ECOLOGY LETTERS

Ecology Letters, (2020) doi: 10.1111/ele.13628

LETTER

Long-term change in the avifauna of undisturbed Amazonian rainforest: ground-foraging birds disappear and the baseline shifts

Philip C Stouffer,[1,2*†]
Vitek Jirinec,[1,2†]
Cameron L. Rutt,[1,2,3†]
Richard O. Bierregaard Jr,[2]
Angélica Hernández-Palma,[1,2,4]
Erik I. Johnson,[1,2,5]
Stephen R. Midway,[6]
Luke L. Powell,[1,2,7]
Jared D. Wolfe[1,2,8] and
Thomas E. Lovejoy[2,9]

Abstract

How are rainforest birds faring in the Anthropocene? We use bird captures spanning > 35 years from 55 sites within a vast area of intact Amazonian rainforest to reveal reduced abundance of terrestrial and near-ground insectivores in the absence of deforestation, edge effects or other direct anthropogenic landscape change. Because undisturbed forest includes far fewer terrestrial and near-ground insectivores than it did historically, today's fragments and second growth are more impoverished than shown by comparisons with modern 'control' sites. Any goals for bird community recovery in Amazonian second growth should recognise that a modern bird community will inevitably differ from a baseline from > 35 years ago. Abundance patterns driven by landscape change may be the most conspicuous manifestation of human activity, but biodiversity declines in undisturbed forest represent hidden losses, possibly driven by climate change, that may be pervasive in intact Amazonian forests and other systems considered to be undisturbed.

Keywords

Amazonia, biodiversity erosion, Biological Dynamics of Forest Fragments Project, bird communities, bird declines, climate change, community change, defaunation, rainforest, shifting baseline.

Ecology Letters (2020)

INTRODUCTION

Tropical forest loss has spurred concern over declining biodiversity. Landscape ecology, rooted in island biogeography, provides insights into how forest cover, fragment size, matrix composition, and edge effects influence populations or communities across altered landscapes (Sekercioglu *et al*., 2007; Martensen *et al*., 2012; Wolfe *et al*., 2015; Pfeifer *et al*., 2017; Fletcher *et al*., 2018). These concepts predict how configuration of remaining forest, matrix and regeneration affect rainforest taxa (Dent and Wright, 2009; Hanski *et al*., 2013; Pfeifer *et al*., 2017). Critically, assessing how landscape change affects biodiversity usually involves comparing results from disturbed areas with baseline metrics from the least disturbed setting. If data from disturbed and control sites are collected concomitantly, the approach becomes a space-for-time substitution analysis, even if this is not mentioned explicitly (e.g. Pickett, 1989; Fig. 1). The comparison describes the current pattern, but may not reveal mechanisms or trajectory in a non-stationary environment (Damgaard, 2019).

Biodiversity change in tropical forests may also occur in the absence of landscape change, although revealing these patterns requires long-term sampling of sites within undisturbed forest. A network of tree community plots has shown altered plant communities and ecosystem properties consistent with climate change (e.g. Esquivel-Muelbert *et al*., 2019). As tropical tree communities and climate undergo directional change, rainforest animal communities may also be experiencing long-term changes distinct from landscape effects (e.g. Brawn *et al*., 2017). Unfortunately, the level of sampling that has revealed patterns for plants is generally not available for animals. Unlike tree community studies from multiple sites sampled across decades, results showing trends for animals in intact tropical forest are compromised by narrow spatial or temporal sampling, local disturbance, or landscape change (Whitfield *et al*., 2007; Visco *et al*., 2015; Blake and Loiselle, 2016; Lister and Garcia, 2018; Willig *et al*., 2019).

To understand how rainforest biodiversity will change from the multiple pressures of the Anthropocene (Dirzo *et al*., 2014), we need to disentangle processes resulting from deforestation-driven landscape context (e.g. Pfeifer *et al*., 2017) from those occurring in intact forest in the absence of landscape effects (e.g. Esquivel-Muelbert *et al*., 2019). For

[1]*School of Renewable Natural Resources, Louisiana State University AgCenter and Louisiana State University, Baton Rouge, LA 70803, USA*
[2]*Biological Dynamics of Forest Fragments Project, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas 69011, Brazil*
[3]*Department of Biology, George Mason University, Fairfax, VA 22030, USA*
[4]*Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Avenida Paseo Bolívar 16-20, Bogotá, D.C, Colombia*
[5]*National Audubon Society, 5615 Corporate Blvd. #600b, Baton Rouge, LA 70808, USA*
[6]*Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, LA 70803, USA*
[7]*School of Biological and Biomedical Sciences, Durham University, Durham DH1 3LE, UK*
[8]*College of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI 49931, USA*
[9]*Department of Environmental Science and Policy, George Mason University, Fairfax, VA 22030-4444, USA*
**Correspondence: E-mail: pstouffer@lsu.edu*
†These authors contributed equally to this work.

© 2020 John Wiley & Sons Ltd

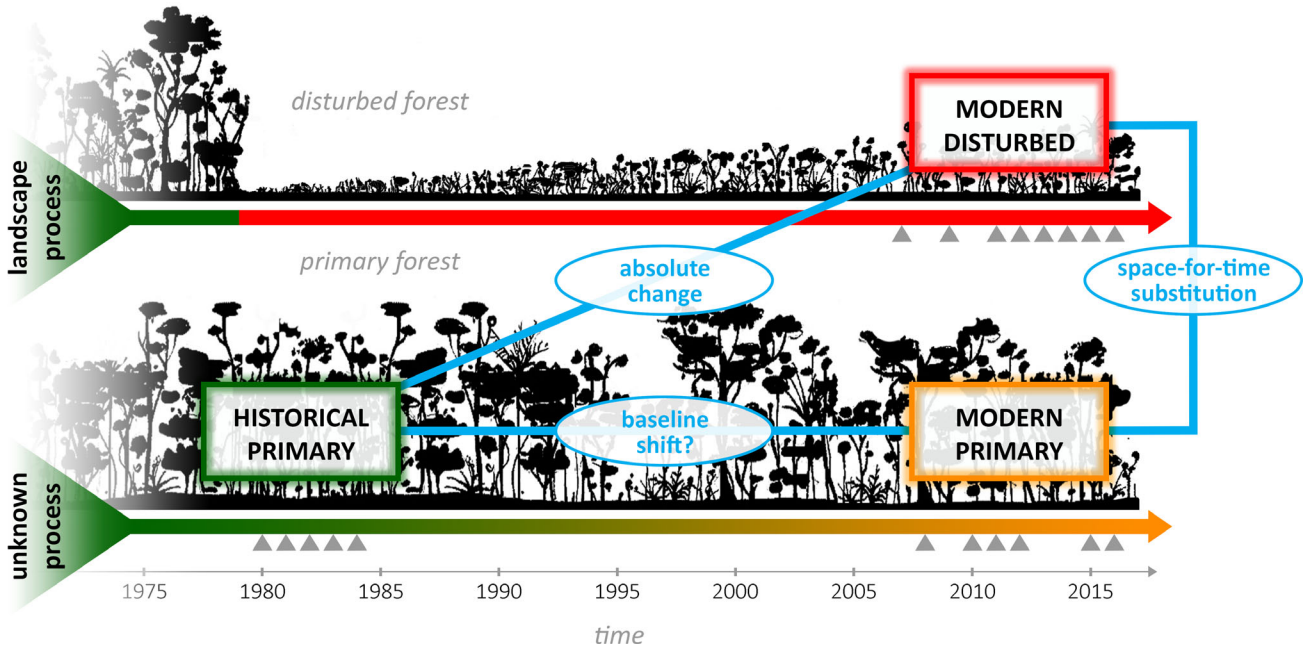

Figure 1 Biotic change drivers and research approaches. The typical space-for-time substitution used to assess landscape processes, in this case beginning with forest clearing in 1979, will be misleading if communities in undisturbed primary forest have changed (baseline shift). Triangles indicate years of sampling included in our analysis.

