179–196. https://doi.org/10.1016/j.agee.2011.11.007.

Ehrenbergerová L., Šenfeldr M., Habrová H., 2017. Impact of tree shading on the microclimate of a coffee plantation: a case study from the Peruvian Amazon. Bois For. Trop. 334, 13–22. https://doi.org/10.19182/bft2017.334.a31488.

Ewers, R.M., Banks-Leite, C., 2013. Fragmentation impairs the microclimate buffering effect of tropical forests. PloS One 8, e58093. https://doi.org/10.1371/journal.pone.0058093.

Fick, S.E., R.J. Hijmans, 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086.

Freeman, B.G., Scholer, M.N., Ruiz-Gutierrez, V., Fitzpatrick, J.W., 2018. Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. P. Natl. Acad. Sci. USA 115, 11982–11987. https://doi.org/10.1073/pnas.1804224115.

Frishkoff, L.O., Karp, D.S., Flanders, J.R., Zook, J., Hadly, E.A., Daily, G.C., M'Gonigle, L.K., 2016. Climate change and habitat conversion favour the same species. Ecol. Lett. 19, 1081–1090. https://doi.org/10.1111/ele.12645.

Gardner, J.L., Symonds, M.R.E., Joseph, L., Ikin, K., Stein J., Kruuk, L.E.B., 2016. Spatial variation in avian bill size is associated with humidity in summer among Australian passerines. Clim. Change Responses 3, 3–11. https://doi.org/10.1186/s40665-016-0026-z.

Garfinkel, M., Minor, E., Whelan, C.J., 2021. Using faecal metabarcoding to examine consumption of crop pests and beneficial arthropods in communities of generalist avian insectivores. Ibis. https://doi.org/10.1111/ibi.12994.

Garrigues, R., Dean, R., 2014. Birds of Costa Rica: a field guide. 2nd Ed. Bloomsbury Publishing, London, UK.

Gerson, A.R., McKechnie, A.E., Smit, B., Whitfield, M.C., Smith, E.K., Talbot, W.A., McWhorter, T.J., Wolf, B.O., 2019. The functional significance of facultative hyperthermia varies with body size and phylogeny in birds. Funct. Ecol. 33, 597–607. https://doi.org/10.1111/1365-2435.13274.

Gomes, L.C., Bianchi, F.J.J.A., Cardoso, I.M., Fernandes, R.B.A., Fernandes Filho, E.I., Schulte, R.P.O., 2020. Agroforestry systems can mitigate the impacts of climate change on coffee production: A spatially explicit assessment in Brazil. Agr. Ecosyst. Environ. 194, 106858. https://doi.org/10.1016/j.agee.2020.106858.

Granados-Montero, M., Avelino, J., Arauz-Cavallini, F., Castro-Tanzi, S., Ureña, N., 2020. Leaf litter and *Mycena citricolor* inoculum on the American leaf spot epidemic. Agron. Mesoam. 31, 77–94. https://dx.doi.org/10.15517/am.v31i1.36614.

Guo, F., Lenoir, J., Bonebrake, T.C., 2018. Land-use change interacts with climate to determine elevational species redistribution. Nat. Commun. 9, 1315. https://doi.org/10.1038/s41467-018-03786-9.

Hartig, F., 2021. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.4. http://florianhartig.github.io/DHARMa/.

Hoegh-Guldberg, O., Jacob, D., Taylor, M., Bindi, M., Brown, S., Camilloni, I., et al., 2018. Impacts of 1.5ºC Global Warming on Natural and Human Systems. In: Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (eds.)]. In Press

Jetz, W., Wilcove, D.S., Dobson, A.P., 2007. Projected impacts of climate and land-use change on the global diversity of birds. PLoS Biol 5, e157. https://doi.org/10.1371/journal.pbio.0050157.

Jha, S., Bacon, C.M., Philpott, S.M., Méndez, V.E., Läderach, P., Rice, R.A., 2014. Shade Coffee: Update on a Disappearing Refuge for Biodiversity. BioScience 64, 416–428. https://doi.org/10.1093/biosci/biu038.

Johnson, M.D., 2000. Effects of Shade-Tree Species and Crop Structure on the Winter Arthropod and Bird Communities in a Jamaican Shade Coffee Plantation. Biotropica 32, 133-145. https://doi.org/10.1111/j.1744-7429.2000.tb00456.x.

Jucker, T., Hardwick, S.R., Both, S., Elias, D.M.O., Ewers, R.M., Milodowski, D.T., Swinfield, T., Coomes, D.A., 2018. Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. Global Change Biol. 24, 5243–5258. https://doi.org/10.1111/gcb.14415.

Lasiewski, R.C., Dawson, W.R., Bartholomew, G.A., 1970. Temperature regulation in the little Papuan frogmouth, *Podargus ocellatus*. Condor 72, 332–338. https://doi.org/10.2307/1366012.

Latimer, C.E., Smith, O.M., Taylor, J.M., Edworthy, A.B., Owen, J.P., Snyder, W.E., Kennedy, C.M., 2020. Landscape context mediates the physiological stress response of birds to farmland diversification. J. Appl. Ecol. 57, 671–680. https://doi.org/10.1111/1365-2664.13583.

Lighton, J.R., 2008. Measuring Metabolic Rates. Oxford Univ. Press, New York, NY.

Lin, B.B., 2007. Agroforestry management as an adaptive strategy against potential microclimate extremes in coffee agriculture. Agr. Forest Meteorol. 144, 85–94. https://doi.org/10.1016/j.agrformet.2006.12.009.

Lister, B.C., Garcia, A., 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. P. Natl. Acad. Sci. USA 115, E10397–E10406. https://doi.org/10.1073/pnas.1722477115.

Maclean, I.M.D., Duffy, J.P., Haesen, S., Govaert, S., De Frenne, P., Vanneste, T., Lenoir, J., Lembrechts, J.J., Rhodes, M.W., Van Meerbeek, K., 2021. On the measurement of microclimate. Methods Ecol. Evol. 12, 1397–1410. https://doi.org/10.1111/2041-210X.13627.

Mata, A., 2010. Metabolic rate and specific dynamic action of the Red-legged Honeycreeper, a nectar-feeding Neotropical passerine. Comp. Biochem. Phys. A 157, 291–296. https://doi.org/10.1016/j.cbpa.2010.07.018.

McKechnie, A.E., Wolf, B.O., 2004. Partitioning of evaporative water loss in white-winged doves: Plasticity in response to short-term thermal acclimation. J. Exp. Biol. 207, 203–210. https://doi.org/10.1242/jeb.00757.

Mitchell, D., Snelling, E.P., Hetem, R.S., Maloney, S.K., Strauss, W.M., Fuller, A., 2018. Revisiting concepts of thermal physiology: Predicting responses of mammals to climate change. J. Anim. Ecol. 87, 956–973. https://doi.org/10.1111/1365-2656.12818.

Montejo-Kovacevich, G., Martin, S.H., Meier, J.I., Bacquet, C.N., Monllor, M., Jiggins, C.D., Nadeau, N.J., 2020. Microclimate buffering and thermal tolerance across elevations in a tropical butterfly. J. Exp. Biol. 223, jeb220426. https://doi.org/10.1242/jeb.220426.

Moreira, S.L.S., Pires, C.V., Marcatti, G.E., Santos, R.H.S., Imbuzeiro, H.M.A., Fernandes, R.B.A., 2018. Intercropping of coffee with the palm tree, *macauba*, can mitigate climate change effects. Agr. Forest Meteorol. 256–257, 379–390. https://doi.org/10.1016/j.agrformet.2018.03.026.

Muggeo, V.M., 2008. “segmented: an R Package to Fit Regression Models with Broken-Line Relationships.” R News 8, 20–25. https://cran.r-project.org/doc/Rnews/.

Nilsson, J.Å., Molokwu, M.N., Olsson, O., 2016. Body Temperature Regulation in Hot Environments. PloS One 11, e0161481. https://doi.org/10.1371/journal.pone.0161481.

Perfecto, I., Rice, R.A., Greenberg, R., Van der Voort, M.E., 1996. Shade coffee: A disappearing refuge for biodiversity. BioScience 46, 598–608. https://doi.org/10.2307/1312989.

Pollock, H.S., Cheviron, Z.A., Agin, T.J., Brawn, J.D., 2015. Absence of microclimate selectivity in insectivorous birds of the Neotropical forest understory. Biol. Conserv. 188, 116–125. https://doi.org/10.1016/j.biocon.2014.11.013.

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Riddell, E.A., Iknayan, K.J., Wolf, B.O., Sinervo, B., Beissinger, S.R., 2019. Cooling requirements fueled the collapse of a desert bird community from climate change. P. Natl. Acad. Sci. USA 116, 21609–21615. https://doi.org/10.1073/pnas.1908791116.

Sales, L.P., Galetti, M., Pires, M.M., 2020. Climate and land-use change will lead to a faunal "savannization" on tropical rainforests. Global Change Biol. 26, 7036–7044. https://doi.org/10.1111/gcb.15374.

Schooler, S.L., Johnson, M.D., Njoroge, P., Bean, W.T., 2020. Shade trees preserve avian insectivore biodiversity on coffee farms in a warming climate. Ecol. Evol. 10, 12960–12972. https://doi.org/10.1002/ece3.6879.

Şekercioğlu, C.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D., Sandi, R.F., 2002. Disappearance of insectivorous birds from tropical forest fragments. P. Natl. Acad. Sci. USA 99, 263–267. https://doi.org/10.1073/pnas.012616199.

Şekercioğlu, C.H., Loarie, S.R., Oviedo Brenes, F., Ehrlich, P.R., Daily, G.C., 2007. Persistence of forest birds in the Costa Rican agricultural countryside. Conserv. Biol. 21, 482–494. https://doi.org/10.1111/j.1523-1739.2007.00655.x.

Şekercioğlu, C.H., Schneider, S.H., Fay, J.P., Loarie, S.R., 2008. Climate change, elevational range shifts, and bird extinctions. Conserv. Biol. 22, 140–150. https://doi.org/10.1111/j.1523-1739.2007.00852.x.

Senior, R.A., Hill, J.K., Benedick, S., Edwards, D.P., 2018. Tropical forests are thermally buffered despite intensive selective logging. Global Change Biol. 24, 1267–1278. https://doi.org/10.1111/gcb.13914.

Siles, P., Harmand, J.M., Vaast, P., 2010. Effects of *Inga densiflora* on the microclimate of coffee (*Coffea arabica* L.) and overall biomass under optimal growing conditions in Costa Rica. Agroforest. Syst. 78, 269–286. https://doi.org/10.1007/s10457-009-9241-y.

Steiger, S.S., Kelley, J.P., Cochran, W.W., Wikelski, M., 2009. Low metabolism and inactive lifestyle of a tropical rain forest bird investigated via heart-rate telemetry. Physiol. Biochem. Zool. 82, 580–589. https://doi.org/10.1086/605336.

Stiles, F.G., Skutch, A., 1989. A Guide to the Birds of Costa Rica. Cornell Univ. Press, Ithaca, NY.

Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B., Thomas, C.D., 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. Oikos, 120, 1–8. https://doi.org/10.1111/j.1600-0706.2010.18270.x.

van Vliet, H.E., Stutchbury, B.J., Newman, A.E., Norris, D.R., 2020. The impacts of agriculture on an obligate grassland bird of North America. Agr. Ecosyst. Environ. 287, 106696. https://doi.org/10.1016/j.agee.2019.106696

Weathers, W., 1977. Temperature regulation in the dusky munia, *Lonchura fuscans* (Cassin) (Estrildidae). Aust. J. Zool. 25, 193–199. https://doi.org/10.1071/ZO9770193.

Weathers, W., 1997. Energetics and thermoregulation by small passerines of the humid, lowland tropics. Auk 114, 341–353. https://doi.org/10.2307/4089237.

Worthington, A.H., 1989. Adaptations for avian frugivory: assimilation efficiency and gut transit time of *Manacus vitellinus* and *Pipra mentalis*. Oecologia, 80, 381–389. https://doi.org/10.1007/BF00379040

Zhang, Y., Fueglistaler, S., 2019. Mechanism for increasing tropical rainfall unevenness with global warming. Geophys. Res. Lett. 46, 14836–14843. https://doi.org/10.1029/2019GL086058.

Chapter 3. Physiologically vulnerable or resilient? Tropical birds, global warming and re-distributions

Otto Monge, Ivan Maggini, Christian H. Schulze, Stefan Dullinger, Leonida Fusani

Abstract
Tropical species are considered to be more threatened by climate change than those of other world regions. This increased sensitivity to warming is thought to stem from a low physiological capacity to withstand temperature fluctuations and to the assumption that many tropical species already live near the limits of heat tolerance under current climatic conditions. For birds, despite thorough documentation of community-level rearrangements, such as biotic attrition and elevational shifts, there is no consistent evidence of physiological sensitivity to warming. In this paper, we provide an integrative outlook into the physiological response of tropical birds to thermal variation and provide insights regarding their capacity to face warming. In short, evidence from the literature suggest that the assumed physiologically sensitivity to warming attributed to tropical biotas do not seem to be a fundamental characteristic of tropical birds. Tropical birds do possess the physiological capacities to deal with fluctuating temperatures, including high-elevation species. Moreover, those living in hot and arid environments are fitted to withstand elevated levels of heat. However, there are still many unaddressed points that hinder a more complete understanding of the response of tropical birds to warming. As an example, we do not know much about species' cooling capacities when exposed to combined gradients of heat and humidity, particularly in montane species. In addition, climate effects on tropical birds will interact with those of rapidly expanding and intensifying land use creating increased levels of microclimatic stress in disturbed ecosystems. Further research into how tropical birds from many different ecological contexts handle warming will increase our understanding of current and future community rearrangements in tropical birds.

