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Review

Patterns and causes of understory bird declines in human-disturbed tropical forest landscapes: A case study from Central America

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ABSTRACT

Tropical forest understory birds are declining globally for unknown reasons, indicating an urgent need to understand the causes. We review and synthesize studies investigating causes of these declines focusing on the Sarapiquí region of the Caribbean slope of Costa Rica. We discuss evidence for five potential causes of population declines motivated by current understanding of the effects of fragmentation, disturbance of remnant forests, climate change, and their possible interactions: (1) reduced forest area increases the probability of stochastic extirpation; (2) reduced connectivity among forest patches decreases population rescue opportunities; (3) degradation of preferred microhabitats due to, for example, abundant large mammals, jeopardizes specialized birds' foraging opportunities; (4) high nest predation rates reduce productivity below replacement levels; and (5) changes in macro- and microclimate increase energetic demands and reduce survival. Our review documents how tropical forest loss and degradation likely impact understory birds through a variety of direct, indirect, and interrelated causes spanning multiple temporal and spatial scales and levels of biological organization. We propose that the processes affecting understory birds in the Sarapiquí region may be broadly representative of threats experienced by rainforest understory birds pantropically. Effective conservation will require consideration of such diverse and interacting factors.

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1. Introduction

Tropical communities are threatened globally (Newbold et al., 2014). Effective conservation of tropical species requires determining why their populations are declining and identifying the ecological and life history traits associated with persistence or loss. Although many correlates of extinction risk have been identified such as habitat fragmentation (Haddad et al., 2015), mechanistic studies of declines are surprisingly infrequent. Considerable recent interest has focused on avian declines in particular. While we recognize that tropical forests are losing their avifaunas, the causes of these extirpations are poorly understood (Sodhi et al., 2004, 2011). The biodiversity stakes are high because these communities are diverse and provide essential ecosystem services such as insect control (Blake and Loiselle, 2009; Maas et al., in preparation; Şekercioğlu, 2006; Terborgh et al., 1990).

Insectivorous birds have emerged as a guild of particular concern in tropical rainforest understory (Robinson, 1999, 2001; Şekercioğlu et al., 2002; Sigel et al., 2006, 2010). Many of these species possess traits that increase sensitivity to disturbance including having large territories (and thus, low population density and large area requirements), poor dispersal capabilities, and preferences for old growth or interior forest habitat (Lees and Peres, 2008, 2010; Robinson, 1999; Şekercioğlu and Sodhi, 2007; Şekercioğlu et al., 2002; Sodhi et al., 2004; Stouffer and Bierregaard, 1995). Microhabitat specialization resulting from diet and/or foraging specialization is also common in this guild, including reliance on dense understory vegetation, sparse leaf litter, or particular types of arthropods or fruits (Fitzpatrick, 1980; Marra and Remsen, 1997; Michel et al., 2015, in press; Sherry, 1984; Stratford and Stouffer, 2013). Nest type and placement by many of these birds (e.g., open-cup, ground, and pendulous nests) may elevate predation risk from a variety of predators (Oniki, 1979; Sieving, 1992; Sigel et al., 2010; but see Sigel et al., 2006; Young et al., 2008). Finally, the tropical forest understory guilds contain many small-bodied birds (Karr, 1971) that must feed frequently due to high mass-specific metabolic rate exacerbated by large surface area to body mass ratio (Calder, 1974). A consequence of such physiological traits is sensitivity to climatic change (Canaday, 1997; Karr and Freemark, 1983; Stratford and Robinson, 2005) and thus greater vulnerability to extinction (Boyle and Sigel, 2015; Owens and Bennett, 2000).

Here we take advantage of a well-studied tropical region, the Sarapiquí River watershed on the Caribbean slope of Costa Rica, as a case study to examine the causes of understory bird population declines in fragmented and otherwise disturbed tropical forests. Given the correlates of avian declines listed above and this region's ecological history, five core hypotheses (grouped into four categories) emerge as likely causes of decline: (1a) Loss of intact old-growth forest has reduced available habitat for bird species with strong preferences for this habitat type. (1b) Fragmentation also prevents dispersal-limited understory birds from moving between isolated habitat patches. (2) Microhabitat availability has declined even within intact forest; specifically, increased abundance of collared peccaries (*Pecari tajacu*, a native omnivorous mammal) has reduced an important microhabitat (dense liana tangles) needed by many specialized insectivores, including mixed-species flock participants. (3) Nest predation by a specialized predator, the bird-eating snake (*Pseustes poecilonotus*) has disproportionately impacted ground/understory nesters in connected forest more than in fragments or contiguous forest. (4) Physiological stressors linked to changing temperature and rainfall regimes are resulting in declines of small-bodied birds. In the following sections we review evidence from the Sarapiquí region of Costa Rica for each of these hypotheses, and consider each of these causes in a broader tropical perspective. Finally, in order to develop comprehensive conservation recommendations, we interpret causes in terms of their associated spatio-temporal scales and levels of biological organization.

2. Methods

We reviewed published literature by searching Web of Science, Google Scholar, Science Direct, and the Searchable Ornithological Research Archive. Search terms included combinations of the following: Sarapiquí, Costa Rica, forest, rainforest, disturb*, fragment*, climate change, avian, understory, bird*, decline, mechanism, cause*. We supplemented these searches with targeted efforts to locate references recommended by colleagues or otherwise identified during the literature search.

We assessed recent (1997–2012) land use in the Sarapiquí River watershed through analysis of land cover datasets in ArcMap 10.1 (ESRI, Redlands, CA). We merged the 1997–2000 Land Use dataset from the Earth Observation Systems Laboratory and Fondo Nacional de Financiamento Forestal (http://cro.ots.ac.cr/en/la-selva/gis/laselva_gis/index.html) with the 2012 MODIS Land Cover type dataset (MCD12Q1). The MCD12Q1 data product was obtained through the online Data Pool at the NASA Land Processes Distributed Active Archive Center (LP DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota (https://lpdaac.usgs.gov/data_access). Additional spatial data layers (rivers, reserve boundaries, and a digital elevation model) were obtained from the La Selva Biological Station Geographic Information Systems Laboratory (http://cro.ots.ac.cr/en/laselva/gis/laselva_gis/index.html).