animals, this represents a formidable challenge due to the difficulty of achieving adequate sampling in space and time (Visco *et al.*, 2015). If animal patterns are changing in the absence of landscape change, it would represent a sobering warning that simply preserving forest does not maintain rainforest biodiversity in a static condition. Moreover, abundance changes within continuous primary forest would show that the baseline used to determine contemporary landscape-level effects has shifted. Unfortunately, this could dampen encouraging results that suggest recovering landscapes will support rainforest taxa even as primary forest continues to be cleared (Dent and Wright, 2009). The most meaningful assessment of modern communities should be against a baseline from undisturbed forest that accounts for changes in recent decades, rather than relying only on inference from space-for-time substitution (França *et al.*, 2016; De Palma *et al.*, 2018; Soga and Gaston, 2018).

The Biological Dynamics of Forest Fragments Project (BDFFP), north of Manaus, Brazil, offers the opportunity to examine long-term changes in understorey bird abundance from primary forest plots unaffected by local landscape effects. In addition to undisturbed forest, about 10% of the forested area has been removed or fragmented, revealing landscape effects on birds (Stouffer, 2020). Using standardised bird capture data from undisturbed primary forest plots sampled decades apart and from fragments and second growth in the modern disturbed landscape, we address two objectives (Fig. 1). First, we assess abundance change in primary forest between 1980–1984 and 2008–2016. From this analysis, we identify the species and guilds that have changed in this interval in the absence of landscape effects. These are birds responding to as-yet unknown processes that may be operating throughout the vast Amazonian rainforest. Second, we use a parallel analysis to assess abundance change between the historical primary forest and the modern disturbed landscape. These results reveal the extent to which the 'undisturbed' forest baseline has shifted, with reduced abundance in the modern primary forest compounding landscape effects for vulnerable species.

METHODS

Study area

The BDFFP includes three adjacent *c.* 15 000 ha rainforest parcels about 80 km north of Manaus, Brazil (2°20'S, 60°W; Fig. S1). Beginning in the 1970s, limited clearing of primary rainforest produced a mosaic of pastures and forest fragments, although the entire area remains embedded in a vast expanse of undisturbed forest (Gascon and Bierregaard, 2001). Additional forest clearing in the area slowed over the 1980s and generally ceased by about 1990. Across the BDFFP, overall forest cover has persisted at > 90% for as long as LANDSAT imagery has been available to analyse (since 1985; Rutt *et al.*, 2019a). The forest is typical *terra firme* rainforest, growing on nutrient-poor soils characteristic of the Guiana Shield (Gascon and Bierregaard, 2001). Rainfall at Reserva Ducke, about 60 km to the south, averages *c.* 2550 mm/year, peaking in March through May (Aleixo *et al.*, 2019).

Site selection

In the early 1980s, BDFFP researchers sampled birds in many plots within continuous primary forest in anticipation

© 2020 John Wiley & Sons Ltd

that the plots would become isolated (see Bird sampling); the objective was to examine community change following isolation. Eleven plots were eventually isolated and have been sampled through 2016. By the late 1980s, it became apparent that additional forest would not be cleared, and sampling ceased in almost all continuous forest sites. For our historical sample, we chose 34 sites in continuous forest that had been sampled 4-9 times in 1980-1984 (Fig. S1; $n = 3$ sites sampled 4 times, $n = 1$ site sampled 5 times, $n = 29$ sites sampled 6 times, and $n = 1$ site sampled 9 times). Primary forest sites we analysed were originally delineated without any systematic selection process. These sites were spread over a linear distance of > 35 km between the two most distant sites. For our modern sample, we used 21 continuous forest sites each sampled 4-6 times from 2008 to 2016 ($n = 7$ sites sampled 4 times, $n = 5$ sites sampled 5 times, $n = 9$ sites sampled 6 times). These sites were not the same sites sampled in the 1980s, but they spanned approximately the same area, with maximum separation of > 40 km between the two most distant sites.

Sites in the two primary forest samples were similar representations of the broader landscape; most sites in both time periods were < 3 km of a site from the other time period (Fig. S1). The mean distance of a modern site to the nearest historical site was 2536 m (range 54–6580 m, SD = 2080 m). Sites were at least 200 m from any edge, beyond the reach of the vast majority of the many edge effects measured at the BDFFP, including reduced understorey bird abundance (Powell *et al*., 2013; Laurance *et al*., 2004; 2018). On average, sites in both samples were > 900 m from any edge, and were distributed similarly in both samples (Fig. S2). Logistics of sampling birds along trails within delineated plots led to some clumping of sites. We controlled for this effect, which was present in both time periods, using a similar distribution of sites with regard to distance among sites (Fig. S3; mean distance in both samples > 400 m).

For the modern disturbed landscape, we included 15 sites: $n = 4$ 1-ha fragments; $n = 3$ 10-ha fragments; and $n = 8$ sites in second growth, sampled 5–21 times from 2007 to 2016. These sites were selected to capture landscape variation across the disturbed areas of the BDFFP (see map and additional details in Rutt *et al*., 2019b). Hereafter we use 'historical primary forest' and 'modern primary forest' to refer to the continuous primary forest sites and 'modern disturbed landscape' for sites in fragments and second growth.

Bird sampling

The protocol for mist-netting birds has remained consistent (Stouffer *et al*., 2006). A site sample corresponds to the same line of nets run repeatedly. A continuous line of 16 nets (or 8 nets in 1-ha sites in the modern disturbed landscape), with the bottom trammel set at ground level, was opened at 0600. Nets were typically left open until 1400. Net material (polyester), length (12 m), height (*c*. 2.5 m) and mesh size (38 mm) have remained constant. Captured birds were identified, processed and released on site. Net lines were run for one day at a time, generally at intervals of > 1 month. We only included samples from the dry season (June–November).

Bird data

The main strength of mist net sampling is its standardisation, essentially free from observer bias. Capture probability differs among species based on their behaviour; we compare capture rates within species or by combining similar species by guild (see Analysis). Our analysis should not be construed as a measure of absolute abundance, but we consider variation within species among samples to be driven by differences in relative abundance. We excluded raptors, kingfishers and species captured < 5 times. This filtering eliminated canopy species that almost never descend to net level, as well as birds too large to be reliably sampled with mist nets. The forest understorey community at our site includes almost exclusively permanent residents not known to make any seasonal movements (Rutt *et al*., 2017). Long-distance migrants are extremely rare, but we excluded these few captures as well as one intratropical migrant, *Geotrygon montana* (Stouffer and Bierregaard, 1993). We also excluded *Pachysylvia muscicapina*, a canopy species with > 5 captures, and *Cyanoloxia rothschildii*, an uncommon species of uncertain guild affiliation. We categorised the remaining species into 12 feeding or substrate guilds (Table S1). Based on behavioural observations and faecal samples, most species in our sample do not eat fruit at our site. To distinguish species that at least sometimes eat fruit, our frugivore guilds include the few species that are strongly frugivorous (e.g. manakins) as well as species that only occasionally eat fruit at our site (e.g. *Momotus momota* and *Tachyphonus surinamus*). We divided woodcreepers into three guilds based on their behaviour: the obligate army-ant follower *Dendrocincla merula* is included with two antbirds (*Pithys albifrons* and *Gymnopithys rufigula*) in the army-ant follower guild; three species that often attend ant swarms, but seldom join mixed-species flocks, comprise the ant-woodcreeper guild; and the remaining species, which all participate in mixed-species flocks, are simply categorised as the woodcreeper guild.