Keywords: bird conservation, ecophysiology, thermal stress

Introduction

Anthropogenic climate change can be particularly pervasive in tropical ecosystems (Laurance et al. 2011; Foden et al. 2013; see Box 1). For example, recent predictions suggest that end-of-century temperatures could surpass the realized thermal limits of proportionally more organisms in the Tropics than at higher latitudes (Trisos et al. 2020). In consequence, re-distributions and re-arrangements of tropical communities are expected to occur more frequently (Freeman et al. 2021). Distributions would shift along elevational gradients, with species at the mountain-tops being particularly disadvantaged because they would have no more space to escape towards (Marris 2007; Freeman et al. 2018). In turn, the lowest elevations would suffer from biotic attrition, because upward shifts and local extinctions of their biotas may not be compensated by species moving in from still warmer areas (Colwell et al. 2008).

Birds in the tropical regions of the world have responded to climate change in a variety of ways. For example, long-term losses of lowland bird richness have been related to increases in maximum temperatures and to the frequency of extreme typhoons (38% attrition; Tsai et al. 2015) as well as to variations in seasonal rainfall (27% attrition; Curtis et al. 2021). Additionally, strong La Niña events, that caused increased rainfall, were associated to lowland abundance declines (Blake & Loiselle 2015). Concerning elevational movements, predominant upslope shifts are occasionally accompanied by downslope shifts and absence of change as well as shifts in only the lower elevation limit, only the upper or both (Peh 2007; Forero-Medina et al. 2011; Campos-Cerqueira et al. 2017; Freeman et al. 2018; Neate-Clegg et al. 2021). Mountain-top extinctions have so far only be reported from a montane bird community in the Andes (Freeman et al. 2018). Furthermore, across tropical regions, montane birds have shifted upslope either at pace with (Freeman & Class-Freeman 2014; Freeman et al. 2018) or slower than the elevational temperature rate of change (Forero-Medina et al. 2011).

Distributional shifts are expected to increase the abundance of warm-adapted species across elevational gradients (i.e. "thermophilization"; Fadrique et al. 2018). This can happen when mid- and high-elevation birds decline in abundance at their lower margin while lowland species increase at their upper (Williams & de la Fuente 2021), promoting the transition of montane communities towards ones of lower elevations (Neate-Clegg et al. 2021). In the lowlands, thermophilization can occur when rainforest birds are replaced by species from warm and dry regions (Curtis et al. 2021).

It is commonly assumed that the main driver of the observed distributional rearrangements in tropical biotic communities is thermal sensitivity (Laurance et al. 2011; Khaliq et al. 2014) because many organisms are thought to possess low tolerance to temperature variation (Tewksbury et al. 2008) and to live near their upper thermal limits already under current climatic conditions (Trisos et al. 2020). These assumptions have been derived from the narrow distribution ranges of many tropical species, which apparently suggest narrow thermal niches and hence high thermal sensitivity (Colwell et al. 2008; Laurance et al. 2011). Yet, sound empirical evidence for these assumptions from physiological studies is surprisingly scarce. In fact, most studies that measured thermal tolerance in relation to the warming expected over the next decades focused on tropical ectotherms so far [e.g. *Anolis* lizards (Logan et al. 2014); ants (Tizón et al. 2014); littoral snails (Marshall et al. 2015); amphibians (von May et al. 2019)].

Identifying whether warming directly impacts tropical organisms or not could have deep implications for understanding the nature of community-level responses to climate change. Birds can become physiologically vulnerable to warming when the intolerance of rising temperatures worsen into an inability to efficiently cool down the body when facing extremely high heat. The upper thermal limits would be subsequently surpassed and local extinctions may follow. This scenario was proven to be behind the collapse of a sub-tropical avian desert community (Riddell et al. 2019) but no cases have been reported so far in the Tropics. It has also been suggested that warming-induced thermal stress within native distributions might lead to redistributions into areas where temperatures match preferred values. In this context, organisms would chase their thermal niche elsewhere when rising temperatures exceed their narrow tolerance levels (Colwell et al. 2008). However, to date such a direct physiological trigger of distributional changes has not been documented in tropical birds.

In contrast to the tenet of prevailing narrow thermal niches in tropical birds, a growing body of literature shows that at least certain tropical birds possess a relatively broad thermal tolerance (Freeman et al. 2018; Pollock et al. 2021) and can even withstand predicted levels of warming (e.g. a 4 ºC increase: Thompson et al. 2015). In addition, the “true” thermal tolerance of tropical lowland biotas to future warming might be underestimated given the absence of current analogues of hotter areas with which to compare (Feely & Silman 2010). In other words, true thermal niches of lowland birds may actually be wider than currently realized ones, because warmer conditions could be managed but do not currently occur across species ranges (Shoo et al. 2005; Freeman & Beehler 2018; Burner et al. 2019). Indeed, a number of tropical bird communities have resisted climate warming so far, with no significant overall change in elevation limits of individual species (Campos-Cerqueira et al. 2017), small changes in overall abundance (Roselli et al. 2017) and even abundance increases, especially at high elevations, of warm- and cold-adapted understory species alike (Dulle et al. 2016).

In a general sense, a too narrow focus on climate change as a driver of tropical bird diversity changes bears the risk of overlooking more imminent threats such as anthropogenic habitat alterations (Caro et al. 2022). Indeed, it might even prompt scientists to debate the contribution of climate change in direct organismal responses (Oliver & Morecroft 2014). In addition, the interaction between climate change and other prominent processes of the Anthropocene, especially land-use change, can be critical for improving predictions of biotic vulnerability in tropical regions (Brodie et al. 2012; Harris et al. 2014, Newbold et al. 2020). Finally, even when local or regional climatic trends correlate with biodiversity changes, or are indeed causal drivers, physiological vulnerability might not play a role (Cahill et al. 2013). For example, some elevational shifts and abundance changes in tropical birds have been more related to the distribution and availability of habitat and resources, mostly linked to rainfall, than to increases in temperature (Forero-Medina et al. 2011; Rosselli et al. 2017; Freeman et al. 2018; Neate-Clegg et al. 2020).

In summary, the drivers of recent re-arrangements in tropical bird communities are not yet well understood. In this paper, we review the existing literature with a focus on one particular aspect, namely the supposed thermal sensitivity of tropical birds and the resulting vulnerability in the face of a warming climate. Specifically we asked: are tropical birds characterized by narrow thermal tolerances? Are they currently living close to their upper thermal limits? And, consequently, are they particularly vulnerable to warming from a physiological standpoint? What is the role of microclimatic alterations, such as the ones driven by land-use change, in their vulnerability or resilience to warming? For this, we: *i*) examined the physiological mechanisms that underlie the response of tropical birds to variation in temperatures and to high levels of heat (including the role of humidity); *ii*) analysed the relationships between changes in land use, microclimate and thermal tolerance; and *iii*) identified knowledge gaps and future directions of research that can expand our understanding of how vulnerable or flexible tropical birds can be to the effects of global warming.

Box 1. Global warming in the Tropics

Global mean temperatures are expected to continue rising during this century, with magnitudes depending on the amount of greenhouse gases emitted: up to 2.6ºC under a moderate and up to 4.7ºC under a high emissions scenario (Lee et al. 2021). In tropical regions, the variability in average temperatures is expected to increase within the next decades – e.g. by ~10% in the Sahel and Southeast Asia and ~15% in the Amazon per degree of global warming (Bathiany et al. 2018). This variation may also increase the intensity of hot days, becoming ~24% hotter than the average day in tropical land (Byrne 2021).

Even though yearly temperatures fluctuate less in the Tropics than at higher latitudes, warming normalized by temperature variation shows that the Tropics are warming more and also experiencing more extreme heat events (Zeng et al. 2021). In tropical Africa, heat waves – consecutive days when temperatures are drastically higher than usual – may extend over 10–50 days per year (Engelbrecht et al. 2015). If a 5ºC warmer future is met, by 2100 some tropical regions could have as much as 120 heat-wave days per season (Perkins-Kirkpatrick & Gibson 2017). To make things worse, deforestation of tropical forests is a major amplifier of climate change. For example, current local warming of more than 5ºC in the Amazon and in Southeast Asia has occurred in deforested lands and equates to the amount of warming predicted for the next 100 years under a worst-case scenario (Zeppetello et al. 2020). Furthermore, the incidence of heat waves will likely be highest in agricultural areas, devoid of forest cover (Im et al. 2017).

Hot days in the Tropics are becoming hotter because they are also dry days (Byrne 2021). Increases in drought stress are expected to occur in tropical regions such as Central America, southeast Africa and Madagascar due to shifts in the wind patterns that determine the rainfall seasonality across the Tropics (Mamalakis et al. 2021). For instance, prolonged dry seasons in southern Amazonia caused droughts during the 2000's and, if the trend continues at even half the rate, by 2090 the dry seasons could be >1 month longer (Fu et al. 2013). Moreover, although African forests appear to be more resistant to short-term drought than forests in the Amazon or southeast Asia (Bennett et al. 2021), long-term drying trends have caused large-scale reductions in rainfall and terrestrial water storage in a Congolese forest (Zhou et al. 2014).

On the other hand, the effect of extreme heat on organisms can be modified by its interaction with air humidity (Zhang et al. 2021) because humidity can interfere with the cooling of an organism's body (Raymond et al. 2017). For example, tropical cyclones can bring intense precipitation over large continental areas (Dominguez & Magaña 2018). The frequency of combined events of dangerously high heat following major tropical cyclones is projected to increase from currently three events per 30-year period to potentially occurring annually, if temperatures rise up to 4ºC in some tropical regions (Matthews et al. 2019).

Physiological features of tropical birds related to vulnerability or flexibility to tolerate climate warming

Main features involved in avian thermal tolerance response

Endotherms possess a variety of physiological mechanisms that allows them to adjust to environmental stressors and avoid negative effects (see Box 2). Of major relevance is the regulation of body temperature (Tb) within a safe range in order to sustain vital functions (Angiletta et al. 2010). For instance, regulated increments in the metabolic activity during exposure to cold serves to generate internal heat (Lowell and Spiegelman 2000). On the other hand, heat loads produced by endogenous metabolic activity as well as those absorbed from the environment are dissipated through cooling mechanisms (Weathers 1981). Generally, in both cases, physiological mechanisms are set to maintain a constant Tb (i.e. normothermic Tb, in birds: ~40–42ºC). Thermoregulation represents a significant share of an endotherm's energetic expenditure when experiencing fluctuations in ambient temperatures (Ta) (McNab 2013). However, the capacity to adapt the regulation of Tb may smooth the energetic trade-off between thermoregulation and other life-history functions such as growth or reproduction (Boyles et al. 2011).

Box 2. Avian basal metabolism, body temperature and heat dissipation in a warmer world

The rate of metabolic expenditure of resting endotherms remains at a minimum (basal metabolic rate, BMR) across a given range of ambient temperature (Ta). This range (thermo-neutral zone, TNZ) is bounded by lower and upper critical Ta limits (LCL and UCL, respectively) and varies, along with BMR, across ecological contexts (McNab 2013). For instance, BMR in birds can decrease along environmental gradients for different species (Tieleman et al. 2002), or for populations of the same species (Maldonado et al. 2012), and the TNZ limits can shift to lower Ta in highland versus lowland individuals (Castro et al. 1985). Traditionally, the TNZ has been regarded as ecologically important for the adaptation to thermal stress because outside of it an increased amount of metabolic energy is invested into maintaining constant body temperature (Tb) (Scholander 1950; Fristoe et al. 2015). In consequence, it has been stated that as long as Ta remains within the TNZ, birds are in a thermoregulatory "safe zone", but when Ta is deviates beyond the critical limits, survival is threatened or fitness reduced (Khaliq et al. 2014). However, the possible consequences of a climate-change driven shift in Ta in relation to the TNZ are not straightforward. First, because Tb can be regulated outside the TNZ through physiological and behavioural strategies and many endotherms may actually live at Ta above their UCL (Mitchell et al. 2018; Freeman et al. 2020). Second, because Tb can increase while Ta is within the limits of the TNZ (Weathers 1977; Weathers 1997), even reaching hyperthermic levels (Withers & Williams 1990). For better insights into possible effects of climate change on avian thermoregulation it is hence reasonable to jointly examine the variation in the rate of metabolism along with the physiological mechanisms for heat dissipation.

Birds lose heat by evaporating water through the respiratory tract (evaporative water loss, EWL) – enhanced by panting – or via the skin (cutaneous water loss, CWL). However, since most birds cannot produce enough water from the metabolism to replace the losses, several mechanisms are triggered in order to conserve water and avoid dehydration (Dawson 1982). Facultative hyperthermia is the increase in Tb that approximates and slightly surpasses Ta, thereby letting heat dissipate passively from the body to the surroundings (McKechnie & Wolf 2019) thus reducing the need for evaporative cooling and conserving body water (Gerson et al. 2019). In arid habitats, small birds normally possess low capacities for evaporative cooling which makes them more likely to benefit from the creation of a thermal gradient (Weathers 1981; Gerson et al. 2019). Moreover, because prolonged panting can result in dehydration from EWL and also interfere with efficient food and water consumption (du Plessis et al. 2012; Smit et al. 2016), birds from hot and water-limited environments who start panting at a relatively low Ta are more vulnerable to warming temperatures (Pattinson et al. 2020).

