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Biological Conservation

Review

The effects of climate change on tropical birds

Çağan H. Şekercioğlu [a,b,*], Richard B. Primack [c], Janice Wormworth [d]

[a] Department of Biology, University of Utah, 257 South, 1400 East, Salt Lake City, UT 84112-0840, USA
[b] KuzeyDoğa Derneği, İsmail Aytemiz Cad., İstasyon Mah., 36200 Kars, Turkey
[c] Biology Department, Boston University, Boston, MA 02215, USA
[d] 6-16 St. Neot Ave., Potts Point, NSW 2011, Australia

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ABSTRACT

Birds are among the most widely studied organisms on earth and represent an important indicator group for learning about the effects of climate change – particularly in regard to the effects of climate change on tropical ecosystems. In this review, we assess the potential impacts of climate change on tropical birds and discuss the factors that affect species' ability to adapt and survive the impending alterations in habitat availability. Tropical mountain birds, species without access to higher elevations, coastal forest birds, and restricted-range species are especially vulnerable. Some birds may be especially susceptible to increased rainfall seasonality and to extreme weather events, such as heat waves, cold spells, and tropical cyclones. Birds that experience limited temperature variation and have low basal metabolic rates will be the most prone to the physiological effects of warming temperatures and heat waves. Mostly unknown species' interactions, indirect effects, and synergies of climate change with other threats, such as habitat loss, emerging diseases, invasive species, and hunting will exacerbate the effects of climate change on tropical birds. In some models habitat loss can increase bird extinctions caused by climate change by 50%. 3.5 °C surface warming by the year 2100 may result in 600–900 extinctions of land bird species, 89% of which occur in the tropics. Depending on the amount of future habitat loss, each degree of surface warming could lead to approximately 100–500 additional bird extinctions. Protected areas will be more important than ever, but they need to be designed with climate change in mind. Although 92% of currently protected areas are likely to become climatically unsuitable in a century, for example only 7 or 8 priority species' preferred climatic envelopes are projected to be entirely lost from the African Important Bird Area network. Networks of protected areas need to incorporate extensive topographical diversity, cover wide elevational ranges, have high connectivity, and integrate human-dominated landscapes into conservation schemes. Most tropical bird species vulnerable to climate change are not currently considered threatened with extinction, often due to lack of knowledge; systematically and regularly gathering information on the ecology, and current and future distributions of these species is an urgent priority. Locally based, long-term tropical bird monitoring and conservation programs based on adaptive management are essential to help protect birds against climate change.

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1. Introduction

Climate change is increasingly recognized, along with habitat destruction, as one of the most serious and widespread threats to biological diversity (IPCC, 2007). As scientists search for the best biological indicators of human-induced climate change, birds offer two advantages: first, they are the best-known class of organisms when it comes to climate research (Wormworth and Şekercioğlu, 2011), and second, millions of citizen-scientist birdwatchers track them across the globe, contributing to extensive datasets (Kinzelbach, 1995; www.ebird.org; www.worldbirds.org). For example, the arrival dates of migratory birds feature prominently in the long phenological records of Europe, in part thanks to naturalists like Robert Marsham who began compiling 'Indications of Spring' in 1736 (Lehikoinen et al., 2004).

As a well-studied, globally-distributed indicator group, birds' are excellent bellwethers of climate change effects on biodiversity. Bird distributional shifts have already been linked to climate change (Gregory et al., 2009; Niven et al., 2009; Chen et al., 2011). Unchecked climate change, combined with habitat loss, may lead to the extinctions of hundreds of bird species (Şekercioğlu et al., 2008). Tropical bird species' particular vulnerability to climate change is increasingly recognized (La Sorte and Jetz, 2010; Harris et al., 2011; Sodhi et al., 2011; Wormworth and Şekercioğlu, 2011). Most tropical birds are sedentary, endemic species isolated on tropical mountains (Janzen, 1967; Şekercioğlu et al., 2008) and lowland species without access to higher elevations (Loarie et al., 2009) are likely to face greater risk. However, there are few studies of climate change effects on the bird communities of entire tropical forest regions (Harris et al., 2011), and few tropical bird families have been assessed in their entirety (see the case study, section 2.9).

Yet information on current and predicted climate change impacts on tropical birds could be used to evaluate the suitability of current conservation practices, such as the adequacy of existing protected area networks, and to suggest management strategies to prevent the future decline and extinction of these species. Many physiological, ecological, and biogeographical characteristics that make certain bird species more susceptible to climate change are also present in non-avian groups. Ongoing measures and management regimes to reduce climate change threats to bird communities could also help species in other groups.

With these in mind, we have conducted an extensive review of the literature on the effects of climate change on tropical birds. We searched the Web of Knowledge™ with the keywords climat* AND chang* AND bird* and their variations. We focused on the studies on tropical birds and also read the relevant articles cited in and citing these articles. In a few cases, where tropical examples were not available, we gave temperate examples of phenomena that should be watched for in tropical systems. Two of us (ÇHŞ and JW) spent the past two years reviewing and summarizing the literature on climate change effects on birds for a recent book (Wormworth and Şekercioğlu, 2011).

Our main goals are to outline the existing and potential effects of climate change on tropical bird communities, to examine why certain bird species are more susceptible to climate change, and to discuss how this information can be used to improve the conservation and management of birds and other taxa in the face of escalating climate change.

2. Geography, habitat and range shifts: which species will be most affected?

This section outlines how certain geographical (e.g. mountains) and habitat (e.g. forests) features are likely to interact with climate change to affect tropical birds. It also discusses modeled results of range shifts due to climate change, and their consequences for birds.

Despite the uncertainties in predicting precipitation changes in the tropics, multiple models based on the IPCC A2 Emissions Scenario predict tropical drying trends, "in relatively intense, localized regions at the margins of the convection zones" particularly in the Caribbean/Central America region and equatorial South America (Neelin et al., 2006). Although overall tropical drying trends comprise a significantly larger fraction of the average changes in rainfall, some locations will experience more precipitation, including the equatorial Pacific region of the convection zones, and increased Southeast Asian summer monsoon (Neelin et al., 2006).

Temperature increase is the main driver of climate change-caused habitat loss at higher elevations, whereas precipitation changes are the main cause in lowlands (Enquist, 2002; Li et al., 2009). Because endemism is greater at higher elevations in the tropics (Enquist, 2002), temperature has a greater effect on tropical

vertebrate ranges than does precipitation (McCain, 2009). Temperature, through its effects on evapotranspiration and NPP, also has a crucial effect on vegetation change in the tropics (Delire et al., 2008) and temperature increases are likely to have a greater impact in the loss of tropical endemics than are changes in precipitation. However, past changes in bird communities suggest that major changes in precipitation patterns, such as changes in the monsoon regime, may be more important than temperature changes, particularly if warming is limited to 2 °C (Tyrberg, 2010).

2.1. Montane species

Tropical mountain species are among birds most vulnerable to climate change (Şekercioğlu et al., 2008; Wormworth and Şekercioğlu, 2011). Extinction risk increases as birds' elevational ranges narrow (Fig. 1). In addition, a given elevational range translates into a much smaller area of occupancy at the top of a mountain compared to its base; for example, the top and bottom one-meter bands of a hundred-meter tall square pyramid differ in area by two orders of magnitude. Where warming temperatures reduce many montane species ranges' by forcing them to shift upslope, some species may be driven to local (or global) extinction, particularly species endemic to tropical highlands (Shoo et al., 2005a; Colwell et al., 2008; Gasner et al., 2010; La Sorte and Jetz, 2010; Figs. 2 and 3). Conversely, bird species with access to intact habitats spanning a wide elevational range are expected to be less affected by climate change (Anciaes and Peterson, 2009). Despite the importance to estimates of tropical birds extinctions, few data exist on the potential extent and magnitude of current and future shifts in tropical birds' elevational limits in response to climate change (Bohning-Gaese and Lemoine, 2004; Laurance et al., 2011; Shoo et al., 2006; e.g. Figs. 2 and 3). Yet, studies of 'disappearing climates' further emphasize the threats to birds of tropical mountains. Areas with disappearing climates are expected to be concentrated at the poleward regions of continents, but also in tropical mountain regions, including areas that correspond to biodiversity hotspots (Williams et al., 2007). In this regard, tropical mountain cloud forests deserve special mention for the disproportionately high and concentrated biodiversity they host. For example, widespread epiphytes provide birds with food and nesting
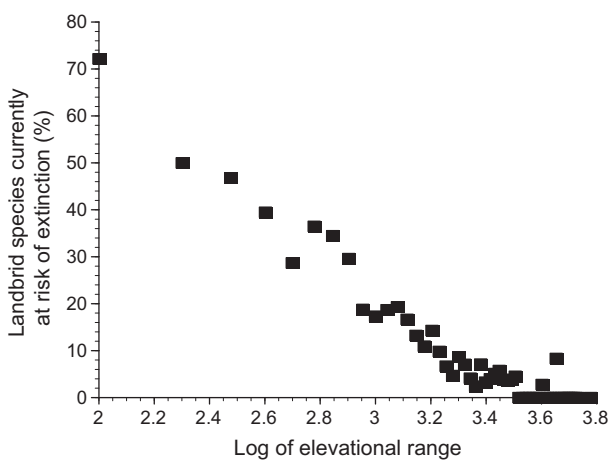
Fig. 1. The relationship between bird extinction risk and elevational range ($r^2 = 0.97$, $p < 0.0001$). The x-axis is the $\log_{10}$ of each species' elevational range rounded up to the nearest hundred meters (upper elevational limit – lower elevational limit). For example, the point corresponding to 2 (=log of 100 m) on the x-axis means that of the 79 bird species that have elevational ranges that are ⩽100 m, 72% are threatened or near threatened with extinction. Reprinted with permission from Şekercioğlu et al. (2008). Climate change, elevational range shifts, and bird extinctions. *Conservation Biology* 22, 140–150.
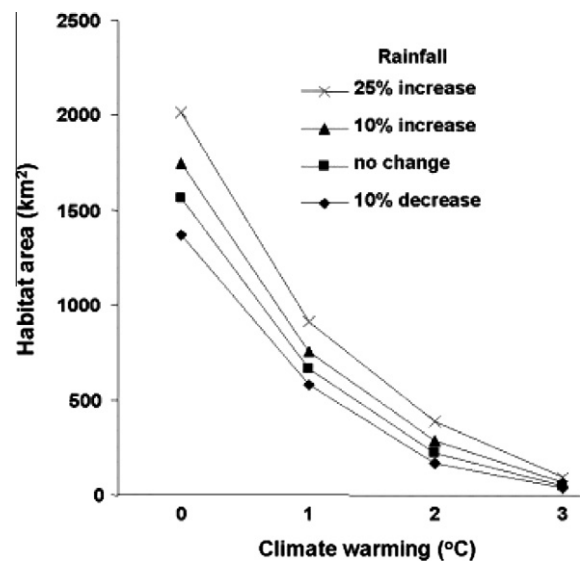
Fig. 2. Predicted area of golden bowerbird habitat in a number of future climate change scenarios including a range of changes in rainfall and from one to three degrees of warming. Reprinted with permission from Elsevier, David W. Hilbert and CSIRO. Hilbert et al. (2004) Golden bowerbird (*Prionodura newtonia*) habitat in past, present and future climates: predicted extinction of a vertebrate in tropical highlands due to global warming. *Biological Conservation* 116, 367–377.

