

RESEARCH ARTICLE

Bird species occupancy trends in Southeast Mexico over 1900–2020: Accounting for sighting record absences

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Handling Editor: Lucie Kuczynski**Abstract**

1. Long-term land-use change impacts tropical bird communities through population-level and functional diversity effects from habitat loss, degradation and fragmentation, leading to land management and conservation challenges.
2. Assessing the temporal impacts of land-use change on occupancy patterns, population change and functional traits of bird species in tropical areas is limited by the treatment of nondetections as true absences or artefacts of low sampling effort during and throughout years.
3. With this in mind, we developed a novel Bayesian species occupancy framework to account for species absences to evaluate bird community changes in Palenque, Chiapas, Mexico, where there is opportunity for study given exceptional records of change across habitats from rainforest to urban centres. We created a novel dataset of population trends for 244 bird species over the years 1900 to 2020 from published short-term field studies, expert field notes and community science pages.
4. Our results show that open area species had higher population increases than forest specialists over time, represented most evidently by the turnover of rainforest specialists for urban species. Modelled influence of functional traits displayed the importance of main habitat types, body mass and habitat and dietary breadth as factors that associated with bird population trends. On average, species with body masses <6.6 and >948.4 g showed decreasing trends, while all other species showed increasing or stable trends.
5. Our findings illuminate the value of accounting for species absences from several data sources to discover long-term species population trends and affiliated functional traits whose preservation requires conservation and land management action to protect bird ecosystem services. Primary forest conservation is key to maintaining populations of habitat and dietary specialists, such as small understorey insectivorous and large frugivorous species. Protecting rare natural savanna patches from conversion to cattle pasture is vital to prevent further extirpation of native granivores and to slow colonization by exotic and invasive species.

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KEYWORDS

Chiapas, extirpation, habitat loss, occupancy modelling, population ecology, presence and absence, species colonization, species turnover

1 | INTRODUCTION

Urbanization and the resulting habitat loss for development and agriculture are major drivers of biodiversity loss in the tropics (Aronson et al., 2014; Kehoe et al., 2017; Sol et al., 2020). The remaining landscapes, often highly fragmented and altered, no longer contain similar levels of intact and undisturbed habitat necessary to maintain natural populations of wildlife (Cazalis et al., 2021; Timmers et al., 2022). The consequences of such changes to tropical wildlife and the long-term viability of tropical ecosystems require urgent attention and study (Dirzo et al., 2014; Li et al., 2022). These threats are impactful and prevalent in the northern Neotropics, which faces one of the highest yearly deforestation rates in the world (Estrada et al., 2020) and is home to rich communities of wildlife, including birds (Echeverri et al., 2022; Falkowski et al., 2020; Hendershot et al., 2020; Patten et al., 2010).

Assessing the long-term impacts of tropical habitat loss on bird occupancy and population trends over time faces limitations from nondetections of certain species—a nondetection could be a result of a true absence of the species, an artefact of low sampling effort or inherent difficulties of detecting certain rare species. True absences can be caused by a range of well-defined pressures on bird community dynamics in the short and long term, including the direct and indirect impacts of natural disasters (e.g. hurricanes; Levey & MacGregor-Fors, 2021) and human activities (e.g. agricultural activities and urbanization; Boesing et al., 2018; Morante-Filho et al., 2021; Patten et al., 2010). If human-driven habitat loss, alteration and fragmentation slow in tropical landscapes, and these areas are allowed to regenerate or are actively managed to increase forest cover, community-level dynamics may not necessarily return to a native baseline of biodiversity before human activities (Dornelas et al., 2014; Pejchar et al., 2018; Roels et al., 2019). Bird biodiversity may also change both in the short and long term from effects of both active (e.g. deforestation, resource extraction and transportation and housing development) and passive (e.g. road effects, urban noise and predation by domestic animals) human activities (Blickley & Patricelli, 2010; Carral-Murrieta et al., 2020; Williams et al., 2020). These effects may shape bird biodiversity over time through local bird species extirpation, colonization and population-level change of susceptible bird groups (Bull et al., 2014; Dornelas et al., 2014; Sodhi et al., 2004).

To properly address the impacts of long-term tropical land-use change on birds and inform conservation strategies, investigations are needed into how bird populations respond and which functional traits are affiliated with responses. Habitat affinity offers value, especially in tropical regions, where many bird species are restricted to undisturbed forested habitats, while others have a high affinity for open habitats, such as tropical savanna and oak woodland

(Hendershot et al., 2020). Body mass has been shown to predict extinction probability, with the smallest and largest species facing the highest risks from habitat loss and modification (Patten et al., 2010; Ripple et al., 2017; Şekercioğlu et al., 2002) and hunting pressures (Palacio et al., 2020; Ripple et al., 2017; Suarez & Zapata-Ríos, 2019) respectively. Forest degradation also impacts sensitive bird groups with strict habitat and dietary needs (Şekercioğlu et al., 2002) through habitat simplification, including forest understorey clearing and planting of homogenous, nonnative vegetation (Huang & Catterall, 2021; Morante-Filho et al., 2021; Paredes et al., 2021). Combined, these actions negatively affect bird species by disrupting and reducing foraging niches, which may reduce species and functional diversity in an area (Hughes et al., 2022; Levey et al., 2021; Remeš et al., 2021). As a result, ecosystem services provided by bird species may change depending on the degree of disturbance to habitats and landscapes (Barros et al., 2019; Echeverri et al., 2022; Morante-Filho et al., 2021). Through the investigation of how functional groups contribute to bird population trends over time, insights can be drawn into the implications of changing bird biodiversity on ecosystem services (Bregman et al., 2016; Echeverri et al., 2020, 2022; Karp et al., 2013), the conservation value of tropical areas (Şekercioğlu et al., 2019) and the most relevant land management needs for susceptible bird species groups (Ibarra-Macias et al., 2011; Luck & Daily, 2003; Remeš et al., 2021).

Here we provide a novel and reproducible Bayesian framework to model bird occupancy pattern curves and assess functional trait attributions to population trends (i.e. slope value of occupancy curves) while utilizing high-quality community science data as a complement to short-term field studies and field notes. Coupling both methods may unveil long-term bird community changes and provide vital temporal context and complements to the 'snapshot' findings of short-term field studies. We provide detailed long-term occupancy records of bird species from a 120-year incidence record of reliably detected species in southeast Mexico and establish which functional diversity traits are affiliated with major increases and declines of bird populations. We used the bird community from Palenque, Chiapas, Mexico to determine which species have likely become extirpated, which have likely colonized novel habitats after human disturbance, and which have undergone no significant changes.