Birds from arid regions have been studied in depth because of their obvious state of risk from warming, but virtually all studies come from sub-tropical deserts. Thus, there are still many uncertainties regarding how tropical birds, especially rainforest and montane species, deal with heat. For example, what is the variation in the physiological responses of individuals, populations and species to heat stress, especially to the critical thermal maximum (CT_{max}) – the Ta at which Tb rises to life-threatening levels (Kendeigh 1969; Boyles et al. 2011)? Thermal environments that demand higher EWL may not be limiting to birds if water lost to EWL is replaced, thereby safely maintaining an efficient cooling capacity. Regular drinking is in fact vital to endure hyperthermia at Ta approaching CT_{max} (Czenze et al. 2020; Freeman et al. 2020). On the other hand, with limited access to water, survival can be compromised with sustained exposure even to non-immediately lethal Ta (Mitchell et al. 2018). Moreover, some species may perish if they are unable to withstand severe hyperthermia, even if adapted to conserve body water (Czenze et al. 2020). Thus, in hot, arid environments, and most likely elsewhere, there will be variation in the degree of vulnerability among bird species depending on their capacity to fulfil cooling requirements (Riddell et al. 2019). Consequently, the link between heat tolerance and the risk of extirpation is not as straightforward as it may seem (Cahill et al. 2013).

Are tropical birds physiologically vulnerable to warming?

Physiological sensitivity to warming could drive biotic attrition and elevational shifts if tropical birds were characterized by a low capacity to handle Ta fluctuations and if they already live close to their heat tolerance limits under current conditions (Figure 1). The basis for assuming these conditions to hold seems to be a perceived climatic stability linked to the thermal aseasonality of the Tropics (Stratford & Robinson 2005; Sheldon et al. 2018). In consequence, climatic variation beyond the currently prevailing limits would create a generalized thermal stress for most species and the incapacity to endure such conditions would push the birds out of their native habitats into more "climatically suitable" areas and/or lead to abundance declines and local extinctions.

Traditionally, the notion of an increased sensitivity of tropical endotherms to temperature variation has been ascribed to the possession of a narrow thermo-neutral zone (TNZ, Scholander 1950); thought to stem from living in thermally stable environments (Bucher 1981). Under this view, many tropical birds would be restricted to habitats where Ta fluctuates along a very narrow range – presumably the TNZ, where Tb is supposed to remain constant with minimal energy input. Thus, when facing spatio-temporal fluctuations in Ta outside TNZ limits, such birds are supposed to become thermally stressed given the need to invest in keeping a constant Tb. For instance, one tropical montane bird species was deemed intolerant to Ta above an upper critical limit (UCL) of merely 31ºC (Weathers & Van Riper 1982).

Previous studies can provide an insight into the physiological responses of tropical birds to variations in Ta and the possibilities of being dependant on thermal stability. Several examples from the literature show that the relationship between TNZ and Tb is in fact highly variable in tropical birds. There are cases in which a very narrow TNZ (e.g. of 2ºC–4ºC) has been identified, but the regulation of Tb outside its limits shows a deal of variation. For example, the montane barred parakeet *Bolborhynchus lineola* keeps a constant Tb at Ta as low as 5ºC (Bucher 1981), but the lowland rainforest spotted antbird *Hylophylax naevioides* face steady decreases in Tb below the lower critical limit (LCL) (Steiger et al. 2009). In addition, Tb in other lowland birds fluctuates outside the TNZ, suggesting a reduced energy input for thermoregulation outside its limits (Bosque et al. 1999; Merola-Zwartjes & Ligon 2000). There are also specific cases in which hyperthermia occurs even within a broad TNZ (Weathers 1977; Withers & Williams 1990). Nonetheless, it seems that the trend for many ecologically diverse tropical birds is for Tb to vary slightly outside broad TNZs of 10ºC or higher (Schuchmann and Schmidt-Marloh 1979a; Merola-Zwartjes 1998; Seavy & McNab 2007; Mata 2010).

In montane species, daily variations in Ta can be followed by Tb rhythms in amplitudes of 5ºC–17ºC (Morrison 1962; Cheke 1970; Schuchmann and Schmidt-Marloh 1979b). Whether these variations in Tb are associated with Ta or not (e.g. to save energy at night), they demonstrate that even the presumably sensitive montane avifaunas can handle continuous fluctuations in Ta. In fact, thermoregulatory costs may not constrain montane birds to distribute at specific elevations (Londoño et al. 2017). Further evidence comes from studies that assessed short- or long-term acclimation responses. For instance, four lowland passerines survived gradual changes in Ta in the range of 0ºC to 40ºC for six months (Cox 1961). Likewise, 13 lowland sunbirds (Nectariniidae) endured continuous exposure to Ta ranging from 5ºC–32ºC for 4–6 consecutive days (Prinzinger et al. 1989) and five finches from arid regions withstood a 24hr period of gradual increases from 18ºC to 42ºC (Marshall & Prinzinger 1989). Thus, it seems unlikely that a narrow tolerance to thermal variation is a fundamental characteristic of tropical birds and that species must be restricted to a specific thermal context in consequence. However, more long-term acclimation studies would be a key contribution to better understand the effects of temporal variations in Ta on their physiological response.

If tropical birds live close to their upper limits of thermal tolerance, their vulnerability would drastically increase when facing sudden and intense heat waves or droughts as well as when experiencing gradual warming. However, the lack of conclusive evidence complicates the interpretation of this assumption. For instance, a 15-year trend of rising maximum local temperatures during the dry season reduced the survival of adult male rufous-and-white wrens *Thryophilus rufalbus*, a species adapted to the hot lowland dry forests in Central America (Woodworth et al. 2018). Nevertheless, as the wren's thermal tolerance was not measured there is no direct indication that the observed response to warming resulted from thermal stress.

The assumption of proximity to the thermal limits was probably conceived by regarding the UCL as a tolerance limit (Figure 1). However, a better indicator of thermal sensitivity is the response of Tb when facing dangerously high levels of heat (see Box 2). In sub-tropical deserts, acute exposure to extreme heat for hours causes lethal dehydration or hyperthermia, while chronic exposure to days or weeks of sustained heat leads to sub-lethal consequences such as loss of body mass and reproductive failure (Conradie et al. 2019). Unfortunately, studies that have measured the long-term response to heat in tropical species are few. Experimental data shows that some lowland and montane tropical birds can endure several days per month at Ta above the local maximum Ta of their habitats, with no apparent effects on body mass (Cox 1961; Lasiewski et al. 1967). In fact, 13 African woodland savannah birds live with Tb that reach up to 45ºC–47ºC during the dry season in their natural habitat (Nilsson et al. 2016). The large majority of information, however, comes from metabolic experiments lasting a few hours. Whether from open or forested lowland and montane habitats, species exhibited only mild hyperthermia when exposed to Ta above 40ºC (Lasiewski et al. 1970; Schuchmann and Schmidt-Marloh 1979a; Schuchmann and Schmidt-Marloh 1979b; Bartholomew et al. 1983; Marshall & Prinzinger 1991), with the highest Tb reaching 47ºC in Panamanian variable seedeaters *Sporophila corvina* (Weathers 1997). On the other hand, some species appeared to be sensitive to heat when becoming hyperthermic after exposure to Ta of just 32ºC (Prinzinger et al. 1989) or failed to survive Ta of 45ºC (Weathers 1977). However, in both cases, uncontrolled humidity inside the chamber where metabolic measurements were taken may have interfered with heat dissipation (Weathers 1977; Prinzinger et al. 1989). In sum, several ecologically diverse tropical lowland birds have been shown to endure acute exposure to high heat. In fact, not only are current Ta around the UCL of many species – in some cases even below – but the projected warming Ta will most likely stay far from eliciting lethal hyperthermia (Pollock et al. 2021). Nevertheless, the large void of information on the response to chronic exposure constitutes a source of uncertainty regarding the long-term capacity of tropical birds to withstand gradual warming.

Finally, thermophilization of bird communities could be triggered by thermal physiology when species vulnerable to deteriorating conditions in their natural habitats emigrate while other species that can tolerate those conditions settle in. For instance, when warming couples with decreasing availability of water sources and cool-adapted species are replaced by warm-adapted species in the hot and humid lowlands (Curtis et al. 2021). Care should be taken, though, to consider when warming is promoting compositional changes to the habitat vegetation that result in turnover of the associated bird communities (Sales et al. 2020; Araújo et al. 2021). In such cases, physiological vulnerability in birds might be erroneously concluded. Thus, whenever thermophilization is suspected, studies should also explore potential changes to habitat associations for the bird species involved.

Along elevational gradients, montane birds are expected to be less tolerant to high Ta than their lowland counterparts. Unfortunately, no study has yet compared the tolerance of heat in tropical bird communities along mountain slopes. The closest examples show differences in the basal metabolic rate (BMR) of >250 species spanning a ~3km elevation gradient in the Andes and lower Tb in highland birds (Londoño et al. 2015, 2017). Spatial differences in heat tolerance could also be measured in horizontal scales at different elevations, between forest and open area bird species. In a study involving 16 ecologically-diverse lowland passerines, the species that foraged exposed to direct sun radiation appeared to possess lower metabolic expenditure (Hails 1983). In turn, no metabolic differences were found between montane open-habitat and forest sunbirds (Nectariniidae) with no further associations between Tb and habitat choice (Seavy 2006). Given that BMR can only partially explain flexibility in thermal tolerance, more data on EWL and Tb are urgently needed for species along diverse ecological and elevational gradients.

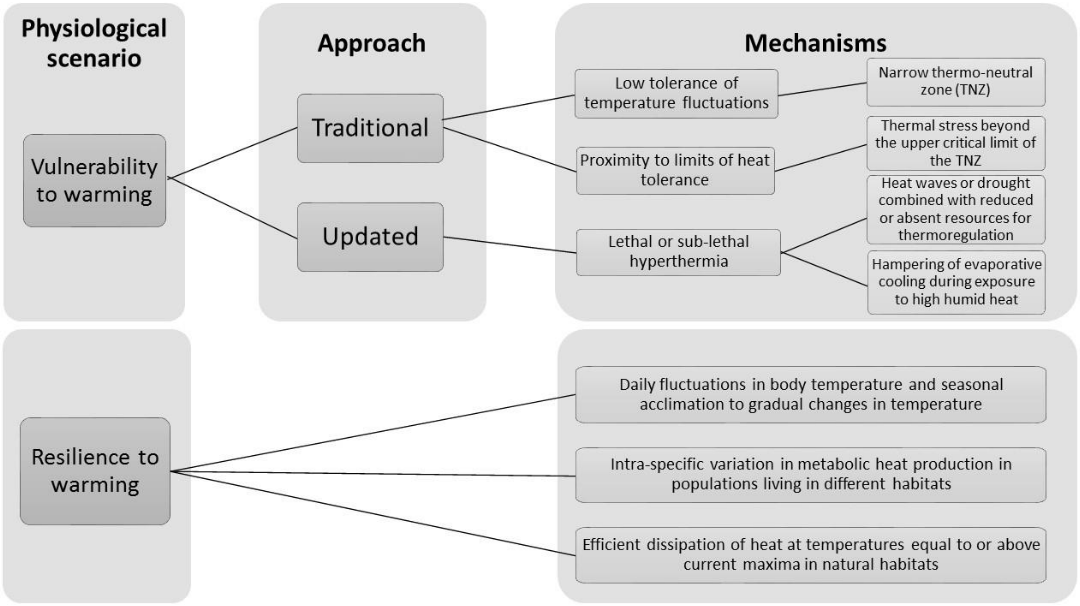


Figure 1. Physiological mechanisms of vulnerability and resilience to warming in tropical birds. The **traditional approach** refers to the assumptions commonly used to describe vulnerability to warming in tropical biotas in general whereas the **updated approach** is based on the literature analysed in this paper involving tropical birds.

What physiological mechanisms can help tropical birds cope with warming?
Analysing the variability of thermoregulatory mechanisms is a first step towards understanding avian sensitivity to warming. Intra-specific research in temperate birds has revealed not only short- and long-term seasonal variation in BMR and evaporative water loss (EWL) (Tieleman et al 2003; Soobramoney et al. 2003; McKechnie et al. 2007; Thompson et al. 2017) but also, and most importantly, that cooling capacity and heat tolerance can vary in proportion to the severity of variation in Ta (Noakes et al. 2016).

Thermoregulatory traits of birds are often considered invariable in vulnerability assessments (e.g. “thermal danger” = future maximum Ta > current UCL; Khaliq et al. 2014). Yet, temporal variation of the UCL in tropical birds highlight their potential for acclimatization and adaptation (Pollock et al. 2019). Even better than estimating thermal safety margins based on the UCL, is to analyse how much heat the birds can tolerate before hyperthermia results in physical damage (Mitchell et al. 2018; Pollock et al. 2021). Indeed, the variation in the capacity to dissipate heat or tolerate hyperthermia at high Ta would provide a clearer picture of the resilience of tropical birds against warming.

Intra-specific variation in birds that inhabit both hot and cool environments can illustrate the capacity of populations of the same species to adapt to different local thermal conditions (Figure 1). In this context, the variation in BMR is relevant because endogenous heat generated by metabolic activity should only make a small contribution to the total heat load, especially at high Ta. Unfortunately, there is a large knowledge gap in intra-specific studies for tropical species. In perhaps the only case, BMR measurements of Puerto Rican tody *Todus mexicanus* individuals from a lowland hot and xeric habitat were lower than for individuals that lived in montane humid forests (Merola-Zwartjes & Ligon 2000). Although Oniki (1975) recorded higher cloacal Tb in xeric-habitat individuals, the Tb measurements reported by Merola-Zwartjes & Ligon

(2000) did not differ between both regions and, thus, no connection could be established between Tb, BMR and habitat. However, the generally low Tb observed in both studies (~37 ºC) seems to protect this species from becoming hyperthermic in either xeric or humid environments (Oniki 1975; Merola-Zwartjes & Ligon 2000). Intra-specific variation in physiological parameters can thus give an idea of how populations of the same species may tolerate warming in different parts of their distribution.

