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Bird conservation in tropical ecosystems: challenges and opportunities

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"What would the world be, once bereft of wet and of wildness?"

Gerard Manley Hopkins

Introduction

Bird conservation is a global mission but most of the key battles are being played out in the tropics. Tropical ecosystems are generally under greater pressure than their temperate counterparts from human population growth, agricultural expansion and a host of related factors. They also support 87% of bird species, many of them highly susceptible to habitat loss or climate change (Şekercioğlu et al. 2012). The concern that many tropical species are therefore destined for extinction has focused much effort towards setting global conservation priorities based on a minimum number of protected areas, often one per species (e.g. Rodrigues et al. 2004; Ricketts et al. 2005). However, this approach is founded on traditional conservation strategies developed in the temperate zone,

and the extent to which it can be applied to tropical birds remains unclear.

Here, we summarize the key attributes of tropical ecosystems and implications for bird conservation. First, we outline threats to key tropical environments. Then we argue that tropical species often differ from their temperate-zone counterparts in ways that pose novel challenges for conservation. We conclude that sustainable conservation of tropical birds and the ecosystem services they provide will be achieved only if attention is focused not merely on current snapshots of species distributions and protected areas but on biotic processes and interactions operating at larger spatial and temporal scales. To support these ideas, we consider (i) why and how tropical ecosystems work in different ways from temperate systems, (ii) the shortcomings of standard conservation strategies when applied to the tropics, and (iii) the

outstanding priorities for policy, practice and future research. The strategies we propose have broad relevance for the management of tropical diversity because birds have long been viewed as a model system for assessing conservation priorities, and act as flagships for numerous conservation programmes (Tobias et al. 2005).

Threats to tropical environments

Lowland tropical forests

Tropical forests support vast numbers of species. They also limit soil erosion, reduce floods, contribute to hydrological cycles, help to stabilize the climate, and generally play a major role in human well-being. Nonetheless, people are currently removing tropical forests at a stupendous rate: an average of 1.2% of rainforest area, equivalent to ~15 million hectares, is destroyed annually (Laurance 2008) (see Chapter 13). One view holds that this process is self-reinforcing, and therefore likely to accelerate, because deforestation opens previously remote regions to agriculture and development, and increases the impact of fires and hunting. An alternative view holds that such forecasts are unduly pessimistic because human populations will become increasingly urbanized, and primary forest loss will be offset by regrowth of secondary forests in depopulated areas (Wright & Muller-Landau 2006). Either way, the pressure on old-growth tropical forests is intense, and set to get much worse in future (Laurance 2006).

Over the next 50 years, the human population is expected to reach 9 billion, with an ever greater proportion climbing the socio-economic ladder (Laurance & Peres 2006). Demand for food is predicted to rise by 70–100% (Godfray et al. 2010), and global industrial activity may expand 3–6-fold over the same period (Soh et al. 2006). The scale of projected increases in overall and per capita consumption of food, timber and countless other products will further stimulate industrial drivers of tropical deforestation, such as cattle ranches, soy farms, paper mills, oil palm plantations, and major highways and infrastructure projects, all of which have expanded markedly during recent decades (Smith et al. 1993; Vargas et al. 2006). Biofuel production from food crops is expected to increase by 170% in the next 10 years (Fargione et al. 2010). Crucially, the spiralling demand for crops and commodities is likely to drive further degradation of large areas of remaining tropical forests, regardless of whether human populations decline in rural areas (Vargas et al. 2006; DeFries et al. 2010). All projections carry with them a degree of uncertainty, yet the precautionary principle dictates that we should prepare for a future in which lowland tropical forests are highly fragmented.

Tropical mountains

Tropical mountains offer hope for conservation because montane habitats often remain relatively intact, at least at higher elevations. They play an essential role as refuges for lowland biodiversity that may otherwise disappear in response to climate warming or habitat loss at lower elevations. They are also important hubs of bird diversification and endemism because of their isolation. However, adaptation to these higher elevation refuges is risky: tropical montane endemics have limited capacity to shift their ranges across unsuitable lowland habitats and are therefore particularly vulnerable to climate change (Şekercioğlu et al. 2008). Moreover, this risk is faced by precisely those species that are least affected by habitat loss in highly threatened lowlands (Pimm 2008).

Tropical islands

Tropical regions contain 45,000 islands over a minimum size of 5ha (Arnberger & Arnberger 2001). Each island supports relatively few species

but many of these are important in terms of rarity and uniqueness (see Chapter 12). Birds endemic to islands often have relatively small geographical ranges, having diverged from continental ancestors through isolation. This isolation has often resulted in the evolution of flightlessness, fearlessness and loss of immunity, rendering island birds poorly adapted to novel anthropogenic pressures, including habitat change and the introduction of alien predators and pathogens (Milberg & Tyrberg 1993). Because of these issues, the arrival of humans on islands in the tropical Pacific led to the disappearance of at least 2000 insular bird species (Steadman 1995). It is no surprise, therefore, that 88% of bird extinctions since 1600 occurred on islands, mainly in the tropics (Butchart et al. 2006).