materials. However, these plants occupy fine-grained climate niches on tree trunks, crooks and branches, and epiphyte mortality can occur under even slight climatic change, with cascading effects on cloud forest communities. With warming, many cloud forests can be expected to experience reduced cloud cover, less water capture and drier ecosystems (WTMA, 2008; Karmalkar et al., 2008) as current climate conditions shift upslope. In the IPCC report, Fischlin et al. (2007) emphasized that tropical mountain cloud forests are among the tropical forest regions where endemics are at "disproportionately high risk of extinction".

Elevational distribution is often used as a proxy for population size. However, in the Wet Tropics of Queensland, highland bird populations (e.g. Fig. 2) may decline even more quickly than suggested by warming-induced range contractions (Shoo et al., 2005b). For most bird populations, their abundance is unlikely to be distributed uniformly across their ranges and across different elevations. Although climate-change induced alterations in abundance patterns have important conservation implications, these changes have not been well studied (Shoo et al., 2005b). Also little understood are potential increases in net primary productivity that may partially ameliorate some of projected impacts of global warming on the biodiversity of tropical highlands (Williams et al., 2010).

Hotter lowland zones tend to isolate the populations of upland tropical birds, which are often sedentary (Janzen, 1967). Tropical montane endemics like Venezuela's endangered scissor-tailed hummingbird (*Hylonympha macrocerca*) or regal sunbird (*Nectarinia regia*) of East Africa (Fig. 3) have limited capacity to shift their ranges across such unsuitable habitat to other mountain ranges, which could make such birds particularly vulnerable to extinction from climate change. Yet, because tropical mountains tend to have low human populations and more intact habitat relative to tropical lowlands, most tropical montane bird species, like golden bowerbirds (*Prionodura newtoniana*), have been considered to be of least conservation concern – but now face the looming threat of climate change (Şekercioğlu et al., 2008; Shoo et al., 2005a; Fig. 2). Due to limited data, climate change is only recently being incorporated into the assessments of extinction likelihood (BirdLife International, 2008), but it is increasingly realized that
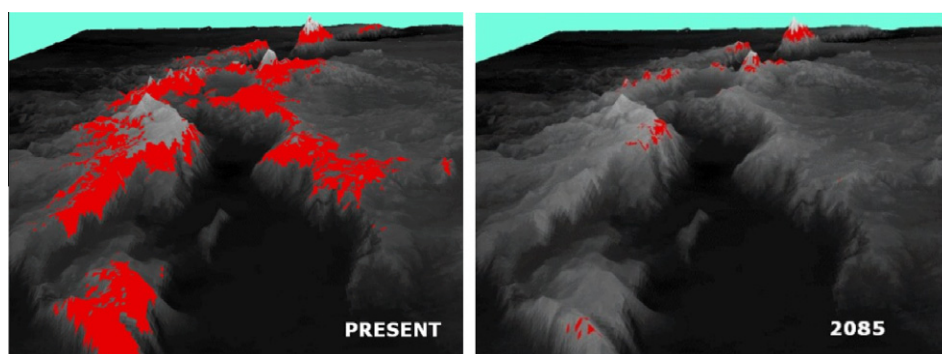
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Fig. 3. Modeled future range of regal sunbird (*Nectarinia regia*). Reprinted with permission from BirdLife International (2008) Groundbreaking work will help Africa's biodiversity combat climate change. URL: http://www.birdlife.org/news/news/2008/07/rwanda_meeting.html.

in the long term, "it may be the most serious threat of all" (BirdLife International, 2008; Hilton-Taylor et al., 2009).

2.2. Species of tropical coastal and island ecosystems

Effects of climate change on tropical coastal forests, such as mangrove forests, are even less known. Tropical coastal ecosystems are disappearing at a rapid rate and are highly sensitive to both climate change and concomitant sea level rise (Waycott et al., 2009). The loss of these coastal habitats should concern us greatly because they provide key ecosystem functions and services (Şekercioğlu, 2010a), such as reducing the damage caused by tsunamis.

Tropical forests and bird communities on oceanic islands are especially vulnerable to climate change. More than any other habitat, these communities have already suffered greatly from introduced invasive species and exploitation (BirdLife International, 2011). Island ecosystems have been drastically modified, and most still experience ongoing habitat loss. This includes the loss of land area due to rising sea levels resulting from global climate change (Kingsford et al., 2009). Coastal flooding is likely to reduce the extent of coastal wetlands on small islands, and increases in the number of extreme events, including a possible increase in the number of intense tropical cyclones, could degrade tropical forests that are often small in extent, and may be slow to regenerate (Mimura et al., 2007). Many threatened tropical island endemics such as the critically endangered mangrove finch (*Camarhynchus heliobates*) on the Galapagos Islands, endangered Abbott's booby (*Papasula abbotti*) on Christmas Island, and critically endangered Cozumel thrasher (*Toxostoma guttatum*) of Mexico now face the additional threat of climate change.

Tropical seabirds reliant on coastal zones and islands are also vulnerable, particularly during the breeding season (e.g. Ancona et al., 2011). Tropical seabirds of Australia's Great Barrier Reef are vulnerable not just to warming events that affect their foraging success (Peck et al., 2004; Erwin and Congdon, 2007), but also to sea level rise that could inundate the low-lying coral cays which host their breeding colonies. Most cays are less than three metres above the high water mark, and low-lying cays, which are preferred by most seabirds, could be flooded in the future during storm surges or even at high tide (Hulsman & Devney, 2010).

2.3. Birds in extensive lowland forests

For species in extensive low-lying areas such as the Amazon and Congo basins, where topographical diversity is lacking, climate change poses an additional challenge. As climate warms, many types of vegetation and dependent organisms – including fruit trees

and insects that many birds depend on – may be expected to shift their distributions to track their preferred microclimates. Broadly speaking, this would entail dispersal toward the poles or to higher altitudes (Gregory et al., 2009; Janzen, 1967; Niven et al., 2009; Pounds et al., 1999; Shoo et al., 2006). Where upslope shifts are made possible due to the proximity of mountains, this may require relatively short dispersal distances for vegetation and dependent species. Yet in extensive flat areas, where mountains are few and far between, such as the Amazon basin and the Congo basin, plant and animal communities may need to move far greater distances to track their climate preferences (Anciaes and Peterson, 2009; Loarie et al., 2009; Menon et al., 2009; Peterson et al., 2002, 2001; Şekercioğlu et al., 2008). Poor dispersers, such as birds of the forest interior (e.g., endangered Congo peafowl, *Afropavo congensis* and vulnerable rufous twistwing, *Cnipodectes superrufus*), may not be able to make these range shifts. Furthermore, tropical lowland communities may experience net biotic attrition, as a result of the species moving to higher elevations not being replaced by other species (Colwell et al., 2008).

2.4. Birds in non-forest habitats

Although relevant studies of tropical birds have mainly focused on forest species (e.g. Pounds et al., 1999; Shoo et al., 2005a), thousands of tropical bird species inhabit diverse open habitats such as savanna, *cerrado*, grasslands, *karoo*, scrub, deserts, and human-dominated areas. Recently, Marini et al. (2009) modeled the expected effects of climate change on the distributions of 26 widespread bird species of the *cerrado*. This ecosystem has the largest extent of tropical savanna worldwide, and 44% of its approximately 10,000 plant species are endemic. Projected range size contractions of up to 80% will affect various savanna (e.g. near threatened coal-crested finch, *Charitospiza eucosma*) and grassland (e.g. vulnerable lesser nothura, *Nothura minor*) species, and species with smaller ranges (Marini et al., 2009). Range shifts of 175–200 km towards southeastern Brazil are predicted, but the dispersal of species could be thwarted because that region has high levels of human population and development (Marini et al., 2009). Extensive deforestation of the Brazilian Atlantic forest further exacerbates the effects of climate change (Loiselle et al., 2010).

2.5. Aquatic birds in the tropics

Climatic models have focused mainly on terrestrial species. However, the diversity patterns of aquatic birds such as waders, ducks, and geese differ from those of terrestrial bird species (Ramirez-Bastida et al., 2008). Coastal regions, which often have high bird diversity, will be affected by rising sea levels. Yet,

because coastal wetlands are often bounded by agriculture and settlements, opportunities for range shifts are limited. These wetlands include Florida's Everglades and its globally important colonies of roseate spoonbills (*Platalea ajaja*), wood storks (*Mycteria americana*), and other waterbirds. Vast coastal swamps in northern Australia are also at risk, including Kakadu, which harbors more than 280 bird species. Only marginally above sea level, these tropical wetlands have already proven to be vulnerable to salt water incursion. Yet this region's sea level rise is currently occurring at four times the global average rate. Exacerbated by tropical storms, sea level rise could cause these highly productive wetland areas to be transformed into salt pans, greatly degrading their potential to host bird populations (Traill et al., 2010; Garnett and Brook, 2011). On the other hand, salt-tolerant coastal marshes are likely to expand and this could benefit the species that prefer these wetlands.