We expected long-term land-use change and exchange of rainforest for cattle pasture in the study area to impact species occupancy trends over time. We predicted that landscape-level replacement of primary forest has led to extirpations of sensitive bird species and functional groups (e.g. primary rainforest specialists, such as understorey insectivores and large-bodied frugivores) and the colonization of novel habitats, such as cattle pasture, by open area specialists (e.g. ground foraging omnivores and granivores; Jirinec et al., 2022;

Patten & Smith-Patten, 2012). We predicted that smaller body mass, lower dietary and habitat breadth and species that forage for insects and nectar will equally influence negative species trends, while larger body mass, higher dietary and habitat breadth and ground foraging guilds will influence positive species trends (Levey et al., 2021; Patten & Smith-Patten, 2011).

2 | MATERIALS AND METHODS

2.1 | Study site

We conducted the study in Palenque, Chiapas in southeastern Mexico. Specifically, we targeted the landscape located between the natural protected area of Palenque National Park (PNP hereafter; 17.4785°N, 92.0476°W) and the town of Palenque (17.5095°N, 91.9823°W), located about 8 km from PNP (Figure S1, Supporting Information). The study area is composed of forested patches of varying sizes and connectivity to PNP and forests of Indigenous Peoples' lands (e.g. Ch'ol and Tzeltal people). The original vegetation, which consisted of mature tropical rainforest, was partially and gradually converted to pasturelands and plantations 50–70 years ago and continued until 2002 (Figueroa & Sánchez-Cordero, 2008). Embedded in introduced pasture grassland and plantations include small remnant forest fragments that once formed part of an extensive vegetation corridor that connected the northern Selva Lacandona with the rainforests of Central America (Patten et al., 2011) and provide habitat for native avifauna (Ibarra-Macias et al., 2011; Levey et al., 2021). With the establishment of PNP in 1981 to protect the Mayan ruins of Palenque, approximately 900 ha of mature primary forest have remained after the widespread introduction of grasslands for cattle (Figures S1–S3, Supporting Information). Secondary forest cover has increased over the past few decades, likely due to tourism development (Figures S1–S3, Supporting Information). The combination of habitats and diverse avifauna attracts birding tourism from Mexico and around the world to observe rare tropical rainforest and savanna bird species, influencing Palenque's standing as the top tourism destination in Chiapas (Gobierno de México, 2022).

2.2 | Data collection

2.2.1 | Construction of bird species list and incidence data

To assemble a baseline list of species detected or presumed to be present in Palenque before 1970, we used a series of published works, specimen collections, field notes, sound recordings and museum collections from Palenque (see Patten et al., 2011 for a full list of published works and museum collections). From 1970 to 2020, we used the following sources to add to the baseline list of bird species of Palenque: (1) survey visits from 1967 to 2009 listed

in Patten et al. (2011), (2) a 10-month field study from 2019 to 2020 (Levey et al., 2021), (3) field notes from reputable birders (see Patten et al., 2011 for a full list of contributors) and (4) observations uploaded to the community science pages eBird (<http://ebird.org/>) and iNaturalist (<http://inaturalist.org/>). eBird is a community science project from the Cornell Lab of Ornithology that allows a user to upload checklists of bird species detected with a measure of sampling effort (Sullivan et al., 2009), while iNaturalist accepts photos or sound recordings of an individual bird at one point in time (Unger et al., 2021). Each site requires a time and date for observations and is vetted by regional expert volunteers and through crowd-sourcing identification and review. Given the potential for erroneous data on each site due to user malpractice (e.g. false reports of species to enhance personal listing totals) or legitimate identification mistakes, we filtered records beyond the data quality checks from volunteer reviewers of each site to include reports only from observers with extensive experience in the area and observations with a photo or audio documentation or substantial field notes, especially for uncommon and rare species in the area (Patten et al., 2011). To date, the Palenque municipality has received eBird data from 801 birders, and iNaturalist has received bird data from 220 naturalists. We used the latest AOS supplement to the checklist of North and Middle American Birds (Chesser et al., 2022) for all scientific names of species. The data used in this study did not require ethical approval from an animal ethics committee.

2.3 | Statistical analyses

2.3.1 | Modelling absence

A great challenge for analyses of occurrence data, particularly data from a sighting record, is how best to treat absence. If we assume no identification errors, which generally is a safe assumption if observers are at all skilled, then a presence can be taken at face value—the false positive rate can be treated as 0. An absence, by contrast, cannot be determined with certainty—there are too many ways in which one may obtain a false negative. Survey efforts play a key role. It is axiomatic that years with few surveys are more likely to generate false negatives than are years with many surveys. The pattern of the sighting record itself also matters because temporal autocorrelation affects the probability of a record in a given year. A species seen in, say, each of three consecutive years is more likely to be seen the subsequent year than is a species not seen in a decade. A species' detectability is another key factor that influences the false negative. Some species are conspicuous and easy to find, while others are secretive, seldom seen and may be passed over if not vocalizing.

We modelled absence before data analysis. The first probability we estimated was the false negative given the survey effort. Except for recent years (2004–2020), there are no good data on actual effort. We estimated effort in the i th year via a standard species accumulation curve, fit with a Michaelis–Menten equation:

$$S = \frac{S_{\text{MAX}} N_i}{m + N_i},$$

where S is species richness, N is survey effort, S_{MAX} is an estimate of the curve's asymptote and m is a metric of how quickly the curve approaches that asymptote (Colwell & Coddington, 1994). Algebraic rearrangement allows us to solve for N_i :

$$N_i = \frac{mS}{S_{\text{MAX}} - S}.$$

We set S_{MAX} to 250 species, the approximate richness for Palenque over the past 120 years, vagrants, and strays excluded (Patten et al., 2011). Simulation trials suggested $m = 0.7$ as a reasonable estimate, in that estimated N was sensible and neither too low nor too high. With the estimate of N_i , we estimated the probability of encounter of the j th species in the i th year as

$$p_i = (1 - d_j)^{N_i},$$

where d_j is the detectability of the j th species (Bayley & Peterson, 2001). We lacked a direct estimate of d_j , which would have been ideal, so as a proxy we used the number of years a species was recorded across the years in which survey data were available ($n = 60$). An alternative to this approach, if objective data were available for population trends, would be to use presence per year across some window wherein a given species was known to occur, discounting all years with objectively determined absence.