Today, island birds are coming under increasing pressure from human exploitation and invasive species (see Chapter XX [Cross-ref invasives chapter]). For example, it is thought that various species of rat (*Rattus*) have been introduced, accidentally or otherwise, to 90% of the world's islands (Jones et al. 2008; Oppel et al. 2010). Other threats vary case by case. The popularity of some tropical islands as places to live or visit makes them susceptible to rapid coastal development, overfishing or disease. On St Lucia, for example, roughly 40% of habitat occupied by the white-breasted thrasher (*Ramphocinclus brachyurus*), an endangered species with a global population of roughly 1200 individuals, is slated for potential tourist development (Young et al. 2010). Likewise, Bataille et al. (2009) provide evidence that tourism drives the ongoing introduction of avian malaria vectors (e.g. *Culex quinquefasciatus*) from mainland Ecuador to the Galapagos Islands, transported by cruise boats and aeroplanes.

New insights into threats facing tropical avifaunas

The litany of threats outlined above is broadly familiar but its ultimate impact on birds remains debatable. BirdLife International (2000) predicted that 13% of bird species may be extinct or consigned to extinction within 100 years, most of them due to tropical deforestation and hunting. Given the scale of potential impact, the time is ripe for a more detailed assessment of the ecological processes underlying decline and extinction in tropical birds.

Demography and life-history

Tropical birds differ from their temperate-zone counterparts in numerous ways but three factors have a disproportionate impact on the survival of populations. First, a far larger proportion of tropical species are highly sedentary, presumably as a result of climatic (and thus resource) stability. For example, year-round territories are defended by only nine (4.5%) of 193 North American forest bird species, whereas the same figure rises to 379 (51%) of 739 Amazonian bird species (Salisbury et al. 2012). Second, tropical species have lower reproductive output. They tend to lay only two-egg clutches, whereas temperate birds lay 4–13 eggs per clutch (Jetz et al. 2008). Third, their ranges are often patchy and population densities low (Donlan et al. 2007). At one locality in Amazonian Peru, for example, 106 (35%) of 329 resident species occurred at densities of <1 pair/100 ha, with a median abundance (i.e. average population density) across all species of 2.5 pairs/100 ha (Terborgh et al. 1990). This contrasts with the last remaining primeval European forests, where the median abundance of >50 forest bird species is much higher, at 10–30 pairs/100 ha (Wesołowski et al. 2006). Indeed, median abundance of European forest birds often exceeds the maximum estimated population density in Amazonia (*Cercomacra cinerascens* at 20 pairs/100 ha), providing a striking illustration of the relative rarity of tropical birds.

This combination of low dispersal, low reproductive output and low population density suggests that tropical birds are more sensitive to habitat fragmentation or disturbance, and less able to recover after population bottlenecks (Stratford & Robinson 2005; Soh et al. 2006).

Most importantly, it implies that a far greater area of intact habitat is required to protect viable populations. Judging only by the population densities reported above, an area 4–12 times higher on average per species may be required. However, the added constraints of low dispersal and low reproductive output, as well as significant numbers of extreme low-density species, suggest that diverse tropical bird communities can only be conserved in much larger areas.

Dispersal and migration

The term 'sedentary' fails to convey the extreme dispersal limitation of insectivorous birds in tropical forests, many of which are unable or unwilling to cross relatively minor gaps such as roads (Stratford & Robinson 2005; Laurance et al. 2009). In experimental tests, 50% of rainforest understorey species struggled to cross 100 m gaps (Moore et al. 2008), and comparative studies suggest that thousands of tropical bird species face this problem (Stratford & Robinson 2005; Salisbury et al. 2012). This contrasts sharply with the situation in temperate-zone habitats where gap aversion is rare. Amongst European woodland birds, for example, even the wren (*Troglodytes troglodytes*) is able to cross broad (>100 m) gaps in habitat, as long as low vegetation is present.

Unsurprisingly, limited mobility is an overlooked determinant of extinction risk in birds. Two-thirds of the planet's bird species are sedentary, and 74% of sedentary species live exclusively in the tropics. Of sedentary species, 26% are globally threatened or near threatened with extinction, compared to 10% of migratory species (Şekercioğlu 2007). Projections of land bird extinctions expected from the combined effects of climate change and habitat loss also indicate that sedentary bird species are approximately five times more likely to go extinct by 2100 than migratory birds (Şekercioğlu et al. 2008). This partly reflects the disadvantages of a sedentary lifestyle when it comes to tracking moving climate optima. Despite the greater risks

to tropical sedentary bird species, they have generally been neglected in comparison to northern hemisphere migratory species that have laws and conventions dedicated to them (e.g. Neotropical Migratory Bird Conservation Act in the USA). For example, between 1990 and 2007, international agencies provided the island of Hispaniola (i.e. the Dominican Republic and Haiti) with more than $1.3 million for migratory bird research, compared with only $300,000 for the study of resident birds, including several rare endemics (Latta & Faaborg 2009).