Birds of peat swamp forests are also of concern. Of all forest types, peat swamp forests are the most vulnerable to fires, particularly during droughts and El Niño years (Posa et al., 2011). These fires can take months to extinguish. They also exacerbate climate change by causing the release of massive amounts of carbon stored in these peat forests, adding to the global greenhouse gas burden.

Unfortunately, no global analyses have been undertaken to model the expected changes in tropical wetland/coastal habitats in response to climate change scenarios. Additional factors such as hunting, disease, and habitat loss further threaten tropical wetland species (Traill et al., 2009, 2010). Given their dependence on water, tropical aquatic birds will be particularly vulnerable to climate change.

2.6. Arid zone species

Arid zone species, such as desert cisticola (*Cisticola aridulus*), are assumed to be resilient to high temperatures and low humidity. However, these species are already exposed to extreme conditions and are often dependent on seasonal rains, as well as on aquatic habitats such as riparian forests, seasonal and permanent waterholes, lakes, and rivers (Schneider and Griesser, 2009). We have limited knowledge of how future changes in temperature may affect rainfall patterns, and how further increases in already high temperatures and/or changes in rainfall regimes may affect the availability of other sources of water and food. The disappearance of water sources is likely to be devastating for these "oasis" communities, and the added stress of higher temperatures and possibly scarcer rainfall could test the tolerances of even these seemingly hardy species. Even small temperature increases can greatly increase the amount of birds' evaporative water loss. Hotter weather due to climate change is expected to test the ability of desert birds to sustain their water balance, and climate change is expected to lead to more frequent episodes of catastrophic mortality by the 2080s. Modeling suggests that small desert birds will require 150–200% more water during the hottest period of the day to survive predicted increases in maximum daily temperature (McKechnie and Erasmus, 2006; McKechnie and Wolf, 2010).

2.7. Birds in human-dominated landscapes

Ecologists tend to focus their studies on relatively intact ecosystems, but this limits our ability to predict climate change impacts on human-dominated ecosystems (Felton et al., 2009). Because human-dominated lands make up a large and growing subset of tropical ecosystems, it would be worthwhile to gather more data about birds that are impacted by human activity. Some human activities and human-dominated areas can be modified to allow birds to survive, and research may identify the changes needed to foster this. For example, some forest birds, such as silver-throated tanagers (*Tangara icterocephala*), orange-billed nightingale-thrushes (*Catharus aurantiirostris*), and white-throated thrushes (*Turdus assimilis*) persist in the agricultural landscapes of southern Costa Rica by either adapting to coffee plantations or by focusing their activities on remnant trees, riparian strips, and small forest fragments (Şekercioğlu et al., 2007). As human-dominated ecosystems increasingly surround intact ecosystems, improving the conservation capacity of human-dominated tropical countryside will be critical. This will include increases in landscape connectivity and other improvements that optimize the potential for species to carry out range shifts in response to climate change.

2.8. Projected impacts of range shifts on tropical birds

Modeled shifts in species' ranges in the Neotropics indicate that those in the tropical parts of the Mexican and Andean mountains, and in the biodiversity hotspot of Central America could be the most affected by climate change (Lawler et al., 2009). In 80% of climate change scenarios, these regions are expected to lose 25–38% of their endemic species (Lawler et al., 2009). The Brazilian Atlantic forests and the southern and western boundaries of the Brazilian *cerrado* are also likely to experience high species turnover. Hundreds of restricted-range species are expected to be at the risk of extinction as a result of climate change (Lawler et al., 2009). Climate change is likely to exacerbate the conservation status of this region's already threatened bird species, such as the endangered horned guan (*Oreophasis derbianus*) in the cloud forests of Mexico and Guatemala, endangered Cochabamba mountain-finch (*Compsospiza garleppi*) in the Bolivian Andes, vulnerable red-fronted parrotlet (*Touit costaricensis*) in Costa Rica and Panama, critically endangered kinglet calyptura (*Calyptura cristata*) in the Brazilian Atlantic forest, and also critically endangered blue-eyed ground-dove (*Columbina cyanopis*) in the Brazilian *cerrado*. In sub-Saharan Africa, bird species projected to undergo the greatest range contractions inhabit the temperate areas of the Cape (e.g., the vulnerable Knysna warbler, *Bradypterus sylvaticus* in South Africa), the Horn of Africa (e.g., the endangered Warsangli linnet, *Carduelis johannis* in Somalia), East Africa (e.g., the endangered Sharpe's longclaw, *Macronyx sharpie* in Kenya), and montane (e.g., the vulnerable Usambara eagle-owl, *Bubo vosseleri* in Tanzania) and semi-arid (e.g., the critically endangered Liben lark, *Heteromirafra sidamoensis,* in Ethiopia) habitats (Huntley et al., 2006). Although Afrotropical birds associated primarily with equatorial and moist tropical forest habitats are expected to experience relatively less change in their distributions (Huntley et al., 2006), species in extensive, flat lowlands, such as the Congo basin, will need to move much greater distances than species in mountainous areas (Loarie et al., 2009).

In Southeast Asia, some tropical forest bird species have apparently already begun to shift their ranges in response to increased temperatures. Peh (2007) used data from field guides to show that 94 common resident species of Southeast Asian forests, such as the little forktail (*Enicurus scouleri*), brown bush warbler (*Bradypterus luteoventris*), and russet sparrow (*Passer rutilans*), shifted the upper, lower or both boundaries of their distributions to higher altitudes from 1971 to 1999.

Tropical montane birds in Peru also appear to be shifting upslope in response to warming (Forero-Medina et al., 2011). In the Cerros del Sira, the elevational limits of birds from the same species vary from peak to peak, implying that birds' range margins are unlikely to be a simple response to temperature. Yet these bird species show a consistent upslope range shifts in response to warming from 1969 to 2010. Nevertheless, their shifts lag behind warming, and this may reflect an indirect response to temperature via gradual alteration of their food supplies, habitat, or other interactions (see Section 5).

Where ecosystems migrate in response to temperature change, the availability of habitats and resources for bird species may be disrupted as well. Different types of birds will have varying rates of success in coping with these changes. Success may depend on whether birds' preferred food sources successfully track climate change and shift to these new vegetation zones or, alternatively, how well the bird species adapt to new vegetation and food sources. The important concern for conservation planners is thus not only how to protect tropical birds now, but also how to determine the rate at which birds and associated tropical ecosystems will migrate over time so that future habitats can also be protected.

Loarie et al. (2009) calculated an index of the velocity required for ecological communities to keep up with climate change (Fig. 4). Although this velocity is not uniform across habitats and regions, in general terms, 92% of protected areas are likely to become climatically unsuitable in a century, especially in grasslands, savannas, deserts, and mangroves (Loarie et al., 2009). Nevertheless, an analysis of African Important Bird Areas (IBA) indicates that all but 7–8 priority species' will retain some of their preferred climatic envelopes in the IBA network, showing the importance of carefully designed protected area networks (Hole et al., 2009). Protected areas will remain vital, but will need to be enlarged based on future range shift projections. Under climate change, protected area planning must consider not only the current habitat needs of a given species or community, but also the areas that could accommodate future needs as temperatures warm. Ideally, habitat corridors should be used to provide high connectivity between protected areas, but this will require better integration of human-dominated landscapes into conservation schemes. Equally important, protected areas must assess potential barriers to migration, both natural – rivers, oceans, and unsuitable soils – and human-made, including settlements, farmlands, and coastal fortifications. The problem of extensive protected areas losing bird populations due to climate change (Mac Nally et al., 2009) makes it essential to integrate human-dominated landscapes into conservation areas.

2.9. Manakins: a case study

The family Pipridae (manakins) is endemic to the Neotropical region. The roughly 45 species in this family are limited to various forest habitats and nearby second growth. Ranging from lowlands to montane forest, manakins prefer relatively humid conditions, even in drier areas, where they are limited to gallery forest (Snow, 2004). Because these species are restricted to Neotropical forest habitats, consist of dozens of species with varied geographic distributions and ecological preferences, and have wide-ranging elevational distributions, manakins provide an ideal opportunity to model climate change effects on the distribution of a tropical bird family. Anciaes and Peterson (2009) used ecological niche modeling (Peterson et al., 2001) to model manakins' ecological niches, based on these birds' present distributions and climatic preferences. They then combined these models with climatic projections for the mid-21st century. The results indicate that manakin species limited to the lowland habitats of the Amazon basin and *cerrado* (e.g. the helmeted manakin, *Antilophia galeata*) will be the most affected. That is, these species would need to move relatively greater distances to track their environmental niches. These species are expected to lose 80% of their habitable area; moreover 20% of the *cerrado* manakin species are expected to go extinct. In other ecoregions dominated by mountains, predicted loss of potential area (16–50%) and expected extinctions (0–5%) are much lower. This demonstrates the importance of topographic diversity in buffering against forced range shifts due to climate change. The researchers also predicted that manakin distributions will become more fragmented, highlighting the conservation challenge climate change will pose for many tropical bird groups.