We treated the pattern of occurrences as a sighting record to account for temporal autocorrelation. The probability of extirpation in the i th year given a pattern of sightings is estimated as

$$e_i = \frac{Y_k - Y_{k-1}}{i - Y_{k-1}},$$

Solow and Roberts (2003), where i is the focal year, Y_k is the year in which the species was last recorded relative to the focal year, and Y_{k-1} is the year in which the species was penultimately recorded relative to the focal year. For example, if the focal year is 2003, the last record before 2003 was in 1998, and the next most recent record before 2003 was 1994, then the probability the species persists in 2003 is $(1998 - 1994) / (2003 - 1994) = 0.44$. This equation can be 'turned around' as

$$c_i = \frac{Y_{k+1} - Y_k}{Y_{k+1} - i},$$

to estimate the probability that a species has colonized a site. These last two probabilities are not independent of each other, so we conservatively retained the lowest for any given year. Each metric was initialized to 1.0, so an inability to estimate a metric meant that it was 1.0 for that year. If a species was not detected, its probability of absence for a given year was estimated as the product of p_i and $\min(e_i, c_i)$. An alternative to the minimum would be use of the median, which would dampen negative trends and sharpen positive trends because

estimated absence would tend to be brought nearer to $p = 0.5$, a veritable coin flip.

2.3.2 | Statistics

We used Bayesian beta regression, with the proportion of slope estimates as a response (i.e. the 'probability of direction' [pd], the proportion of the posterior probability density of that has the same sign as that distribution's median), to estimate a species' trend from 1900 to 2020. Estimates were obtained via custom JAGS code (run via R package Rjags; Plummer, 2019) for the model:

$$y_i \sim B(\alpha_1, \alpha_2)$$

$$\alpha_1 \leftarrow \mu_i \phi$$

$$\alpha_2 \leftarrow (1 - \mu_i) \phi$$

$$\text{logit}(\mu_i) \leftarrow \beta_0 + \beta_1 x_i$$

$$\phi \sim \Gamma(1, 0.001)$$

$$\beta_0 \sim \text{Cauchy}(0, 1 / 2.5^2) [0,]$$

$$\beta_1 \sim \text{Laplace}(0, \lambda)$$

$$\lambda \sim U(0.01, 100),$$

where y_i is the response variable (i.e. pd of trend), $\sim B()$ refers to data distributed as beta with shape parameters α , μ is the central tendency of the distribution, ϕ is the dispersion (distributed as gamma with rate and shape indicated; see below), β_0 and β_1 are the intercept and slope respectively (with priors following Gelman, 2006) and λ is the standard deviation of the slope (distributed as uniform; the inverse square of this value is used in the JAGS model).

Any annual probability equal to 0 or 1 was adjusted upward or downward, respectively, by 0.01 so as not to violate conditions of a beta distribution, for which the response interval is (0,1), not [0,1]. Our model assumed constant variation across years in uncertainty by use of a constant shape parameter for dispersion, ϕ . A slope was interpreted as meaningful if the 95% highest density credible interval (from R package HDINTERVAL; Meredith & Kruschke, 2020) did not overlap 0, whereas if 95%–97.5% of slopes in the posterior probability distribution were positive or negative (i.e. its pd), the slope was interpreted as suggestive. For those species with a long sighting record, dating from the early part of the 20th century to 2020, the slope will be biased upward purely because survey frequency was annual or nearly so in the last quarter of the dataset but infrequent and spotty in the first quarter. We analysed these species a second time with the Bayesian beta regression adjusted to account for the biased slopes (adjustment entailed use of data only from 1970 onward as well as estimating a slope derived solely from an increase in

survey intensity and using that estimate as a baseline). Those species that had genuinely increased continued to exhibit a positive trend, but for other species, the trend disappeared when sighting record bias was removed.

Resultant slopes from beta regression, one for each of 244 species, were used as response variables in subsequent analyses to assess which species-specific ecological traits best accounted for the trend. We used the species attributes body mass (log-transformed; Dunning, 2008), dietary class (plant, animal), diet (carnivore, frugivore, granivore, herbivore, insectivore, nectarivore, piscivore; >1 possible; Levey et al., 2021), dietary breadth (tally of diets; 1–5), foraging stratum (water, ground, understorey, lower, upper, bark, aerial; >1 possible; Parker III et al., 1996), strata (tally of strata 1–3; Parker III et al., 1996), foraging method (flycatching, hang-gleaning, gleaning, hawking, hover-snatching, manipulation, pouncing, probing, snatching; Remeš et al., 2021), motility (sedentary, migratory), affinity (forest, open), habitat (freshwater, primary edge, secondary edge, savanna, scrub, secondary forest, primary forest, urban; >1 possible; Levey et al., 2021) and habitat breadth (tally of habitats used; 1–6). We used Bayes factors (Kass & Raftery, 1995) to assess how well a model provided support against H_0 (e.g. an intercept-only model). Bayes factors, a ratio of a parameterized model's likelihood against H_0 , allow one to rank competing models akin to now-standard procedures that use information criteria, but they incorporate an element of effect size as well. Long-standing categories for evidence against H_0 (Kass & Raftery, 1995) are that a Bayes factor <3.2 indicates there is little to no support for H_A , the model in question, whereas a factor of 3.2–10 indicates 'substantial', 10–100 'strong' and >100 'decisive' evidence against H_0 . (Bayes factors <1 provide evidence for H_0 against H_A and can be interpreted in the same categories as $1/\text{Bayes Factor}$) Estimates were obtained via the 'general-Test' function in the R package BAYESFACTOR (Morey & Rouder, 2018). For any attribute well-supported in final models, we determined which specific classification (e.g. which diet) or cutoff, as well as directionality of relationship (+ or –), using Bayesian model averaging (R package BMA; Raftery et al., 2021). Unlike standard model selection techniques founded on information criteria, BMA incorporates uncertainty in the process as it estimates variable importance from a posterior probability distribution of a combination of all candidate models (Hinne et al., 2020). We completed all analyses using R software (R Core Team, 2022).