3. Causes of understory bird decline

3.1. Sarapiquí land use history, avifauna, and regional context

The Sarapiquí region was historically covered by tropical wet forest, receiving approximately 4000 mm of rain annually (Holdridge, 1967). This forest cover declined to approximately 70% by 1963, and ∼55% today (Read et al., 2001; Fig. 1). Mature forest loss slowed following a 1996 ban on deforestation, but agricultural expansion into pasture and secondary forest interferes with forest regeneration (Fagan et al., 2013). The remaining mature forest is largely restricted to ecological reserves, including Braulio Carrillo National Park, which encompasses 47,000 ha of primarily old-growth forest that extends up to ∼3500 masl (McDade and Hartshorn, 1994), La Selva Biological Station (hereafter La Selva), Tirimbina Biological Reserve (hereafter Tirimbina), and several
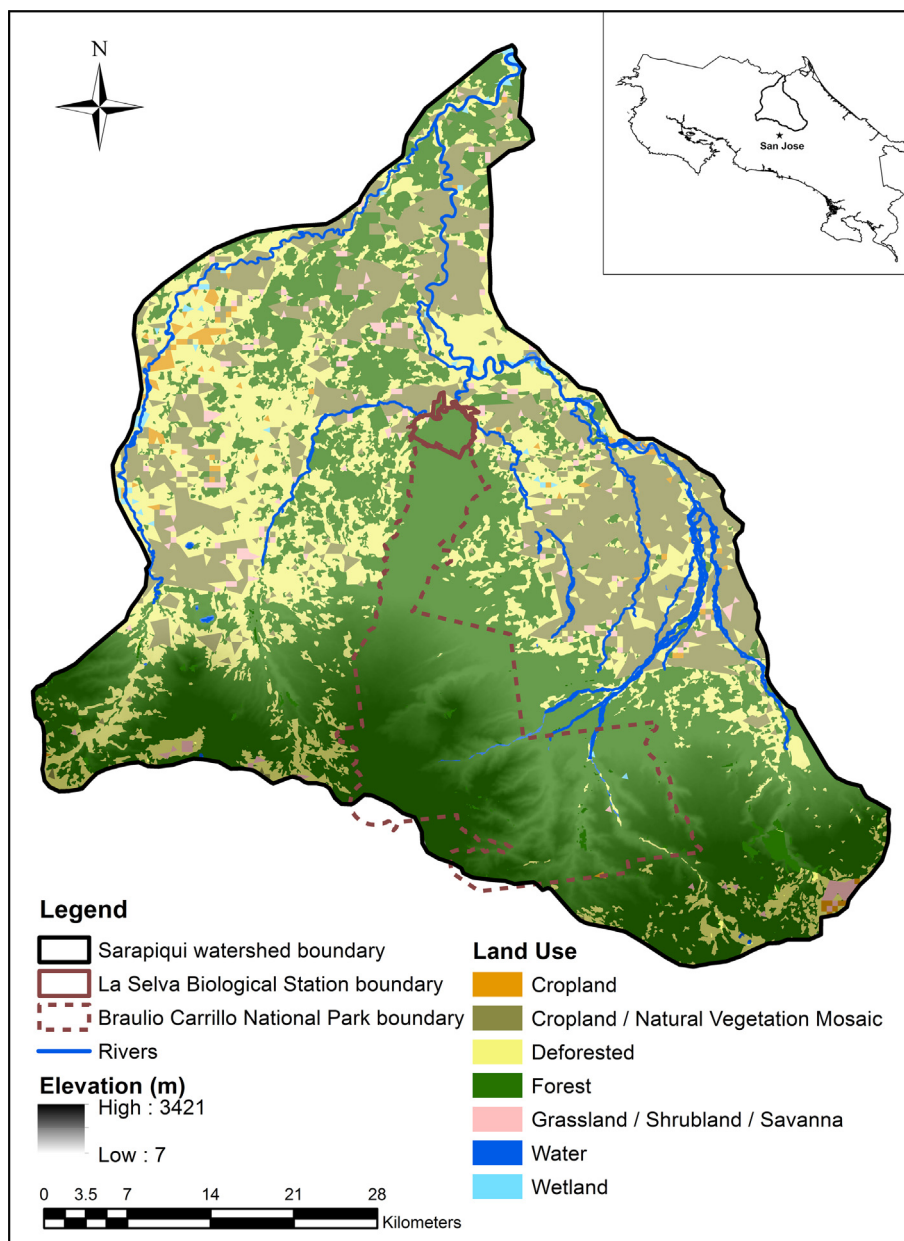
Fig. 1. Land use, rivers, protected area and watershed boundaries, and elevation in the Sarapiquí River watershed, compiled from data sets collected during 1997–2012.

other private reserves as well as scattered forest fragments in a matrix of pasture and cropland (Read et al., 2001; Fig. 1).

Despite the 45% forest cover loss, the Sarapiquí region may represent a best-case scenario for Neotropical agricultural landscapes. An estimated 80% of vegetation in the Mesoamerican Hotspot (spanning Mexico and Central America) has been cleared for agriculture (Harvey et al., 2008), and 84–93% of the Brazilian Atlantic Forest has been deforested (Ribeiro et al., 2009). The Sarapiquí region has a high remnant forest cover even within Costa Rica, e.g., compared to the Coto Brus region in southwestern Costa Rica with an estimated 27% forest cover (Daily et al., 2001), though the Panama Canal region has an estimated 53% forest cover (Rompre et al., 2009). In this context, the fragmentation effects on birds described herein take on even greater importance, as many other Neotropical regions have experienced far greater deforestation than the Sarapiquí region.

Besides regional deforestation, local landscapes and faunal assemblages also affect the avifaunal community both directly and indirectly (Sigel et al., 2010). For example, corridors can facilitate forest bird movements, just as pastures and agricultural crops inhibit movements. Elevational corridors are thought to enhance altitudinal migration (Blake and Loiselle, 2000). Despite La Selva's connection to Braulio Carrillo National Park's large area of forest by an elevational corridor, its rapid rise in elevation and extensive historical deforestation along La Selva's southern and western edges (Read et al., 2001) may have effectively isolated some lowland-restricted species because there is substantial species turnover between 500 and 1000 masl (Blake and Loiselle, 2000). Where present, secondary forest provides additional habitat and dispersal opportunities for some understory species, but even older secondary forest may be unsuitable for many forest-dependent birds (Barlow et al., 2007). Roaming large mammals like peccaries

can damage vegetation, but they are largely extirpated from fragments due to hunting, while notably abundant in some protected areas like La Selva (Michel et al., 2013; Romero et al., 2013). Though peccaries are native, their effects on tropical vegetation are similar to those of feral wild boar (*Sus scrofa*) and javaporcos (wild boar – domestic pig *S. scrofa domesticus* hybrids), which damage both crops and native vegetation in southeastern South America (Barrios-Garcia and Ballari, 2012).

The bird community in the Sarapiquí region of Costa Rica's Caribbean slope was first described by Slud (1960) at La Selva. The first systematic bird censuses were conducted there in the late 1970s by TWS, and repeated by Bruce Young in the 1990s (Sigel et al., 2006). Together with other qualitative assessments of the bird community through the end of the twentieth century (Levey and Stiles, 1994; Stiles, 1983; Zook et al., 1999) a picture emerged of the responses of birds at La Selva and throughout Sarapiquí to regional landscape changes. Specifically, understory insectivores and species that participate in mixed-species flocks declined significantly between 1960 and 1999, concurrent with regional forest loss (Sigel et al., 2006). The avian community also varies elevationally. Species richness is similar between 50 and 1500 m, but is lower in the range of 1500–2000 m, and insectivores are less prevalent above 1000 m (Blake and Loiselle, 2000). Upslope from the lowlands, forests are less fragmented, and it is likely that bird communities are more intact. However, possible effects of climate change on birds in montane Costa Rica have not been well studied.