Analysis

For individual species, we used Bayesian hierarchical models to estimate changes in relative bird abundance among the three datasets (Fig. 1). In a previous study, we conducted a space-for-time substitution analysis based on the difference in capture rates between the modern primary forest and the modern disturbed landscape samples to determine the effect of forest disturbance (Rutt *et al*., 2019b). Similarly, to test for long-term changes in bird abundance in the absence of landscape disturbance (a baseline shift), we derived species-specific change estimates based on differences between the historical primary forest samples and the modern primary forest samples. Finally, to examine the effect of forest disturbance on birds while accounting for a baseline shift (absolute change), we calculated the difference between the historical primary forest and the modern disturbed landscape samples.

The Bayesian hierarchical framework enables independent modelling of species presence/absence and abundance, given that a species is present. The analytical process leading to vulnerability estimates from the modern disturbed landscape sample is described elsewhere (Rutt *et al*., 2019b); the same

© 2020 John Wiley & Sons Ltd

approach was used to generate the long-term change estimates within primary forest. Briefly, we used a hierarchical Bayesian framework to model vulnerability or long-term change from count data. We began with a hierarchical zero-inflated Poisson model,

$$w_i \sim \text{Bernoulli}(\psi_i)$$

where ψ_i represents the probability that a species occurs at a given site, accounting for species that are absent from individual sites (where $i = site \times species$ observations). If $w_i = 1$, the species was observed at that site, and we estimated counts (C_i) with the parameter λ, which we further model with a linear predictor,

$$C_i \sim \text{Poisson}(w_i \times \lambda_i)$$
$$\lambda_i = \alpha_{j(i)} + \beta_{j(i)} x_i + A_i$$

The linear predictor includes a random intercept (α_j) and random slope (β_j) for j species, giving each species a vulnerability estimate based on x_i, a dummy variable with two levels (historical/modern or disturbed/primary). A_i is an offset to account for different sampling effort among sites. This process was identical for comparison of historical primary forest and modern primary forest (measuring long-term change in the absence of landscape effects) and comparison of historical primary forest and modern primary forest with the modern disturbed landscape (revealing the shifted baseline). For both analyses we only included species with five captures combined between the two samples.

We ran three parallel Markov chains for all models, with each chain starting at its own randomly generated value. The first 10 000 iterations of each chain were discarded, with the remaining 10 000 thinned by removing every third iteration, resulting in a total of 10 000 saved iterations per model. These remaining values allowed us to characterise the posterior distribution, which we assessed visually for convergence using trace plots and plots of posterior distributions, as well as the Brooks–Gelman–Rubin statistic, R, where values < 1.1 indicate convergence. We considered a parameter significant if the posterior distribution did not overlap zero at the 95% credible interval (CRI). All models were fit in JAGS with the R package 'R2jags' (Su and Yaima, 2020).

We compared communities among sites and treatments with NMDS and Jaccard similarity index (R package 'vegan' with the metaMDS and betadiver functions [Oksanen *et al.*, 2019]). The NMDS was based on species-specific capture rates at each site (captures, excluding same-day recaptures, per unit sampling effort [mist net hours]). We calculated Jaccard indices for all pairwise comparisons of sites in both the historical and the modern samples.

RESULTS

Of the 79 species that could be compared between the historical primary forest and the modern primary forest samples, 9 (11%) were less common in the modern primary forest sample, 8 (10%) were more common in the modern primary forest sample and 62 (78%) showed no significant change (Fig. 2a). Of the species with 95% CRIs overlapping zero, 38 species showed mean decreases and 24 showed mean increases. The magnitude of decreases and increases were roughly equivalent. Abundance change corresponds to a log scale, indicating that eight species at least doubled in abundance and eight species saw their abundance reduced by at least 50%. Lowered abundance led to considerable reduction in naïve occupancy across sites: 14 species were present at less than half the proportion of sites in the modern primary forest as in the historical primary forest (Table S1).

Abundance changes did not represent a random scatter of species. Rather, systematic differences in abundance emerged among guilds (Fig. 3a). Near-ground insectivores and terrestrial insectivores declined most strongly. These two guilds, totalling 21 species, included 11 of the 14 species with the greatest mean declines (Fig. 2a; guild assignments in Table S1, detailed results for individual species in Supporting Information). For example, *Isleria guttata, Sclerurus caudacutus* and *Microcerculus bambla,* three species in these guilds, were present at > 50% of sites in the historical sample but in <20% of sites in the modern primary forest. Only the midstorey frugivore guild increased significantly since the 1980s. These seven species include four of the eight species with the greatest mean increases (Fig. 2a). Midstorey insectivore species showed variable responses, resulting in an overall increase for the guild. Five guilds (woodcreepers, understorey frugivores, army-ant followers, ant-following woodcreepers and understorey insectivores), comprising 25 species, showed almost no change between the historical primary forest and the modern primary forest samples. Hummingbirds and gap insectivores declined, but not significantly.

Comparing the modern disturbed landscape with historical primary forest revealed greater declines than when compared with modern primary forest (Fig. 2b, results for individual species in Supporting Information). Of the 38 species that declined in the modern disturbed landscape based on comparison with modern primary forest (open red circles), 25 (66%) showed a greater magnitude of change when compared with historical primary forest (closed red circles), in some cases by an order of magnitude (1 unit on the y-axis). This included greater decreases for 18 of the 20 species previously identified as having the greatest declines (Rutt *et al.*, 2019b). Overall, species that declined in the modern disturbed landscape compared to modern primary forest declined even more when they were compared to historical primary forest (Fig. S4). Few species increased in the modern disturbed landscape, but those that did also increased more in comparison to historical primary forest.

The historical primary forest baseline allowed us to consider an additional 10 species that were too rare to analyse in the modern primary forest or the modern disturbed landscape (closed circles unpaired with open circles in Fig. 2b; see also Rutt *et al.*, 2019b). With a sample size adequate for analysis, they showed extreme declines in modern disturbed landscape, with two terrestrial insectivores and one understorey insectivore among the 15 species that declined the most between the historical primary forest and the modern disturbed landscape.

Collapsing species into guilds revealed large differences in abundance between the historical primary forest and the modern disturbed landscape for insectivore guilds (Fig. 3b). Terrestrial insectivores and near-ground insectivores showed > 3-