3 | RESULTS

We compiled a list of 378 bird species reliably detected in Palenque during the 1900–2020 time frame, including 241 residents (63.8%) and 137 winter visitors, migrants and vagrants (36.2%). For data analysis, we reduced the species list to 244 species to include only residents, over-summering Nearctic migrants (e.g. *Chordeiles acutipennis*), altitudinal migrants that have historically spent lengthy periods in Palenque (e.g. *Turdus assimilis*) and summer breeders (e.g. *Elanoides forficatus*, *Ictinia plumbea*, *Progne chalybea*, *Myiodynastes*

luteiventris and *Legatus leucophaeus*). Of these 244 species, we classified 26 as carnivores (10.6%), 45 as frugivores (18.4%), 22 as granivores (9%), 3 as herbivores (1.2%), 124 as insectivores (50.6%), 14 as nectarivores (5.7%) and 10 as piscivores (4.1%). Due to a low overall count of scavenger species and likeness to carnivores, we added the feeding guild to the carnivore category.

Overall, 25 species had a decreasing trend and 43 species had an increasing trend (see Table 1 for the top 20 of each category). We detected 23 (9.4%) species with a strong negative trend and 32 (13.1%) species with a strong positive trend (i.e. 95% highest density credible intervals did not include 0, so >97.5% of estimates that comprised the posterior distribution were negative or positive). Forest specialists accounted for 81.6% of species with a strong decreasing trend, and open area specialists accounted for 62.5% of species with a strong increasing trend (Figure 1). For decreasing species, forest specialists represented four feeding guilds while open area specialists represented two feeding guilds (Figure 1). For increasing species, forest and open area specialists contained six feeding guilds alike (Figure 1). The mean posterior probability distribution of the mean population trend for forest specialists was significantly lower than for open area specialists (Figure 2).

The 20 bird species with the strongest negative trends (Table 1) consisted of 17 primary forest specialists, two tropical savanna species and one secondary forest species (see Figure 3 for examples of individual species trends). The 20 species with a strong positive trend consisted of 10 open area species common in introduced pasturelands, six insectivores and a nectarivore common in secondary forests, three wetland and flooded pasture species, and one urban species (Table 1 and see Figure 3 for examples of individual species trends).

Body mass attributed to negative species trends, on average, for body masses of approximately <6.6 and >948.4 g and positive species trends for body masses between 6.6 and 948.4 g (Figure 4). For habitat and dietary breadth, our results show a stepwise pattern of decreasing to increasing population trend for high to low dietary and habitat breadth specificity (Figure 5). Estimated Bayes factors indicated decisive support for models of a trend that included various combinations of habitat breadth, dietary breadth, primary habitat, body mass and dietary class, with the 'best' model over 8600× more likely than a null model (Table 2 and Table S1, Supporting Information). The stratum at which a species tends to occur and its principal foraging method also contributed to decisive models, but such models ranked well below models that excluded these attributes (Table 2 and Table S1, Supporting Information).

4 | DISCUSSION

Long-term land-use change in biodiverse areas heavily impacts bird species populations and functional groups, creating bird biodiversity conservation challenges for areas that depend on the ecosystem services of native biodiversity (Echeverri et al., 2022). In this study, we developed a novel framework by which we could estimate absence from a detection/nondetection record from 1990 to 2020 in

TABLE 1 Ranked list of the 20 bird species exhibiting the strongest negative and positive population trends in Palenque from 1900 to 2020. Trend refers to the slope value for the occupancy probability curves from 1900 to 2020

Decreasing			Increasing		
Scientific name	Common name	Trend	Scientific name	Common name	Trend
<i>Columbina minuta</i>	Plain-breasted Ground Dove	-0.068	<i>Falco femoralis</i>	Aplomado Falcon	0.0514
<i>Tunchiornis ochraceiceps</i>	Tawny-crowned Greenlet	-0.0612	<i>Tyrannus savana</i>	Fork-tailed Flycatcher	0.0507
<i>Claravis pretiosa</i>	Blue Ground Dove	-0.0449	<i>Cyanocorax yncas</i>	Green Jay	0.0495
<i>Colinus virginianus</i>	Northern Bobwhite	-0.042	<i>Passer domesticus</i>	House Sparrow	0.0492
<i>Piranga leucoptera</i>	White-winged Tanager	-0.0409	<i>Tigrisoma mexicanum</i>	Bare-throated Tiger Heron	0.0481
<i>Penelope purpurascens</i>	Crested Guan	-0.04	<i>Icterus gularis</i>	Altamira Oriole	0.0478
<i>Lanio aurantius</i>	Black-throated Shrike-Tanager	-0.0399	<i>Bubulcus ibis</i>	Cattle Egret	0.0463
<i>Microrhopias quixensis</i>	Dot-winged Antwren	-0.0387	<i>Cathartes burrovianus</i>	Lesser Yellow-headed Vulture	0.0453
<i>Heliodytes barroti</i>	Purple-crowned Fairy	-0.0374	<i>Chondrohierax uncinatus</i>	Hook-billed Kite	0.042
<i>Malacoptila panamensis</i>	White-whiskered Puffbird	-0.0363	<i>Mimus gilvus</i>	Tropical Mockingbird	0.0416
<i>Eucometis penicillata</i>	Grey-headed Tanager	-0.0359	<i>Burhinus bistriatus</i>	Double-striped Thick-knee	0.0407
<i>Lipaugus unirufus</i>	Rufous Piha	-0.0355	<i>Butorides virescens</i>	Green Heron	0.0407
<i>Uropsila leucogastra</i>	White-bellied Wren	-0.0344	<i>Peucaea botterii</i>	Botteri's Sparrow	0.0403
<i>Microcerculus philomela</i>	Nightingale Wren	-0.0343	<i>Caracara cheriway</i>	Crested Caracara	0.04
<i>Icterus prothemelas</i>	Black-cowled Oriole	-0.033	<i>Zenaida asiatica</i>	White-winged Dove	0.0393
<i>Caryothraustes poliogaster</i>	Black-faced Grosbeak	-0.0327	<i>Busarellus nigricollis</i>	Black-collared Hawk	0.0357
<i>Lophornis helenae</i>	Black-crested Coquette	-0.0321	<i>Sclerurus guatemalensis</i>	Scaly-throated Leaf-tosser	0.0337
<i>Notharchus hyperrhynchus</i>	White-necked Puffbird	-0.0313	<i>Icterus cucullatus</i>	Hooded Oriole	0.0331
<i>Pachyramphus cinnamomeus</i>	Cinnamon Becard	-0.0286	<i>Heliomaster longirostris</i>	Long-billed Starthroat	0.0325
<i>Icterus mesomelas</i>	Yellow-tailed Oriole	-0.0262	<i>Troglodytes aedon</i>	House Wren	0.032

terms of the probability of a false negative before running species trend analyses, lending higher confidence in our results than if we had considered species absences as true and not a function of low sampling effort. We used several credible data sources on bird biodiversity from the lowland tropical rainforest of Palenque, Chiapas (Patten et al., 2010). We then used a Bayesian statistical framework to estimate species population trends and connect relevant functional traits to population trend increases and declines.