3. Evolution and adaptation: slow lives in a fast-paced new world

This section focuses on the aspects of tropical bird species' life histories and ecologies that may affect their capacity to adapt to
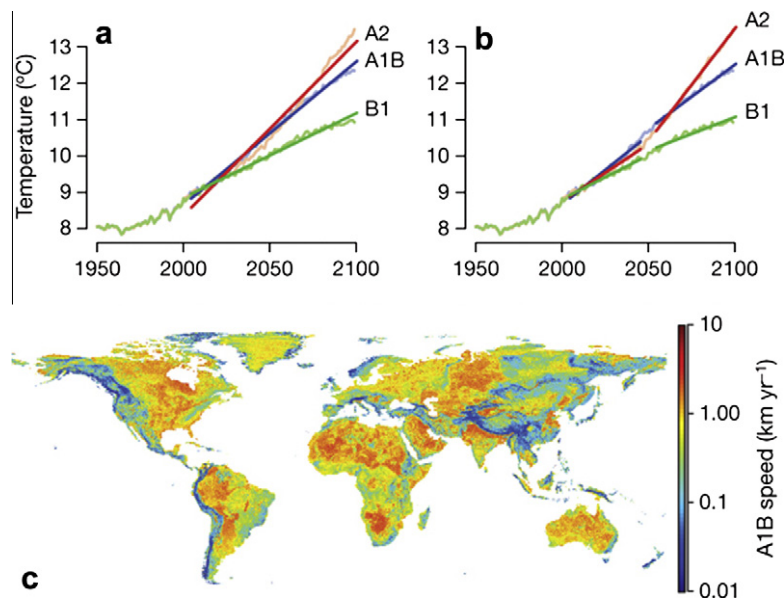
Fig. 4. The velocity of temperature change globally. (a) Temporal gradients calculated from 2000–2100 across three emissions scenarios (A2, A1B and B1). (b) Temporal gradients calculated from 2000–2050 and 2050–2100 across three emissions scenarios. Trends plotted here are the average of the global land surface. (c) A global map of climate velocity calculated using the 2050–2100 Special Report on Emissions Scenarios (SRES) A1B emissions scenario temporal gradient. This is the instantaneous local velocity along Earth's surface needed to maintain constant temperatures at a location, and has a global mean of 0.42 km year^{-1}. For example, in a dark red area, vegetation would need to shift 10 km year^{-1} to keep up with climate change. Reprinted with permission from Loarie et al. (2009) The velocity of climate change. *Nature* 462, 1052–1055.

climate change. Climate change also has evolutionary consequences (Bonaccorso et al., 2006). For some species, adaptive responses such as phenotypic plasticity, learning, and maternal effects, along with migration rates, are unlikely to be sufficient to keep pace with climate change, and the rate of microevolution will be the primary determinant of their ability to adapt to climate change (Visser, 2008). Yet most vertebrates will be unable to evolve rapidly enough to adapt to anthropogenic climate change, exacerbated by extensive habitat loss (Njabo and Sorenson, 2009); bird species will be lost at a far higher rate than the rate of the evolution of new species.

On actual and ecological islands, geographic isolation and long-term environmental stability are among the features that promote endemism and speciation, yet these same features make island species especially vulnerable to environmental change (Fordham and Brook, 2010). Tropical mountain areas, for example, have been the centers of speciation and endemism due to their isolation (Voelker et al., 2010) and long-term habitat stability (Fjeldsa and Lovett, 1997; Graham et al., 2006). In Africa, Pliocene climate change has driven the speciation of African forest birds like the Cameroon mountain greenbul (*Andropadus montanus*) by causing lowland forest retraction and rapid isolation of montane forests (Njabo and Sorenson, 2009; Voelker et al., 2010). Ongoing climate change will further isolate tropical montane forests.

However, species' ecological niches are unlikely to evolve substantially during the decadal time-scales over which climate change is expected to take place (see references in Anciaes and Peterson, 2009), especially for organisms with long generation times (e.g. seabirds, parrots, cassowaries). Compared to birds in temperate regions, many tropical bird species experience less seasonality and more stable temperature and humidity regimes. These conditions favor birds with "slower" lives, that is, those with "k-selected" life histories characterized by smaller clutch sizes (Jetz et al., 2008a), lower productivity, and longer life spans (Wiersma et al., 2007). Consequently, tropical bird species with less demographic flexibility than their temperate counterparts are unlikely to evolve as quickly in response to rapid climatic change. Moreover, recent research suggests that high-elevation birds have life-history strategies similar to those of low-latitude birds (Tieleman, 2009). This raises further concern about tropical high-elevation species with particularly slow life histories (see above). Not only are high-elevation birds particularly susceptible to climate change, but most high-elevation endemic bird species are found in the tropics.

As long-lived homeotherms, many tropical birds' population growth rates should be less affected by climate change induced variability in their demographic rates (e.g. survival, reproduction, or growth) than those of short-lived species like insects (Morris et al., 2008). Furthermore, research has shown that tropical populations, through their long-term persistence during periods of climate change, have accumulated more genetic variability relative to populations in more temperate areas (and likely at higher elevations in the tropics). Populations of the latter groups have been frequently eliminated during colder periods, or have gone through more population bottlenecks, and thus possess reduced genetic variability (Hewitt, 1996).

Although tropical birds are longer-lived, on average, than their temperate relatives (Wiersma et al., 2007), the advantage of longer lifespans is likely to be negated by other factors that make tropical birds more vulnerable, such as smaller clutch sizes (Jetz et al., 2008a), more sedentary habits (Şekercioğlu, 2007), and lower tolerance of climatic variability (Seavy, 2006; Weathers, 1997).

Not all effects of climate change are negative, and changes in temperature and precipitation regimes will benefit some species. How a bird's life history will respond to climate change may be unexpected and hard to predict, as shown by male northern mockingbirds (*Mimus polyglottos*). This non-tropical species demonstrates more elaborate sexual displays with increased climatic variability (Botero et al., 2009). Warmer temperatures may alter birds' reproductive strategies, countering some negative demographic effects of climate change, and enabling some species to expand to new areas (Jarvinen, 1994), but this is yet to be demonstrated in the tropics.

Conversely, "r-selected" bird species with short generation times, large clutches, multiple broods, and the ability to re-nest after losing an entire clutch, are also more likely to recover from adult, juvenile, and nest mortality caused by extreme weather and other climate change effects (Angert et al., 2011). Generalist species that can use a wide range of habitats and/or feed on different kinds of food are less threatened with extinction (Şekercioğlu, 2011). These species are expected to be more likely to adapt to or even benefit from climate change, often at the expense of specialists. Overall, many traits that reduce birds' likelihood of extinction to other threats are also likely to prove advantageous in coping with climate change (Wormworth and Şekercioğlu, 2011).

Nevertheless, climate change will not benefit many species. Because individualistic responses are likely, climate change could bring about the formation of novel communities and even lead to community disassembly, especially in diverse tropical communities with a wide range of life histories.

3.1. How physiology and microclimate impact tropical bird species' ability to adapt

Current understanding of interspecific variation in physiological traits is limited and needs further study. However, we can make some general observations about how these factors will influence tropical bird species' ability to adapt to climate change (Bernardo et al., 2007). In comparison to ectotherms, endothermic birds are more likely to be indirectly affected by climate change via its impacts on vegetation in their communities, rather than via direct effects on physiology (Aragon et al., 2010). Nevertheless, an increasing number of studies hint at the vital role birds' physiological responses to climate change will play (McKechnie, 2008; McNab, 2009).

Birds living in hotter and drier habitats (e.g. Somali bee-eater, *Merops revoilii*) often show physiological adaptations, such as reduced thermal conductance (Weathers, 1997), lower evaporative water loss (Weathers and Greene, 1998), and higher heat tolerance, exemplified by variable seedeaters (*Sporophila aurita*; Weathers et al., 2001). Open habitat sunbirds in Uganda (e.g. scarlet-chested Sunbird, *Nectarinia senegalensis*) have reduced thermal conductance, better insulation and greater ability to tolerate fluctuating temperatures than do forest sunbirds (Seavy, 2006). Lowland and open-country bird species that have adapted to higher temperatures are likely to tolerate temperature increases better than highland species and species of the forest interior (Weathers, 1997). Furthermore, climate change can favor open-country species' penetration into climatically-compromised forest remnants (Laurance, 2004). One theory is that while birds that are thermal specialists perform at a high level but within a narrow band of body temperatures, thermal generalists can perform at a low level across a wide range of temperatures and maintain a lower body temperature during heat stress (Boyles et al., 2011).

Changes in temperature and humidity will also have indirect effects on avian activity and behavior. If birds avoid sites with unfavorable climates, this could reduce important activities such as feeding and breeding displays (Walsberg, 1993). Many tropical forest species, such as silver-throated tanagers (*Tangara icterocephala*) in Costa Rica, spend a lot of time in the cool and humid forest interior, but they display and forage in exposed areas, such as song perches and fruiting canopy trees. Intensive radio-tracking

combined with constant monitoring of habitat temperature and humidity revealed that these birds track temperature and humidity differences as small as 0.8 °C and 4.2%, respectively (Şekercioğlu et al., 2007).

Physiological limitations also shape habitat selection. In tropical forests, holes or hollows in trees are critical resources for many birds because they provide safe nesting cavities and microclimatic refugia from higher outside temperatures (Isaac et al., 2008). Cavity-nesting behavior has recently been shown to be a critical factor in determining avian clutch size, illustrating the importance of cavities (Jetz et al., 2008a). As global temperatures increase, tree hollows are expected to become more important to birds than ever (Isaac et al., 2008). However, the large, older trees most likely to have these cavities are often those first logged in tropical forests; even in protected forests, dead trees that provide hollows are often collected for firewood. Increasing scarcity of such older trees, combined with temperature-sensitive species' growing need for tree hollows, suggest that cavity-nesters such as woodpeckers, owls, and parrots will face more competition for the remaining hollows. They may need to compete for these resources not only with other birds, but also with cavity-dwelling mammals (Isaac et al., 2008). In Monteverde, Costa Rica, climate change has already enabled keel-billed toucans (*Ramphastos sulfuratus*), cavity-nesting nest predators, to expand their range into the highlands, where they now compete with the montane forest specialist resplendent quetzals (*Pharomachrus mocinno*) for nest holes, as well as preying on quetzal nests (Pounds et al., 1999).

3.2. Basal metabolic rate in tropical birds: implications for survival

Basal metabolic rate (BMR), the standard measure of the energy cost of maintenance, has been called "the obligatory cost of living for endotherms" (Barcelo et al., 2009). Although knowledge of BMR is critically important to determine birds' physiological tolerance to climate change, data on BMR and how it varies among tropical birds is limited. BMR is not a fixed, taxon-specific trait, but has high phenotypic flexibility (McKechnie, 2008). Compared to ectotherms, birds have more physiological flexibility to respond to temperature changes, but the degree of flexibility also varies greatly among bird species (McKechnie, 2008).