The forests of Costa Rica's Sarapiquí region are generally representative of lowland Neotropical wet forest in forest composition and community assemblages, and thus the ecological processes and responses to human disturbance described here for the Sarapiquí are likely relevant beyond the immediate region. Refugio Bartola, connected to the 260,000 ha Indio Maíz Biosphere Reserve in southeastern Nicaragua, is a much larger reserve by comparison, and largely similar to La Selva in its bird community, precipitation, and forest composition, although rainfall is higher and *Dipteryx panamensis* is a more dominant forest tree at Bartola compared to dominance by *Pentaclethra macroloba* at La Selva (Hartshorn and Hammel, 1994; Múnera-Roldán et al., 2007). La Selva has also been compared with Barro Colorado Island (BCI), an island of tropical moist (not wet) forest in the Panama Canal region. La Selva and BCI originally shared a similar community of insectivores, and this guild has suffered declines and extirpations in both forests; however, some patterns are inconsistent, such as an increase in abundance of antwrens and persistence of mixed-species flocks on BCI (Sigel et al., 2010). Biological Dynamics of Forest Fragmentation Project (BDFFP) in Amazonian Brazil, a little less than half the size of the Sarapiquí region at ~100,000 ha, is also a well-studied lowland Neotropical forest. Unlike the Sarapiquí, the BDFFP landscape was created for experimental purposes. It receives less rain, has a more pronounced dry season, and is entirely protected from hunting (Bierregaard et al., 1992; Laurance et al., 2002), whereas only few of the Sarapiquí's remaining forests are so protected. Patterns of avian decline are similar in these two regions, with understory insectivores being among the most affected guilds (Laurance et al., 2011). Another well-studied Neotropical site, Cocha Cashu in Peru, is only ~1000 ha, but better represents contiguous old-growth forest, as it is disturbed little by humans and lies within the 1.6 million ha Manú National Park (Terborgh et al., 1990). There are an estimated 550 bird species present at Cocha Cashu, surpassing La Selva's 467 recorded species. The avian communities of all of the aforementioned sites have (or once had) diverse communities of understory insectivorous birds (Robinson and Terborgh, 1990; Sigel, 2007).

3.2. Reduced habitat area and connectivity

3.2.1. Habitat loss

Tropical deforestation often leaves islands of forest surrounded by non-forest matrix, such as pastures, plantations, buildings, and roads. In forest fragments, as on islands, area and isolation from continuous forest influence species richness and composition (Watling and Donnelly, 2006). In forest fragments, however, processes such as edge effects and matrix composition also influence species richness, and it is challenging to tease these processes apart from area effects (Banks-Leite et al., 2010; Laurance, 2008; Lees and Peres, 2006). Habitat loss and fragmentation inevitably reduce bird population size, increasing the likelihood of stochastic extirpation. Many Neotropical forest species have large territory sizes (e.g., 53 ha for *Phaenostictus mcleannani* and 200 ha for *Lipaugus unirufus*; (Chaves-Campos and DeWoody, 2008; Sigel, 2007), and consequently low population densities making such species susceptible to area effects (Robinson et al., 2000a; Terborgh et al., 1990).

In the Sarapiquí region, forest loss has created forested islands of varying size. Sigel (2007) compared bird diversity in four sites in the region (La Selva, Tirimbina, and two small fragments surrounded by banana plantations), using Refugio Bartola in Nicaragua as a control site. As predicted by the species-area relationship, estimated bird species richness—estimated by point counts for a subset of each reserve—was highest in the control site (111 spp), followed by La Selva (77 spp, 1200 ha of primary forest) and Tirimbina (65 spp, 345 ha), and significantly lower in small fragments surrounded by banana plantations (58 spp, 35.4 ha and 53 spp, 24.6 ha; Matlock et al., 2002; Sigel, 2007). Species may continue to decline and disappear from these sites, as time lags in extirpations may occur up to 100 years after isolation (Brooks et al., 1999) and regional deforestation occurred 30–40 years ago. Continued monitoring is necessary to assess the effects of time lags and evaluate the impact of local reforestation projects (Matlock et al., 2002; Pagiola, 2008).

3.2.2. Dispersal limitation

The dispersal-limitation hypothesis was developed from island biogeography and metapopulation concepts, and posits that organisms may be unable or unwilling to cross hostile matrix to re-colonize fragments undergoing extirpation (MacArthur and Wilson, 1967). However, it is difficult to test. Although birds' flight may generally reduce vulnerability to dispersal barriers, we know little about their dispersal, and some tropical understory birds disperse surprisingly poorly. A problem testing the dispersal-limitation hypothesis is that patterns of species occurrence in terrestrial landscapes may be misleading, saying little about processes like population resilience and likelihood of recolonization and rescue. For example, a frequent assumption is that species occupying a majority of fragments in a landscape must be good dispersers (Boscolo and Metzger, 2011; Uezu et al., 2005; With and King, 1999), but this pattern may arise instead because species persist at a site for long periods due to high survival and strong site-faithfulness (e.g., Gill and Stutchbury, 2006; Morton and Stutchbury, 2000; Woltmann and Sherry, 2011). Also, natal dispersal may be greater than breeding dispersal, and thus more important for understanding the impacts of fragmentation on adult distributions in tropical forest birds. Unfortunately, natal dispersal is poorly studied in all birds, not just tropical, and low nesting success in many tropical birds makes natal dispersal challenging to study in practice (Ricklefs and Bloom, 1977; Robinson, 2009; Robinson et al., 2000b; Rompré and Robinson, 2008; Visco, 2015; With and King, 1999).

Despite the challenges associated with studying dispersal limitation, mounting evidence suggests that poor dispersal ability

reduces the persistence of tropical understory birds in fragmented landscapes. Even birds that can disperse well in unfragmented landscapes such as obligate ant-followers still suffer extinctions after habitat isolation (Ferraz et al., 2007), likely because area requirements are unmet, leaving less mobile species to persist in small and isolated patches (Şekercioğlu, 2007; Van Houtan et al., 2007). Rigorous tests of dispersal limitation come from three main types of data: mark-recapture, displacement trials, and molecular genetics. Mark-recapture studies reveal that some tropical birds regularly move between forest fragments, clearly not limited in their movements by the matrix (Barlow et al., 2006; Stouffer and Bierregaard, 1995, 2007). Importantly, in two of these studies the matrix was secondary forest, which may be more permeable to birds than agricultural or human-inhabited landscapes.

Displacement trials entail capturing, releasing, and observing whether individual birds return to their home range. Compelling evidence for limited flight capacity of tropical birds comes from Panama, where a number of species were shown to be physically incapable of flying 200–300 m over open water, thereby demonstrating that Barro Colorado Island (a true island) contains closed populations of several understory species (Moore et al., 2008). Similarly, in more typical terrestrial contexts, some understory birds were hesitant to cross even 50 m of non-forest habitat despite strong motivation to do so (Ibarra-Macias et al., 2011). Nevertheless, a number of studies have demonstrated the propensity for some understory individuals to return after being displaced at distances up to 1.4 km, provided that there are minimal gaps and at least some forest cover (Castellón and Sieving, 2006; Kennedy and Marra, 2010; Laurance et al., 2004, 2005).

Molecular genetic data (e.g., microsatellites) are increasingly valuable for providing evidence of genetically-relevant dispersal processes over larger geographic and time scales than typical for behavioral studies such as displacement trials (Haig et al., 2011; Sunnucks, 2011). In the Sarapiquí, high mean pairwise relatedness in isolated fragments suggests that individuals produced in fragments infrequently emigrate, implying that most individuals did not disperse into those fragments (Woltmann et al., 2012; W.D. Robinson and S. Woltmann, unpublished data). Consequently, individuals must be breeding with related individuals. Over time, such inbreeding will inevitably have negative demographic consequences (Frankham, 1998, 2005).