© 2020 John Wiley & Sons Ltd

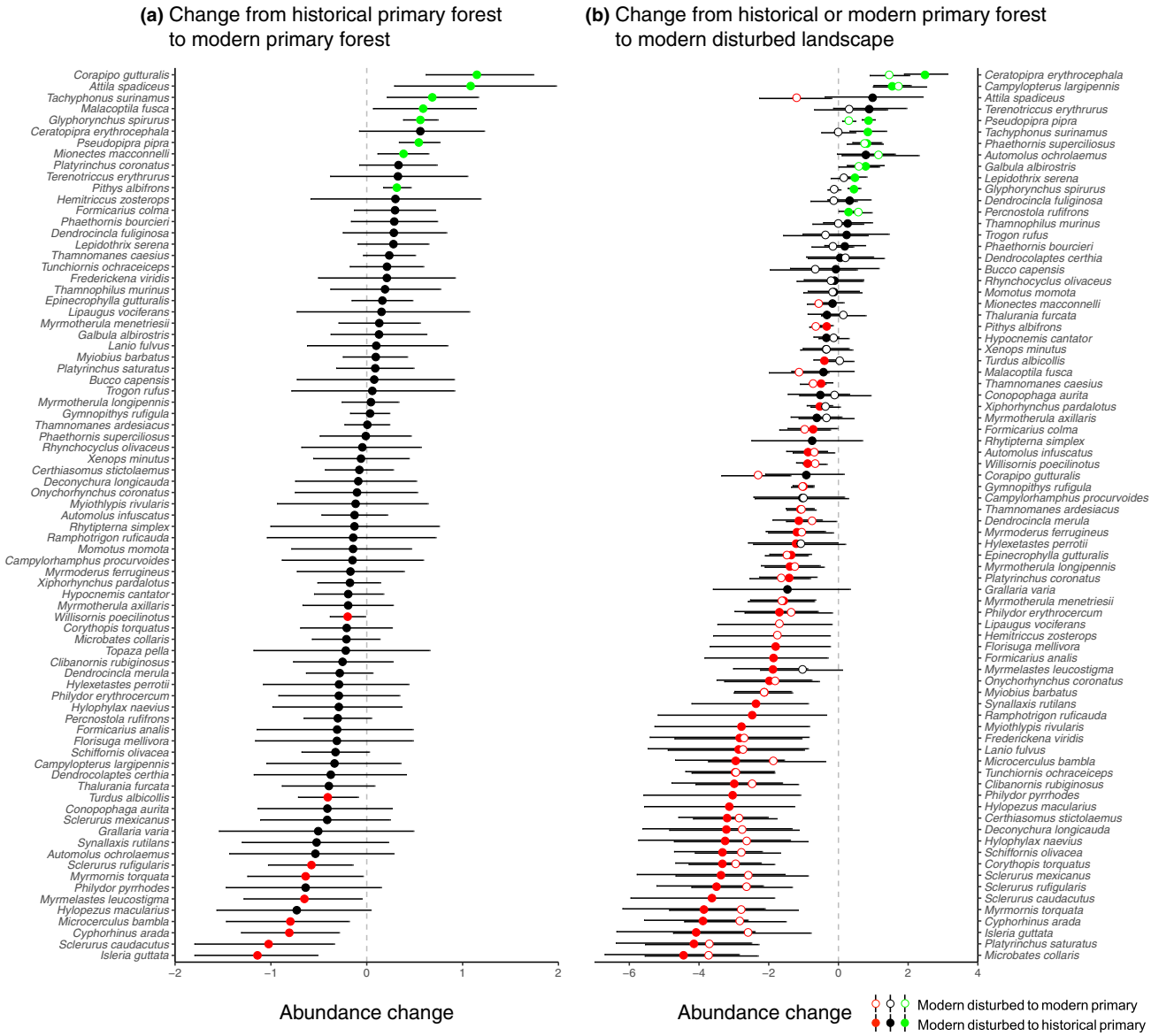

Figure 2 (a) Mean and 95% credible intervals (CRI) of bird abundance change in primary forest between historical and modern samples. Coloured circles (red for declining, green for increasing) indicate CRIs that do not overlap zero. (b) Mean and 95% CRIs comparing abundance in the modern disturbed landscape with abundance in historical primary forest and modern primary forest.

fold negative change, an amplification of their temporal change within primary forest (Fig. 3a). Riparian insectivores, woodcreepers and understorey insectivores also showed strong negative change.

Community-level ordination (Fig. 4) revealed that the modern primary forest sites differed significantly from the historical primary forest sites (function envfit $r^2 = 0.250$, $P < 0.001$). NMDS cluster centroid SEs for the two time periods did not overlap, and only one site fell within the centroid SE ellipse for the other time period. The historical primary forest sample showed less variation among sites, as indicated by a smaller centroid SE. Modern disturbed landscape communities differed considerably among sites, as expected based on including small forest fragments and secondary forest of various ages, but clustered more closely to modern primary forest than to historical primary forest, illustrating the shifted baseline for primary forest sites. Historical primary forest sites had slightly higher Jaccard similarity than modern primary forest sites. In both samples, distance contributed little to similarity; the variation among sites was comparable for sites < 5 km apart and for sites > 25 km apart (Fig. S4).

DISCUSSION

Long-term declines in undisturbed forest

We analysed bird captures from three datasets: the modern (2007–2016) disturbed landscape of forest fragments and second growth, and continuous primary forest from two time periods (historical primary forest in 1980–1984 and modern

© 2020 John Wiley & Sons Ltd

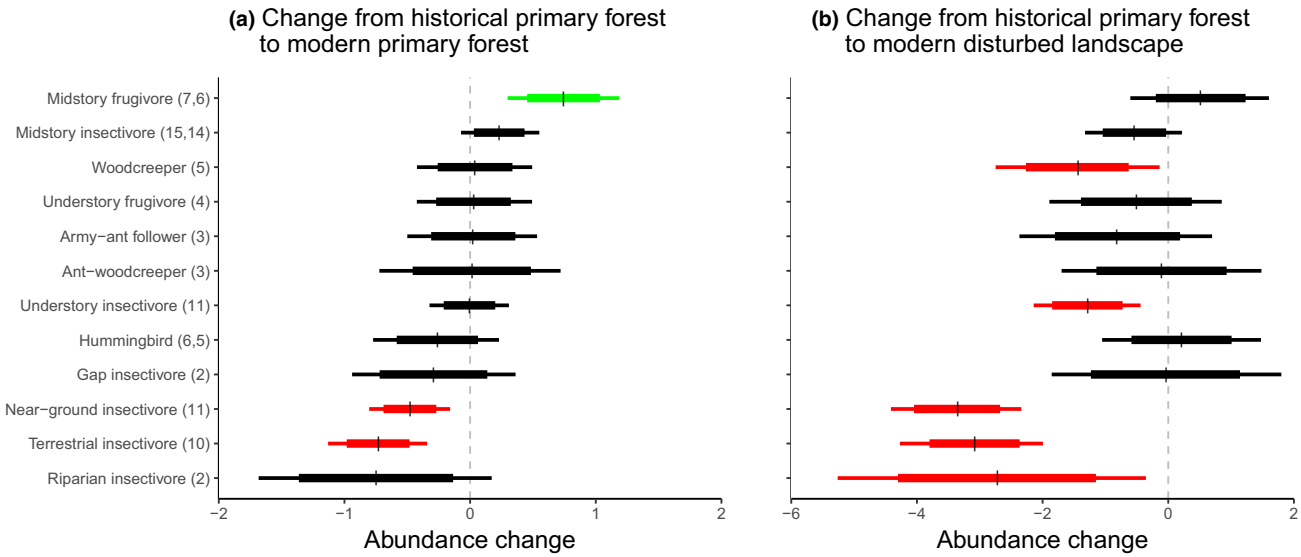

Figure 3 (a) Guild-level change in abundance between historical primary forest and modern primary forest. (b) Guild-level change in abundance between historical primary forest and the modern disturbed landscape. In both panels, bars indicate 80 and 95% CRIs, coloured if the 95% CRI does not overlap zero. Parentheses indicate number of species in each guild, with two numbers given for sample sizes that differ between a and b. Notice the x-axis scale differs between panels. Guild assignments from Table S1.