Although year-round territorial systems make up the largest component of tropical avifaunas, a different set of risks is faced by many frugivores and nectarivores. Telemetry studies show that these birds are typically mobile because they track patchy food resources. Unlike temperate-zone birds, however, they are often unable to cross degraded landscapes. Classic examples include elevational migration in white-ruffed manakins (*Corapipo altera*) (Boyle 2008) and unpredictably complex annual movements over hundreds of kilometres in the three-wattled bellbird (*Procnias tricarunculata*) (Powell & Bjork 2004). In effect, these movements compound the challenges of designing effective protected area networks because isolated reserves will fail to provide sufficient coverage for many species.

Physiological constraints and preferences

Most tropical birds experience lower climatic variability than do their temperate-zone counterparts, both within and between years (Ghalambor et al. 2006). They are therefore thought to have lower thermal plasticity (Stratford & Robinson 2005). The evidence from a geographical study of rufous-collared sparrows (*Zonotrichia capensis*) supports the hypothesis that populations in stable environments are less able to adapt to novel environmental conditions (Cavieres & Sabat 2008). Moreover, there are good reasons to expect tropical birds to be relatively intolerant of temperature

fluctuation: in particular, they have lower basal metabolic rates (BMR; Wiersma et al. 2007; McNab 2009), whereas species with higher BMRs are more adaptable to climate change (Bernardo et al. 2007). In general, therefore, tropical birds are likely to be constrained by narrower environmental niches, reduced tolerance of thermal stress and habitat change (Janzen 1967; Stratford & Robinson 2005; Şekercioğlu et al. 2012).

Biotic interactions

In terms of genetic diversity, 80% of the tree of life could be retained even when approximately 95% of species are lost (Nee & May 1997); the only problem is that the resulting ecosystems would not work! Healthy ecosystems depend on associations between hosts and parasites, predators and prey, seeds and seed dispersers, and so on. These networks are the lifeblood of biodiversity. They are particularly important in tropical ecosystems because co-evolutionary associations tend to increase in abundance towards the equator (Schemske et al. 2009). In effect, the complex architecture of food webs and other biotic interactions in tropical ecosystems increases the likelihood of cascading co-extinctions, and cautions against a simplistic view of phylogenetic diversity (PD) as a means to prioritize conservation action (see Chapter 1).

Tropical birds offer good examples of finely tuned interactions, as they have more specialized dietary niches than their temperate-zone counterparts (Belmaker et al. 2012). The most clear-cut cases are nectarivores. For example, some species of hummingbird with highly specialized bills (e.g. sword-billed hummingbird, white-tipped sicklebill, etc.) can only forage on, and pollinate, very few species of flowering plants. Thus, the survival of specialist nectarivores and their associated foodplants is tightly interwoven via co-evolutionary adaptations. Similarly, frugivorous birds dictate the fate of forests. Many tropical trees produce large, lipid-rich fruits adapted for animal dispersal, so

the disappearance of frugivores can have serious consequences for forest regeneration, even when the drivers of habitat loss and degradation are controlled.

The impact of bird declines on ecosystem function and services

Ecosystem services are 'the set of ecosystem functions that are useful to humans' (Kremen 2005). In general, increased biodiversity in a particular environment is thought to increase ecosystem efficiency and productivity, and decrease susceptibility to perturbation. Birds play a role as 'mobile link' animals connecting habitats and ecosystems through their movements (Lundberg & Moberg 2003), and providing services such as pollination, seed dispersal, nutrient deposition, pest control and scavenging (Şekercioğlu 2006; Wenny et al. 2011). Thus, the ongoing decline in bird species is likely to have far-reaching ecological consequences, from the spread of disease and loss of agricultural pest control to the extinction of plants dependent on avian pollinators and seed dispersers (Şekercioğlu et al. 2004).

In the tropics, large frugivorous birds are particularly threatened by hunting and habitat fragmentation, which can have significant consequences for shade-tolerant, late successional tree species with large seeds (e.g. Lauraceae, Burseraceae, Sapotaceae). For example, in the East Usambara mountains of Tanzania, the endemic tree *Leptonychia usambarensis* (Sterculiaceae) is dependent on avian seed dispersers such as greenbuls (*Andropadus* spp.), most of which are rare or absent in small forest fragments (Cordeiro & Howe 2003). This results in lower seed removal, shorter dispersal distance, greater seedling aggregation under the parent trees, and reduced recruitment in fragments than in continuous forest (Cordeiro & Howe 2003). Similarly, previous studies have shown that overhunting of large frugivores (e.g. guans, toucans, hornbills) has a detrimental

impact on recruitment of bird-dispersed trees in humid forests of Amazonia (Terborgh et al. 2008) and India (Sethi & Howe 2009). In effect, widespread losses of avian frugivores may result in the domination of short-lived pioneer trees, with long-term effects cascading through plant communities (Şekercioğlu et al. 2004; Terborgh et al. 2008). They also mean that the potential for long-distance dispersal is declining for many plant species at precisely the time when flexible range shifts are becoming more important because of land use and climate change.