Tropical xeric birds are adapted to endure heat in their habitats. For instance, some lark species (Alaudidae) respond to increasing aridity along their distributions with lower phylogeny-independent rates of EWL, suggestive of a plastic response among species (Tieleman et al. 2002). Yet, how likely are such species to tolerate Ta even higher than the ones currently experienced across their distributions? Some tropical xeric species that frequently utilize surface water can tolerate experimental Ta above 45ºC (similar to the maximum Ta of the study areas at the time of the experiments) by increasing EWL and dissipating all metabolic and exogenous heat (Dawson & Bennett 1973; Withers & Williams 1990). A similar response to high heat was found in a species that relies on succulent vegetation for water in dry ecosystems (Ehlers & Morton 1982). In all of these cases, hyperthermia developed and was sustained from Ta 45ºC upwards. It appears that some tropical birds from extremely hot and water-limited environments can tackle high Ta with efficient heat dissipation and body water conservation strategies, but they may still be sensitive to heat waves and drought as it might push them beyond their tolerance limits.

Heat stress in tropical birds has been measured mostly in species from lowland habitats. Less is known about montane species. Metabolic measurements of three tropical highland hummingbirds (Trochilidae) showed that at Ta of 36ºC, which is well above the local maxima of their habitats, Tb was maintained at normothermic levels (Lasiewski et al. 1967; Wolf & Hainsworth 1972). Presumably, such Ta would likely be encountered by these hummingbirds in the lower margins of their highland distributions (e.g. at ~2000 m) and would certainly be tolerated. Other hummingbird species, from middle-elevations and lower, experienced mild hyperthermia when exposed to Ta of 33ºC–35ºC (Schuchmann and Schmidt-Marloh 1979a; Schuchmann and Schmidt-Marloh 1979b). Evidently, more studies are needed to better understand the physiological vulnerability of montane, and especially highland, species to warming.

Humidity and avian thermoregulation in the Tropics

Air moisture is a relevant factor in the avian thermoregulatory response to heat. For example, humidity along with Ta can directly affect Tb regulation in birds (Gardner et al. 2016). However, the combined effects of humidity and heat have not been as exhaustively studied as the impacts of Ta alone (i.e. dry heat; Rogers et al. 2021). Humid heat can severely hamper the efficacy of evaporative cooling in endotherms (Buzan & Huber 2020) when the water vapour pressure in the surrounding air exceeds that of the body surfaces from which water is used to dissipate heat at high Ta (Boyles et al. 2011). Birds that mainly loose water through their skin seem to be more affected than those which dissipate heat through the respiratory tract (e.g. by panting; Gerson et al. 2014). Moreover, exposure to high humid heat could have a generalized effect across avian taxa of generating more metabolic heat than can be lost through evaporative cooling (van Dyk et al. 2019). Unfortunately, physiological studies that examine the response of tropical birds to concomitant gradients of Ta and humidity are rare. Lasiewski et al. (1967) recorded a steady decrease in EWL in the highland giant hummingbird *Patagona gigas* across an experimental range of relative humidity reaching 90% at Ta of 25ºC. More recently, Londoño et al. (2017) found that highland birds from the Peruvian Andes were able to tolerate the 33ºC Ta typical of the hot and humid lowland rainforest; however, the experimental relative humidity reached a maximum of only 45% during metabolic trials.

Because the combination of high humidity and high heat is more prevalent in the Tropics than in other climatic zones, tropical birds might frequently resort to dissipating heat convectively via facultative hyperthermia instead (Gardner et al. 2016; van Dyk et al. 2019). In lowland areas with high dew points, facultative hyperthermia may overcome the limitations of the diminished scope for evaporative dissipation of heat loads (Weathers 1997). This strategy can allow tropical rainforest birds to remain active (e.g. foraging or flying) when exposed to intense sun radiation (Weathers 1977). Non-evaporative heat dissipation through body structures is an effective thermo-tolerance mechanism to survive in tropical hot-humid habitats. For instance, the bill plays a key role in the adaptive thermoregulatory response of birds (Tattersall et al. 2017). Large-beaked species, such as toucans (Ramphastidae) and hornbills (Bucerotidae), dissipate ~20–60% of total body heat through the bill (Tattersall et al. 2009; van de Ven et al. 2016). Notably, the positive association between bill size and humidity appears to be phylogenetically independent and more likely to be determined by environmental conditions (Gardner et al. 2016). For example, larger bills have been measured in individuals of temperate and migratory passerines that live in water-limited, humid and hot habitats (Greenberg et al. 2012; Luther & Greenberg 2014). Finally, other avian body structures can work for the same thermoregulatory purpose. For example, southern cassowaries (*Casuarius casuarius*) dissipate more heat at high Ta through their head casques than through their bills (Eastick et al. 2019).

Tropical birds show adaptations to thrive in hot and humid habitats but virtually nothing is known about their potential response to joint variations in humidity and Ta. On one hand, while non-evaporative heat loss can be highly advantageous in this context, there might still be shortcomings. For example, the thermoregulatory advantage of larger bills in 36 Australian passerines faded in highly humid sites that also experienced very high maximum temperatures during the summer (e.g. above 40ºC; Gardner et al. (2016). At the same time, EWL in Australian budgerigars (*Melopsittacus undulatus*) can remain constant along an experimental gradient of water vapour pressure at Ta reaching 30ºC (Eto et al. 2017). Undoubtedly, more research is needed to improve our understanding of how the combined effects of heat and humidity can affect thermoregulation in tropical birds.

Microclimate, land-use changes and thermoregulation

The combination of habitat loss and climatic stress may conduce to elevated chances of biotic attrition and changes in elevational distributions (Guo et al. 2018). The loss of natural habitat cover creates a thermal disequilibrium in which microclimate Ta increases, influencing the responses of biotic communities (Zellwegger et al. 2020). For instance, while conversion to agriculture can diminish total abundance in avian communities, warming can alter species-specific abundances because of differences in heat tolerance (Bowler et al. 2018). Even if species manage to survive habitat conversion not only would they experience higher levels of local warming but further habitat loss may result in heat waves and drought challenging their thermal limits (Senior et al. 2017). This scenario of high vulnerability might apply to tropical birds that are partially or completely resilient to deforestation – e.g, those that manage to survive in hot and dry lowland regions dominated by intensive agriculture (Frishkoff et al. 2016). Montane birds that survive in intensively cultivated lands do not seem to be as severely affected from exposure to current disrupted microsite temperatures, but may be physiologically challenged by warming in the upcoming decades (Monge et al. 2022). Yet, what could the outcome be for species associated with the forest interior?

The "microclimate hypothesis" proposes that tropical birds choose cool, moist and dark microsites within forests and that changes to these conditions bring physiological vulnerability (Patten & Smith-Patten 2012). This hypothesis was formulated to explain why terrestrial and understory insectivores are particularly vulnerable to the loss of tropical forests, given that clearing and fragmentation create bright, warm and dry forest edges (Pollock et al. 2015; Patten & Smith-Patten 2012; Jirinec et al. 2022). A recent study that quantified the light and thermal niches of understory Amazon rainforest birds, found that species indeed selected dark, cool microsites (Jirinec et al. 2022). However, exposure to midday Ta of 34–36ºC in tree gaps caused variation in Tb among species, averaging ~41ºC but surpassing 43ºC in some cases (Jirinec et al. 2022). The maximum values could be interpreted as mild hyperthermia, plausibly resulting from a combined exposure to heat and humidity. Yet, this was the condition in tree gaps at midday, meaning that the species could move to close-canopy sites away from the gaps during those hottest hours, especially considering that large natural gaps in the Amazon forest can be <1 ha in area and total gap area be <2% of the entire forest tract (Hunter et al. 2015). Moreover, Ta and light intensity are often correlated (i.e. brighter sites are also warmer). If this is the case, then the species may not be necessarily selecting cool sites, but dimmer sites which turn out to be cool sites where solar radiation is low. In support, eye size tends to be large in tropical forest understory birds conferring them high optical resolution in the dark but increasing their susceptibility to light (Ausprey 2021). Indeed, unravelling the degree of thermal stress, if any, of forest-dependent birds inside tropical rainforests is a pending research avenue. More urgent is to investigate their physiological response during exposure to conditions at the forest edges, where the most drastic microclimatic changes take place.

Finally, a series of recent declines of terrestrial and understory insectivores and whole-community turnover inside undisturbed tropical forests have also been observed but, while intuitively linked to climate change, the proximate causes remain unknown (Blake & Loiselle 2015; Curtis et al. 2021; Stouffer et al. 2021; Pollock et al. 2022). The influence of negative indirect effects (e.g. variations in resource availability) offer a plausible explanation for these patterns (Lister & García 2018; Neate-Clegg et al. 2020), especially if those resources are involved in maintaining effective thermoregulation when climatic conditions harshen. For instance, the lack of permanent water sources coupled with the intensity of the dry season could have fuelled the disappearance of rainforest insectivores in an isolated lowland rainforest in Panama (Curtis et al. 2021). In this study region, a >30-year trend in longer dry seasons also negatively affected recruitment and population growth rates in 15 bird species (Brawn et al. 2017). Hopefully, more work would help to unravel if, when and how thermoregulation is related to these puzzling trends.

Knowledge gaps and future research directions

There is a wealth of quantitative information on the thermal tolerance of many tropical bird species. This empirical data allowed us to assess whether the physiological response of birds matched the assumptions of thermal vulnerability to warming, thought to underlie rearrangements in tropical biotic communities. In essence, a narrow thermal tolerance and a proximity to thermal limits does not appear to be the prevailing pattern in tropical birds, not even for high-elevation species which are also alarmingly underrepresented in studies. The observed responses, from the individual to the community level, may result from synergies between land-use change and microclimate variation or from indirect effects of climate change on natural habitats and key resources. Nevertheless, there are still unaddressed topics which limit our knowledge about potential sources of thermal sensitivity (summarized in Table 1).

First and foremost, most studies have focused on the BMR and the TNZ. For analyses of vulnerability or flexibility to climate change to be complete, a close examination of the abilities for heat dissipation is a requirement. Ideally, more data on the long-term response should be produced because chronic exposure to heat can impair vital functions over time when birds become unable to dissipate heat efficiently (Conradie et al. 2019). Thus, future studies should consider a careful selection of key parameters to measure vulnerability to warming and how these react to seasonal climatic variation and anomalies. Of such, the EWL and the CT_{max} have informed assessments of the probability of extirpation and survival in sub-tropical birds that inhabit arid zones in which Ta variation has intensified as a consequence of climate change (Albright et al. 2017; Riddell et al. 2019). In the Tropics, humidity is an influencing factor for avian thermoregulation but it is also highly variable, being dependant on patterns of precipitation (Chadwick et al. 2016). Changes in rainfall could be particularly problematic to small tropical birds given that their reliance on passive heat dissipation could put them at risk during episodes of very high humid heat (Gardner et al. 2016; Gerson et al. 2019). Researchers might analyse the combinations of humidity and Ta that severely hamper effective heat dissipation and are detrimental to survival, to determine species-specific degrees of vulnerability. Additionally, more intra-specific studies of species that inhabit environmental gradients (e.g. Ta, precipitation, aridity) could allow the identification of populations more vulnerable to warming as well as physiological features which could make them more resilient (Tieleman et al. 2002; Cavieres & Sabat 2008). Likewise, analysing plastic responses to heat stress of populations along elevational gradients would provide greater insights into their flexibility to warming, especially of those at middle and high elevations.

Finally, we would like to underscore the relevance of considering the human disturbance of natural habitats as the leading cause of vulnerability for birds in the tropical regions (Caro et al. 2022). Tropical birds have long been severely impacted by deforestation, with long-term abundance declines of terrestrial and understory insectivores of up to 95 % in isolated forest fragments in the Amazon region (Stouffer et al. 2006). Unfortunately, recent estimations of deforestation across the Tropics are alarming. Rapid clearing and degradation has resulted in great losses of lowland and upper montane forests in Papua New Guinea (Shearman et al. 2009), of African rainforest (Ernst et al. 2013), dry forest and woodlands (Bodart et al. 2013) and of rainforest in the Amazon, largely occurring during periods of severe drought (Bullock et al. 2020). Tropical birds are well adapted to the abiotic conditions of their natural habitats, but the changes in land use disrupt this balance. In fact, the combination of habitat alterations and climatic variations can drive patterns of extinction and colonization shifts in tropical birds (Beale et al. 2013). Therefore, we believe that the key areas that need to be assessed in order to determine the physiological vulnerability of tropical birds to warming are those directly affected by human activities.

Table 1. Knowledge gaps that hinder understanding of the physiological response of tropical birds to warming and suggested lines of research to tackle those gaps. The column with example references contain a sample of studies, mostly carried out on birds from extra-tropical regions, that can help to guide research avenues in the Tropics.

Knowledge gaps	Suggested lines of research	Example references
More data on EWL and Tb	Move beyond solely analysing BMR, the TNZ and its limits and assess cooling capacities through the quantification of EWL, heat tolerance limits and resistance of hyperthermia. Identify areas that challenge effective heat dissipation and increase the risk of lethal hyperthermia, resulting in abundance declines and local extinctions.	Cunningham et al. (2013); Albright et al. (2017); Conradie et al. (2020); Riddell et al. (2019)
Long-term response to sustained levels of warming	Analyse the physiological effects of sustained heat along with survival estimates, changes in body mass, risk of dehydration over consecutive days, limits to cognitive and motor abilities relevant for survival, among others.	Thompson et al. (2015); Conradie et al. (2019); Danner et al. (2021)
Assess thermal tolerance along mountain slopes	Intra- and inter-specific comparisons of heat tolerance at different zones along elevational gradients.	Soobramoney et al. (2003); Thompson et al. (2017)
Direct or indirect drivers of thermophilization	Consider assessing the directional shifts in plant community composition and changes to habitat structure that promote turnovers towards warm-adapted plants and possible cascading effects on bird communities.	Fadrique et al. (2018) and Esquivel-Muelbert et al. (2018) evidenced thermophilization shifts of Andean and Amazonian forest plant communities, respectively
The role of humidity in thermoregulation during hot days	Quantify heat dissipation at joint gradients of air humidity and temperature above Tb and examine morphological adaptations between populations along ecological gradients to tackle elevated humid heat.	Greenberg et al. (2012); Gerson et al. (2014); Luther & Greenberg (2014); Gardner et al. (2016) identified combinations of humidity and Ta that increased

Knowledge gaps	Suggested lines of research	Example references
		vulnerability for tropical Australian passerines
Interactive effect of land-use conversion on microclimates	Measure heat tolerance across treatments or gradients of human disturbance along with microclimate variables.	Monge et al. (2022) measured the physiological response to heat and predicted consequences of exposure to maximum microsite temperatures on tropical birds in forest, low-, and high-intensity agriculture
Physiological response of declining forest-interior species	Test capacity for evaporative cooling during acute and chronic exposure to heat, especially of understory insectivores. Intra- and inter-specific analysis including the forest interior as well as forest edges.	