Our results supported our predictions and showed that long-term land-use change in Palenque has influenced the widespread replacement of extirpated rainforest specialists for open area colonizers. We detected more decreasing feeding guilds from forest habitat relative to open habitat, and we detected an equal and larger range of feeding guilds within the increasing species group in both forested and open habitats, building upon existing trends of increased heterogeneity of functional diversity at the community level uncovered by previous work in the area (Levey et al., 2021; Patten et al., 2010). Species with

the smallest and largest masses, restricted dietary breadth, and plant feeding categories (e.g. nectar, fruit and seeds) in the community experienced negative population trends, while species with intermediate body masses, high dietary and habitat breadth, and 'meat' feeding categories (e.g. meat, fish and insects) in the community exhibited positive population trends. Our Bayesian framework for modelling species absence before calculating estimated species population trends and results provide key computational contributions to bird ecological studies that aim to use a variety of data sources when long-term studies are lacking and empirical evidence of long-term bird biodiversity responses to land-use change respectively.

4.1 | Body size affects risk only at its extremes

Consequences of land-use change in the tropics are often reflected in diversity changes of species with certain body masses

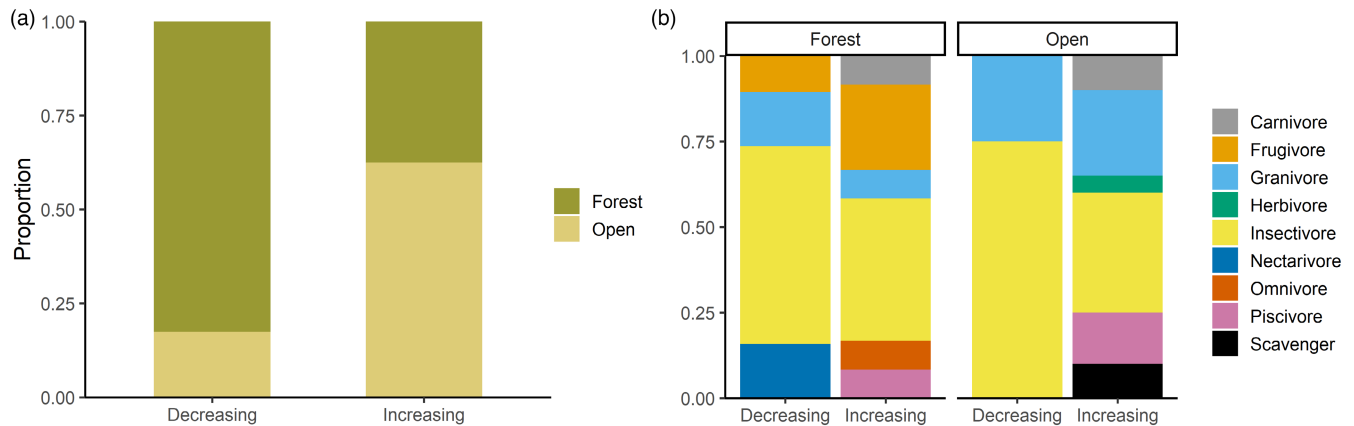


FIGURE 1 Proportion of (a) forest and open habitat specialist bird species that are decreasing and increasing and (b) species assigned to feeding guilds that are decreasing and increasing from forest and open habitats.

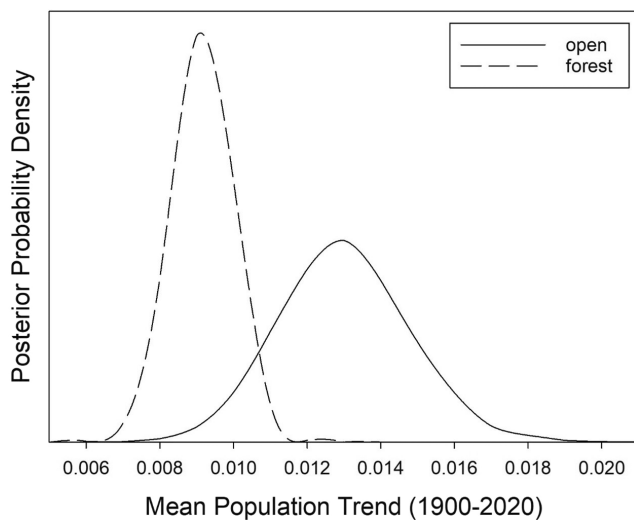


FIGURE 2 Distributions of posterior probability densities and mean population trends (i.e. slope values of the probability of occurrence) for open area and forest specialist bird species from 1900 to 2020. Forest specialists had a significantly lower mean population trend than open area specialists.

(Patten & Smith-Patten, 2011; Ripple et al., 2017; Şekercioğlu et al., 2002). Bird species with small and large body masses face a higher risk of population declines and extirpation after habitat disturbance (Ripple et al., 2017). For birds with smaller body masses, habitat disturbance (Remeš et al., 2021), loss and fragmentation (Şekercioğlu et al., 2002) have been shown to have filter species with low dispersal capacities and sensitive nesting and dietary requirements (Boesing et al., 2021). In Palenque, the smallest species declines include hummingbirds (e.g. *Phaethornis longirostris*, *P. striigularis* and *Campylopterus hemileucurus*) commonly found in primary and secondary forest understorey. We also found declines in understorey insectivores, including species that were commonly found foraging in mixed-species swarm flocks (e.g. *Eucometis penicillata*, *Lanio aaurantius* and *Tunchiornis ochraceiceps*). These species require dense understorey vegetation to display and sing, forage and nest in hanging palm leaves (Morante-Filho et al., 2018). Species with larger body masses

have a recorded history of extirpation in the Neotropics (Almeida et al., 2022), and at Palenque, large cracids (*Penelope purpurascens* and *Crax rubra* respectively) and raptors (Buechley et al., 2019; e.g. *Harpia harpyja* and *Spizaetus ornatus*) respectively, have declined or been extirpated from hunting and habitat loss. Patten et al. (2010) noted that both small and large species have become extirpated from Palenque due to the isolation and size reduction of the protected area. We note the declines of these small and large species and highlight their functional traits to signal potential ecosystem service losses to local agriculture, seed dispersal, trophic level disruptions and social and economic ramifications of emblematic bird species loss. Mechanistically, a species' dietary or habitat breadth, alone or in combination, could be the key predictor of species trend, and quantification of breadth may be the best surrogate for ecological specialization, theoretically an important indicator of extinction risk (Patten & Smith-Patten, 2011).