Meanwhile, the susceptibility of insectivorous birds to habitat degradation and fragmentation may cause a different set of problems. Insectivores often control invertebrate populations and play a significant role in limiting foliage damage in tropical forests (van Bael et al. 2010) and plantations (Greenberg et al. 2000; Kellermann et al. 2008; van Bael et al. 2008; Mooney et al. 2010). This form of control of insect herbivores can be economically important in agricultural regions. For example, bird-mediated predation of the coffee berry borer (*Hypothenemus hampei*) in Jamaican coffee plantations saves farmers $310/ha per year (Johnson et al. 2010).

Finally, tropical scavengers such as vultures provide one of the most important yet under-appreciated ecosystem services. Avian scavengers worldwide comprise the most threatened avian functional group, with about 40% of the species being threatened or near threatened with extinction (Şekercioğlu et al. 2004). Because of the loss of decomposition services provided by vultures, increased disease transmission and consequent health spending are likely. Markandya et al. (2008) suggested that the spiralling Indian dog population, which increased by 7.25 million between 1992 and 2003, could be caused by the 90–99% declines in vultures. Partly based on the associated surge of ~48,000 additional rabies deaths, they estimated that the health costs attributable to vulture declines were US$ 18 billion (Markandya et al. 2008).

What are the implications for biodiversity conservation?

Armed with this information about tropical environments and their native species, we can explore the implications for conservation strategies. The following sections deal with major threats to biodiversity at a global scale, highlighting the type and scale of impact they may have on tropical ecosystems.

Habitat fragmentation

Millions of hectares of tropical forests exist in fragments and many thousands of new fragments are created every year (Sodhi et al. 2011). These exist in a variable matrix of land uses, and consequently the loss of avian diversity is highly site dependent (Sodhi et al. 2011). Nevertheless, some patterns have emerged. Understorey insectivores, for instance, tend to be particularly sensitive to fragmentation (Peh et al. 2005; Barlow et al. 2006; Yong et al. 2011). This may be because other dietary guilds, including frugivores, granivores and nectarivores, are often dispersive, non-territorial and naturally adapted to exploit patchy resources, and therefore better equipped to cross gaps and travel through degraded landscapes. This process is highlighted by studies in Amazonia showing that fragments are primarily inhabited by bird species with good dispersal abilities or high tolerance of the non-forest matrix (Lees & Peres 2008). A key latitudinal difference linked to dispersal ability involves the likelihood of recolonization after local extinction. This is illustrated by the fact that temperate bird species dropping out from forest fragment avifaunas often recolonize within a few years if source populations are found nearby, whereas tropical species rarely return to the community unless the habitat linking the fragment to the source population actually recovers (see Stratford & Robinson 2005).

Another issue influencing the survival of bird populations is elevated predation in forest fragments. For example, in the Eastern Arc mountains of Tanzania, seven common understorey bird species, e.g. forest batis (*Batis mixta*), suffered 2–200 times lower rates of nest success in fragments versus continuous forest (Newmark & Stanley 2011). Similar reductions in reproductive success appear to be widespread in forest fragments, and at least partly linked to higher densities of nest predators, including rodents, raccoons, mongooses and snakes, as well as greater visibility of nests to hawks and other arboreal predators (Chalfoun et al. 2002). Importantly, the density and diversity of nest predators are typically far higher in tropical than temperate regions, again suggesting that fragmentation has a greater negative impact on tropical birds (Stratford & Robinson 2005).

Climate change

Most studies of the impacts of climate change on biodiversity have focused on boreal or temperate regions, perhaps because it is often assumed that the threat of warming increases towards the poles. However, the tropics are a far more likely setting for climate-mediated mass extinctions, for three main reasons. First, the direct impact of global warming will be severe in tropical mountains, where high-elevation climates will shrink or disappear (Ohlemüller et al. 2008). Second, species inhabiting extensive lowlands may find it difficult to cope with further warming or to migrate towards cooler refuges (Wright et al. 2009). And third, the sheer diversity of tropical lineages means that these threats will affect large numbers of bird species. Specifically, if a warming climate threatens taxa restricted to tropical highlands (≥ 500 m asl), this would amount to approximately 10% of the world's ~10,000 bird species, including the majority of those currently considered to be safeguarded from land use change (Pimm 2008; Harris et al. 2011). In

contrast, the melting of polar ice caps attracts much more media attention despite affecting a relatively small number of bird species, most of which have large global ranges.

Previous studies indicate that tropical organisms are as likely as temperate organisms to track moving climates (Pounds et al. 1999; Colwell et al. 2008). Although the full impact of this process under global warming is difficult to predict, it is likely to force many bird species uphill in the montane tropics, reducing their ranges, sometimes entirely (Shoo et al. 2005; Şekercioğlu et al. 2008; Wormworth & Şekercioğlu 2011; Şekercioğlu et al. 2012). For example, the potential habitat of the golden bowerbird (*Prionodura newtonia*), a montane forest species endemic to Australia, would be reduced by 98% if temperatures rose by 3 °C (Hilbert et al. 2004). Likewise, a 4 °C increase would result in almost complete removal of the Pantepui vegetation of Venezuela (Nogue et al. 2009), presumably with devastating effects on 30–40 endemic bird species, e.g. rose-collared piha (*Lipaugus streptophorus*).