BMR is especially flexible in migratory birds (McNab, 2009), and this fact suggests that sedentary tropical birds that live in habitats with low climatic variability are likely to have less flexible BMRs. This inference is supported by an analysis of 71 bird species' responses to the 2003–2004 heat wave in France (Jiguet et al., 2006). Whereas bird species with the widest thermal range (e.g. carrion crow, *Corvus corone*) were least affected, birds with the narrowest thermal range (e.g. rook, *Corvus frugilegus*) suffered significant population declines (Jiguet et al., 2006). The study concluded that a bird species' thermal range is a reliable predictor of its resilience to extreme temperatures. This suggests that thousands of tropical forest bird species that currently experience limited temperature variation will be among the most susceptible birds to the physiological effects of warming climates and heat waves. Similar studies are needed in the tropics. Where the frequency of such heat waves increases, selection pressure will mount and will favor birds that can cope, with thermal generalists likely having an advantage (Boyles et al., 2011).

Birds of lower trophic levels, such as frugivores and granivores, tend to have higher BMRs than those at higher trophic levels, such as insectivores (Sabat et al., 2009). Migratory bird species, which experience a wider range of temperatures, also have higher BMRs (McNab, 2009). On the other hand, non-passerines, flightless birds, island birds, and tropical birds tend to have lower BMRs (McNab, 2009; Wiersma et al., 2007). Because higher BMR enables the use of a wider range of thermal environments, increases dispersal ability, and improves adaptability to climate change (Bernardo et al., 2007), birds with lower BMR (e.g., dusky antbird, *Cercomacra tyrannina* or wedge-billed woodcreeper, *Glyphorhynchus spirurus*) are at a disadvantage. Most studies of birds' responses to climate change focus on migratory, mainland passerines of temperate habitats. This limited focus suggests that our understanding of birds' metabolic capacity to adapt to climate change could be overly optimistic and unrealistic for most of the world's sedentary, tropical bird species.

The speed and magnitude of a bird's BMR response may also depend on the prevailing temperature of its environment (McKechnie, 2008). Tropical montane birds that experience lower temperatures (e.g. Papuan mountain-pigeon, *Gymnophaps albertisii*) are likely to show slower responses to future climate change than lowland species. Yet, BMR responses may be critical: even risk-taking and predator avoidance behavior have been shown to be influenced by BMR (Moller, 2009). BMR variability's importance as a shaper of birds' responses to climate change demonstrates why studies of tropical birds' physiological responses to climate change constitute an urgent research priority.

4. Role of mobility and migration

Due to their high mobility, birds are better able to disperse in response to climate change than many other organisms. However, even seemingly rapid distribution shifts may not be sufficient to track climate change (Devictor et al., 2008). Most tropical bird species and their habitats will not be able to shift fast enough or far enough to track their preferred climate envelopes, particularly in flat, lowland areas (Loarie et al., 2009).

Long-distance migratory bird species that have high mobility are expected to suffer fewer extinctions from climate change than sedentary species (Şekercioğlu et al., 2008). Higher mobility provides migratory birds with a higher capacity to deal with global change than sedentary (non-migratory) birds. Such sedentary species are already 2.6 times more threatened with extinction than are long-distance migratory bird species (Şekercioğlu, 2007). Long-distance migratory birds comprise less than a fifth of all the bird species (Şekercioğlu, 2007), so if non-migratory species prove to be relatively more threatened by climate change (Cox, 2010), this will affect most of the world's bird species. Based on 60 different scenarios to estimate bird extinctions that will result from a combination of climate change and habitat loss by the year 2100, Şekercioğlu et al. (2008) showed that sedentary birds are five times more likely to go extinct in the 21st century than are long-distance migrants.

However, some migratory bird species are also highly vulnerable to climate change. Many migratory birds spend most of the year on their wintering grounds in the tropics. Migratory birds that winter in the tropics have their own unique challenges, as they are exposed to the multiple effects of climate change on their breeding grounds, wintering grounds, and during their migrations (Ahola et al., 2007; Both et al., 2006; Huntley et al., 2006). Climate change may result in range reductions at both ends of the journeys of some migratory species such as lesser whitethroat (*Sylvia curruca*) and garden warbler (*Sylvia borin*) (Doswald et al., 2009). Climate change could also render key stopover sites unsuitable, and extend the overall migratory journey of some birds (Huntley et al., 2006). Breeding bird surveys showed that while sedentary bird species and short-distance migrants in Denmark increased since 1974, numbers of long-distance trans-Saharan migrants declined 1.3% per year (Heldbjerg and Fox, 2008).

An estimated 2.1 billion birds migrate every year between Europe and Africa alone (Hahn et al., 2009). Shifts and reductions in the wintering ranges of migratory birds may have impacts on tropical bird communities as well. Barbet-Massin et al. (2009) project that by 2100, climate change could cause the ranges of 37 of 64

trans-Saharan migrants (e.g. collared flycatcher, *Ficedula albicollis* and thrush nightingale, *Luscinia luscinia*) to shrink, as well as shift by an average 500 km. This could result in major decreases in the richness of bird communities in Africa (Barbet-Massin et al., 2009).

If migratory birds experience increasingly severe food shortages on their wintering grounds due to reduced rainfall, this could affect non-breeding performance and influence their time of departure for their breeding grounds (Studds and Marra, 2007). Changes in tropical wintering habitats also create a disadvantage for migrants' subsequent performance on their breeding grounds. Female American redstarts (*Setophaga ruticilla*) wintering in high-quality habitat produce more young and fledge offspring weeks earlier than females from poor-quality wintering habitat (Norris et al., 2004). Some migratory birds that are unable to synchronize their migratory timing with climate change driven shifts in phenology already demonstrate negative consequences (Ahola et al., 2007; Both et al., 2006). Birds already adapted to environments with unpredictable climates are also likely to better tolerate climate change (Canale et al., 2010). This includes nomadic birds that can move large distances when faced with droughts, floods, and other extreme weather events.

5. Interspecific interactions and indirect effects

Most models of climate change effects on future species distributions do not take into consideration interactions between species because data regarding such interactions are limited. However, changes in biotic associations can be as important as changes in temperature and precipitation, if not more so (Dunn et al., 2009; Jankowski et al., 2010).

Preston et al. (2008) showed that including biotic associations in climate change models reduced habitat availability for endangered California plant, butterfly, and bird species by 68–100%, as opposed to a climate-only model. The potential habitat of the threatened coastal California gnatcatcher (*Polioptila californica californica*), a habitat specialist restricted to semi-arid coastal scrublands in California and Mexico, would be greatly reduced under a warmer climate, compared to models that considered climate only, without accounting for this kind of biotic factor (Preston et al., 2008). They indicated that incorporating biotic interactions in climate models is especially important for habitat specialists and species strongly dependent on other species. Such traits typify tropical bird communities. Between-species interactions, mostly unknown to ecologists, will influence how climate change affects tropical birds.

Indirect effects of climate change that act via interspecific interactions have been little studied, but can be surprising and substantial. The insights garnered from findings of species-poor temperate studies do not bode well for tropical bird communities with more species, more interactions, and more possibilities for the interactions to go wrong. Climate-induced changes in the temporal partitioning of the breeding period can lead to changes in interspecific competition that have fatal consequences (Ahola et al., 2007). For example, the closer pied flycatchers breed in time to their sedentary competitor, the great tit (*Parus major*), the more likely the flycatchers are to attempt to take over tit nests (Ahola et al., 2007). These attempts can be fatal for flycatchers. Since climate change affects breeding phenology, it could alter the balance of these competitive interactions.

Similarly, in the tropical cloud forests of Monteverde, Costa Rica, increased temperatures caused a reduction in dry season mist frequency and in the lifting of the cloud base (Pounds et al., 1999). This, in turn, has led to some lowland bird species expanding their distributions upwards. In the same region, Jankowski et al. (2010) showed that interspecific aggression was a critical factor in constraining the elevational ranges of forest songbirds. The high elevation specialist slaty-backed nightingale-thrush (*Catharus fuscater*)

was the most submissive of the species tested. This indicates that the slaty-backed nightingale-thrush is likely to lose ground to the more aggressive, lower elevation black-headed nightingale-thrush (*Catharus mexicanus*) if the latter species expands to higher elevations in response to the warming temperatures in the region (Jankowski et al., 2010). An estimated one third of threatened tropical mountain species have ranges that border with congeners that are widespread, lower-elevation species (Jankowski et al., 2010). One hypothesis holds that climate warming could permit lowland tropical species, if they are relatively aggressive and therefore dominate their upland congeners, to expand upslope, forcing subordinate higher-elevation species to retreat upslope in their shrinking mountaintop ranges (Jankowski et al., 2010). However, if a high-elevation species is dominant it may hold the upslope shifts of competitors in check even as climates warm.

Novel inter-species interactions due to climate change are not limited to birds. One of the most fascinating and unexpected examples of negative climate change impacts on songbirds has been caused by edible dormice (*Glis glis*) in the Czech Republic (Adamik and Kral, 2008). With increasing spring temperatures, the cavity-nesting dormice are emerging earlier from winter hibernation. However, only one of four cavity-nesting bird species in the region advanced its breeding dates. This combination has led to high brood losses caused by intensified nest predation by dormice, whose populations have increased due to favorable weather combined with good seed mast years. As Adamik and Kral (2008) point out, "changes in climate might affect organisms at various trophic levels with often unexpected outcomes... [and] ...species most at risk are those at different trophic levels that do not shift at the same rate or in the same direction as their food resources, predators or competitors". Populations of forest snakes, which are major predators of tropical forest birds, nestlings and eggs, may increase to the detriment of bird populations; however, this relationship has not yet been explored by ecologists.

Effects of climate change on tropical seabirds have received little attention, but changes in sea surface temperatures can reduce marine prey availability for seabirds (Becker et al., 2007; Le Bohec et al., 2008; Watanuki et al., 2009). Many seabird species have a critical sea surface temperature threshold, above which (as often is the case during El Niño years) the lack of prey leads to unsustainable chick mortality (Boersma, 1998; Erwin and Congdon, 2007). In addition, age and sex-related variation in climatic influence on demographic parameters of tropical seabirds (Oro et al., 2010) can lead to different effects of climate change on different ages and sexes of the same species. Reduced prey directly affects seabird productivity (Cury et al., 2011), but it can also influence impoverished island ecosystems, where seabird droppings (guano) provide critical nutrient inputs to these ecosystems (Croll et al., 2005; Şekercioğlu, 2006b). An interesting example of climate change-induced interactions affecting a tropical bird community comes from seabird nesting islands near the Great Barrier Reef of Australia. A decrease in seabird prey due to an increase in sea-surface temperatures has also meant a reduction in seabirds, in their guano, and in the resulting nutrient input for plants on seabird nesting islands (Greenslade, 2008). With fewer nutrients, native *Pisonia* trees become more susceptible to outbreaks of a sap-feeding herbivore and its attendant ant (Greenslade, 2008). In turn, the loss of *Pisonia* trees reduces important nesting sites for seabirds like black noddies (*Anous minutus*) and wedge-tailed shearwaters (*Puffinus pacificus*), illustrating the complicated web of interactions through which climate change effects reverberate.