4.2 | 'Winners' versus 'losers'

Faunal homogenization is the tendency in many anthropogenically disturbed habitats as various disturbance-tolerant species replace disturbance-sensitive species, a situation that indirectly creates ecological winners and losers (Filgueiras et al., 2021). Our results show that over 120 years, widespread conversion of forest to homogenous cattle pasture in the 1960s and 1970s has, as expected, driven higher population increases in open area bird species relative to rainforest specialists. Patten et al. (2010) reported that 15 understorey insectivorous and large canopy frugivorous species have been extirpated from the study area. Smaller patch size and higher fragmentation combine to drive declines in insectivorous birds specializing in understorey foraging (Patten et al., 2010; Şekercioğlu et al., 2002) and in frugivorous species dependent on large fruiting trees (Luck & Daily, 2003), especially species with lower dispersal capacities (Levey et al., 2021). Loss of forest species likely is a result of their sensitivity to light, higher penetration of which is inevitable as a forest's footprint decreases

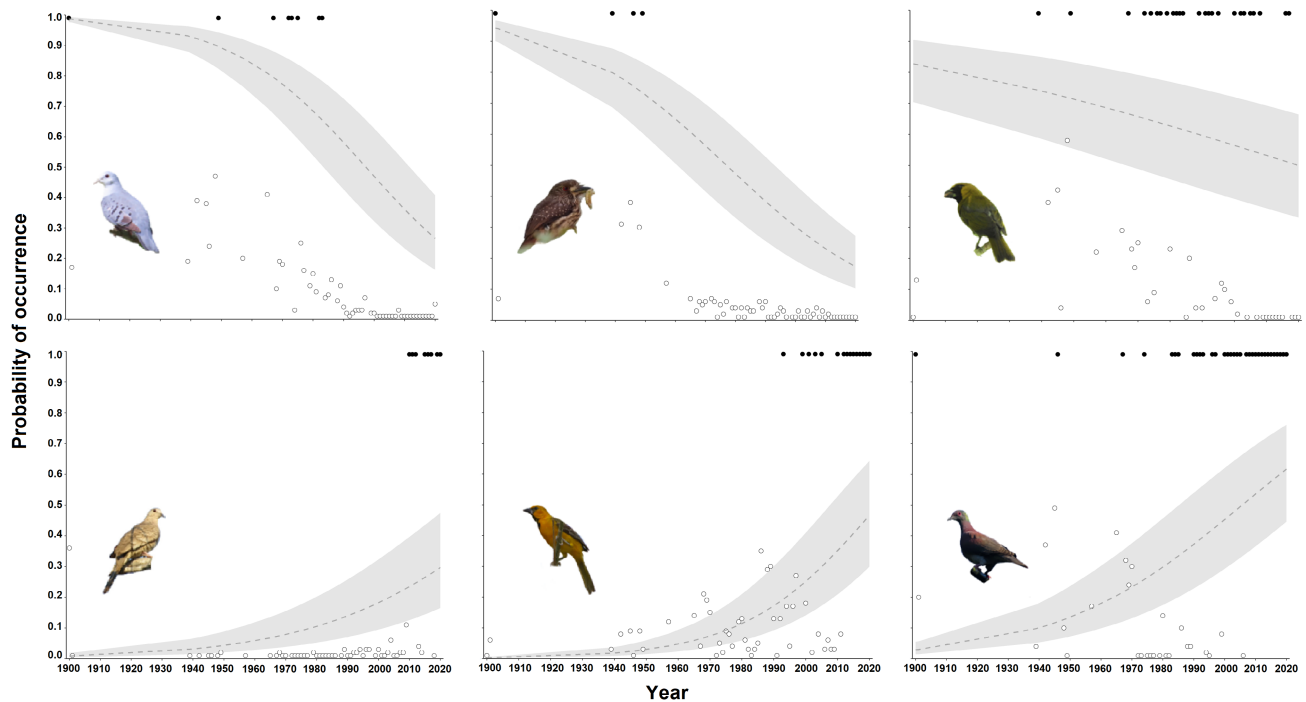


FIGURE 3 Examples of bird species exhibiting decreasing (top row) and increasing (bottom row) estimated trends, represented by occurrence probability (dashed line) and 95% credible interval (grey shading), over the 1900–2020 time frame from Palenque, Chiapas. Notable changes to the tropical lowland rainforest of the area occurred in the 1960s and 70s with the establishment of widespread introduced grasslands for cattle ranching. Open circles represent absence and modelled occurrence probability, and filled circles represent an observed presence in a given year. Top row, from left to right: Granivorous Blue Ground Dove (*Claravis pretiosa*; slope = -0.045), insectivorous white-whiskered Puffbird (*Malacoptila panamensis*; slope = -0.047), and frugivorous black-faced Grosbeak (*Caryothraustes poliogaster*; slope = -0.033). Bottom row, from left to right: Granivorous Inca Dove (*Columbina inca*; slope = 0.021), insectivorous Altamira Oriole (*Icterus gularis*; slope = 0.048), and frugivorous pale-vented Pigeon (*Patagioenas cayennensis*; slope = 0.012). Photo credit: DRL.

(Jirinec et al., 2022; Patten & Smith-Patten, 2012), setting up species of forest interior as losers. Conversely, these same patch size and fragmentation drivers can lead to higher species (Falkowski et al., 2020) and functional diversity in disturbed landscapes relative to protected areas, even after accounting for species extirpations (Levey et al., 2021). This may be achieved by maintaining a baseline group of species that successfully forage and nest throughout a heterogeneous landscape, the increase in forest edge and grassland species, and colonizing species raising community functional diversity (García et al., 2014).