This so-called 'escalator to extinction' may be exacerbated by competitive interactions, a problem particularly relevant to tropical birds because of strong interspecific territoriality between elevational replacement species (Jankowski et al. 2010). Finally, warming could expose montane birds to an array of new pathogens, predators and competitors that migrate upslope (Bradshaw et al. 2009; Wright et al. 2009). For these reasons, tropical high-elevation specialists could be among the most endangered species on earth if global temperatures rise (Williams et al. 2003; Ricketts et al. 2005; Şekercioğlu et al. 2008).

Birds of tropical lowlands face a different set of problems. Current projections suggest that, by 2100, 75% of modern lowland tropical forests will experience mean annual temperatures warmer than the warmest forests known today, i.e. >28 °C (Wright et al. 2009). This represents an increase of 2–4 °C from present-day temperatures, well below the upper realistic bound of 6.4 °C (IPCC 2007).

Thus, lowland species may be ill suited to further warming because they are already close to their tolerance limits (Weathers 1997; Colwell et al. 2008; Wright et al. 2009). In conjunction, latitudinal range shifts to cooler environments are unlikely because there is virtually no latitudinal temperature gradient in the tropics (Colwell et al. 2008). In other words, the escape route to cooler climates is closed to many lowland tropical species, particularly those living far from the nearest topographical relief, e.g. central Amazonia (Loarie et al. 2009; Wright et al. 2009). This contrasts with the situation at higher latitudes, where latitudinal climatic gradients are a permanent feature.

Tropical islands are likely to fare little better. Many rare island endemics are restricted to the montane zone where the extent of suitable habitat could recede dramatically in response to warming (Fordham & Brook 2010). Moreover, climatic fluctuations can seriously threaten bird populations. For example, El Niño conditions, characterized by high sea temperature and rainfall in the Equatorial Pacific, are associated with disrupted oceanic food webs. Specifically, they tend to switch off the Cromwell current, thereby reducing fish stocks and causing population crashes in Galapagos penguins (*Spheniscus mendiculus*), an endangered species with a population of around 1500 individuals (Vargas et al. 2006, 2007). They also promote vector-borne diseases (Gilbert & Brindle 2009; Kolivras 2010). El Niños are natural cyclical phenomena but the frequency of severe events has increased sevenfold over the last century; moreover, global warming is predicted to drive further increases in their frequency and intensity (Timmermann et al. 1999). Although these changes may have severe consequences for island birds and ecosystems, they are overshadowed by the threat of warming to atolls and other low-lying oceanic islands. Here, extreme climatic perturbations and sea-level rises may have a catastrophic impact on human welfare and livelihoods, as well as wildlife (Barnett & Adger 2003).

Pathogens and disease

Diversity, virulence and abundance of pathogens are all higher in the tropics. Moreover, since many pathogens are sensitive to temperature, rainfall and humidity, climate warming has the potential to increase pathogen development and survival rates, disease transmission and host susceptibility (Harvell et al. 2002; Garamszegi 2011). This is coupled with the problem of range shifts through introductions, invasions and climate-related expansions and contractions of distributions. Such processes can lead to parasites becoming pathogenic when established in novel environments or in contact with susceptible new hosts. The results for birds can be devastating. In Hawaii, for example, more than half of the native avifauna became extinct due to avian malaria and other introduced pathogens (LaPointe et al. 2010). Upward shifts in mosquito distribution predicted from continued global warming will further reduce the refuge habitat available, with serious implications for some of the surviving Hawaiian endemics: a predicted 2°C rise will probably eliminate all remaining disease-free forested refugia in Hawaii in the next century (Benning et al. 2002). Montane avifaunas throughout the tropics could be similarly threatened by changes in the distribution of hosts and vectors caused by land use and climate change (Harvell et al. 2002).

Invasive species

Invasive plants, predators and pathogens are present on islands worldwide but they are more likely to cause catastrophic declines in the tropics. This is partly because tropical islands support many endemic species with tiny ranges and populations, and also because they provide suitable environments for invasive species to thrive. Introductions can have major negative impacts on tropical birds, particularly on island endemics that have evolved without predation pressure. For example, the

predatory brown tree snake (*Boiga irregularis*) was introduced to the island of Guam shortly after World War II, causing the extirpation or serious decline of 17 of the island's 18 native bird species (Wiles et al. 2003). Most island extinctions have been caused by similar events, with feral cats and rats being the most damaging culprits (see Chapter XX [XREF INVASIVES CHAPTER]). Invasive plants and pathogens can also have strongly deleterious impacts. The red quinine tree (*Cinchona pubescens*), for example, is causing drastic changes to the native plant community of the Galápagos Islands, and is destroying the breeding habitat of the Galápagos rail *Laterallus spilonotus* (Shriver et al. 2010). The main line of defence against invasive species is eradication schemes, which are often costly but sometimes highly effective (e.g. Donlan et al. 2007).