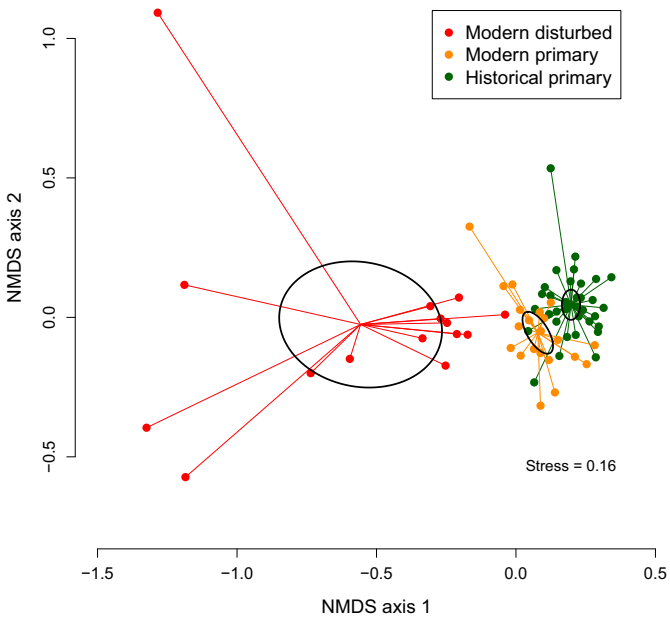

Figure 4 NMDS ordination of bird community composition, with each point representing a site. Ellipses indicate one standard error of the cluster centroid.

primary forest in 2008–2016). We found two important trends. First, abundance of many species has declined within primary forest (Fig. 2a). Second, bird abundance in the modern disturbed landscape is more divergent from the historical sample, reflecting the shifting baseline in the primary forest (Fig. 2b). Most notably, primary forest communities have fewer terrestrial and near-ground insectivores now than they did in the 1980s (Fig. 3a). Nearly all species in these two guilds are now less common. Previous research at the BDFFP and elsewhere has confirmed vulnerability of terrestrial insectivores to landscape processes (Powell *et al.*, 2015), but our new results reveal reduced abundance in the absence of landscape change.

Our design permits confidence that these results are robust and representative of widespread changes in central Amazonian *terra firme* rainforest since the 1980s. Historical and modern samples were collected in the dry season over multi-year intervals from 55 sites that were well separated in space, but sampled identically (Fig. S1). By sampling over multiple years, our results should not be biased by years with unusual weather conditions. By sampling over the same > 40 km swath of rainforest in both time intervals, our results should not be biased by topography or other local processes (Figs. S3 and S5). Total deforested area in this >1500 km^2 landscape is < 10% and has not changed appreciably since the 1980s. Although disturbance has encroached from the south, the area remains connected to vast intact forest, especially to the north (Rutt *et al.*, 2019a). We conclude that processes operating within continuous primary forest have driven the temporal changes we documented. This distinguishes our design and clarifies our interpretation compared to site-specific observations from unique landscapes, multisite comparisons that also include landscape change, or space-for-time comparisons (Castellon and Sieving, 2006; Hanski *et al.*, 2013; Visco *et al.*, 2015; Keinath *et al.*, 2016; Nowakowski *et al.*, 2017).

Potential mechanisms

Other long-term research at the BDFFP allows us to identify possible mechanisms for our results and tentatively discount others. Bird communities in primary forest have not been

© 2020 John Wiley & Sons Ltd

altered in any significant way by invasive bird species, even in small fragments (Rutt *et al*., 2019a; Stouffer, 2020). Neither have invasive predators, competitors, or pathogens been identified for birds. Pathogens seem an unlikely mechanism for the declines we observed, as the strongly affected guilds include species from multiple families, most including close relatives with little long-term change (Table S1). Hunting and trapping is minimal at the BDFFP, surely with no meaningful direct consequence for small birds. Large mammals capable of forest alteration (Visco *et al*., 2015) do not appear to have increased. We know almost nothing about nest predation or other sources of nest failure, but declining species are not restricted to a particular nesting strategy. Rather, they include burrow, cavity and open cup nesters that nest at all times of the year (Stouffer *et al*., 2013). More likely explanations connect birds to changes in food resources, microhabitat conditions, or forest structure within primary forest.

Foraging height is highly stratified in Amazonian bird communities (Terborgh *et al*., 1990; Thiollay, 1994; Walther, 2002). For guilds that declined most strongly (terrestrial and near-ground insectivores), their only significant avian competitors for food are army-ant followers. Ant-following birds consume arthropods flushed out of the litter or low vegetation by marauding ants (Willis and Oniki, 1978). As a guild, army-ant followers showed little change between the historical and modern primary forest samples (Fig. 3a), suggesting that food resources were still available to them in the modern primary forest, or that they outcompeted terrestrial insectivores for limited resources. Ant followers and ground insectivores differ, however, in an important way relevant to their foraging opportunities. Ant followers show extreme specialisation in their association with ants, but consume a broad variety of prey. This prey is concentrated along the front of the advancing swarm, resulting in strong behavioural interactions as birds jockey for prime foraging access (Willis and Oniki, 1978). Terrestrial and near-ground insectivores move along the forest floor as solitary individuals or family groups, often employing specific foraging strategies, such as tossing leaves (*Sclerurus* spp. or *Myrmornis torquata*) or gleaning arthropods from the underside of low leaves (*Corythopis torquatus*). As such, these species should be tied to more specific microhabitats or resources than ant followers, as is also revealed by ant followers being more common in second-growth forest and better colonisers through younger second growth (Stouffer and Bierregaard, 1995; Stouffer *et al*., 2011; Wolfe *et al*., 2015). This habitat plasticity is especially pronounced for *Pithys albifrons*, the smallest and most common ant follower, which increased in abundance between the historical and the modern primary forest samples (Fig. 2a).

Species using higher strata of the understorey showed mixed responses between the historical and modern primary forest samples (Fig. 3a). No guild showed a significant decline, although several individual species among hummingbirds and understorey frugivores are now less abundant (Fig. 2a). In general, it appears that both the species linked to the intricate network of obligate mixed-species flocks (Mokross *et al*., 2014), and the large number of understorey species that do not join flocks, have been relatively stable in the primary forest. Interestingly, one of the species that has increased in recent decades is *Glyphorynchus spirurus*, the smallest woodcreeper. This ubiquitous species has small area requirements, relatively broad habitat associations and opportunistically joins flocks (Johnson *et al*., 2011; Darrah and Smith, 2014). These behavioural characteristics appear to have served it well over recent decades.

The only guild to show an increase in the modern sample was midstorey frugivores (Fig. 3a), a heterogeneous collection of species linked through inclusion of at least some fruit in their diet, in contrast to the near-absolute insectivory of the various insectivore guilds. This suggests that frugivory or dietary plasticity may have been advantageous for these species in recent decades (Bender *et al*., 2017). Some of the species with the greatest increases in the modern samples are strongly frugivorous (e.g. three manakins among the top seven increasing species, Fig. 2a). Developing second growth, edges, and small fragments provide the small fruits used by these birds; increased abundance of fruit resources may drive increased abundance of frugivores in the modern disturbed landscape (Wieland *et al*., 2011; Sousa *et al*., 2017). Even so, early successional trees do not increase in the primary forest beyond *c*. 200 m from edges (Laurance *et al*., 2006), so this effect seems unlikely as a driver of increased midstorey frugivores in the modern primary forest compared to historical primary forest.

Forest structural change may have real effects on bird abundance, but could also contribute to capture probability independent of actual abundance (Remsen and Good, 1996). Our most important result—declining abundance of terrestrial and near-ground insectivores—should not be compromised by vagaries of capture probability, as these species almost never ascend above net level. Many midstorey species, however, regularly use strata above net height, so pervasive changes in forest structure or microclimate (Walther, 2002) could influence the height at which these species forage or move through the forest, in turn affecting their capture rates.