As noted above, foraging items and habitat breadth often affiliated with population trend variance in our results. Landscape-wide land-use change in the area converted what was once homogenous lowland rainforest into a mix of habitats, especially today (Levey et al., 2021). The mix of habitats, each on their own small, degraded or composed of nonnative vegetation and between a high contrast cattle pasture matrix, is unfavourable for primary forest and dietary specialists that require large plots of undisturbed habitat (Boesing et al., 2021). The landscape has favoured bird species with inherent dietary and habitat flexibility that thrive in a combination of forest, forest edge, plantations, agricultural land and urban settings (e.g. *Turdus grayi*, *Quiscalus mexicanus*, *Saltator maximus*, *Myiozetetes similis* and *Pitangus sulphuratus*). This phenomenon is coupled with an imbalance of bird species occupying new habitats created by

disturbance (*Tigrisoma mexicanum*, *Butorides virescens*, *Zenaida asiatica*, *Quiscalus mexicanus*, *Dendrocygna autumnalis* and *Icterus gularis*), including more generalist species replacing forest specialists in disturbed portions of the landscapes and a lack of species occupying habitat of disturbed portions of primary forest (Levey et al., 2021).

In the decade since the work of Patten et al. (2010), we found evidence of further declines and apparent novel and surprising extirpations of other strict primary rainforest species. These species include upper canopy dwelling species (*Patagonioenas nigrirostris*, *Icterus prothemelas*, *Caryothraustes poliogaster* and *Vireolanius pulchellus*), ground, mid-level and understorey insectivorous species (*Dysithamnus mentalis*, *Thamnistes anabatinus*, *Terentotriccus erythrurus* and *Aimophila rufescens*) and savanna species (*Molothrus oryzivorus* and *Tiaris olivaceus*). We also detected evidence for the establishment of eight breeding species in the area since 2010, including three wetland species (*Porphyrio martinica*, *Dendrocygna autumnalis* and *Aramides axillaris*), four urban specialists (*Passer domesticus*, *Streptopelia decaocto*, *Columbina inca* and *Columba livia*) and one open, dry woodland species (*Poliophtila caerulea*). Of the species representing new breeding records, all have occupied areas with heavy disturbance, which is a noted trend for the invasive doves and sparrow (MacGregor-Fors et al., 2010; Martínez-Ruiz & De Labra-Hernández, 2022) and may signal a homogenization of habitat and dietary generalist species diversity in

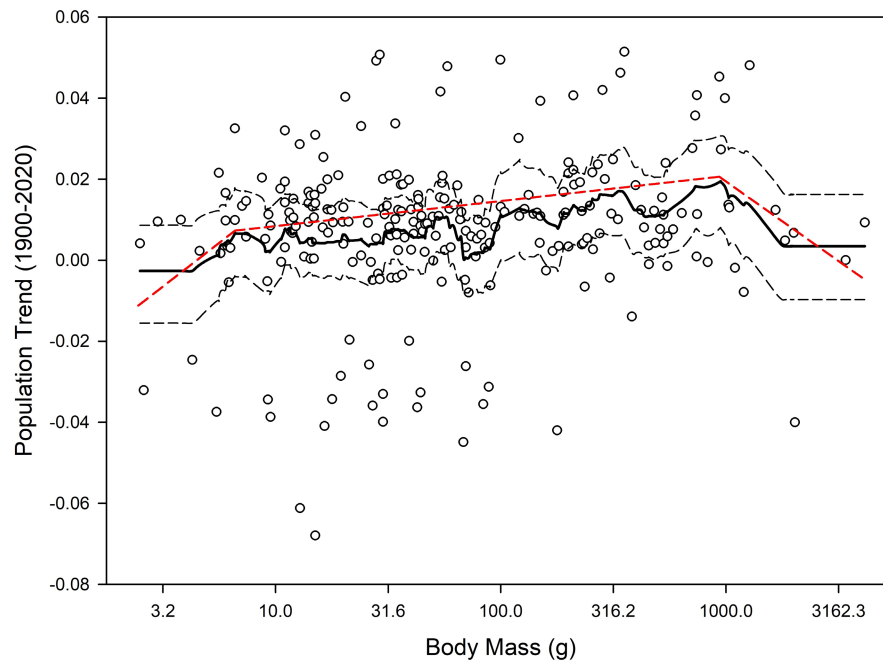


FIGURE 4 Relationship between population trend from 1900 to 2020 and log-transformed body mass for all bird species (represented by unfilled circles). Displayed here is the output of Bayesian nonlinear regression analysis (analogous to a standard least squared-based LOESS regression, itself akin to moving average approaches), including a best fit line in bold between two credible interval lines. Species at the tail ends of the best fit line and body mass distribution (i.e. smallest and largest body masses) exhibited either a stable or negative change in population trend. Species between the tail ends exhibited an average increase in population trend: On the basis of piecewise regression, a negative trend appears below 6.6 g and above 948.4 g. The red line represents a piecewise regression atop the moving average-type fit to highlight the relative trend decreases at the tails of the distribution.