5.1. Ecosystem functions and services

As the above example illustrates, tropical bird species not only interact with one another, but also provide key ecosystem functions

and services by interacting with other organisms such as seed dispersers, pollinators, predators, nutrient dispersers, scavengers, and ecosystem engineers (Şekercioğlu, 2006a; Wenny et al., 2011). Avian ecological functions and ecosystem services are important in many tropical communities, but the influence of climate change on these services is little understood. Bird pollination is more important in the tropics than in the temperate zone, except in Australia, where bird pollination peaks in the temperate regions (Ford, 1985). Although bird pollination has often been considered relatively unimportant in comparison to insect pollination, climate change may increase its importance. This is exemplified by some Caribbean islands, where bird pollination increased with higher rainfall, while insect pollination decreased (Gonzalez et al., 2009).

Ecosystem functions and services become even more important with the increasing variability climate change brings. Mazia et al. (2009) showed that during the wet year of an ENSO cycle, excluding insectivorous birds such as thorn-tailed rayaditos (*Aphrastura spinicauda*) and white-crested elaenias (*Elaenia albiceps*) from tree saplings in an Argentinean *Nothofagus* forest resulted in twice as much leaf damage by insects as was observed during a drought year. These results indicate that large-scale climatic events can influence the strength of trophic cascades, but our understanding of such variable effects on ecosystem function, especially in the tropics, is limited (Van Bael et al., 2004).

6. Destructive synergies: climate change exacerbates other environmental stressors

Climate change is expected to physiologically stress organisms and force species and entire communities to shift their distributions. Yet climate change will also affect biodiversity by synergistically interacting with, and often exacerbating, other environmental stressors such as habitat loss, emerging diseases, invasive species, hunting, or pollution (Brook et al., 2008; Laurance and Useche, 2009; Reino et al., 2009). However, these synergies are often overlooked in climate change research. One review found that about half of the papers in climate change literature considered climate change separately from other threatening processes (Felton et al., 2009). Tropical birds seem to be particularly vulnerable to the synergisms between climate change and hunting, and between climate change and habitat loss in the form of agriculture (Laurance and Useche, 2009). Nevertheless, remaining uncertainties about temperature and precipitation projections for the tropics (Vera et al., 2006) and the responses of tropical forests to changes in CO$_2$, temperature, and rainfall (Feeley et al., 2007; Laurance and Useche, 2009; Phillips et al., 1998) limit our ability to predict future synergies.

6.1. Habitat loss

Extensive habitat loss in the tropics will continue to interact with and exacerbate the effects of climate change on tropical birds, especially endemic and range-restricted species (Jetz et al., 2007; Şekercioğlu et al., 2008). Şekercioğlu et al. (2008) quantified the relative impact of habitat loss on bird extinctions caused by climate change by combining IPCC, 2007 climate change scenarios (IPCC, 2007) with Millennium Ecosystem Assessment habitat loss scenarios (MA, 2005). In the "worst case" surface warming estimate of 6.4 °C by 2100, (which may yet be an underestimate (Stainforth et al., 2005)), Şekercioğlu et al. (2008) estimated that the worst case habitat loss estimates in the "Order from Strength" scenario (MA, 2005) could result in over 2500 land bird extinctions and could increase bird extinctions from climate change by about 50% when compared with the best-case estimates from the "Adaptive Mosaic" scenario (Fig. 5). Furthermore, the authors showed the sensitivity of bird extinctions to the combined effects of climate change and habitat loss to be quadratic. This means that
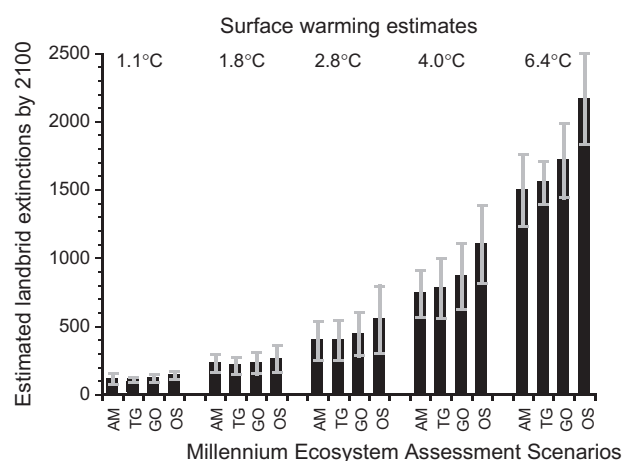
Fig. 5. Number of world landbird species projected to be committed to extinction by 2100 on the basis of the estimates of various surface-warming estimates (IPCC, 2007), three possible shifts in lower elevational limit, and Millennium Assessment habitat-change scenarios (MA, 2005; AM, adaptive mosaic; GO, global orchestration; OS, order from strength; TG, technogarden). Bars show the results of an intermediate amount of elevational shift, where lower limits of 50% of lowland (⩽500 m) bird species are assumed to move up in response to surface warming. "Error bars" indicate best-case (0% move up) or worst-case (100% move up) climate warming scenarios. Reprinted with permission from Şekercioğlu et al. (2008). Climate change, elevational range shifts, and bird extinctions. *Conservation Biology* 22, 140–150.

extinctions increase faster than would be expected from a one-to-one relationship with surface warming. With increasing amounts of baseline warming and habitat loss, each additional °C of surface warming is expected to result in more bird extinctions, ranging from approximately 100 to 500 additional extinctions (Şekercioğlu et al., 2008). The number of extinctions rapidly increase past 1.8 °C of surface warming, as do the additional extinctions from the climate change-habitat loss interaction effect. This emphasizes the critical importance of restraining global warming to less than 2 °C by 2100. However, an analysis of the most recent emissions pledges during the December 2011 international climate-change negotiations in Durban indicates that the world is headed for 3.5 °C of warming by the year 2100 (Tollefson, 2011). Warming of 3.5 °C could result in 600–900 of nearly 8500 land bird species worldwide being committed to extinction (Şekercioğlu et al., 2008; Fig. 5), in the absence of any conservation action. 87% of all bird species and 89% of all land bird species occur in the tropics (Çağan H. Şekercioğlu, unpublished data).

Vegetation also displays a non-linear sensitivity to lapse rate. Lapse rates are lower in the tropics, especially in more humid areas, and this implies that tropical forests will be forced to shift further than temperate forests for every °C of surface warming (Şekercioğlu et al., 2008). However, most models of climate change effects on community shifts are based on data from temperate ecosystems (e.g. Chen et al., 2011), where lapse rates tend to be higher.

6.2. Hunting

Other factors, such as hunting, also interact with climate change and exacerbate its effects on tropical bird populations. Traill et al. (2009, 2010) developed one of the few spatially explicit population viability models for a tropical waterfowl species, the magpie goose (*Anseranas semipalmata*), to simulate population responses to the synergy of hunting, climate change, and increased disease prevalence due to climate change. Without hunting, the simulated disease outbreaks (Traill et al., 2009) or wetland loss due to sea level rise

(Traill et al., 2010), even when they increased due to climate change, rarely threatened meta-population viability, and only when there was high mortality and regular disease outbreaks. With current hunting pressure, however, the population response switched from a threshold response to a linear one, and the threat to meta-population viability from a disease outbreak or wetland loss increased significantly. It is necessary to consider the synergies of climate change with various factors simultaneously, rather than in isolation.

6.3. Invasive species

While climate change poses a crisis for many specialized tropical bird species, it presents opportunities to other, more invasive species that will expand their ranges into more temperate regions (Reino et al., 2009). The expansion of invasive species will result in new communities and ecological interactions with consequences that are often hard to predict, but are likely to be negative for some species. For example, rose-ringed parakeets (*Psittacula krameri*), are highly social and could aggressively compete for food and nesting cavities with other birds (Pithon and Dytham, 2002). Further expansion of their distributions in Europe could come at the expense of other native cavity-nesting species (Leech and Crick, 2007). Other tropical and subtropical bird species that are either introduced by people or expand their ranges naturally are becoming established in new localities, where native birds now have to compete with them (Bohning-Gaese and Lemoine, 2004).

6.4. Emerging diseases and shifting disease vectors

Increases in the prevalence of infectious diseases provide some of the most important examples of a destructive synergy with climate change effects. Changes in temperature, humidity and precipitation will affect many pathogens, and climate warming is likely to "…increase pathogen development and survival rates, disease transmission, and host susceptibility… [Most] host-parasite systems are predicted to experience more frequent or severe disease impacts with warming" (Harvell et al., 2002). Some recent examples from the tropics include the expansion of avian malaria with increasing temperature (Williams, 2010) and climate change (Garamszegi, 2011), *Plasmodium* (malaria) and *Trypanosoma* avian blood parasites being linked to temperature and rainfall (Sehgal et al., 2011), and a rise in coral diseases (Harvell et al., 2002). An expansion of malaria-carrying mosquitoes into Hawaiian highland forests could threaten many Hawaiian endemic bird species (e.g. the rare and declining akiapolaau, *Hemignathus munroi*, endemic to the island of Hawaii). Native birds of the Hawaiian Islands had no experience with malaria or mosquitoes before they were introduced to the islands in the nineteenth century (Freed et al., 2005). With increasing warming, the elevational distributions of the 13 °C isotherm (above which malaria does not occur) and the 17 °C isotherm (below which malaria is year-round and high-risk) are expected to move upslope (Atkinson and LaPointe, 2009). This is expected to greatly reduce the disease-free refugia in high-elevation forest habitat (by up to 96%), where malaria is low-risk or is found only seasonally (Atkinson and LaPointe, 2009). As avian malaria is found throughout the world, similar climate-related increases in disease prevalence among tropical birds (such as montane endemics) will be widespread, and will be most threatening to species with little or no evolutionary experience of various parasites. However, there are few long-term studies on the subject.