Forest-scale patterns associated with climate change have been described at the BDFFP and throughout the Amazon, although little is known about changes to the forest floor or lowest vegetation stratum. In general, tree biomass is increasing in the Amazon (Baker *et al*., 2004; Brienen *et al*., 2015; Feldpausch *et al*., 2016). A trend of increasing tree mortality and increasing soil water deficit (Baker *et al*., 2004; Brienen *et al*., 2015; Esquivel-Muelbert *et al*., 2019) may mean additional woody debris on the forest floor. Continuous primary forest plots at the BDFFP reveal increased tree mortality and recruitment as well as directional composition changes to favour faster-growing species, lianas, and species that tolerate drier conditions (Laurance, 2004; Laurance *et al*., 2014; Esquivel-Muelbert *et al*., 2019). CO_2 enrichment has been postulated as a mechanism for these changes, although changes in drought frequency or rainfall seasonality also seem plausible (reviewed in Laurance *et al*., 2018). The central Amazon has seen less change in rainfall and less extreme drought events than elsewhere in the Amazon (Jiménez-Muñoz et al. 2016; Almeida *et al*., 2017; Esquivel-Muelbert *et al*., 2019); if these factors affect bird populations, we would expect even more extreme results elsewhere in Amazonia. Links from climatic or microhabitat variation in space and time to population trends have been elusive or equivocal for rainforest birds (Pollock

© 2020 John Wiley & Sons Ltd

et al., 2015; Visco *et al*., 2015). Even so, climate change has been postulated as the ultimate driver of upslope distribution changes for tropical montane birds, despite the proximal mechanism remaining unknown (Freeman *et al*., 2018).

The shifting baseline

A major research focus at the BDFFP has been to document how understorey populations and communities respond to the dynamic landscape mosaic (Laurance *et al*., 2011). We assumed that the limitation to bird community recovery from deforestation was sufficient connectivity and second-growth development to allow primary forest species to use other elements of the landscape (Stouffer *et al*., 2006; Wolfe *et al*., 2015; Stouffer, 2020). However, our current analysis reveals that the primary forest avifauna itself has changed. Continued recovery of bird communities in second growth will approach a new baseline that is not representative of the community of the early 1980s. In addition to terrestrial and near-ground insectivores, a much larger suite of species in fragments and second growth also declined from the historical primary forest baseline. Conversely, some omnivores and frugivores appear to be successful throughout the modern landscape. The general concordance of landscape effects and long-term change for individual species and guilds suggests that these effects combine in an additive way. Winners in the modern disturbed landscape are doing better, and losers are doing worse, than modern data reveal (Fig. S4). The species whose baselines have shifted may be predictable in many landscapes: they will be terrestrial and near-ground insectivores. Although vulnerability of these birds has been identified repeatedly (Powell *et al*., 2015), our results add another level to the pattern. Some terrestrial and near-ground birds are now so rare in the primary forest that an assessment across the modern landscape would not reveal a difference associated with disturbance, masking the reality that both the disturbed landscape and the primary forest are now depauperate. For example, the terrestrial insectivore *Sclerurus caudacutus* occurred in no modern disturbed sites, but because it occurred in just 10% of modern primary forest sites it might be assessed as simply a rare species throughout the landscape. In fact, it was present at > 50% of the primary forest sites in the 1980s, so it has only become a rare species in recent decades.

This shifting baseline has important implications for interpreting contemporary biodiversity assessments (De Palma et al. 2018; Soga and Gaston, 2018). Studies that evaluate the risk to rainforest species following disturbance (Hudson *et al*., 2014; Moura *et al*., 2016; Hatfield *et al*., 2018) may underestimate the divergence of vulnerable taxa from an unknown older baseline. Similarly, landscape effects on ecological function of modern Amazonian bird communities may underestimate function loss since the 1980s (Bregman *et al*., 2016). Recovery of secondary forest or certain types of agroforestry can increase diversity of rainforest taxa (Phillips *et al*., 2017; Rocha *et al*., 2018; Şekercioğlu *et al*., 2019), but the magnitude of gains depends upon the baseline for comparison. The pattern we describe unfolded over > 30 years, suggesting that stability over shorter samples (Beaudrot *et al*., 2016) may not necessarily imply the absence of a longer-term trend (Damgaard, 2019).

Our quantitative assessment of biotic change over decades in 'undisturbed' sites makes an important empirical contribution to understanding Anthropocene defaunation (Dirzo *et al*., 2014). Declines in Amazonian birds reinforce patterns that have emerged in other taxa from datasets that are less standardised or less suitable for parsing landscape effects from long-term changes (Ceballos *et al*., 2017; Hallmann *et al*., 2017; Lister and Garcia, 2018). Where data are available, researchers should maintain sampling to accompany the trajectory of long-term change, even if only to document how far conditions are falling from the historical baseline.

ACKNOWLEDGEMENTS

The authors thank the many banders and *mateiros* who contributed to the fieldwork, staff at the BDFFP for their logistical help, colleagues for helpful discussions, Karl Mokross for the trees in Fig. 1, and reviewers at Ecology Letters for suggestions that improved the manuscript. Funding: PCS: NSF 0545491 and 1257340; National Institute of Food and Agriculture, US Department of Agriculture, McIntire Stennis projects #94098 and #94327. ROB and TEL: World Wildlife Fund-US, MacArthur Foundation, Andrew W. Mellon Foundation, U.S. Agency for International Development, U.S. National Aeronautics and Space Administration, Brazil's Ministry for Science and Technology (all from the 1980s- no grant numbers available). This is publication No. 802 of the BDFFP Technical Series and No. 54 of the Amazonian Ornithology Technical Series of the INPA Collections Program. The manuscript was approved by the Director of the Louisiana State University Agricultural Center as manuscript number 2020-241-34872.

CONFLICT OF INTERESTS

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

PCS, VJ, CLR, ROB and TEL conceived the project. PCS, ROB and TEL administered the project and curated the data. PCS, CLR, ROB, AHP, EIJ, LLP and JDW collected the data. VJ, CLR and SRM performed the analysis. PCS, VJ and CLR prepared the manuscript, with review contributions from all authors.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13628.

DATA AVAILABILITY STATEMENT

Data are archived at Dryad https://doi.org/10.5061/dryad.s1rn8pk5s.

REFERENCES

Aleixo, I., Norris, D., Hemerik, L., Barbosa, A., Prata, E., Costa, F. *et al*. (2019). Amazonian rainforest tree mortality driven by climate and functional traits. *Nat. Clim. Change*, 9, 384–388.

© 2020 John Wiley & Sons Ltd

Almeida, C.T., Oliveira, J.F., Delgado, R.C., Cubo, P. & Ramos, M.C. (2017). Spatiotemporal rainfall and temperature trends throughout the Brazilian Legal Amazon, 1973–2013. *Int. J. Climatol.*, 37, 2013–2026.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A. *et al.* (2004). Increasing biomass in Amazonian forest plots. *Philos. T. R. Soc. B.*, 359, 353–365.

Beaudrot, L., Ahumada, J.A., O'Brien, T., Alvarez-Loayza, P., Boekee, K., Campos-Arceiz, A. *et al.* (2016). Standardized assessment of biodiversity trends in tropical forest protected areas: The end is not in sight. *PLoS Biol.*, 14, e1002357.

Bender, I.M.A., Kissling, W.D., Bohning-Gaese, K., Hensen, I., Kuhn, I., Wiegand, T. *et al.* (2017). Functionally specialised birds respond flexibly to seasonal changes in fruit availability. *J. Anim. Ecol.*, 86, 800–811.