Conclusions

We conclude that there is little empirical evidence in support of the assumption that tropical birds have particularly narrow thermal tolerances. By contrast, based on our literature review, we propose that many tropical birds are resilient enough to tolerate thermal variation within the range of predicted future levels of warming. Thus, we concur with Pollock et al. (2021) that tropical birds are no more physiologically threatened by warming in the short-term than birds at other latitudes. Most likely, the hotspots of direct avian physiological vulnerability reside in arid regions outside the Tropics [e.g. southern Africa (Conradie et al. 2019); Australia (McKechnie et al. 2012); North American southwest (Albright et al. 2017)]. However, this does not mean that tropical birds are physiologically insensitive to warming in general. An increase of 5 ºC, as in worst-case scenarios, could prove challenging to birds from open areas who rely on Tb–Ta gradients for passive heat dissipation, as this strategy would demand higher levels of hyperthermia. An equally vulnerable group are birds from xeric habitats if water sources become absent or reduced during heat waves. Also, the consistent changes in rainfall regimes, which can produce more intense wet and dry seasons (Chadwick et al. 2015; Brawn et al. 2016), have the potential to alter the frequency of stronger humid-heat events that have proven to be detrimental to small songbirds (Gardner et al. 2016). Climate change is the world's greatest concern at the scientific and public-opinion level but this has taken the focus away from other, more imminent, threats to biodiversity such as anthropogenic habitat loss and degradation (Caro et al. 2021). In fact, land-use change does not only affect tropical bird diversity directly, but may reinforce climate-driven threats by altering the microclimate birds are exposed to (Monge et al. 2022). Therefore, adaptive measures such as protecting vast areas covered by forest (Stouffer et al. 2011), especially along ecological gradients (Brodie et al. 2012) or, alternatively, improving land management strategies (Oliver & Morecroft 2014) are the most promising approaches to safeguard the diversity of tropical birds.

Acknowledgements

This work was funded by the Costa Rican Ministry of Science and Technology (Nº MICITT-PINN-CON-2-1-4-17-1-008) and by the Faculty of Life Sciences of the University of Vienna.

References

Albright TP, Mutiibwa D, Gerson AR, Smith EK, Talbot WA, O'Neill JJ, et al. 2017. Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. Proc. Natl. Acad. Sci. 114:2283–2288. doi:10.1073/pnas.1613625114.

Angilletta MJJr, Cooper BS, Schuler MS, Boyles JG. 2010. The evolution of thermal physiology in endotherms. Front. Biosci. 2:861–881. doi:10.2741/e148.

Araújo I, Marimon BS, Scalon MC, Fauset S, Junior BHM. 2021. Trees at the Amazonia-Cerrado transition are approaching high temperature thresholds. Environ. Res. Lett. 16:034047. doi:10.1088/1748-9326/abe3b9.

Ausprey IJ. 2021. Adaptations to light contribute to the ecological niches and evolution of the terrestrial avifauna. Proc. R. Soc. B 288:20210853. doi:10.1098/rspb.2021.0853.

Bartholomew GA, Vleck CM, Bucher TL. 1983. Energy metabolism and nocturnal hypothermia in two tropical passerine frugivores, *Manacus vitellinus* and *Pipra mentalis*. Physiological Zoology 56:370–379.

Bathiany S, Dakos V, Scheffer M, Lenton TM. 2018. Climate models predict increasing temperature variability in poor countries. Sci. Adv. 4:eaar5809.

Beale CM, Baker NE, Brewer MJ, Lennon JJ. 2013. Protected area networks and savannah bird biodiversity in the face of climate change and land degradation. Ecol. Lett. 16:1061–1068. doi:10.1111/ele.12139.

Bennett AC, Dargie GC, Cuni-Sanchez A, Mukendi JT, Hubau W, Mukinzi JM, et al. 2021. Resistance of African tropical forests to an extreme climate anomaly. Proc. Natl. Acad. Sci. 21:e2003169118.

Blake JG, Loiselle BA. 2015. Enigmatic declines in bird numbers in lowland forest of eastern Ecuador may be a consequence of climate change. PeerJ 3:e1177. doi:10.7717/peerj.1177.

Bodart C, Brink AB, Donnay F, Lupi A, Mayaux P, Achard F. 2013. Continental estimates of forest cover and forest cover changes in the dry ecosystems of Africa between 1990 and 2000. J. Biogeogr. 40:1036-1047. doi:10.1111/jbi.12084.

Bosque C, Pacheco MA, Siegel RB. 1999. Maintenance energy costs of two partially folivorous tropical passerines. Auk 116:246–252.

Bowler DE, Heldbjerg H, Fox AD, O'Hara RB, Böhning-Gaese K. 2018. Disentangling the effects of multiple environmental drivers on population changes within communities. J. Anim. Ecol. 87:1034–1045. doi:10.1111/1365-2656.12829.

Boyles JG, Seebacher F, Smit B, McKechnie AE. 2011. Adaptive thermoregulation in endotherms may alter responses to climate change. Integr. Comp. Biol. 51:676–690.

Brawn JD, Benson TJ, Stager M, Sly ND, Tarwater CE. 2017. Impacts of changing rainfall regime on the demography of tropical birds. Nat. Clim. Chang. 7:133–136. doi:10.1038/nclimate3183.

Brodie J, Post E, Laurance WF. 2012. Climate change and tropical biodiversity: a new focus. Trends in ecology & evolution, 27:145–150. doi:10.1016/j.tree.2011.09.008.

Bucher TL. 1981. Oxygen consumption, ventilation and respiratory heat loss in a parrot, *Bolborhynchus lineola*, in relation to ambient temperature. J. Comp. Physio. B 142:479–488.

Bullock EL, Woodcock CE, Souza C, Olofsson P. 2020. Satellite-based estimates reveal widespread forest degradation in the Amazon. Glob. Change Biol. 26:2956– 2969. doi:10.1111/gcb.15029.

Burner RC, Styring AR, Rahman MA, Sheldon FH. 2019. Occupancy patterns and upper range limits of lowland Bornean birds along an elevational gradient. J. Biogeogr. 46:2583– 2596. doi:10.1111/jbi.13691.

Buzan JR, Huber M. 2020. Moist heat stress on a hotter Earth. Ann. Rev. Earth and Planet. Sci. 48:623–655.

Byrne MP. 2021. Amplified warming of extreme temperatures over tropical land. Nat. Geosci. 14:837–841. doi:10.1038/s41561-021-00828-8.

Cahill AE, Aiello-Lammens ME, Fisher-Reid MC, Hua X, Karanewsky CJ, Yeong Ryu H, et al.. 2013. How does climate change cause extinction? Proc. R. Soc. B 280:20121890. doi:10.1098/rspb.2012.1890.

Campos-Cerqueira M, Arendt WJ, Wunderle JM, Aide TM. 2017. Have bird distributions shifted along an elevational gradient on a tropical mountain? Ecol. Evol. 7:9914–9924. doi:10.1002/ece3.3520.

Castro G, Carey C, Whittembury J, Monge C. 1985. Comparative responses of sea level and montane rufous-collared sparrows, *Zonotrichia capensis*, to hypoxia and cold Comp. Biochem. Physiol. A 82:847-850.

Caro T, Rowe Z, Berger J, Wholey P, Dobson A. 2022. An inconvenient misconception: Climate change is not the principal driver of biodiversity loss. Conserv. Lett. 15:e12868. doi:10.1111/conl.12868.

Cavieres G, Sabat P. 2008. Geographic variation in the response to thermal acclimation in rufous-collared sparrows: are physiological flexibility and environmental heterogeneity correlated? Funct. Ecol. 22:509–515. doi:10.1111/j.1365-2435.2008.01382.x.

Chadwick R, Good P, Martin G, Rowell DP. 2016. Large rainfall changes consistently projected over substantial areas of tropical land. Nat. Clim. Change 6:177–181. doi:10.1038/nclimate2805.

Cheke RA. 1970. Temperature rhythms in African montane sunbirds. Ibis 113:500–506. doi:10.1111/j.1474-919X.1971.tb05184.x.

Colwell RK, Brehm G, Cardelús CL, Gilman AC, Longino JT. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the Wet Tropics. Science 322:258– 261. doi:10.1126/science.1162547.

Conradie SR, Woodborne SM, Cunningham SJ, McKechnie AE. 2019. Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. Proc. Natl. Acad. Sci. 116:14065–14070.

Conradie SR, Woodborne SM, Wolf BO, Pessato A, Mariette MM, McKechnie AE. 2020. Avian mortality risk during heat waves will increase greatly in arid Australia during the 21st century. Conservation Physiology 8: coaa048.

Cox GW. 1961. The relation of energy requirements of tropical finches to distribution and migration. Ecology 42:253–266.

Cunningham SJ, Martin RO, Hojem CL, Hockey PAR. 2013. Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly-warming arid savanna: a study of common fiscals. PLoS ONE 8:e74613. doi :10.1371/journal.pone.0074613.

Curtis JR, Robinson WD, Rompré G, Moore RP, McCune B. 2021. Erosion of tropical bird diversity over a century is influenced by abundance, diet and subtle climatic tolerances. Sci. Rep. 11:10045. doi:10.1038/s41598-021-89496-7.

Czenze ZJ, Kemp R, van Jaarsveld B, Freeman MT, Smit B, Wolf BO, et al. 2020. Regularly drinking desert birds have greater evaporative cooling capacity and higher heat tolerance limits than non-drinking species. Funct. Ecol. 34:1589–1600. doi:10.1111/1365-2435.13573.

Danner RM, Coomes CM, Derryberry EP. 2021. Simulated heat waves reduce cognitive and motor performance of an endotherm. Ecol. Evol. 11:2261–2272. doi:10.1002/ece3.7194.

Dawson WR. 1982. Evaporative losses of water by birds. Comp. Biochem. Physiol. A 71:495–509. doi:10.1016/0300-9629(82)90198-0.

Dawson WR, Bennett AF. 1973. Roles of metabolic level and temperature regulation in the adjustment of western plumed pigeons (*Lophophaps ferruginea*) to desert conditions. Comp. Biochem. Physiol. A 44:249–266.

Dominguez C. Magaña V. 2018. The role of tropical cyclones in precipitation over the tropical and subtropical North America. Front. Earth Sci. 6:19. doi:10.3389/feart.2018.00019.

Du Plessis KL, Martin RO, Hockey P, Cunningham SJ, Ridley AR. 2012. The costs of keeping cool in a warming world: Implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. Glob. Change Biol. 18:3063–3070.

Dulle HI, Ferger SW, Cordeiro NJ, Howell KM, Schleuning M, Böhning-Gaese K, et al. 2016. Changes in abundances of forest understorey birds on Africa's highest mountain suggest subtle effects of climate change. Divers. Distrib. 22:288–299.

Eastick DL, Tattersall GJ, Watson SJ, Lesku JA, Robert KA. 2019. Cassowary casques act as thermal windows. Sci. Rep. 9:1966. doi:10.1038/s41598-019-38780-8.

Ehlers R, Morton ML. 1982. Metabolic rate and evaporative water loss in the least seed-snipe, *Thinocorus rumicivorus*. Comp. Biochem. Physiol. A 73:233–235.

Engelbrecht F, Adegoke J, Bopape M-J, Naidoo M, Garland R, Thatcher M, et al. 2015. Projections of rapidly rising surface temperatures over Africa under low mitigation. Environ. Res. Lett. 10:085004.

Ernst C, Mayaux P, Verhegghen A, Bodart C, Christophe M, Defourny P. 2013. National forest cover change in Congo Basin: deforestation, reforestation, degradation and regeneration for the years 1990, 2000 and 2005. Glob. Change Biol. 19:1173–1187. doi:10.1111/gcb.12092

Esquivel-Muelbert A, Baker TR, Dexter KG, Lewis SL, Brienen RJW, Feldpausch TR, et al. 2019. Compositional response of Amazon forests to climate change. Glob. Change Biol. 25:39–56. doi:10.1111/gcb.14413.

Eto EC, Withers PC, Cooper CE. 2017. Can birds do it too? Evidence for convergence in evaporative water loss regulation for birds and mammals. Proc. R. Soc. B 284:20171478.
doi:10.1098/rspb.2017.1478.

Fadrique B, Báez S, Duque Á, Malizia A, Blundo C, Carilla J, et al. 2018. Widespread but heterogeneous responses of Andean forests to climate change. Nature 564:207–212. doi:10.1038/s41586-018-0715-9.

Feeley KJ, Silman MR. 2010. Biotic attrition from tropical forests correcting for truncated temperature niches. Glob. Change Biol. 16:1830–1836. doi:10.1111/j.1365-2486.2009.02085.x.