The central role of synergisms

At a local scale, the fate of tropical biodiversity is typically shaped by a suite of factors: biotic, abiotic and socio-economic (Seddon et al. 2000). It is often the inevitable interactions and synergisms between these factors that pose the greatest threat of all (Dobson et al. 2006; Brook et al. 2008; Tylianakis et al. 2008). For example, as habitat declines, hunting pressure often increases, a twin threat responsible for an elevated extinction risk in tropical vertebrates (Laurance & Useche 2009). Likewise, the fragmentation of tropical forest increases the risk of fires, further reducing avian diversity (Barlow et al. 2006).

The importance of synergisms in tropical ecosystems is highlighted by the issue of climate change. While many species coped perfectly well with wide temperature fluctuations and other stressors during their evolutionary history (Balmford 1996), none did so in a heavily human-modified environment with numerous additional barriers to dispersal. This is important because the inherent low dispersal ability of many tropical bird species means that they are often unable to disperse across agricultural

landscapes (Gillies et al. 2011). Thus, those species forced to disperse polewards or uphill by climate change may now find that human settlements and agricultural areas stand in the way (Şekercioğlu et al. 2008). Unfortunately, this outcome is likely to be extremely common because mid-elevations are among the most densely populated and heavily cultivated lands in the tropics. People preferentially settle this elevational band because of its pleasant climate and suitability for a range of important cash crops, including coffee, tea and coca. It therefore seems likely that human activity is reducing the ability of many species to track climates, with potentially disastrous effects on long-term survival prospects.

Even discounting the problem of dispersal constraints, climate change may significantly exacerbate a number of threats to tropical birds (Şekercioğlu et al. 2012). Contemporary communities of birds, plants, pathogens and other interacting species will be disassembled by individualistic range shifts, such that novel communities of species will mix in the future (Laurance & Peres 2006; Thuiller 2007). There will be winners and losers in these new interactions, and the outcome across entire networks of species may produce unanticipated effects on ecosystems (Parmesan 2006). Overall, the dramatic pace of contemporary habitat loss, combined with the synergistic effects of future climatic change, overhunting, emerging pathogens and many forms of habitat degradation, could sharply increase the rate of species extinctions (Tylianakis et al. 2008).

Governance, legislation and economics

Many tropical nations are too poorly equipped, financially and institutionally, to cope with the current rate of environmental change (Butchart et al. 2006). This problem is further exacerbated by widespread corruption (Barrett et al. 2001; Lee & Jetz 2008). The triumvirate of poverty, weak institutions and corrupt officials

leads to the destruction or mismanagement of protected areas, and the uncontrolled exploitation of natural resources at the whim of global markets (Smith et al. 2003). Rising prices for commodities, such as gold, can unleash a surge of tropical deforestation by making exploitation profitable in regions formerly too remote to be affected (Swenson et al. 2011). Biofuel crops, such as sugar cane, oil palm or soy, grow best at low latitudes, and thus escalating demands are creating an incentive for converting tropical habitats to farmland (Laurance 2006; Laurance & Peres 2006; Brook et al. 2008). These mechanisms can now operate rapidly and with dramatic consequences, not least because infrastructural projects have opened up trade routes, making the exploitation of once remote regions economically viable. For example, the Trans-Oceanica Highway links the Brazilian soya belt of Acre and Mato Grosso with Peruvian ports, such that the expanding markets of China and other Asian countries have direct influence on the deforestation frontiers of southern and western Amazonia (Tobias et al. 2008b).

Knowledge

A final piece in the jigsaw is knowledge, or lack thereof. The quality of information about tropical birds lags far behind that available for the temperate zone in terms of taxonomy (Tobias et al. 2008a), population size (Tobias & Seddon 2002; Seddon & Tobias 2007) and conservation status (Tobias & Brightsmith 2007). Taxonomic revisions tend to reveal that many tropical bird species consist of more than one cryptic species, each with global ranges and populations smaller than previous estimates (Lohman et al. 2010). The scale of taxonomic uncertainty in the tropics suggests that conservation issues need to be re-evaluated, as many analyses are sensitive to estimates of global range (e.g. Rodrigues et al. 2004; Vale et al. 2008). Moreover, latitudinal bias in knowledge is not restricted to taxonomy: for example, only a tiny number of long-term

climate datasets originate from the tropics, in contrast to many thousands from Europe or North America (Rosenzweig et al. 2008).

Towards long-term and broad-scale strategies for the conservation of tropical ecosystems

Most conservation efforts and priority-setting exercises focused on tropical systems have attempted to apply strategies developed in the temperate zone. Many rely on species as units of conservation; others emphasize metrics such as phylogenetic diversity (PD), such that conservation may target the maximum amount of 'evolutionary history'. However, the preceding sections outline several reasons why these approaches may fail in the tropics. Up to this point we have dwelt on the underlying problems; the following sections focus on conservation priorities and solutions.

Protected areas and beyond

Between 1994 and 2004, the extinction of 16 bird species was prevented through a combination of habitat protection, control of invasive species and captive breeding (Butchart et al. 2006). For example, wild populations of Seychelles magpie-robin (*Copsychus sechellarum*) increased from approximately 15 to 136 individuals, and Mauritius kestrel (*Falco punctatus*) from four to 500–800 individuals. These targeted schemes, often costing millions of dollars per species, are clearly effective in some cases. However, they only involve <10% of critically endangered bird species, suggesting that conservation efforts and funding need to be greatly expanded.