Combining genetic data with information about the movement behavior of adults and juvenile birds reveals dispersal patterns at fine spatial scales. In the Sarapiquí lowlands, adult chestnut-backed antbirds were unlikely to disperse (~32% switched territories or left the study area in 5 yr). Furthermore, juveniles were capable of acquiring and defending territories within the same site as their parents (Woltmann and Sherry, 2011), and genetic parentage assignment techniques enabled Woltmann et al. (2012b) to infer natal dispersal distances in chestnut-backed antbirds of typically <2 km. Thus, even within intact forest, this understory bird disperses little. Territory switching rates in chestnut-backed antbirds are roughly comparable to those found in dusky antbird (*Cercomacra cinarescens*), in which 47% of individuals switched territories during an eight-year study (Morton et al., 2000). However, in buff-breasted wrens (*Thryothorus leucotis*): only ~10% of the individuals studied switched territories during a 3-year study (Gill and Stutchbury, 2006). More study is needed to consider adult dispersal in a broader context.

3.3. Microhabitat and dietary specialization

Many tropical understory forest-interior birds specialize in microhabitats for foraging and feeding. For example, frugivores often feed from many plant species, but some specialize on substrates (e.g., fruits of epiphytes or hemiepiphytes; Boyle et al., 2011) and others forage on only one or a few plant families, exemplified by olive-backed euphonia (*Euphonia gouldi*) and white-vented euphonia (*E. minuta*) specialization on mistletoe berries (Snow, 1971). Similarly, many understory insectivores are stereotyped foragers or diet specialists (Fitzpatrick, 1980; Marra and Remsen, 1997; Sherry, 1984). For example, some insectivores consume diverse arthropods from one substrate, such as dead leaves in the case of checker-throated antwren (*Epinecrophylla fulviventris*; (Gradwohl and Greenberg, 1980; Rosenberg, 1993).

Many tropical forest-interior birds forage in a limited number of microhabitats (Marra and Remsen, 1997; Sherry, 1984; Stratford and Stouffer, 2013). For example, at least 457 bird species forage, nest, and/or roost in tangles of lianas (i.e., woody vines; Michel et al., 2015). Lianas support abundant and diverse arthropod resources such as planthoppers (Sherry, 1984; Wolda, 1979). Dense liana tangles also trap falling dead leaves that shelter arthropods, creating food pockets attractive to antwrens and other understory insectivores (Gradwohl and Greenberg, 1980; Michel et al., 2015).

Dietary and microhabitat specialization should make forest-interior birds relatively vulnerable to altered vegetation structure or food availability. Indeed, species with narrow trophic-niche widths are less likely to persist following logging and fragmentation than species that feed on a wider range of prey types (Edwards et al., 2013). At La Selva, the forest-interior understory birds that continue to decline (Boyle and Sigel, 2015) include many mixed-species flocking insectivores (Sigel et al., 2006, 2010), many of which specialize on liana tangles (Michel et al., in press). Many of these same Sarapiquí species persist in nearby, smaller forest reserves (e.g., Tirimbina; B.J. Sigel, unpublished data; Michel et al., in press). This pattern of regionally patchy decline hints at causes that affect vegetation locally, rather than direct effects of limited forest area. Many such changes in vegetation structure and, consequently avian microhabitat, frequently occur at fragment edges (Didham and Lawton, 1999). Yet vegetation structure responds to multiple drivers even within large, intact forest reserves far from edges (Michel and Sherry, 2012).

Large mammals, particularly ungulates, shape vegetation structure locally through both trophic (e.g., eating leaves, roots, seeds) and non-trophic (e.g., trampling, wallowing) effects (Beck, 2005; Paine, 2000). By reducing vegetation biomass and changing vegetation structure, abundant native large mammals impact a wide variety of other animals, including birds (Foster et al., 2014). At La Selva, the collared peccary (*Pecari tajacu*) has rebounded from near-extirpation in the 1970s (unlike the now extirpated white-lipped peccary; *Tayassu pecari*) to become unusually abundant today (Michel et al., in press; Romero et al., 2013), concurrent with understory bird declines. Collared peccaries are far more abundant at La Selva (14–66/km^2) than either Tirimbina (3/km^2) or Bartola (4/km^2; Michel et al., in press; Romero et al., 2013). The mechanisms facilitating La Selva's high collared peccary densities remain unknown, but may be linked to the rarity of large predators (e.g., jaguars) combined with limited hunting pressure and availability of supplemental food in adjacent croplands (Michel and Sherry, 2012). Freedom from competition with the larger white-lipped peccary may also contribute to La Selva's high collared peccary abundance (Romero et al., 2013), but it does not explain the lack of similar population expansion in other tropical reserves from which *T. pecari* was extirpated, including Tirimbina and Bartola.

Seven of La Selva's declining understory insectivorous bird species forage selectively in liana and vine tangles, and an eighth nests in lianas (Michel et al., 2015, in press; Sigel et al., 2010). For example, checker-throated antwrens (*Epinecrophylla fulviventris*),
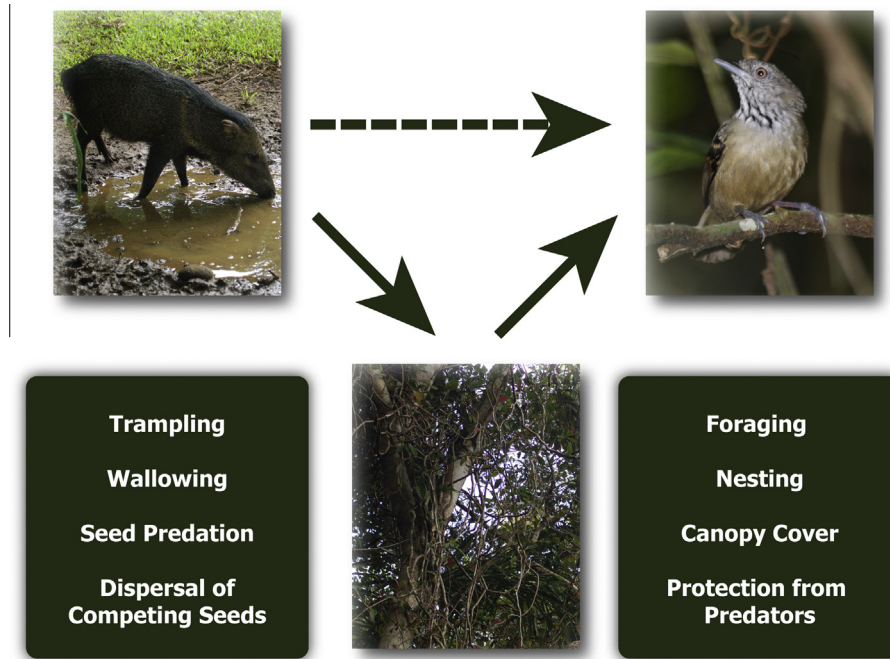
Fig. 2. Proposed direct (solid arrows) and indirect (dashed arrow) effects of abundant collared peccaries (*Pecari tajacu*; top left) on lianas (bottom center) and understory birds (checker-throated antwren, *Epinecrophylla fulviventris*; top right) in the Sarapiquí River watershed. Potential effects of peccaries on lianas are described in the bottom left, and benefits lianas provide to birds are described in the bottom right. (*Photo attribution – peccary*: *Nicole Michel*; *checker-throated antwren*: *Dominic Sherony*; *liana tangle*: *Nicole Michel. This work is licensed under the Creative Commons Attribution 3.0 Unported License. To view a copy of this license, visit* http://creativecommons.org/licenses/by/3.0/.)