Foden WB, Butchart SHM, Stuart SN, Vié J-C, Akçakaya HR, Angulo A, et al. 2013. Identifying the world’s most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. PLoS ONE 8:e65427. doi:10.1371/journal.pone.0065427.

Forero-Medina G, Terborgh J, Socolar SJ, Pimm SL. 2011. Elevational ranges of birds on a tropical montane gradient lag behind warming temperatures. PLoS ONE 6:e28535. doi:10.1371/journal.pone.0028535.

Freeman BG, Class-Freeman AM. 2014 Rapid upslope shifts in New Guinean birds illustrate strong distributional responses of tropical montane species to global warming. Proc. Natl. Acad. Sci. 111:4490–4494. doi:10.1073/pnas.1318190111.

Freeman BG, Beehler BM. 2018. Limited support for the “abundant centre” hypothesis in birds along a tropical elevational gradient: implications for the fate of lowland tropical species in a warmer future. J. Biogeogr. 45:1884–1895. doi:10.1111/jbi.13370.

Freeman BG, Scholer MN, Ruiz-Gutiérrez V, Fitzpatrick JW. 2018. Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. Proc. Natl. Acad. Sci. U.S.A. 115:11982–11987. doi:10.1073/pnas.1804224115.

Freeman BG, Song Y, Feeley KJ, Zhu K. 2021. Montane species track rising temperatures better in the tropics than in the temperate zone. Ecol. Lett. 24:1697–1708. doi:10.1111/ele.13762.

Freeman B, Sunnarborg J, Townsend-Peterson A. 2019. Effects of climate change on the distributional potential of three range-restricted West African bird species. Condor 121:duz012. doi:10.1093/condor/duz012.

Freeman MT, Czenze ZJ, Schoeman K, McKechnie AE. 2020. Extreme hyperthermia tolerance in the world's most abundant wild bird. Sci. Rep. 10:13098. doi:10.1038/s41598-020-69997-7.

Frishkoff LO, Karp DS, Flanders JR, Zook J, Hadly EA, Daily GC, et al. 2016. Climate change and habitat conversion favour the same species. Ecol. Lett. 19:1081–1090. doi:10.1111/ele.12645.

Fristoe TS, Burger JR, Balk MA, Khaliq I, Hof C, Brown JH. 2015. Metabolic heat production and thermal conductance are mass-independent adaptations to thermal environment in birds and mammals. Proc. Natl. Acad. Sci. 112:15934–15939.

Fu R, Yin L, Li W, Arias PA, Dickinson RE, Huang L, et al. 2013. Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. Proc. Natl. Acad. Sci. 110:18110–18115. doi:10.1073/pnas.1302584110.

Gardner JL, Symonds MRE, Joseph L, Ikin K, Stein J, Kruuk LEB. 2016. Spatial variation in avian bill size is associated with humidity in summer among Australian passerines. Clim. Change Responses 3:3–11. doi:10.1186/s40665-016-0026-z.

Gerson AR, Smith EK, Smit B, McKechnie AE, Wolf BO. 2014. The impact of humidity on evaporative cooling in small desert birds exposed to high air temperatures. Physiol. Biochem. Zool. 87:782–795.

Gerson AR, McKechnie AE, Smit B, Whitfield MC, Smith EK, Talbot WA, et al. 2019. The functional significance of facultative hyperthermia varies with body size and phylogeny in birds. Funct. Ecol. 33:597–607. doi:10.1111/1365-2435.13274.

Greenberg R, Cadena V, Danner RM, Tattersall G. 2012. Heat loss may explain bill size differences between birds occupying different habitats. PLoS ONE 7:e40933. doi:10.1371/journal.pone.0040933.

Guo F, Lenoir J, Bonebrake TC. 2018. Land-use change interacts with climate to determine elevational species redistribution. Nat. Commun. 9:1315. doi:10.1038/s41467-018-03786-9.

Hails C. 1983. The metabolic rate of tropical birds. Condor 85:61–65. doi:10.2307/1367889.

Harris JBC, Putra DD, Gregory SD, Brook BW, Prawiradilaga DM, Sodhi NS, et al. 2014. Rapid deforestation threatens mid-elevational endemic birds but climate change is most important at higher elevations. Divers. Distrib. 20:773–785.

Hunter MO, Keller M, Morton D, Cook B, Lefsky M, Ducey M, et al. 2015. Structural dynamics of tropical moist forest gaps. PLoS ONE 10:e0132144. doi:10.1371/journal.pone.0132144.

Im E-S, Pal JS, Eltahir EAB. 2017. Deadly heat waves projected in the densely populated agricultural regions of South Asia. Sci. Adv. 3:e1603322.

Jirinec V, Rodrigues PF, Amaral BR, Stouffer PC. 2022. Light and thermal niches of ground-foraging Amazonian insectivorous birds. Ecology 103:e3645. doi:10.1002/ecy.3645.

Kendeigh SC. 1969. Energy response of birds to their thermal environment. Wilson Bull. 81:441–449.

Khaliq I, Hof C, Prinzinger R, Böhning-Gaese K, Pfenninger M. 2014. Global variation in thermal tolerances and vulnerability of endotherms to climate change. Proc. R. Soc. B 281:20141097.

Lasiewski RC, Weathers WW, Bernstein MH. 1967. Physiological responses of the giant hummingbird, *Patagona gigas*. Comp. Biochem. Physiol. 23:797–813.

Lasiewski RC, Dawson WR, Bartholomew GA. 1970. Temperature regulation in the little Papuan frogmouth, *Podargus ocellatus*. Condor 72:332–338. doi:10.2307/1366012.

Laurance WF, Useche DC, Shoo LP, Herzog SK, Kessler M, Escobar F, et al. 2011. Global warming, elevational ranges and the vulnerability of tropical biota. Biol. Conserv. 144:548–557 doi:10.1016/j.biocon.2010.10.010.

Lee J-Y, Marotzke J, Bala G, Cao L, Corti S, Dunne JP, et al. 2021. Future global climate: scenario-based projections and near term information. In: Climate change 2021: the physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, et al. (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 553–672, doi:10.1017/9781009157896.006.

Lister BC, Garcia A. 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. Proc. Natl. Acad. Sci. 115:E10397–E10406. doi:10.1073/pnas.1722477115.

Logan ML, Cox RM, Calsbeek R. 2014. Natural selection on thermal performance in a novel thermal environment. Proc. Natl. Acad. Sci. 111:14165–14169. doi:10.1073/pnas.1404885111

Londoño GA, Chappell MA, Castañeda MdR, Jankowski JE, Robinson SK. 2015. Basal metabolism in tropical birds: Latitude, altitude, and the ‘pace of life’. Funct. Ecol. 29:338–346.

Londoño GA, Chappell MA, Jankowski JE, Robinson SK. 2017. Do thermoregulatory costs limit altitude distributions of Andean forest birds? Funct. Ecol. 31:204–215.

Lowell B, Spiegelman B. 2000. Towards a molecular understanding of adaptive thermogenesis. Nature 404:652–660. doi:10.1038/35007527.

Luther D, Greenberg R. 2014. Habitat type and ambient temperature contribute to bill morphology. Ecol. Evol. 4:699–705. doi:10.1002/ece3.911.

Maldonado K, Bozinovic F, Cavieres G, Fuentes CA, Cortés A, Sabat P. 2012. Phenotypic flexibility in basal metabolic rate is associated with rainfall variability among populations of rufous-collared sparrow. Zoology, 115:128–133. doi:10.1016/j.zool.2011.09.005

Mamalakis A, Randerson JT, Yu JY, Pritchard MS, Magnusdottir G, Smyth P, et al. 2021. Zonally contrasting shifts of the tropical rain belt in response to climate change. Nat. Clim. Chang. 11:143–151. doi:10.1038/s41558-020-00963-x.

Marris E. 2007. The escalator effect. Nat. Clim. Change. 1:94–96. doi:10.1038/climate.2007.70.

Mata A. 2010. Metabolic rate and specific dynamic action of the red-legged honeycreeper, a nectar-feeding Neotropical passerine. Comp. Biochem. Phys. A 157:291–296. doi:10.1016/j.cbpa.2010.07.018.

Marschall U, Prinzinger R. 1991. Comparative ecophysiology of 5 different species of Estrildidae. J. Ornithol. 132:319–323.

Marshall DJ, Rezende EL, Baharuddin N, Choi F, Helmuth B. 2015. Thermal tolerance and climate warming sensitivity in tropical snails. Ecol. Evol. 5:5905–5919. doi:10.1002/ece3.1785.

Matthews T, Wilby RL, Murphy C. 2019. An emerging tropical cyclone–deadly heat compound hazard. Nat. Clim. Chang. 9:602–606. doi:10.1038/s41558-019-0525-6.

McKechnie AE, Wolf BO. 2019. The physiology of heat tolerance in small endotherms. Physiology 34:302–313. doi:10.1152/physi ol.00011.2019.

McKechnie AE, Chetty K, Lovegrove BG. 2007. Phenotypic flexibility in the basal metabolic rate of laughing doves: responses to short-term thermal acclimation. J. Exp. Biol. 210:97–106. doi:10.1242/jeb.02615.

McKechnie AE, Hockey PAR, Wolf BO. 2012. Feeling the heat: Australian landbirds and climate change, Emu 112:1–7. doi:10.1071/MUv112n2_ED.

McNab BK. 2013. The ecological energetics of birds in New Guinea. Bull. Fla. Mus. Nat. Hist. 52:95–159.

Merola-Zwartjes M. 1998. Metabolic rate, temperature regulation, and the energetic implications of roost nests in the bananaquit (*Coereba flaveola*). Auk 15:780–786.

Merola-Zwartjes M, Ligon J. 2000. Ecological energetics of the Puerto Rican tody: Heterothermy, torpor, and intra-island variation. Ecology 81:990–1003.

Mitchell D, Snelling EP, Hetem RS, Maloney SK, Strauss WM, Fuller A. 2018. Revisiting concepts of thermal physiology: Predicting responses of mammals to climate change. J. Anim. Ecol. 87:956–973. doi:10.1111/1365-2656.12818.

Monge O, Schulze CH, Dullinger S, Fusani L, Maggini I. 2022. Unshaded coffee imposes a heavier load on thermoregulation than shaded coffee for birds in a tropical mountainous region. Glob. Ecol. Conserv. 36:e02117. doi:10.1016/j.gecco.2022.e02117

Morrison P. 1962. Modification of body temperature by activity in Brazilian hummingbirds. Condor 64:315–323. doi:10.2307/1365371

Neate-Clegg MHC, O'Brien TG, Mulindahabi F, Şekercioğlu ÇH. 2020. A disconnect between upslope shifts and climate change in an Afrotropical bird community. Conserv. Sci. Pract. 2:e291. doi:10.1111/csp2.291.

Neate-Clegg MHC, Stuart SN, Mtui D, Şekercioğlu ÇH, Newmark WD. 2021. Afrotropical montane birds experience upslope shifts and range contractions along a fragmented elevational gradient in response to global warming. PLoS ONE 16:e0248712. doi:/10.1371/journal.pone.0248712.

Newbold T, Oppenheimer P, Etard A, Williams JJ. 2020. Tropical and Mediterranean biodiversity is disproportionately sensitive to land-use and climate change. Nat. Ecol. Evol. 4:1630–1638. doi:10.1038/s41559-020-01303-0.

Nilsson JÅ, Molokwu MN, Olsson O. 2016. Body temperature regulation in hot environments. PloS ONE 11:e0161481. doi:10.1371/journal.pone.0161481.

Noakes MJ, Wolf BO, McKechnie AE. 2016. Seasonal and geographical variation in heat tolerance and evaporative cooling capacity in a passerine bird. J. Exp. Biol 219:859–869. doi:10.1242/jeb.132001.

Oliver TH, Morecroft M.D. 2014. Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. WIREs Clim. Change 5:317–335. doi:10.1002/wcc.271.

Oniki Y. 1975. Temperatures of some Puerto Rican birds, with note of low temperatures in todies. Condor 77:344–344.

Patten MA, Smith-Patten BD. 2012. Testing the microclimate hypothesis: light environment and population trends of Neotropical birds. Biol. Conserv. 155:85–93.

Pattinson NB, Thompson ML, Griego M, Russell G, Mitchell NJ, Martin RO, et al. 2020. Heat dissipation behaviour of birds in seasonally hot arid-zones: are there global patterns? J. Avian Biol. 51. doi:10.1111/jav.02350.

Peh KS-H. 2007. Potential effects of climate change on elevational distributions of tropical birds in Southeast Asia. Condor 109:437–441. doi:10.1093/condor/109.2.437.

Perkins-Kirkpatrick SE, Gibson PB. 2017. Changes in regional heatwave characteristics as a function of increasing global temperature. Sci. Rep. 7:12256. doi:10.1038/s41598-017-12520-2.

Pollock HS, Cheviron ZA, Agin TJ, Brawn JD. 2015. Absence of microclimate selectivity in insectivorous birds of the Neotropical forest understory. Biol. Conserv. 188:116–125. doi:10.1016/j.biocon.2014.11.013.

Pollock HS, Brawn JD, Agin TJ, Cheviron ZA. 2019. Differences between temperate and tropical birds in seasonal acclimatization of thermoregulatory traits. J. Avian Biol. 50.

Pollock HS, Brawn JD, Cheviron ZA. 2021. Heat tolerances of temperate and tropical birds and their implications for susceptibility to climate warming. Funct. Ecol. 35:93–104. doi:10.1111/1365-2435.13693.

Pollock HS, Toms JD, Tarwater CE, Benson TJ, Karr JR, Brawn JD. 2022. Long-term monitoring reveals widespread and severe declines of understory birds in a protected Neotropical forest. Proc. Natl. Acad. Sci. 119:e2108731119. doi:10.1073/pnas.2108731119.