Aside from financial constraints, it is doubtful whether this fire-fighting approach is viable from the perspective of ecosystem function. Small or fragmented populations will cease to play a significant ecological role, and thus

conservation strategies assuming that species will survive in a few isolated reserves are unlikely to result in healthy tropical ecosystems. Only by maintaining large, interconnected populations can we avoid numerous species being officially extant but functionally extinct (Sodhi et al. 2011). Thus, conservation needs to focus not only on protected areas but the broader landscape context in which reserves are embedded. This is especially important in the humid tropics, where the fate of avian diversity within protected areas is often inextricably linked to the surrounding agricultural matrix (Harvey et al. 2008).

Lowland and mid-elevation forests of tropical Asia (Peh et al. 2005), Africa (Norris et al. 2010) and Meso-America (Harvey et al. 2008) are tightly coupled agro-forestry systems, with most habitats supporting rural livelihoods. Amazonia is inexorably going this way. A priority for birds is to promote landscape configurations that connect reserves, maintain a diverse array of habitats and retain high structural and floristic complexity (Koh 2008; Chazdon et al. 2009). In particular, the preservation of forest remnants, including riparian strips, secondary forests and individual trees, helps birds to move between forest patches and even breed in human-dominated landscapes (Şekercioğlu et al. 2007; Martensen et al. 2008; Dent & Wright 2009).

Promoting these features is a huge challenge, particularly in areas suited to mechanized agriculture. Where possible, engagement is required to ensure that farmers are stakeholders in creating landscapes that preserve birds as well as rural livelihoods (Harvey et al. 2008). One successful blueprint involves Payment for Ecosystem Service schemes, such as those operating in Costa Rica, which motivate landowners to maintain forest patches and watershed reserves (Sodhi et al. 2011)(see Chapter 4). These measures need to be expanded where possible, and coupled with outreach and education initiatives, to ensure that we preserve key ecosystem processes as well as populations of rare species.

Conservation priorities: too much pattern, not enough process

The idea that conservationists need to focus on the processes sustaining biodiversity is not new (Smith et al. 1993; Moritz 2002), but it has proved difficult to incorporate into conservation strategies. The approach requires us to see beyond the current pattern of extant species, and to consider longer-term evolutionary perspectives. But what perspectives are these? There is a tendency to assume that by using molecular phylogenies to map conservation priorities, we have somehow captured the evolutionary process but a phylogeny is as much a pattern as anything else (Losos 2011). Instead, the defining attributes of process-based conservation are (i) the preservation of genetic, phenotypic and functional diversity below the species level; (ii) the maintenance of abundance so that lineages continue to perform their ecological functions across their natural ranges; and (iii) the promotion of conditions necessary for long-term population connectivity and dispersal, even under climate and land use change scenarios.

The contrasts between pattern-based and process-based conservation are striking. A pattern-based approach tends to prioritize rare endemics, many of which are only narrowly divergent from their closest relatives, by preserving small populations in isolated reserves. A process-based approach does not target these potentially ephemeral 'twigs' of the tree of life, and attempts instead to sustain the underlying mechanisms that provide the impetus for adaptation and speciation. This can be achieved in different ways. One method is to focus attention on all genetically and phenotypically distinct lineages within species (Moritz 2002); another is simply to maintain the context for selection, rather than protecting phenotypes *per se* (Thomassen et al. 2011). A key practical component is the maintenance of habitat heterogeneity and connectivity within and between reserves, particularly where this

captures genetic variation across environmental gradients (Moritz 2002).

Aldo Leopold famously observed that 'to keep every cog and wheel is the first precaution of intelligent tinkering', meaning that all parts of ecosystems should be saved, even though their function may be unclear. Conservationists worldwide have tended to interpret 'parts' as 'species'. However, this misses the point that in all ecosystems the essential cogs and wheels are adaptation, connection and interaction – in other words, not patterns but processes. Incorporating this viewpoint into the bigger picture of conservation thinking is particularly vital in the tropics.

Key measures to preserve healthy tropical avifaunas

With the goal of managing tropical ecosystems and preventing further declines in tropical birds, we propose a list of conservation and research priorities. Although these are designed with birds in mind, similar strategies will greatly improve our chances of preserving a vast proportion of tropical biodiversity in resilient, functional and flexible ecosystems (Hole et al. 2009).