Blake, J.G. & Loiselle, B.A. (2016). Long-term changes in composition of bird communities at an "undisturbed" site in eastern Ecuador. *Wilson J. Ornithol.*, 128, 255–267.

Brawn, J.D., Benson, T.J., Stager, M., Sly, N.D. & Tarwater, C.E. (2017). Impacts of changing rainfall regime on the demography of tropical birds. *Nat. Clim. Change*, 7, 133–136.

Bregman, T.P., Lees, A.C., MacGregor, H.E.A., Darski, B., de Moura, N.G., Aleixo, A. *et al.* (2016). Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. *Proc. Roy. Soc. B-Biol Sci*, 283, 20161289.

Brienen, R.J.W., Phillips, O.L., Feldpausch, T.R., Gloor, E., Baker, T.R., Lloyd, J. *et al.* (2015). Long-term decline of the Amazon carbon sink. *Nature*, 519, 344–348.

Castellon, T.D. & Sieving, K.E. (2006). Landscape history, fragmentation, and patch occupancy: Models for a forest bird with limited dispersal. *Ecol. Appl.*, 16, 2223–2234.

Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl Acad. Sci. USA*, 114, E6089–E6096.

Damgaard, C. (2019). A critique of the space-for-time substitution practice in community ecology. *Trends Ecol. Evol.*, 34, 416–421.

Darrah, A.J. & Smith, K.G. (2014). Ecological and behavioral correlates of individual flocking propensity of a tropical songbird. *Behav. Ecol.*, 25, 1064–1072.

De Palma, A., Sanchez-Ortiz, K., Martin, P.A., Chadwick, A., Gilbert, G., Bates, A.E., *et al.* (2018). Challenges with inferring how land-use affects terrestrial biodiversity: Study design, time, space and synthesis. In: *Next Generation Biomonitoring*, Pt 1 (eds Bohan, D.A., Dumbrell, A.J., Woodward, G. & Jackson, M.). Academic Press, Cambridge, MA, pp. 163–199.

Dent, D.H. & Wright, S.J. (2009). The future of tropical species in secondary forests: A quantitative review. *Biol. Conserv.*, 142, 2833–2843.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J. & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345, 401–406.

Esquivel-Muelbert, A., Baker, T.R., Dexter, K.G., Lewis, S.L., Brienen, R.J.W., Feldpausch, T.R. *et al.* (2019). Compositional response of Amazon forests to climate change. *Glob. Change Biol.*, 25, 39–56.

Feldpausch, T.R., Phillips, O.L., Brienen, R.J.W., Gloor, E., Lloyd, J., Lopez-Gonzalez, G. *et al.* (2016). Amazon forest response to repeated droughts. *Global Biogeochem. Cy.*, 30, 964–982.

Fletcher, R.J., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J. *et al.* (2018). Is habitat fragmentation good for biodiversity? *Biol. Conserv.*, 226, 9–15.

França, F., Louzada, J., Korasaki, V., Griffiths, H., Silveira, J.M. & Barlow, J. (2016). Do space-for-time assessments underestimate the impacts of logging on tropical biodiversity? An Amazonian case study using dung beetles. *J. Appl. Ecol.*, 53, 1098–1105.

Freeman, B.G., Scholer, M.N., Ruiz-Gutierrez, V. & Fitzpatrick, J.W. (2018). Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proc. Natl Acad. Sci. USA*, 115, 11982–11987.

Gascon, C. & Bierregaard, R.O. Jr. (2001). The Biological Dynamics of Forest Fragments Project. In: *Lessons from Amazonia* (eds Bierregaard, R.O., Gascon, C., Lovejoy, T.E. & Mesquita, R.). Yale University Press, New Haven, CT, pp. 31–42.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H. *et al.* (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One*, 12, e0185809.

Hanski, I., Zurita, G.A., Bellocq, M.I. & Rybicki, J. (2013). Species-fragmented area relationship. *Proc. Natl Acad. Sci. USA*, 110, 12715–12720.

Hatfield, J.H., Orme, C.D.L., Tobias, J.A. & Banks-Leite, C. (2018). Trait-based indicators of bird species sensitivity to habitat loss are effective within but not across data sets. *Ecol. Appl.*, 28, 28–34.

Hudson, L.N., Newbold, T., Contu, S., Hill, S.L.L., Lysenko, I., De Palma, A. *et al.* (2014). The PREDICTS database: A global database of how local terrestrial biodiversity responds to human impacts. *Ecol. Evol.*, 4, 4701–4735.

Jiménez-Muñoz, J.C., Mattar, C., Barichivich, J., Santamaŕa-Artigas, A., Takahashi, K., Malhi, Y. *et al.* (2016). Record-breaking warming and extreme drought in the Amazon rainforest during the course of El Niño 2015–2016. *Sci. Rep.- UK*, 6, 33130.

Johnson, E.I., Stouffer, P.C. & Vargas, C.F. (2011). Diversity, biomass, and trophic structure of a central Amazonian rainforest bird community. *Rev. Bras. Ornitol.*, 19, 1–16.

Keinath, D.A., Doak, D.F., Hodges, K.E., Prugh, L.R., Fagan, W., Sekercioglu, C.H. *et al.* (2016). A global analysis of traits predicting species sensitivity to habitat fragmentation. *Glob. Ecol. Biogeo.*, 26, 115–127.

Laurance, S.G.W., Stouffer, P.C. & Laurance, W.F. (2004). Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. *Conserv. Biol.*, 18, 1099–1109.

Laurance, W.F. (2004). Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature*, 428, 171–175.

Laurance, W.F., Andrade, A.S., Magrach, A., Camargo, J.L.C., Valsko, J.J., Campbell, M. *et al.* (2014). Long-term changes in liana abundance and forest dynamics in undisturbed Amazonian forests. *Ecology*, 95, 1604–1611.

Laurance, W.F., Camargo, J.L.C., Fearnside, P.M., Lovejoy, T.E., Williamson, G.B., Mesquita, R.C.G. *et al.* (2018). An Amazonian rainforest and its fragments as a laboratory of global change. *Biol. Rev.*, 93, 223–247.

Laurance, W.F., Camargo, J.L.C., Luizao, R.C.C., Laurance, S.G., Pimm, S.L., Bruna, E.M. *et al.* (2011). The fate of Amazonian forest fragments: A 32-year investigation. *Biol. Conserv.*, 144, 56–67.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A.C., Fearnside, P.M., Ribeiro, J.E.L. *et al.* (2006). Rain forest fragmentation and the proliferation of successional trees. *Ecology*, 87, 469–482.

Lister, B.C. & Garcia, A. (2018). Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proc. Natl Acad. Sci. USA*, E10397–E10406.

Martensen, A.C., Ribeiro, M.C., Banks-Leite, C., Prado, P.I. & Metzger, J.P. (2012). Associations of forest cover, fragment area, and connectivity with Neotropical understory bird species richness and abundance. *Conserv. Biol.*, 26, 1100–1111.

Mokross, K., Ryder, T.B., Côrtes, M.C., Wolfe, J.D. & Stouffer, P.C. (2014). Decay of interspecific avian flock networks along a disturbance gradient in Amazonia. *Proc. Roy. Soc. B-Biol Sci*, 281, 20132599.

Moura, N.G., Lees, A.C., Aleixo, A., Barlow, J., Berenguer, E., Ferreira, J. *et al.* (2016). Idiosyncratic responses of Amazonian birds to primary forest disturbance. *Oecologia*, 180, 903–916.