7. Seasonality and variability

The stereotypical view of tropical bird life history has been that of a lack of seasonality compared to that of temperate birds. However, detailed and long-term studies are revealing that many species, such as Panama's spotted antbirds (*Hylophylax naevioides*), experience seasonality due to wet-dry season cycles (Tye, 1992; Wikelski et al., 2003, 2000). One of the few known examples of tropical birds' phenological responses to climate variation comes from Cameroon, where individual bird species switch from breeding in the wet season in the lowlands to breeding in the dry season in the highlands (e.g. little greenbul, *Andropadus virens* and African thrush, *Turdus pelios*). This observation suggests the types of responses possible under climate change (Tye, 1992).

In mountains, heavy rainfall, high humidity, and low temperatures during the wet season often prevent birds from breeding, including species that are more typical of the drier and hotter lowlands, where they normally prefer to breed in the wet season (Tye, 1992). It is likely that many tropical bird species will shift their breeding periods in response to changes in temperature and rainfall regimes. If climate change results in a mismatch between a critical reproductive cue such as the photoperiod (Wikelski et al., 2000) and the optimal temperature and rainfall regime for reproductive success, population declines may be the result. Changes in the frequency and severity of tropical storms also have important implications for the ecology and conservation of tropical birds (Boyle et al., 2010).

Research on the effects of climate change has almost entirely focused on the changes in average temperature, and to a lesser extent, in rainfall. However, changes in weather events (Reside et al., 2010) and seasonality can be equally important, particularly in the tropics, where seasonality is less pronounced than in the temperate zone and where organisms are adapted to fewer climatic fluctuations and extremes. Nevertheless, some tropical forests may be able to adapt to changes in seasonality better than temperate forests because the relative unpredictability of seasonality in the tropics may have selected for more flexible responses to seasonality (Corlett and LaFrankie, 1998). Although temperatures show relatively little variation in the tropics, rainfall shows some seasonality even in the wettest tropical areas, and many tropical regions experience a distinct dry season that results in periods of low food availability.

For birds and other animals, however, increases in rainfall seasonality and consequent increases in resource bottlenecks are likely to exacerbate the expected impacts of changes in temperature and precipitation regimes (Williams and Middleton, 2008). This is particularly the case for extended dry periods when birds experience a scarcity of food resources such as nectar, fruit, and insects. As many tropical birds time their breeding with increased resource abundance typical of the wet season (e.g. white-throated thrush, *Turdus assimilis*), longer and less predictable dry seasons, droughts, and seasonal asynchrony as a result of climate change can affect the migrations and reproductive performance of tropical birds, lead to the mistiming of life history events, and potentially result in population declines (Corlett and LaFrankie, 1998; Şekercioğlu, 2010b; Williams and Middleton, 2008). Greater climatic seasonality, especially of the dry periods, is thought to be linked to lower bird densities in the bird communities of Australia's Wet Tropics rainforest (Williams and Middleton, 2008), supporting the hypothesis that more climatically-stable areas are more diverse (Pianka, 1966). Long-distance migratory birds wintering in the tropics can also experience disadvantages, such as reduced body mass prior to migration, due to drier conditions in wintering habitat (Smith et al., 2010).

A different challenge faces the Mauritius kestrel, *Falco punctatus.* This formerly critically endangered island endemic breeds later in wetter springs. Senpathi et al. (2011) found that spring rainfall is now 60% more frequent in their study area than it was in 1962, and for each extra day of rainfall, birds delayed breeding by half a day. Later breeding has negative repercussions for Mauritius kestrel nesting success, because it increases the breeding risks associated with climate conditions later in the reproductive season: nests are more likely to be flooded, exposing chicks to hypothermia; and

adults are more likely to face adverse hunting conditions due to wet weather (Senpathi et al., 2011).

Because we have limited understanding of how changes in rainfall seasonality will effect tropical bird populations and species richness of bird communities, more tropical studies are needed.

7.1. Extreme weather events

Global warming, by increasing the amount of energy and humidity in the climate system, also increases climatic variability. This is likely to increase the magnitude and frequency of extreme weather events, such as heat waves, droughts, floods, cold spells, "once-in-a-century" storms and tropical cyclones (IPCC, 2011). Such extreme weather events can be as destructive to plants and bird communities as higher average temperatures and changes in rainfall patterns, if not more so. It may be possible for a bird species to cope with a 2 °C change in average temperature, but if that results in an increase in extreme weather events that destroy critical habitat or make foraging impossible (Boyle et al., 2010), the species can decline towards extinction (Martinez-Morales et al., 2009). The balance of evidence points to increases in the numbers of intense tropical cyclones (though tropical cyclone frequency could decrease overall). This would predominantly affect tropical bird communities, especially species living in coastal and island habitats (Lee et al., 2008; Martinez-Morales et al., 2009; Safford and Jones, 1998), like the Cozumel thrasher (*Toxostoma guttatum*). Furthermore, habitats damaged by tropical cyclones may be very slow to recover if their regeneration depends on seed dispersal by birds (Hjerpe et al., 2001). At present, few population models account for the adverse effects of more frequent or intense extreme weather events.

El Niño and La Niña cycles can have particularly dramatic effects on tropical forest birds, depending on the extent and severity of aseasonal rainfall and droughts that result from these inter-annual patterns of climate variation (Jaksic, 2004). Some tropical birds, especially granivores and insectivores, can respond rapidly to the effects of El Niño-driven rainfall changes, including increases in plant and insect productivity. For example, on the Galapagos Islands, land birds thrive during El Niño years while seabird breeding success plummets. Long-term studies are needed to understand how these responses affect bird population cycles (Jaksic, 2004).

Fires are also extreme climate-related events with major repercussions for wild bird populations. Fire frequency and area burned is expected to increase in many world regions, both as a result of climate change and human alteration of habitat. One study of tropical savannah species in northern Australia indicated that an increase in fire frequency late in the dry season would have a negative effect via decreases in predicted ranges of almost all bird species (98% of those studied) restricted to this habitat (Reside et al., 2012). In Papua New Guinea, a 2007 research expedition also documented the vulnerability to fire of the Papuan harrier (*Circus spilothorax*), which breeds in damp grassland and floodplains at the start of the dry season. Two of the first nests ever recorded were consumed by fire within five weeks of their discovery. In response to the risk of higher fire frequency on Papua New Guinea under climate change, it has been proposed that these harriers be listed as vulnerable (Simmons and Legra, 2009). Tropical forest fires are becoming larger, more frequent and severe, even in forests where they were formerly infrequent (Cochrane, 2003).

8. Discussion

Change has been a feature of Earth's climate throughout time. However, although past climate change has often been of lesser magnitude and speed, it has nevertheless resulted in major upheavals in the planet's ecosystems and dependent organisms (Huntley et al., 2006). Even in the most rapid past episodes of natural climate change during the transitions between glacial and interglacial periods (Schneider, 1989), when some local temperatures rose as much as 8 °C in a few decades (IPCC, 2007), the average global temperature increased by about 5 °C over 5000–7000 years (Huntley et al., 2006). The current rate of global temperature increase is extremely rapid by comparison – one or two orders of magnitude greater than that observed in the past.

The planet's average temperature is expected to increase by 1.1–6.4 °C this century, according to the Intergovernmental Panel on Climate Change (IPCC, 2007). The potential role of little-known or even unknown feedback loops makes the upper limit hard to predict, and an average temperature increase of up to 11 °C may be possible (Stainforth et al., 2005). Already, most tropical climates are the warmest they have been in the past two million years (Bush, 2002) and "...global climate is thus projected to be at least as warm, by the end of the present century, as it has been at any time during the evolution of most of the world's present diversity of organisms" (Huntley et al., 2006).

Some argue that species will simply adapt as they have done during past episodes of climate change. This argument is unrealistically optimistic not only because of the large magnitude and high rate of global change, but also because species must now contend with more than 7 billion human beings who consume most of the planet's resources and eliminate wildlife habitats. Human population is expected to reach 9 billion by 2050 and this is expected to lead to further land clearing (MA, 2005) and greenhouse gas emissions (IPCC, 2007). This will further complicate other species' ability to carry out range shifts, the response thought to have dominated biodiversity's reaction to past episodes of climatic change (Huntley et al., 2007). Biodiversity is highest in the tropics, but the numbers of subsistence and smallholder farmers are also the greatest (Hannah et al., 2002). Although these people will be highly exposed to climate change effects, their ability to cope will be limited. Their efforts to adapt will lead to further clearance or degradation of forests and other habitat (Easterling et al., 2007).

Although a recent meta-analysis has shown that in areas of greatest warming average latitudinal shifts of species have been generally adequate to track temperature changes (Chen et al., 2011), due to the scarcity of suitable data, only 2 out of 22 studies meta-analyzed were from the tropics (15 of 36 comparisons were from a single UK study), and neither tropical study was on birds. Compared to temperate species that often experience a wide range of temperature on a yearly basis, tropical species, especially those limited to tropical forests with stable climates, are less likely to keep up with rapid climate change. Projected climate change will lead to conditions unprecedented for millions of years, and as a result, bird species' equator-ward limits (and likely their lower elevation limits) may retreat roughly in equilibrium with climate change, whereas their pole-ward (and higher elevation) limits are likely to lag behind (Huntley et al., 2006). Range expansion typically requires the concomitant expansion of bird habitat, which generally entails the range expansion of plants that may be long-lived and slow to disperse. Range expansion of vegetation may be relatively slow, even across suitable terrain not occupied by people. Together, these factors indicate that habitat expansion to newly suitable areas will not take place quickly enough to make up for habitat losses due to climate change, especially for relatively sedentary tropical forest species. Rapid range reductions will result, and equatorial populations with higher genetic diversity will be among the first ones to go (Huntley et al., 2006; Şekercioğlu et al., 2008).