dot-winged antwrens (*Microrhopias quixensis*), and ruddy-tailed flycatchers (*Terenotriccus erythrurus*) have declined severely at La Selva (Sigel et al., 2010) where populations are lower (0.60–1.3 birds/100 ha) than Tirimbina (2.2–28.3 birds/100 ha) or Barro Colorado Island (BCI; 25.6–256 birds/100 ha; Michel et al., in press; Robinson, 2001). Structural equation models reveal that, across six sites in Costa Rica, Nicaragua, and Panama, collared peccaries have negative direct and indirect effects (i.e., mediated by vine and liana density and cover) on abundance of these same three species (Michel et al., in press) (Fig. 2). Moreover, other common causes of tropical understory bird decline cannot explain the spatial patterns observed in these species: dispersal limitation is greater at BCI (a true island) than La Selva despite higher abundance of many forest interior insectivores in the former; and climatic conditions are similar at La Selva, Tirimbina, and Bartola, while drier and more seasonal at BCI (Michel et al., in press). At least one understory insectivore, western slaty antshrike (*Thamnophilus atrinucha*), also has similar nest survival rates in the Sarapiquí (including La Selva) and at BCI (Tarwater and Kelley, 2010; Young et al., 2008).

This research suggests that collared peccary alteration of understory and canopy vegetation structure likely contributes to declines of understory birds through a combination of preferred foraging microhabitat loss and microclimatic change (Michel and Sherry, 2012; Michel, 2012; Michel et al., in press). Similar indirect effects of large mammals on vegetation and birds have been described in both temperate environments, e.g., increased abundance of riparian songbirds in Yellowstone National Park, US, following wolf reintroduction (Olechnowski and Debinski, 2008); and tropical environments, e.g., Lago Guri, Venezuela, where herbivores indirectly alter bird diversity and persistence (Feeley and Terborgh, 2008). These interactions illustrate how changing abundances of an ecologically important species such as the collared peccary may potentially lead to complex and arguably eccentric ecological results. Such effects could be representative of keystone species loss in other Neotropical forests.

3.4. Elevated nest predation

At temperate latitudes nest predation tends to be higher in fragmented forest relative to contiguous forest (Donovan et al., 1995; Luck, 2003; Tewksbury et al., 2006) and in forest edges relative to interiors (Batary and Baldi, 2004). Reasons for this pattern include reduced vegetation cover in degraded and fragmented forest reducing availability of well-camouflaged nesting sites (Martin, 1992). The greater edge-to-interior ratio of fragments is also generally thought to allow predator influx from surrounding habitats (Tewksbury et al., 2006; Thompson, 2007). Mesopredators—usually mid-trophic level mammals (e.g., foxes)—are often opportunistic nest predators (Crooks and Soule, 1999). More abundant nest predators may result from mesopredator release in temperate forest fragments that have lost apex predators.

In fragmented tropical landscapes, elevated nest predation can also reduce avian productivity causing population declines (Sodhi et al., 2004; Stratford and Robinson, 2005; Stratford and Stouffer, 1999; Willis, 1974). However, we often fail to see the same relationships between fragmentation and predation in Neotropical forest as we do in temperate forests (Lahti, 2009; Stratford and Robinson, 2005). For example, several Neotropical studies have found no evidence of edge effects on nesting birds (e.g., Carlson and Hartman, 2001; Chiarello et al., 2008; Cooper and Francis, 1998). Tropical forest fragmentation can affect the vegetation and physical environment up to 400 m from the edge (Laurance et al., 2002), potentially modifying nest site vulnerability nearer to edges. Yet the few Neotropical studies that have demonstrated elevated predation risk in fragments or near edges are all based on data from artificial nests (i.e., Carlson and Hartman, 2001; Chiarello et al., 2008; Cooper and Francis, 1998; Galetti et al., 2009; Gibbs, 1991; Sieving, 1992). Such results may not reflect true risk to nesting birds (Moore and Robinson, 2004; Roper, 1992; Zanette, 2002). Studies using real nests are infrequent because finding sufficient tropical bird nests is often logistically challenging (Robinson et al., 2000b). Precautions to minimize nest disturbance

are critical, although a meta-analysis indicated that if camera monitoring does have an effect, it tends to be in the direction of increasing nest success (Richardson et al., 2009). Two recent studies from the Sarapiquí region using real nests found no evidence of elevated nest predation near edges (Visco and Sherry, 2015; Young et al., 2008). These findings suggest that tropical nest predators are likely neither edge species nor elevated in abundance in the surrounding matrix. Young et al.'s (2008) study also found higher nest predation rates in fragments and at La Selva (80%) relative to contiguous forest of Braulio Carrillo National Park (BCNP, 50%) for several understory species pooled together. However, pooling species may obscure important species-specific patterns; for example, chestnut-backed antbird experiences nest predation rates of 64–72% in fragments compared to 95% at La Selva and 79% in contiguous forest (Visco and Sherry, 2015).

Such spatial patterns of nest predation offer a potential demographic explanation for why some understory species have declined at La Selva relative to contiguous forest, although nest predation apparently cannot explain losses from smaller fragments. The causes of high nest predation at La Selva remain unclear, potentially resulting from higher predator abundance or foraging activity compared to both the fragments and higher-elevation contiguous forest. Alternatively, densities of understory birds may be so much lower at La Selva than other habitats (due to decline and/or elevational patterns) that there are fewer total bird nests, so the predators depredate a greater proportion of the available nests.

At least nine species of birds breeding at La Selva are known to nest in vines and lianas and/or use liana material in the construction of their nests at least occasionally (Michel et al., 2015). This includes two species – buff-throated foliage-gleaner (*Automolus ochrolaemus)* and streak-chested antpitta (*Hylopezus perspicillatus)* – that experienced recent severe population declines at La Selva (Sigel et al., 2010). Thus declining availability of lianas (Michel et al., in press) and, particularly, liana tangles that provide dense cover and protection from predators (Michel et al., 2015), could also contribute to reduced numbers, and potentially to reduced success, of nests at La Selva.

Sarapiquí's understory nesting birds are primarily depredated by a specialized nest predator, *Pseustes poecilonotus*, the bird-eating snake. *P. poecilonotus* was responsible for 80% of video-documented chestnut-backed antbird nest predations (*N* = 46; Visco and Sherry, 2015; see also Robinson et al., 2005). Snakes in general were responsible for all recorded nest predations in both lowland La Selva (60–100 masl) and higher-elevation (400 masl) forest in BCNP (Visco and Sherry, 2015). Considering the lower predation rate in BCNP compared to La Selva, perhaps its cooler climate limits ectothermic snakes' abundance or activity levels (see Sperry et al., 2008). Despite this regional variation, *P. poecilonotus'* disproportionate influence on nest success implies that the presence, absence, or activity of a single predator species can influence nesting bird populations.