Prinzinger R, Lübben I, Schuchmann K-L. 1989. Energy metabolism and body temperature in 13 sunbird species (Nectariniidae). Comp. Biochem. Physiol. A 92:393–402.

Raymond C, Singh D, Horton R. M. 2017. Spatiotemporal patterns and synoptics of extreme wet-bulb temperature in the contiguous United States. J. Geophys. Res. 122: 13 108–13 124. doi:10.1002/2017JD027140.

Riddell EA, Iknayan KJ, Wolf BO, Sinervo B, Beissinger SR. 2019. Cooling requirements fueled the collapse of a desert bird community from climate change. Proc. Natl. Acad. Sci. 116:21609–21615. doi:10.1073/pnas.1908791116.

Rogers CDW, Ting M, Li C, Kornhuber K, Coffel ED, Horton RM, et al. 2021. Recent increases in exposure to extreme humid-heat events disproportionately affect populated regions. Geophys. Res. Lett. 48:e2021GL094183. doi:10.1029/2021GL094183.

Rosselli L, Stiles FG, Camargo PA. 2017. Changes in the avifauna in a high Andean cloud forest in Colombia over a 24-year period. J. Field Ornithol. 88:211–228.

Sales LP, Galetti M, Pires MM. 2020. Climate and land-use change will lead to a faunal "savannization" on tropical rainforests. Glob. Change Biol. 26:7036–7044. doi:10.1111/gcb.15374.

Scholander P, Hock R, Walters V, Johnson F, Irving L. 1950. Heat regulation in some arctic and tropical mammals and birds. Biol. Bull. 99:237–258.

Schuchmann K-L, Schmidt-Marloh D. 1979a. Temperature regulation in non-torpid hummingbirds. Ibis 121: 354–356.

Schuchmann K-L, Schmidt-Marloh D. 1979b. Metabolic and thermal responses to heat and cold in streamertail hummingbirds (*Trochilus polytmus* and *Trochilus scitulus*, Trochilidae). Biotropica 11:123–126.

Seavy NE. 2006. Physiological correlates of habitat association in East African sunbirds (Nectariniidae). J. Zool. 270:290–297. doi:10.1111/j.1469-7998.2006.00138.x.

Seavy NE, McNab BK. 2007. Energetics of East African pycnonotids. Biotropica 39:114–119.

Senior RA, Hill JK, González Del Pliego P, Goode LK, Edwards DP. 2017. A pantropical analysis of the impacts of forest degradation and conversion on local temperature. Ecol. Evol. 7:7897–7908. doi:10.1002/ece3.3262.

Shearman PL, Ash J, Mackey B, Bryan JE, Lokes B. 2009. Forest conversion and degradation in Papua New Guinea 1972–2002. Biotropica, 41:379–390. doi:10.1111/j.1744-7429.2009.00495.x.

Sheldon KS, Huey RB, Kaspari M, Sanders NJ. 2018. Fifty years of mountain passes: a perspective on Dan Janzen's classic article. Am. Nat. 191:553–565. doi:10.1086/697046.

Shoo LP, Williams SE, Hero J-M. 2005. Climate warming and the rainforest birds of the Australian Wet Tropics: Using abundance data as a sensitive predictor of change in total population size. Biol. Conserv. 125:335–343.

Smit B, Zietsman G, Martin RO, Cunningham SJ, McKechnie AE, Hockey PAR. 2016. Behavioural responses to heat in desert birds: Implications for predicting vulnerability to climate warming. Clim. Change Resp. 3:9.

Soobramoney S, Downs CT, Adams NJ. 2003. Physiological variability in the fiscal shrike Lanius collaris along an altitudonal gradient in South Africa J. Therm. Biol. 28:581–594.

Steiger SS, Kelley JP, Cochran WW, Wikelski M., 2009. Low metabolism and inactive lifestyle of a tropical rain forest bird investigated via heart-rate telemetry. Physiol. Biochem. Zool. 82:580–589. doi:10.1086/605336.

Stouffer PC, Bierregaard ROJ, Strong C, Lovejoy TE. 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. Conserv. Biol. 20:1212–1223. doi:10.1111/j.1523-1739.2006.00427.x.

Stouffer PC, Johnson EI, Bierregaard ROJ, Lovejoy TE. 2011. Understory bird communities in Amazonian rainforest fragments: species turnover through 25 years post-isolation in recovering landscapes. PLoS ONE 6:e20543. doi:10.1371/journal.pone.0020543

Stouffer PC, Jirinec V, Rutt CL, Bierregaard ROJ, Hernández-Palma A, Johnson EI, et al. 2021. Long-term change in the avifauna of undisturbed Amazonian rainforest: ground-foraging birds disappear and the baseline shifts. Ecol. Lett. 24:186–195. doi:10.1111/ele.13628.

Stratford JA, Robinson W. 2005. Gulliver travels to the fragmented tropics: Geographic variation in mechanisms of avian extinction. Front. Ecol. Env. 3:85–92.

Tattersall GJ, Andrade DV, Abe AS. 2009. Heat exchange from the toucan bill reveals a controllable vascular thermal radiator. Science 325:468–470.

Tattersall GJ, Arnaout B, Symonds M. 2017. The evolution of the avian bill as a thermoregulatory organ. Biol. Rev. Cambridge Phil. Soc. 92:1630–1656. doi:10.1111/brv.12299.

Tewksbury JJ, Huey RB, Deutsch CA. 2008. Putting the heat on tropical animals. Science, 320:1296–1297. doi:10.1126/science.1159328.

Thompson LJ, Brown M, Downs CT. 2015. The potential effects of climate-change-associated temperature increases on the metabolic rate of a small Afrotropical bird. J. Exp. Biol. 218:1504–1512.

Thompson LJ, Downs CT. 2017. Altitudinal variation in metabolic parameters of a small Afrotropical bird. Comp. Biochem. Physiol. 212:88–96. doi:10.1016/j.cbpa.2017.07.015.

Tieleman BI, Williams JB, Bloomer P. 2002. Adaptation of metabolism and evaporative water loss along an aridity gradient. Proc. R. Soc. B 270:207–214.

Tieleman BI, Williams JB, Buschur ME, Brown CR. 2003. Phenotypic variation of larks along an aridity gradient: are desert birds more flexible? Ecology 84:1800-1815. doi:10.1890/0012-9658(2003)084[1800:PVOLAA]2.0.CO;2.

Tizón R, Wulff JP, Peláez DV. 2014. The effect of increase in the temperature on the foraging of *Acromyrmex lobicornis* (Hymenoptera: Formicidae). Zool. Stud. 53:40. doi:10.1186/s40555-014-0040-4.

Trisos CH, Merow C, Pigot AL. 2020. The projected timing of abrupt ecological disruption from climate change. Nature 580:496–501. doi:10.1038/s41586-020-2189-9.

Tsai CF, Lee YF, Chen YH, Chen WM. 2015. Species turnover in tropical montane forest avifauna links to climate correlates. Glob. Ecol. Conserv. 3:541–552.

van de Ven TMFN, Martin RO, Vink TJF, McKechnie AE, Cunningham SJ. 2016. Regulation of heat exchange across the hornbill beak: functional similarities with toucans? PLoS ONE 11:e0154768. doi:10.1371/journal.pone.0154768.

van Dyk M, Noakes MJ, McKechnie AE. 2019. Interactions between humidity and evaporative heat dissipation in a passerine bird. J. Comp. Physiol. B. 189:299–308. https://doi.org/10.1007/s00360-019-01210-2.

von May R, Catenazzi A, Santa-Cruz R, Gutierrez AS, Moritz C, Rabosky DL. 2019. Thermal physiological traits in tropical lowland amphibians: Vulnerability to climate warming and cooling. PLoS ONE 14:e0219759. doi:10.1371/journal.pone.0219759

Weathers W. 1977. Temperature regulation in the dusky munia, *Lonchura fuscans* (Cassin) (Estrildidae). Aust. J. Zool. 25:193–199. doi:10.1071/ZO9770193.

Weathers W. 1997. Energetics and thermoregulation by small passerines of the humid, lowland tropics. Auk 114:341–353. doi:10.2307/4089237.

Weathers W. 1981. Physiological thermoregulation in heat-stressed birds: consequences of body size. Physiol. Zool. 54:345–361.

Weathers W, van Riper C. 1982. Temperature regulation in two endangered Hawaiian honeycreepers: The palila (*Psittirostra bailleui*) and the Laysan finch (*Psittirostra cantans*). Auk 99: 667–674.

Williams SE, de la Fuente A. 2021. Long-term changes in populations of rainforest birds in the Australia Wet Tropics bioregion: a climate driven biodiversity emergency. PLoS ONE 16:e0254307. doi:10.1371/journal.pone.0254307.

Withers PC, Williams JB. 1990. Metabolic and respiratory physiology of an arid-adapted Australian bird, the spinifex pigeon. Condor 92:961–969.

Wolf LL, Hainsworth FR. 1972. Environmental influence on regulated body temperature in torpid hummingbirds. Comp. Biochem. Physiol. A 41:167–173.

Woodworth BK, Norris DR, Graham BA, Kahn ZA, Mennill DJ. 2018. Hot temperatures during the dry season reduce survival of a resident tropical bird. Proc. R. Soc. B 285:20180176. doi:10.1098/rspb.2018.0176.

Zellweger F, de Frenne P, Lenoir J, Vangansbeke P, Verheyen KK, Bernhardt-Römermann M, et al. 2020. Forest microclimate dynamics drive plant responses to warming. Science, 368:772–775. doi:10.1126/science.aba6880.

Zeng X, Reeves Eyre JEJ, Dixon RD, Arevalo J. 2021. Quantifying the occurrence of record hot years through normalized warming trends. Geophys. Res. Lett. 48:e2020GL091626. doi:10.1029/2020GL091626.

Zeppetello LR, Parsons LA, Spector JT, Naylor RL, Battisti DS, Masuda YJ, Wolff NH. 2020. Large scale tropical deforestation drives extreme warming. Env. Res. Lett. 15:084012. doi:10.1088/1748-9326/ab96d2.

Zhang Y, Held I, Fueglistaler S. 2021. Projections of tropical heat stress constrained by atmospheric dynamics. Nat. Geosci. 14:133–137. doi:10.1038/s41561-021-00695-3.

Zhou L, Tian Y, Myneni R, Ciais P, Saatchi S, Liu YY, et al. 2014. Widespread decline of Congo rainforest greenness in the past decade. Nature 509:86–90. doi:10.1038/nature13265.

General conclusions

Apart from altering natural ecosystems, land use can strongly affect vertebrate diversity via the intensity of management (Semenchuk et al. 2022). This work analyzed the effects of coffee cultivation intensity on bird diversity at the community level as well as on the ability of particular species to tolerate associated local temperature regimes. In a general sense, the simplification of vegetation features in intensified farms resulted in a reduction in species richness and altered phylogenetic and functional diversity. The pervasive effect of intensification was boosted by a lessened capacity of intensified farms to buffer microclimatic maximum temperatures. In other words, coffee cultivated under intensified systems, with reduced vegetation structure and composition, offers fewer resources and less suitable habitat as well as a thermally more hostile environment for birds. Although tropical birds in general possess the capacities to endure changing temperature conditions, these capacities are put to the limit when persisting in simplified landscapes dominated by intensified agriculture.

It has been known for some decades, that the maintenance of heterogeneous vegetation cover inside diversified coffee farms bolsters bird diversity (Perfecto et al. 1996; Greenberg et al. 1997; Bakermans et al. 2012). Specific vegetation features, such as tree height, canopy cover and the diversity of trees have been positively associated with bird richness (Waltert et al. 2005; Gordon et al. 2007). The present work built on this knowledge and investigated five measures of vegetation structure and composition in relation to three dimensions of avian diversity (**Chapter 1**). The initial aim of linking specific vegetation features to these dimensions was achieved by showing that bird richness significantly increased with the amount of large trees that provided greater shade cover, while phylogenetic diversity did so with increasing numbers of crop plants. Also, bird communities tended to be more functionally clustered at sites with more large trees, which means that they shared more traits among them than would be expected at random, indicative of ecological stability at low levels of disturbance (Cooke et al. 2019).

Because tropical bird communities are structured along gradients of elevation, their response to land-use change can also show elevational patterns (Sreekar et al. 2021). Indeed, the effect of vegetation features on specific dimensions of bird diversity were not present at all elevations but occurred at defined elevation zones. For instance, the effect of large trees on functional clustering and positive effect of crop plants on phylogenetic diversity were present at middle elevations only. Taken together, these results underscore the importance of considering the impact of intensification indicators, such as vegetation features, in a broader environmental context. In other words, conservation measures developed for birds in tropical agricultural landscapes might benefit from considering the larger environmental context.

In sum, land-use change reduces the availability of suitable habitat, with subsequent declines in bird richness which then spill into a loss of functional traits and evolutionary lineages as the land use intensifies. This tunes in with the notion that habitat loss and degradation is the biggest threat for biodiversity in the Tropics (Caro et al. 2022).

To recognize the potential mechanisms involved in the loss of avian diversity in intensified agricultural landscapes is a most needed step forward to develop more effective mitigation measures. Habitat loss and degradation can lead to a non-random decline in functional traits and evolutionary lineages in tropical disturbed landscapes (Bregman et al. 2016; Luther et al. 2020). This means that some birds might be more affected than others by land-use change and they might just be functionally and phylogenetically distinct species. Besides the negative effects of habitat loss on forest-dependent birds (e.g. loss of phylogenetic lineages; Frishkoff et al. 2014; Morante-Filho et al. 2017), the increasingly hot and dry conditions of tropical deforested areas (Sales et al. 2020) could further the loss of avian diversity in a similar non-random manner. Indeed, land-use conversion alone can reduce overall bird abundance but differences in heat tolerance can drive abundance declines of specific species (Bowler et al. 2018). This opens an exciting and hitherto unexplored avenue of research; that is, how can heat tolerance determine the loss of functionally and phylogenetically distinct avian taxa in intensified agriculture.