Conservation targets

- Extensive protected areas, i.e. 'megareserves', sustaining viable populations of birds in large areas of intact habitat (Laurance 2005; Peres 2005). These areas are always richer in bird diversity, and more important for bird conservation, than land shared with agricultural productivity (Edwards et al. 2010; Gibson et al. 2011; Phalan et al. 2011).
- Improved yields of tropical crops. This is an important factor in allowing a maximum area of natural habitat to be spared for conservation purposes.
- Improved targeting of clearance and conversion of forests for human land uses. For

example, intensive agricultural development should be focused on grasslands or precleared land, rather than forests, as this limits losses in terms of both carbon balance and bird diversity (Danielsen et al. 2009).
- Island restoration. The eradication of invasive mammals, plants and pathogens is key to preserving avifaunas of tropical islands.
- Connectivity between bird populations. This can be achieved by integrating degraded, secondary and fragmented habitats into conservation schemes. Techniques include minimizing forest fragmentation and fragment degradation, preventing fires, cattle incursions and other types of disturbance, reducing the contrast between fragments and the surrounding non-forest matrix, and increasing fragment connectivity via ecological corridors, riparian strips and landscape restoration. Where feasible, efforts should focus on developing and implementing community schemes and government legislation to maintain these landscape features at deforestation frontiers.
- Intact elevational and ecological gradients. Even supposedly complete gradients, such as Manu National Park in Peru, are currently being truncated or interrupted by habitat degradation. One laudable government-sponsored initiative attempts to connect protected areas from the western lowlands of Ecuador, over the Andes and down into eastern Amazonia, and there is an urgent need to replicate this approach elsewhere to safeguard elevational corridors. The logic of preserving elevational transects extends to all habitat mosaics and ecotones, i.e. gradations between core habitat types. In all cases, land-sparing efforts need to consider that environmental gradients may fluctuate spatially over time.
- Strengthened incentives to promote the sustainable economic use of bird-friendly habitats. This includes much greater emphasis on educating people in tropical nations about the key functional roles played by ecosystems in flood protection, sustainable food production and delivery of clean water (Edwards et al. 2010; Şekercioğlu 2012).

Research agenda

- Promote research focused on tropical birds. Bird behaviour and ecology are fundamental to process-based conservation strategies, yet most work on this subject has targeted temperate-zone taxa (Newmark & Stanley 2011).
- Dispersal. Research should clarify the ability of tropical birds to use human-modified landscapes, cross gaps and navigate corridors, as these are critical aspects of avian life-history from the perspective of landscape management. The recent use of tracking technology to quantify dispersal ability and habitat use (e.g. Gillies & St. Clair 2008; Hawes et al. 2008; Hadley & Betts 2009) should be expanded.
- Understanding biotic interactions. These are complex even in temperate-zone bird communities but in the tropics more research is required to understand the long-term implications of interactions with food plants, prey and parasites. A range of modern tools, from field experiments to phylogenies, should be used to explore the role of interactions in maintaining stable tropical ecosystems.
- Improving knowledge about range and abundance. Most tropical regions remain poorly known in terms of the distribution and abundance of bird species, and how these fluctuate over time. Progress requires field surveys and monitoring exercises, ideally coupled with the development of automated monitoring tools, e.g. song identification software.
- Improving knowledge about taxonomy. Detailed phenotypic and molecular studies are required to revise tropical species limits and relationships in many avian families.
- Conservation potential of agricultural landscapes, including logged and secondary forests. Most studies have looked at bird diversity from the perspective of isolated natural habitat, whereas the matrix of human land uses provides a useful framework for a different set of questions. What are the relative impacts of different agricultural practices on conservation outcomes and ecosystem services? To what extent can species with different ecologies survive in or travel through different crops or marginal habitats? These

questions require a focus on the biodiversity value of plantations and other agricultural habitats, and management practices that maintain connectivity in natural populations (Harvey et al. 2008).
- Long-term population dynamics. The extent to which degraded habitats serve as a 'safety net' for tropical bird populations needs detailed study. It is clear that these habitats support a wide diversity of bird species and are important for conservation (Edwards et al. 2011), yet studies that only consider presence/absence, or even relative abundance, may provide an overly optimistic scenario if surveys detect temporary transients or if degraded habitats act as 'ecological traps' (Part et al. 2007). Thus, we need an improved understanding of underlying population dynamics in key habitats, with a focus on individual fitness, demography, extinction lags, etc.
- Resolving the land-sharing versus land-sparing debate. Retaining habitat patches in the landscape reduces agricultural yield, so that agricultural production needs to spread over larger areas to meet demand (Edwards et al. 2010). More research is required to identify optimum conservation strategies for balancing the trade-off between larger protected areas and a more connected landscape for birds.
- Climate change. Most studies have focused on the temperate zone, and we need to know much more about the physiological constraints, and climate-tracking potential of tropical birds (Stratford & Robinson 2005; Wormworth & Şekercioğlu 2011). For example, a global review of range shifts in response to climate warming was unable to include a single study on tropical birds (Chen et al. 2011).

Conclusions

When it comes to bird conservation, lessons learnt in temperate systems cannot simply be transferred to the tropics. The current practice of preserving tropical species in small numbers of protected areas embedded in an inhospitable matrix is not sustainable. Instead, conservation

efforts should seek to maximize the size of reserves and the connectivity between them. On one hand, land sparing in the form of large pristine blocks of habitat is paramount. On the other hand, we urgently need to harness the potential of agricultural, secondary and degraded habitats as refuges for tropical birds. As part of this process, more attention should focus on developing community-based environmental education, outreach and income generation programmes that support bird conservation initiatives. Only by integrating these approaches, and expanding basic research, can we succeed in preserving tropical avifaunas for the future.

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