While high nest predation rates at La Selva could help explain understory bird declines there, low nest predation rates in other fragments—opposite to the expected pattern—cannot explain regional understory bird declines from fragments. One possibility is that predators, and specifically *P. poecilonotus,* have also declined in fragments. A likely, albeit unconfirmed, possibility is that snake persecution in the region due to the abundance and diversity of venomous snakes that pose a threat to humans may contribute to reduced snake populations of all kinds where humans are most active—e.g., in and around fragments. Moreover, because tropical forest birds tend to be long-lived (Johnston et al., 1997; Moreau, 1944; but see Karr et al., 1990), relatively high nest predation rates alone should rarely doom populations to extirpation. Demographic models reveal that typical adult annual survival rates of 0.75 ± 0.07

can overcome nest predation rates as high as 73% to maintain a stable population (Wilson et al., 2011; Woltmann and Sherry, 2011; Young et al., 2008). However, high survival may not be enough: additive effects of habitat loss, reduced foraging opportunities, and climate change could tip the population balance, resulting in declines (Sodhi et al., 2004).

3.5. Physiological tolerances to changing environments

Changing climate is another factor that could explain rainforest understory bird declines. Exposure to even sublethal climatic conditions could alter behavior, increase stress, and increase energy expenditure, resulting in reduced survival or reproductive success. Climate can also affect avian demography indirectly via food availability. How birds cope with these environmental changes depends on physiological processes such as thermoregulatory capacity and metabolic rates—factors that covary with body size.

3.5.1. Changing climate and microclimate of the Sarapiquí lowlands

In the northern Neotropics, both temperature and precipitation have increased in recent years, and sites influenced by Caribbean precipitation patterns are experiencing more severe precipitation events (Aguilar et al., 2005). Since 1983, La Selva's maximum and minimum temperatures have increased by an average of 0.2 °C per decade (Fig. 3a and b). Mean daily maxima in 2005 and 2008 peaked at nearly 32 °C, approaching the upper critical threshold of 37 °C for some small birds (Powers, 1992; Weathers and Riper, 1982). Over the same 30-year period, rainfall has also increased by an average of 307 mm per decade (Fig. 3d; Clark and Clark, 2011), while the number of days with no precipitation have declined by 20–40 days per decade (Fig 3c; Whitfield et al., 2007). However, the long-term pattern of change in total annual precipitation is still not clear. Over longer time scales (50 yr) La Selva's total annual rainfall appears not to have changed significantly (Clark and Clark, 2011; OTS, 2014).

Independent of global climate processes, local changes to the understory microclimate may have occurred due to vegetation structure change. A common consequence of tropical forest fragmentation is warming and drying of forest edges (Laurance et al., 2002; Stratford and Robinson, 2005). Most forested areas of the Sarapiquí have experienced increased fragmentation and edge:-forest ratio since the 1960s (Joyce, 2011). However, in some areas of Sarapiquí, deforested land surrounding old-growth has reforested (Drake et al., 2002), buffering adjacent understory (Didham and Lawton, 1999). Thus, although edge effects might have contributed to population declines at La Selva and in forest fragments, this probably cannot explain regional avifaunal changes.

Other microclimatic changes may be driven by changing vegetation in Sarapiquí, including tree mortality, reduced tree growth, and the effects of collared peccaries on vegetation structure (Section 3.2). Canopy openings could increase understory light levels—an important factor for light-sensitive species (Patten and Smith-Patten, 2012)—potentially accompanied by increased temperature and decreased humidity (Camargo and Kapos, 1995; Ewers and Banks-Leite, 2013). However, a recent study in Panama found that none of nine understory insectivores exhibited microclimate selectivity, but observed that they avoided areas with high light intensity, suggesting that vegetation-dependent light changes may be more important than microclimate variation (Pollock et al., 2015). Unfortunately, we lack the data to evaluate these vegetation-dependent microclimate and light intensity changes for Sarapiquí.

3.5.2. Direct physiological consequences of changing climate

Body size and understory habitat use are the strongest predictors of current decline in La Selva's avifauna (Boyle and Sigel, 2015). Contrary to predictions from island-biogeography theory,
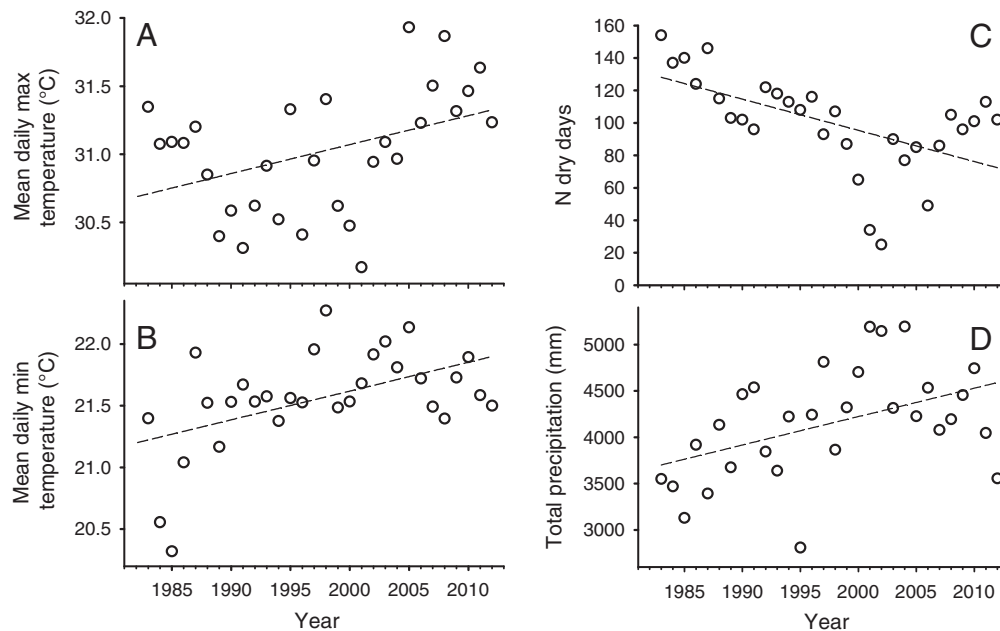
Fig. 3. Organization for Tropical Studies (OTS) Meteorological Data from 1983 to 2012 (OTS, 2014). During this time, mean daily maximum temperatures increased (Panel A, $R^2 = 0.17$, $p = 0.024$), mean daily minimum temperatures increased (Panel B, $R^2 = 0.26$, $p = 0.004$), the number of dry days decreased (Panel C, $R^2 = 0.33$, $p = 0.001$), and total precipitation has increased (Panel D, $R^2 = 0.21$, $p = 0.01$). Data from http://www.ots.ac.cr/meteoro/default.php?pestacion=2.

small-bodied birds are more likely to be declining in the Sarapiquí region, and are declining faster than larger-bodied birds, independent of habitat. The covariation between insectivory and small body size, and the stronger predictive power of body size relative to diet suggest that associations between insectivory and decline may be driven by factors differentially affecting small-bodied species (Boyle and Sigel, 2015).