For the time being, this work intended to unravel the capacity of tropical birds that live in diverse and intensified coffee farms to handle high levels of heat and how this capacity match the daily temperature conditions of the farms (**Chapter 2**). The focus here was on the maximum microclimatic temperatures because these significantly differed between intensified and diverse farms, while there was no significant differences between the latter and the nearest forest patch. Birds had no problem dealing with experimental temperatures that represented the thermal conditions present below that canopy of forests or those at diverse farms. Maximum temperatures in intensified farms increased to such an extent that it was predicted that birds would spend up to three times more of their time during the day cooling down their bodies through evaporation of water from their respiratory tract, than at diversified farms. However, despite this higher demand, the birds were in neither case at an immediate risk of suffering from lethal dehydration. Sub-lethal (i.e. chronic) dehydration, on the other hand, might be possible if birds fail to acquire enough water to replenish the losses, resulting in the decline of body condition and reproductive failure (Conradie et al. 2019). This might seem an unlikely scenario in the moist and cool understory of lush tropical forests or even under the canopy of trees in diversified farms but perhaps not in the most intensified farms, which are completely devoid of trees. Therefore, because many bird species can survive initial destruction and fragmentation of natural habitats, land-use change amplifies the pervasive effects of warming because these species would then have to face altered microclimatic conditions in the newly-created open, drier and hotter converted areas. If vital resources for thermoregulation, such as food items or water sources (Riddell et al. 2019), are lacking then it is likely that only the most heat-tolerant species would be able to persist in intensified coffee-dominated landscapes in the future.

Given that the study sites where the thermal tolerance experiments and measurements of microclimatic temperatures were located at ~1800 m of elevation, it was also possible to analyze the response of the four involved species in the context of their elevational distribution. In essence, tropical montane birds are thought to possess a narrow thermal tolerance, because of the narrowness of the vertical distributions (Janzen 1967; Colwell et al. 2008; Tewksbury et al. 2008). In this case, the distribution of three of the four studied species extended into the lowlands and was only slightly less broad in the fourth of them. Thus, it is likely that these species experience and tolerate temperatures close to the maximum at 1800 m in the lowest parts of their vertical distribution. What are the implications of this? Are other bird species limited to narrower vertical bands indeed less tolerant to heat? Are lowland birds more at risk from warming? Tropical birds whose distributions does not include warm areas might possess truncated thermal niches, which means that they could tolerate hot conditions in certain areas but these do not currently occur within the species' range (Freeman & Beehler 2018; Burner et al. 2019). Accordingly, tropical birds, especially those in the lowlands, might possess the physiological capacity to withstand current and future warming (Pollock et al. 2021). The review that I performed of literature about the physiological features that may explain vulnerability or resilience to warming in tropical birds, appears to point in this direction (**Chapter 3**).

There is a wealth of studies that document the responses of tropical birds to warming in terms of distribution shifts and local extinctions, but the mechanisms behind these responses are not well understood. As a very important first step, more empirical research is needed to quantify the thermal tolerance of tropical birds across ecological, elevational and land-use intensity gradients. Tropical birds possess the physiological capacities to live with the climatic conditions of their natural habitats. If resources are available and reachable, tropical birds may not be particularly threatened by warming (Pollock et al. 2021). The problem arises when the natural climatic conditions of their habitats are disrupted by land-use change. Thermoregulation would be challenged because heat waves and drought are more severe in converted lands (Sales et al. 2020). This situation, summed up to the loss of suitable habitat, might set the stage for local extinctions and distribution shifts.

A general conclusion of this thesis work is that the same measures that can mitigate the impact of agricultural use on the dimensions of avian diversity (e.g. agroforestry) could also reduce the risk that climate change poses to birds that thrive in agriculture-dominated landscapes. For instance, I found that native and crop trees, which are large and provide canopy cover, promote several aspects of avian diversity within shaded coffee farms and such features might also be crucial to maintain buffered microclimatic temperatures for birds, namely shade and a variety of food resources. Low-intensity agroforestry hence appears an appropriate means to lower the pressure that interacting land use and climate change will pose on tropical bird diversity in the future

References

Bakermans, M. H., Rodewald, A. D., Vitz, A. C., Rengifo, C., 2012. Migratory bird use of shade coffee: the role of structural and floristic features. Agroforest. Syst. 85, 85–94.

Bregman TP, Lees AC, MacGregor HE, Darski B, de Moura NG, Aleixo A, et al. 2016. Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. Proc. R. Soc. B: Biol. Sci. 283:20161289.

Bowler DE, Heldbjerg H, Fox AD, O'Hara RB, Böhning-Gaese K. 2018. Disentangling the effects of multiple environmental drivers on population changes within communities. J. Anim. Ecol. 87:1034–1045.

Burner RC, Styring AR, Rahman MA, Sheldon FH. 2019. Occupancy patterns and upper range limits of lowland Bornean birds along an elevational gradient. J. Biogeogr. 46:2583– 2596.

Caro T, Rowe Z, Berger J, Wholey P, Dobson A. 2022. An inconvenient misconception: Climate change is not the principal driver of biodiversity loss. Conserv. Lett. 15:e12868.

Cooke RSC, Bates AE, Eigenbrod F. 2019. Global trade-offs of functional redundancy and functional dispersion for birds and mammals. Global Ecol. Biogeogr 28:484–495.

Conradie SR, Woodborne SM, Cunningham SJ, McKechnie AE. 2019. Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. Proc. Natl. Acad. Sci. 116:14065–14070.

Freeman BG, Beehler BM. 2018. Limited support for the “abundant centre” hypothesis in birds along a tropical elevational gradient: implications for the fate of lowland tropical species in a warmer future. J. Biogeogr. 45:1884–1895.

Frishkoff LO, Karp DS, M'Gonigle LK, Mendenhall CD, Zook J, Kremen C, et al. 2014. Loss of avian phylogenetic diversity in neotropical agricultural systems. Science 345:1343–1346.

Greenberg, R., Bichier, P., Angon, A. C., Reitsma, R., 1997a. Bird populations in shade and sun coffee plantations in central Guatemala. Conserv. Biol. 11, 448–459.

Janzen DH. Why mountain passes are higher in the tropics. 1967. Am. Nat. 101:233–249.

Luther DA, Cooper W, Wolfe JD, Bierregaard R, Gonzalez A, Lovejoy T. 2020. Tropical forest fragmentation and isolation: Is community decay a random process? Global Ecol. Conserv. 23:e01168.

Morante-Filho JC, Arroyo-Rodríguez V, de Andrade ER, Santos BA, Cazetta E, Faria D. 2017. Compensatory dynamics maintain bird phylogenetic diversity in fragmented tropical landscapes. J. Appl. Ecol. 55:256–266.

Perfecto, I., Rice, R. A., Greenberg, R., Voort, M. E., Van, D. E. R., 1996. Shade Coffee: A Disappearing Refuge for Biodiversity. BioScience 46, 598–608.

Pollock HS, Brawn JD, Cheviron ZA. 2021. Heat tolerances of temperate and tropical birds and their implications for susceptibility to climate warming. Funct. Ecol. 35:93–104.

Riddell EA, Iknayan KJ, Wolf BO, Sinervo B, Beissinger SR. 2019. Cooling requirements fueled the collapse of a desert bird community from climate change. Proc. Natl. Acad. Sci. 116:21609–21615.

Semenchuk P, Plutzar C, Kastner T, Matej S, Bidoglio G, Erb, K-H, et al. 2022. Relative effects of land conversion and land-use intensity on terrestrial vertebrate diversity. Nat. Commun. 13:615.

Sales LP, Galetti M, Pires MM. 2020. Climate and land-use change will lead to a faunal "savannization" on tropical rainforests. Glob. Chang. Biol. 26:7036–7044.

Sreekar R, Si X, Sam K, Liu J, Dayananda S, Goodale U, et al. 2021. Land use and elevation interact to shape bird functional and phylogenetic diversity and structure: Implications for designing optimal agriculture landscapes. J. Appl. Ecol. 58:1738–1748.

Appendices

Appendix from Chapter 2

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

Table A.1. 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 (ºC)
Cabanis's wren	Inflection T_a (ºC)	-	34.72 (33.98 – 35.45)	33.00 (24.62 – 41.39)	-
	β_{below} ($ºC^{-1}$)	-	0.03 (0.02 – 0.03)	0.01 (-0.00 - 0.04)	-
	β_{above} ($ºC^{-1}$)	-	0.15 (0.13 – 0.17)	-	-
Silver-throated tanager	Inflection T_a (ºC)	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} ($ºC^{-1}$)	-0.02 (-0.05 – 0.01)	0.03 (0.02 – 0.04)	0.03 (0.02 – 0.03)	-0.04 (-0.08 – 0.01)
	β_{above} ($ºC^{-1}$)	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 (ºC)	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} ($ºC^{-1}$)	-0.02 (-0.03 – -0.01)	0.02 (0.01 – 0.02)	0.04 (0.04 – 0.05)	0.04 (0.01 – 0.07)
	β_{above} ($ºC^{-1}$)	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 (ºC)	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} ($ºC^{-1}$)	-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} ($ºC^{-1}$)	0.01 (-0.00 – 0.02)	0.07 (0.05 – 0.09)	0.10 (0.03 – 0.15)	0.20 (0.11 – 0.32)

Summary

The conversion of natural habitats in the tropical regions of the world, boosted by the intensification of the land management, promotes the decline in the richness and abundance of birds. However, data on the effects that land use has on avian functional roles, phylogenetic lineages and thermal stress is still scarce. The purpose of this Ph.D. thesis was to assess the response of tropical birds to the separate and combined effects of land-use change and climate warming, using the coffee crop in Costa Rica as the study system. In Chapter 1, I analyzed the role of coffee cultivation intensity on the taxonomic, functional and phylogenetic dimensions of avian diversity and determined that the most contributing vegetation elements affected avian diversity differently at specific elevations. In Chapter 2, I combined measurements of microclimatic temperatures inside coffee farms cultivated at different levels of intensity and of heat tolerance in four focal bird species to predict that exposure to heat increases ~3-fold in farms lacking vegetation. However, even the maximum temperature reached in these high-intensity farms were tolerated by all species. Finally, Chapter 3 consisted of an integrative review of the physiological features of tropical birds related to vulnerability or resilience to warming. I found that the most important knowledge gaps involve the estimation of heat tolerance, especially the long-term response, in mountain and forest-interior birds as well as those living in converted lands. This thesis work provides novel information on joint assessments of avian diversity in coffee farms and heat tolerance in agricultural lands with different intensity levels. All in all, areas under intensified land-use are hotspots of decline of avian diversity in tropical landscapes. However, more empirical evidence is needed to determine whether the causes of current and possible future decline are related to habitat loss, intolerance of heat or both.

Zusammenfassung

Die Umwandlung natürlicher Lebensräume in den tropischen Regionen der Welt, verstärkt durch die Intensivierung der Landnutzung, fördert den Rückgang der Artenvielfalt und des Vogelreichtums. Daten zu den Auswirkungen von Landnutzung auf die ökologischen Funktionen, phylogenetische Abstammungslinien und den thermischen Stress bei Vögeln sind jedoch noch selten. Das Ziel dieser PhD-Arbeit bestand darin, die Reaktion tropischer Vögel auf die getrennten und kombinierten Auswirkungen von Landnutzungsänderungen und Erwärmung zu bewerten, wobei die Kaffee-Plantagen in Costa Rica als Studiensystem verwendet wurden. In Kapitel 1 habe ich die Rolle der Bewirtschaftungsintensität der Kaffee-Plantagen auf die taxonomischen, funktionalen und phylogenetischen Dimensionen der Vogelvielfalt analysiert. Es zeigte sich, dass verschiedene, zusätzliche Vegetationsstrukturen in Kaffee-Plantagen die Vogelvielfalt in bestimmten Seehöhen unterschiedlich beeinflussten. In Kapitel 2 wurden Messungen der mikroklimatischen Temperaturen in verschieden intensiv bewirtschafteten Kaffeefarmen in Beziehung zur Hitzetoleranz von vier Vogelarten gesetzt. Die Ergebnisse zeigen, dass die Hitzeexposition in Kaffee-Plantagen ohne zusätzliche Vegetationsstrukturen wie Schattenbäume etwa um das Dreifache zunimmt. Selbst die maximale Belastung in den am intensivsten bewirtschafteten Plantagen war allerdings für alle Arten tolerierbar. In Kapitel 3 habe ich die vorhandene Literatur ausgewertet, um die thermische Sensitivität tropischer Vögel gegenüber steigenden Temperaturen abzuschätzen und dabei auch Interaktionen von Klimawandel und Landnutzung berücksichtigt. Ich fand heraus, dass die wichtigsten Wissenslücken die Schätzung der Hitzetoleranz, insbesondere der Langzeitreaktion, bei Gebirgs- und Waldinnenvögeln sowie solchen, die in umgewandelten Ländern leben, betreffen. Diese Dissertation liefert neue Informationen zur gemeinsamen Bewertung der Vielfalt von Vögeln in Kaffeefarmen und der Hitzetoleranz in landwirtschaftlichen Flächen mit unterschiedlicher Nutzungsintensität. Insgesamt sind Gebiete mit intensivierter Landnutzung Hotspots für den Rückgang der Vogelvielfalt in tropischen Landschaften. Die vorliegenden Daten erlauben es allerdings nicht, die aktuellen und vor allem auch die zu erwartenden zukünftigen Verluste eindeutig dem Verlust von Lebensräumen, der fehlenden Hitzeintoleranz oder einer Kombination beider Faktoren zuzuschreiben.