8.1. Future projections and models

Climate-based models of the geographic distributions of species and vegetation are constantly improving, while achieving finer resolution, improved representation of key processes, and more

accurate depiction of oceanic circulation (Karnauskas et al., 2012). However, relatively few climatic stations are available in the tropics, and tropical climate models based on limited data can be a source of uncertainty that may affect the outcomes of species distribution models (Soria-Auza et al., 2010). The utility of such models also hinges on good quality species distribution data. This is particularly challenging when it comes to the often poorly-known distributions of tropical species, some of which may be based on a handful of points from specimens collected a century ago. Jetz et al. (2008b) showed that the distributions of hundreds of bird species in relatively well-known North America, South Africa, and Australia are overestimates. Critically, the level of overestimation was higher for threatened, range-restricted, and specialized birds – those most vulnerable to global change. Therefore, detailed datasets with good data on absence as well as presence is preferable (Huntley et al., 2006). As a further challenge, many models confound occurrence with the probability of detection. To address this, recently developed occupancy models can use basic presence/absence survey data from citizen science projects like bird atlases, while accounting for probability of detection (Altwegg et al., 2008). However, the kind of detailed data provided by bird atlases usually requires hundreds or thousands of dedicated, disciplined, knowledgeable, and well-trained amateur and professional ornithologists – personnel not available in most tropical countries (see below). In these cases, the data from birdwatchers must be put to better use (Şekercioğlu, 2002; www.ebird.org; www.worldbirds.org).

Another concern is that static climate models may be inadequate for mapping future ranges. In fact, even dynamic models may be inadequate in predicting species' ranges, which are also influenced by ecological processes such as species interactions, adaptation, and flexibility in life history (Schwager et al., 2008). Models need to do a better job in considering slowly-changing processes and mechanisms (Schwager et al., 2008) and incorporating species' interactions.

Globally, species with restricted distributions are concentrated in the tropics, and many of these species are already threatened with extinction (Stattersfield et al., 1998). In birds, decreasing range size due to habitat loss increases the likelihood of extinction due to climate change (Schwartz et al., 2006). To make matters worse, model fit also declines for species with smaller ranges, resulting in high uncertainty in predicting climate change extinctions in these species (Schwartz et al., 2006). Excluding these species from conservation management plans could result in their extinction. Conversely, mistakenly including species as threatened when they are actually not could lead scarce conservation resources to be squandered. Uncertainties like these apply even to well-known bird species of eastern United States (Schwartz et al., 2006), but the problems with predicting climate-change driven extinctions for little-known tropical bird species are much greater.

Extensive range shifts and species turnover are expected under climate change. Yet, substantially different model projections can result, depending on both the climate and species distribution models selected (Bellard et al., 2012). Species turnover in response to climate change, along with temperature and precipitation predictions, remain subject to large uncertainties (Diniz et al., 2009; Vera et al., 2006). Despite all the uncertainties involved, a recent comparison of 130 observed and 188 predicted ecological responses to climate change supported the predictions of high extinction risk (MacLean and Wilson, 2011); the corrected mean extinction probability of 10% for the predictions was actually conservative compared to the mean probability of 14% based on the empirical evidence.

8.2. The need for more tropical research

As is generally the case in ecology and conservation, the temperate zone has been the focus of most studies of climate change and most modeling exercises on the changes in species distributions. Fewer than 1% of the long-term climate change data sets come from the tropics (Rosenzweig et al., 2008) and far more tropical ornithological research is needed (Harris et al., 2011; Şekercioğlu, 2012). For example, the above-mentioned global overview of the shifts in species' elevational and latitudinal limits caused by climate change that included only Holarctic studies of birds (in Europe and North America; Chen et al., 2011). Even though most birds species are tropical (Tscharntke et al., 2008) and sedentary (Şekercioğlu, 2007), the lopsided concentration of researchers and long-term datasets in the developed countries of the temperate zone (Rosenzweig et al., 2008) have meant that most of our understanding of climate change impacts on birds is based on the studies of temperate birds that are largely migratory. To comprehensively understand the implications of climate change for avian ecology and bird conservation, many more long-term studies of tropical bird communities are needed (Perry et al., 2011), especially those that consider responses along elevational gradients (e.g. Laurance et al., 2011; Pounds et al., 1999; Shoo et al., 2005a). This necessitates increased funding to establish more long-term, multi-site field research projects (Şekercioğlu, 2012).

Confronted with the relative scarcity of field studies on climate change, ornithologists have found innovative ways to investigate its effects (albeit mostly in temperate regions). They have analyzed differences in bird distribution data in successive field guides (Peh, 2007), probed the notebooks of nineteenth-century amateur naturalists (Primack et al., 2009; Willis et al., 2008), and amassed millions of data points collected by experienced birdwatchers who volunteer for citizen science projects such as the US Breeding Bird Survey (Niven et al., 2009), the European Breeding Bird Atlas (Hagemeijer and Blair, 1997), and e-bird (www.ebird.org). However, amateur interest in birds is less prevalent in tropical countries. These nations are largely characterized by developing economies and less educated populations more concerned with survival than with birdwatching. Nevertheless, the appeal of birds is universal, interest in birds is growing in developing, tropical countries (Şekercioğlu, 2012), and birdwatching can also become a means towards a sustainable livelihood (Şekercioğlu, 2002). Given sufficient opportunity and motivation, people in tropical countries are likely to appreciate birds and rapidly learn to identify them (Paaby et al., 1991). Because most tropical households have low income thresholds, limited funds for research and monitoring can go a long way (Şekercioğlu, 2012). Field guides make bird identification accessible to most of the world's population. The birdwatching tourism market is also global; if people of tropical countries are provided with ornithological training, this can lead to careers that combine bird guiding and scientific data collection. In this way, locally based, long-term bird monitoring programs in the tropics could combine biodiversity monitoring, environmental education, raising local awareness, community-based conservation, and ecotourism development (Şekercioğlu, 2012). Such programs can be successful and cost-effective tools for job creation and poverty reduction in many developing countries.

8.3. The value of protected areas for tropical birds: planning for future change

We urgently need to understand how climate change will affect the capacity of protected areas to harbor species and communities (Willis et al., 2009). Especially in areas prone to drought, climatic extremes reduce food availability – and consequently, breeding success – and can therefore lead to widespread bird population declines even in large reserves (Mac Nally et al., 2009). By contrast, higher, cooler climatic refugia on tropical mountains are disproportionately important for restricted range species, and steep mountains, where human activity is limited, are often afforded

protection from human disturbance. For example, in the Wet Tropics of Queensland, the coolest part of the rainforest harbors 45% of endemic species (Shoo et al., 2011). Such climatically diverse tropical montane areas have buffered cold-adapted species from extinction during past interglacial periods of unusually warm global temperatures (Ohlemuller et al., 2008). However, climate change will disproportionately affect the narrow climatic zones that characterize these centers of species rarity. This will jeopardize many restricted-range species (Ohlemuller et al., 2008), such as the Mt. Apo sunbird (*Aethopyga boltoni*) in the Philippines or the regal sunbird (*Nectarinia regia*) in East Africa (Fig. 3).

We must design networks of protected areas with climate change in mind because this will be critical for conservation (Shoo et al., 2010). The Important Bird Area (IBA) network of Africa includes 1230 sites essential for maintaining populations of priority species (Hole et al., 2009). Climate-induced shifts in the distributions of the breeding birds of sub-Saharan Africa are expected to result in 42% of IBAs showing >50% species turnover (Hole et al., 2009). However, only 7 or 8 priority species' preferred climatic envelopes are projected to be entirely lost from the IBA network, and about 90% of priority species should retain suitable climatic space somewhere. Nonetheless, sophisticated conservation plans will be fruitless unless they are applied effectively in collaboration with local people and decision-makers. Equally, these plans will rely on improvements to landscape connectivity and efforts that make the human-dominated landscapes surrounding protected areas more hospitable to bird populations.

8.4. Research and management

Our limited knowledge of climate change impacts hinders our ability to measure, predict, and prepare for the growing effects of climate change on tropical ecosystems and bird populations (Laurance et al., 2011). Research is urgently needed in the following four main areas: species ecology, climate change impacts on species, range shifts, and management action (Miller-Rushing et al., 2010).

To create effective conservation management plans, it is critical to collect basic ecological data, such as range size, habitat needs, important interactions, evolutionary biology, and climate sensitivity. This data collection must be prioritized and funded (Lankau et al., 2011; Şekercioğlu, 2012). In addition, models that predict climate change impacts must be improved. More accurate models are particularly important to project where different vegetation types and their dependent organisms will move. This will help identify, protect and (in some cases) allow for the purchase of areas where species will shift, along with the habitat corridors that may enable them to do so.

While conservation ecologists should increase their research on tropical birds, conservation practitioners should use an adaptive management framework to mitigate climate change effects on tropical bird communities. Adaptive management will be critical to reduce tropical bird extinctions from climate change. Managers need to publish their findings regularly, so that the lessons learned can be shared and used to improve conservation efforts. This is critical to the success of the adaptive management framework, comprising "the identification of management questions and goals, implementing management practices, testing the effectiveness of the practices, and re-evaluating and revising the practices" (Miller-Rushing et al., 2010).

The first step is to identify and monitor the populations and species at greatest risk from climate change. Long-term management of the designated populations, species, and their habitats must then follow, including new and expanded protected areas, and corridors based on projections of their ranges. Where possible and cost-effective, restoring lands degraded by climate change (or

other factors) in essential localities will bolster tropical bird populations and will buy time for birds to shift to more suitable areas. Finally, for some highly sedentary tropical bird species threatened with extinction, assisted migration may be necessary (Hewitt et al., 2011). This case for capture and relocation of individuals to more suitable localities may be particularly applicable to many tropical forest understory species, birds on low tropical mountains, low-lying island specialists, and sedentary birds whose current and future ranges are not connected.

Nevertheless, such efforts will be temporary fixes if we fail to achieve immediate societal change to reduce consumption, to control the emissions of greenhouse gases, and to stop climate change, in combination with having effective conservation areas that enable organisms to shift in response to climate change that is already happening. Otherwise, we face the prospect of an out-of-control climate that will not only lead to enormous human suffering, but will also trigger the extinction of countless organisms, among which tropical birds will be but a fraction of the total.

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