How might higher temperatures and altered humidity, including more severe rainfall events, affect Sarapiquí birds physiologically? Tropical birds often have narrower temperature optima than temperate counterparts (Stratford and Robinson, 2005). Furthermore, avian temperature tolerance is mediated by humidity: Under dry conditions, some desert birds can cope with temperatures >45 °C, but with even slight increases in humidity their ability to dissipate heat declines dramatically, elevating metabolic costs (Gerson et al., 2014). Tropical birds can detect and respond behaviorally to spatial variation in microclimate (Karr and Freemark, 1983), even when these differences are small (e.g., 0.8 °C, 4.2% humidity; Şekercioğlu et al., 2007). However, doing so may be costly, if not impossible. Obligate understory species typically experience even narrower diurnal swings in temperature and humidity than do birds living in the canopy or forest edge (Stratford and Robinson, 2005). Thus, just as tropical and temperate birds differ in their abilities to survive swings in climatic conditions (Ghalambor et al., 2006; Janzen, 1967), understory birds may have relatively narrow thermal niches and suffer greater adverse consequences of changing climates than birds in other tropical habitats.

Unfortunately, measurements of the breadth and plasticity of thermal neutral zones in tropical forest birds are few. Thermal tolerance in birds is better studied in more extreme environments (McKechnie and Erasmus, 2006; McKechnie and Wolf, 2010; McKechnie, 2008) or exposed non-forested habitats (Weathers, 1997). Deviance from allometric relationships helps identify those guilds with reduced capacity to cope metabolically with climatic variation as a function of body size (Bernardo et al., 2007). Smaller birds, regardless of their habitat, are more sensitive to temperature fluctuations due to well-established relationships between body size and conductance (a measure of the ease of heat

exchange between a birds' body and the environment) (Weathers, 1997). For small Neotropical birds, thermal extremes of 37 °C may approach lethal or near-lethal limits, particularly if such species have evolved relatively low and narrow thermal optima (Weathers and Riper, 1982). Weathers (1997) reports a thermal neutral zone of 28.9–39.2 °C for the 10.9 g variable seedeater (*Sporophila corvina*), a bird commonly found in deforested Neotropical regions. Thermal neutral zones of wet forest understory birds may be even more restricted; conductance of two manakin species is far higher than predicted by allometric equations, and basal metabolic rate (BMR) is far lower (Weathers, 1997). High conductance and low BMR reduce birds' abilities to regulate internal temperature and consequently to tolerate thermal fluctuations (Bucher and Worthington, 1982). Frugivores and granivores typically have higher BMRs than insectivores independent of body size relationships, suggesting a direct link between diet and physiology that could explain declines of the insectivore foraging guild (Sabat et al., 2009).

A variety of tropical forest birds also facultatively drop metabolic rate at night when temperatures cool off to conserve energy (Bartholomew et al., 1983; Bucher and Worthington, 1982; Downs and Brown, 2002; Steiger et al., 2009). If night-time temperatures increase (Fig. 3b; Clark and Clark, 2011), warm nights could deprive understory birds of energy savings from heterothermy. While it appears that selection will likely favor thermal generalists (Boyles et al., 2011), we have few data with which to evaluate the relationship between climatic tolerances and patterns of species decline in Neotropical forests.

As little as we understand the physiological consequences of variation in temperature on tropical understory birds, we know even less regarding the consequences of variation in precipitation regime. Both too much and too little rain likely adversely affects fitness, but we lack empirical or theoretical data to identify precipitation optima—the equivalent of the thermal neutral zone for rain and humidity. In some more seasonally dry Neotropical forests, positive deviations in rainfall have positive demographic effects (Brawn, 2012; but see Dugger et al., 2004), which are likely mediated by food abundance (Brown and Sherry, 2006; Studds and Marra, 2007; Williams and Middleton, 2008). However, in wetter

forests, the reverse may be true. Mounting evidence suggests that in the context of high annual rainfall, further increases in rainfall are stressful to birds; extreme rainfall events trigger facultative short-term movements of tropical birds (Ramos-Olmos, 1983), and both synchronize and influence the magnitude of downhill movements by seasonal altitudinal migrants (Boyle, 2011; Boyle et al., 2010). Severe rainfall in the Sarapiquí region raises corticosterone levels and necessitates short-term fasting (Boyle et al., 2010). Severe rainfall also alters patterns of energy acquisition and storage elsewhere, as observed in rainforest birds in Sarawak (Fogden, 1972). Behavioral and physiological responses occur independently of local food availability (Boyle, 2008), suggesting that heavy rain impedes foraging directly rather than altering food abundance. Heavy rainfall influences reproductive behavior via this same mechanism; foraging and feeding rates decline during torrential rains elsewhere in Central America (Foster, 1974). Due to the allometric relationships between body size, metabolic rate, and capacity for energy storage, small birds run out of energy reserves more quickly than do large birds (Calder, 1974). Thus, precipitation-induced fasts are most likely to penalize small birds.

Because precipitation is the major axis of seasonality in tropical forests, it stands to reason that changes to rainfall regimes will have profound consequences for tropical avifauna. We know, for instance, that rainfall seasonality regulates the timing of breeding in some Neotropical species (Wikelski et al., 2000). While widely hypothesized to reflect an indirect effect of climate on reproduction via food availability, it may be the direct effects of rainfall that limit the ability of tropical birds to nest during the wettest times of the year (Dowsett-Lemaire, 1989; Tye, 1992).

Unfortunately, there are very few mechanistic studies of physiological consequences of climate change on tropical birds (Harris et al., 2011). While slower life histories mean that the longevity of tropical birds could buffer populations from stochastic weather-related events, their low reproductive rates will limit populations' capacity to recover from mortality events (Morris et al., 2008). If we take a regional perspective to species conservation efforts, we might worry less about lowland Central American birds under climate change than birds with no possibility for upslope range shifts such as central Amazonian species. However, until we understand the basis for the losses and declines of lowland avifauna, and the patterns of population change at higher elevations, we will not be able to predict further changes or mitigate on-going losses (Wormworth and Şekercioğlu, 2011). We echo the call for more studies of tropical birds' physiological responses to climate (Şekercioğlu et al., 2012).

4. Synthesis: Characterizing the causes of decline

The foregoing review identifies several likely independent causes of understory bird decline in disturbed tropical forest, but
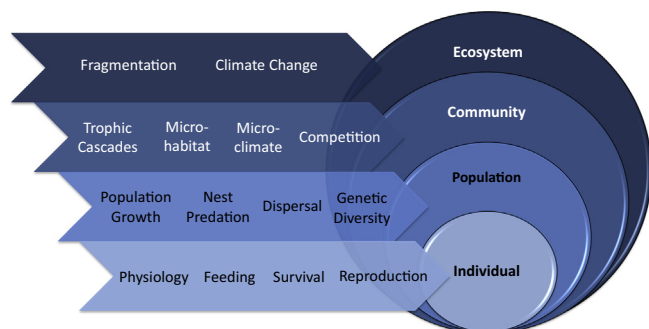

Fig. 4. How causes of understory bird decline primarily act on ecological structure in human-disturbed tropical forest.

we must consider that these factors rarely operate in isolation. Due to the complexity of ecological networks and high biodiversity, tropical forests may be particularly susceptible to "ecological meltdown" (sensu Terborgh et al., 2001) when disturbed. Inter-specific relationships often depend on particular biotic or abiotic conditions that vary across the tropics, even within wet forested regions. Heavy forest fragmentation coupled with human-modified climate disrupts these ecological relationships at multiple levels of organization, which in turn affect each other (Fig. 4). For example, causes of decline that operate at the population level, such as inbreeding depression resulting from limited natal dispersal opportunities, will exert the strongest effects when individuals are simultaneously stressed by individual-level factors such as body condition (Delgado et al., 2010). To make inferences to other regions, we must consider that the structure of these relationships has two consequences: (1) populations of tropical forest birds are vulnerable to a diverse set of disruptions in their interactions, making them particularly vulnerable to human impacts; and (2) forest fragmentation and climate change entail many predictable impacts at particular ecological levels, but the interrelationships among these levels largely depend on the local context.