Nowakowski, A.J., Watling, J.I., Whitfield, S.M., Todd, B.D., Kurz, D.J. & Donnelly, M.A. (2017). Tropical amphibians in shifting thermal landscapes under land-use and climate change. *Conserv. Biol.*, 31, 96–105.

Oksanen, J.F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, P.R.*et al.* (2019). Vegan: Community Ecology Package (version 2.5-6), 2019. https://CRAN.R-project.org/package=vegan.

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J. *et al.* (2017). Creation of forest edges has a global impact on forest vertebrates. *Nature*, 551, 187–191.

© 2020 John Wiley & Sons Ltd

Phillips, H.R.P., Newbold, T. & Purvis, A. (2017). Land-use effects on local biodiversity in tropical forests vary between continents. *Biodivers. Conserv.*, 26, 2251–2270.

Pickett, S.T. (1989). Space-for-time substitution as an alternative to long-term studies. *Long-term Studies in Ecology*. Springer, pp. 110–135.

Pollock, H.S., Cheviron, Z.A., Agin, T.J. & Brawn, J.D. (2015). Absence of microclimate selectivity in insectivorous birds of the Neotropical forest understory. *Biol. Conserv.*, 188, 116–125.

Powell, L.L., Cordeiro, N.J. & Stratford, J.A. (2015). Ecology and conservation of avian insectivores of the rainforest understory: A pantropical perspective. *Biol. Conserv.*, 188, 1–10.

Powell, L.L., Stouffer, P.C. & Johnson, E.I. (2013). Recovery of understory bird movement across the interface of primary and secondary Amazon rainforest. *Auk*, 130, 459–468.

Remsen, J.V. Jr & Good, D.A. (1996). Misuse of data from mist-net captures to assess relative abundance in bird populations. *Auk*, 113, 381–398.

Rocha, R., Ovaskainen, O., Lopez-Baucells, A., Farneda, F.Z., Sampaio, E.M., Bobrowiec, P.E.D. *et al.* (2018). Secondary forest regeneration benefits old-growth specialist bats in a fragmented tropical landscape. *Sci. Rep.- UK*, 8, 3819.

Rutt, C.L., Jirinec, V., Cohn-Haft, M., Laurance, W.F. & Stouffer, P.C. (2019a). Avian ecological succession in the Amazon: A long-term case study following experimental deforestation. *Ecol. Evol.*, 9, 13850–13861.

Rutt, C.L., Jirinec, V., Johnson, E.I., Cohn-Haft, M., Vargas, C.F. & Stouffer, P.C. (2017). Twenty years later: An update to the birds of the Biological Dynamics of Forest Fragments Project, Amazonas, Brazil. *Rev. Bras. Ornitol.*, 25, 277–296.

Rutt, C.L., Midway, S.R., Jirinec, V., Wolfe, J.D. & Stouffer, P.C. (2019b). Examining the microclimate hypothesis in Amazonian birds: Indirect tests of the 'visual constraints' mechanism. *Oikos*, 128, 798–810.

Sekercioglu, C.H., Loarie, S.R., Brenes, F.O., Ehrlich, P.R. & Daily, G.C. (2007). Persistence of forest birds in the Costa Rican agricultural countryside. *Conserv. Biol.*, 21, 482–494.

Şekercioğlu, Ç.H., Mendenhall, C.D., Oviedo-Brenes, F., Horns, J.J., Ehrlich, P.R. & Daily, G.C. (2019). Long-term declines in bird populations in tropical agricultural countryside. *Proceedings of the National Academy of Sciences*, 116(20), 9903–9912.

Soga, M. & Gaston, K.J. (2018). Shifting baseline syndrome: causes, consequences, and implications. *Front. Ecol. Environ.*, 16, 222–230.

Sousa, T.R., Costa, F.R.C., Bentos, T.V., Leal, N., Mesquita, R.C.G. & Ribeiro, I.O. (2017). The effect of forest fragmentation on the soil seed bank of Central Amazonia. *Forest Ecol. Manag.*, 393, 105–112.

Stouffer, P.C. (2020). Birds in fragmented Amazonian rainforest: Lessons from 40 years at the Biological Dynamics of Forest Fragments Project. Condor: Ornithol. Appl., 122, https://doi.org/10.1093/condor/duaa005

Stouffer, P.C. & Bierregaard, R.O. Jr (1993). Spatial and temporal abundance patterns of Ruddy Quail-Doves (*Geotrygon montana*) near Manaus, Brazil. *Condor*, 95, 896–903.

Stouffer, P.C. & Bierregaard, R.O. Jr (1995). Use of Amazonian forest fragments by understory insectivorous birds. *Ecology*, 76, 2429–2445.

Stouffer, P.C., Johnson, E.I. & Bierregaard, R.O. Jr (2013). Breeding seasonality in central Amazonian rainforest birds. *Auk*, 129, 529–540.

Stouffer, P.C., Johnson, E.I., Bierregaard, R.O. Jr & Lovejoy, T.E. (2011). Understory bird communities in Amazonian rainforest fragments: Species turnover through 25 years post-isolation in recovering landscapes. *PLoS One*, 6, e20543.

Stouffer, P.C., Bierregaard, R.O.R, Strong, C. & Lovejoy, T.E. (2006). Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conserv. Biol.*, 20, 1212–1223.

Su, Y.-S. & Yaima, M. (2020). R2jags: Using R to run "JAGS" version 0.6-1. https://CRAN.R-project.org/package=R2jags.

Terborgh, J., Robinson, S.K., Parker, T.A. III, Munn, C.A. & Pierpont, N. (1990). Structure and organization of an Amazonian forest bird community. *Ecol. Monogr.*, 60, 213–238.

Thiollay, J.-M. (1994). Structure, density, and rarity in an Amazonian rain-forest bird community. *J. Trop. Ecol.*, 10, 449–481.

Visco, D.M., Michel, N.L., Boyle, W.A., Sigel, B.J., Woltmann, S. & Sherry, T.W. (2015). Patterns and causes of understory bird declines in human-disturbed tropical forest landscapes: A case study from Central America. *Biol. Conserv.*, 191, 117–129.

Walther, B.A. (2002). Vertical stratification and use of vegetation and light habitats by Neotropical forest birds. *J. Ornithol.*, 143, 64–81.

Whitfield, S.M., Bell, K.E., Philippi, T., Sasa, M., Bolaños, F., Chaves, G. *et al.* (2007). Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proc. Natl Acad. Sci. USA*, 104, 8352–8356.

Wieland, L.M., Mesquita, R.C.G., Bobrowiec, P.E.D., Bentos, T.V. & Williamson, G.B. (2011). Seed rain and advance regeneration in secondary succession in the Brazilian Amazon. *Trop. Conserv. Sci.*, 4, 300–316.

Willig, M.R., Woolbright, L., Presley, S.J., Schowalter, T.D., Waide, R.B., Heartsill Scalley, T. *et al.* (2019). Populations are not declining and food webs are not collapsing at the Luquillo Experimental Forest. *Proc. Natl Acad. Sci. USA*, 116, 12143–12144.

Willis, E.O. & Oniki, Y. (1978). Birds and army ants. *Ann. Rev. Ecol. Syst.*, 9, 243–263.

Wolfe, J.D., Stouffer, P.C., Mokross, K., Powell, L.L. & Anciães, M.M. (2015). Island vs. countryside biogeography: An examination of how Amazonian birds respond to forest clearing and fragmentation. *Ecosphere*, 6, 295.

SUPPORTING INFORMATION

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

Editor, Joshua Lawler
Manuscript received 21 May 2020
First decision made 6 July 2020
Second decision made 19 August 2020
Manuscript accepted 14 September 2020

© 2020 John Wiley & Sons Ltd