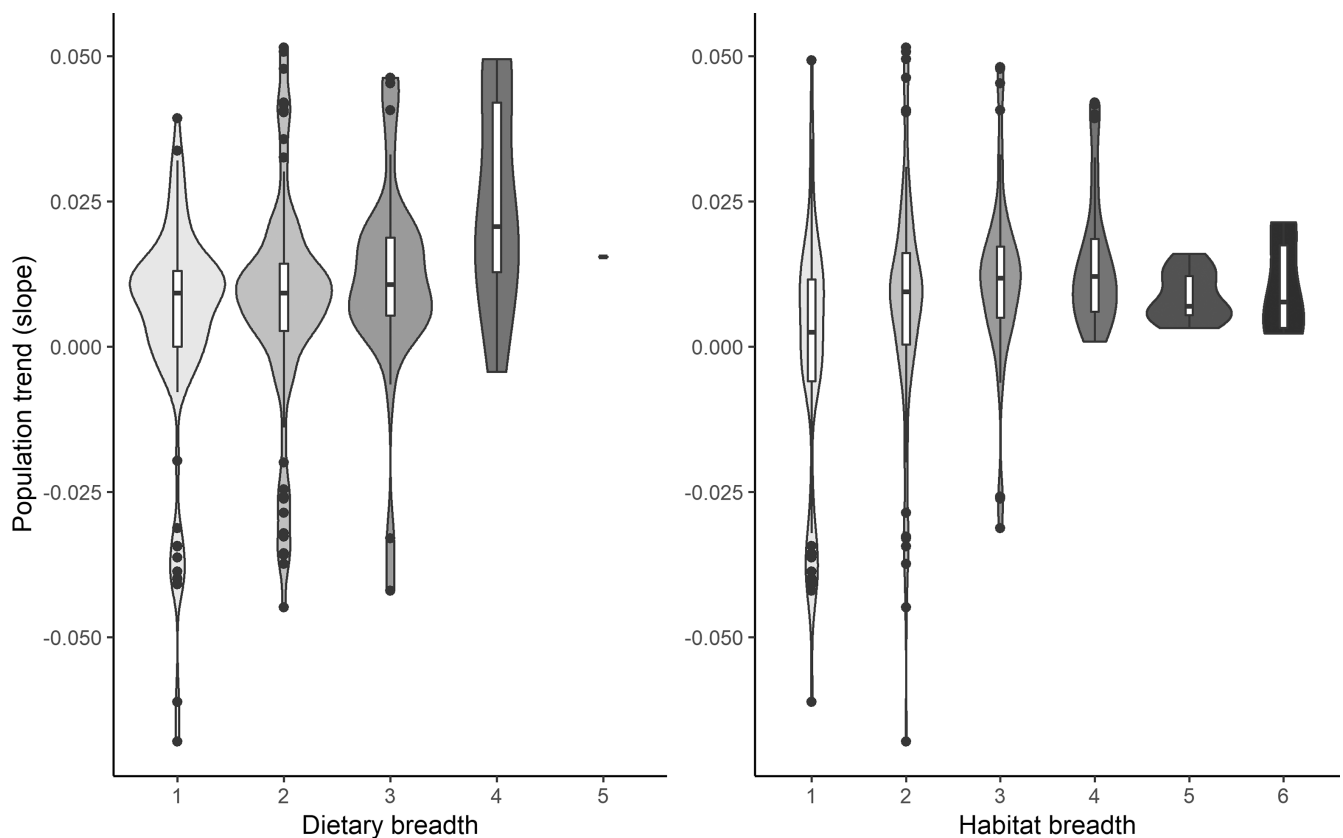


FIGURE 5 Violin plot of population trend slopes and dietary and habitat breadths. Our results highlight the affiliation of dietary and habitat breadth specificity on population trend in a stepwise pattern of decreasing to increasing population trends for high to low dietary and habitat breadth specificity.

Functional trait	Number of top models with trait	Increasing trend	Decreasing trend
Body mass (g)	12	Between 6.6 g and 948.4 g	<6.6 and > 948.4 g
Diet class	8	—	Plant diets
Dietary breadth	18	≥4	—
Foraging stratum	4	Water	—
Foraging method	2	—	Gleaning
Primary habitat	14	Savanna, urban, freshwater	Primary forest
Habitat breadth	18	≥3	—
Motility	0	—	—
Habitat affinity	0	—	—
Diet	0	—	—
Strata	0	—	—

TABLE 2 Summary of functional traits included in the top 22 additive models and the specific ranges for each that affiliated with a negative or positive slope value for species occupancy curves, which we use to infer increasing and decreasing population trend. Bayesian model averaging indicated whether each functional traits was affiliated with increasing or decreasing population trend

disturbed tropical areas of Mexico (Vázquez-Reyes et al., 2017). Functionally, this turnover is skewed towards positive trends of species of animal feeding categories and negative trends of species of the plant diet class (Levey et al., 2021). Specifically, the presence of a positive mean trend of insectivores despite small, primary forest insectivore declines was due to individual positive trends of flycatcher species that thrive in a range of disturbed habitats throughout tropical areas of Mexico (e.g. *Tyrannus melancholicus*, *Myiozetetes similis* and *Pitangus sulphuratus*) and species common in open and drier habitats of the Yucatan peninsula (e.g. *Tyrannus savana*, *Mimus gilvus* and *Troglodytes aedon*). Frugivores and nectarivores declined in response to forest loss and were not replaced by adequate increases in certain species or compensated by colonizing species, highlighting the concerns of ecosystem services losses outside of protected areas.

5 | CONCLUSIONS

Long-term land-use change that replaces tropical rainforest with introduced grassland for cattle can have drastic impacts on bird communities (Hendershot et al., 2020; Levey et al., 2021; Şekercioğlu et al., 2019). Piecing out the relevant functional traits that may help or hinder bird species under such landscape transformation has important conservation and land management implications, especially in areas where bird ecosystem services have historically and presently affected local economy, ecology and cultural identity (Echeverri et al., 2020). To prevent further distancing of the Palenque bird community from its historical and native characteristics, measures are needed to protect habitat for the most at-risk bird species and functional groups. The top opportunity for this goal is outside PNP, where the landscape has undergone widespread changes (Levey et al., 2021). At risk are ecosystem services vital for human well-being, including a reduction of bird tourism in response to species extirpations.

For small insectivores and nectarivores, forest connectivity with PNP and surrounding secondary forest patches needs improvement to raise the effectiveness of the protected area (Mayhew et al., 2019). Large tree retention coupled with understorey clearing must be understood as harmful for many species of wildlife, and the call for increased connectivity must be understood as corridors of native plants at all forest structure levels. Increasing and maintaining native forest corridors, especially with flowering and fruiting trees, will positively impact nectarivores and larger, upper canopy frugivores. Attention also must be paid to rapidly decreasing native savanna in the area, which has been linked to the extirpation of native granivorous species. These habitats must be conserved to protect unique and endemic species for bird tourism and herbivorous insect and rodent control that native savanna species (e.g. *Burhinus bistriatus*, *Columbina minuta* and *Tyto alba*) provide to the area (Daily & Karp, 2015; Echeverri et al., 2022). While these measures may be supported and implemented in areas with a high dependence on tourism, further attention is needed to evaluate tourism impacts on bird biodiversity (Echeverri et al., 2022). Such impacts include increased urbanization (via road, train rail and hotel creation), anthropogenic noise and waste pollution, change to vegetation composition with introduced plants, and trampling of forest trails swollen visitor carrying capacities. These efforts are especially needed in areas that wish to expand urban commodities and increase access to remaining natural areas for projected increases in tourism activity so that conservation and land management efforts are not in vain.

AUTHOR CONTRIBUTIONS

All authors conceived research ideas and questions. Dallas R. Levey and Michael A. Patten designed methodology and performed research. Michael A. Patten wrote and performed Bayesian trend analyses. Dallas R. Levey and Michael A. Patten collected data and performed analyses. Dallas R. Levey led the writing of the manuscript. All authors wrote the paper, contributed to manuscript

revisions, and approved the manuscripts submitted for review and publication.

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CONFLICT OF INTEREST

We declare no sources of conflict of interest.

DATA AVAILABILITY STATEMENT

Data and R code are available at FigShare <https://doi.org/10.6084/m9.figshare.21494421.v1> (Levey et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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