Related to the complexity that ecological networks and human impacts introduce to tropical birds at multiple levels of organization, causes of understory bird declines are unlikely to be independent. Synergies among causes, or interactions in which one cause exacerbates the impacts of another, are probable, but poorly studied in Sarapiquí birds. One general synergy likely occurring in the Sarapiquí is more human over-exploitation of animals where fragmentation increases forest accessibility (e.g., Benchimol and Peres, 2014; Peres, 2001). Hunting quickly eliminated white-lipped peccaries regionally, which likely had important effects on vegetation and possibly collared peccaries (Romero et al., 2013), whose effects on birds were discussed above. Snake persecution, another form of over-exploitation by humans, is a plausible explanation for greater nesting success in fragments by those vulnerable to the bird-eating snake (Visco and Sherry, 2015). Another likely synergy involves dispersal and climate change/fragmentation: Insofar as tropical forest interior birds are poor dispersers, they will be increasingly vulnerable to fragmented landscapes where both edge and climate effects will cause habitat deterioration, and fragment isolation will reduce movements to better habitats and rescue effects.

Time lags also likely play a greater role in persistence of understory bird populations than currently understood. We know that time lags occur between the isolation of populations in fragments and subsequent inbreeding and loss of heterozygosity. Such genetic effects can take decades to hundreds of years to manifest in birds depending on fragment size (Keyghobadi, 2007). Similarly, direct or indirect climatic effects, or changes to vegetation triggering complex trophic interactions that affect individual fitness, could take decades to manifest themselves as population-level effects (Davis, 1986). Over longer timescales, populations with small habitat areas, low genetic diversity, limited food and microhabitat availability, and limited reproduction, or that include physiologically stressed individuals, are likely to be more vulnerable to stochastic disturbance events.

5. Recommendations for research and conservation

5.1. Research recommendations

Our review highlights future strategic research for advancing understanding of threats to Neotropical taxa generally. Undoubtedly we have oversimplified some causes and missed other important threats; nevertheless, this Sarapiquí case study embodies key ideas prevalent in the broader field of tropical forest

biodiversity conservation. Research focused on single species may overlook threats to other species in the community, so we must continue to build natural history inventories and diversify our study subjects. The existence of a baseline community survey was invaluable to this regional assessment, so here we justify the need for baseline avian surveys in any habitat potentially affected by anthropogenic activities (i.e., most habitats on Earth). Additionally, across taxa, research is needed on basic demography such as apparent survival rate and long-term genetic prospects of isolated populations, which are more informative to population resilience than count surveys alone. Peccary and feral pig abundances need quantification where they persist, and researchers should document the effects of both reduced abundance (e.g., via over-hunting) and excessive abundance of these roaming forest ungulates on seed dispersal, vegetation structure, and insect abundance-aspects that directly and indirectly affect insectivorous birds. Nest predator identification was informative of landscape-scale nest predation patterns, and identified what may be a keystone species to breeding bird success in the region. Various nest predators will respond differently to landscape changes, and thus differentially impact the birds therein. We recommend further efforts to identify nest predators across fragmentation gradients and extension of nest monitoring to a broader suite of species. Research on the physiology of tropical birds is scarce, and such information is essential to addressing impacts of climate changes to the understory bird community. Finally, we have identified a couple of likely synergies between the causes of decline on which we focused, but we cannot emphasize enough the need for further research on synergies among impacts, which can greatly and unpredictably exacerbate bird declines. Despite the difficulty of teasing apart stochastic from more deterministic ecological changes given our necessarily restricted temporal and spatial perspective, insights from Sarapiquí should generally apply to Neotropical forests. Indeed, many hypotheses explaining declines arose from results from other sites such as the BDFFP in Brazil (Laurance et al., 2011), and BCI in Panama (e.g., Robinson, 1999).

Efforts to understand threats to tropical taxa are hindered by substantial logistical challenges. For example, quantifying dispersal distances in large, unfragmented landscapes is a priority, but the undisturbed landscapes in which such studies would be possible are extremely scarce. Another logistic challenge is financially supporting the resource- and time-intensive monitoring work required to characterize fragment and reference landscape population trends. Long-term data such as mark-recapture studies are critical to understanding the demographic bottlenecks in declining populations, yet funding for such studies is notoriously difficult to obtain. Funding presently tends to favor large-scale meta-analyses, molecular analyses, and modeling over long-term ecological field research (Sodhi et al., 2011; but see the Stability of Altered Forest Ecosystems project in Borneo, Ewers et al., 2011). Incentivizing the long-term effort and financial commitment involved in targeted experimental studies is crucial for understanding the causes of tropical forest biodiversity loss (Lindenmayer et al., 2012).

5.2. Conservation recommendations

Our review highlights diverse independent and interacting threats to Neotropical understory birds. The studies featured here suggest that understory bird populations may persist temporarily in forested reserves and even some fragments. However, these birds remain vulnerable to multiple threats to persistence, even within a relatively unfragmented tropical agricultural landscape that may represent a "best-case scenario" for Central America or beyond (Daily et al., 2001; Harvey et al., 2008; Ribeiro et al.,

2009). Taken together, these studies predict that the areas with the most vulnerable populations are probably the smallest lowland forest patches that are isolated from large forest tracts and connections to higher altitude forest. Although it is too late for many populations once occupying these areas, fragments can be valuable to land managers, as many contain thriving wildlife populations (Mendenhall et al., 2014; Şekercioğlu et al., 2007) and present opportunities for achieving conservation goals via education and community engagement (e.g., Tirimbina; Tirimbina Biological Reserve, 2010; Turner and Corlett, 1996). Nevertheless, we advocate setting aside large relatively intact tropical forest reserves and increasing connectivity between them, as exemplified by the San Juan-La Selva Biological Corridor that connects multiple lowland and highland forest areas (Fagan et al., 2013; see also Ripple et al., 2014). However, in larger protected forests like La Selva, evidence was consistent with effects of mesoherbivore (e.g., peccary) and/or mesopredator (e.g., bird-eating snake) release, which can have cascading trophic consequences. Importantly, even large reserves need ongoing monitoring to ensure that key ecological processes remain intact.

Regardless of global human impacts, faunal communities inevitably change over time, forming novel ecosystems, so goals to restore ecosystems to "pre-human" states are both unrealistic and ill-advised (Jackson and Hobbs, 2009). If instead our goal is to conserve existing diversity and functioning ecosystems, then tangible solutions exist. Our assessment from this Sarapiquí case study indicates that large, unfragmented reserves with genetically diverse populations, diverse microhabitats, monitored populations of keystone species (e.g., top carnivores, ungulates, and nest predators), and connectivity with climate-buffered higher-altitude forests may provide understory birds the best odds for surviving on-going human-caused disturbances.

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