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Article

Bird Occupancy of a Neotropical Forest Fragment Is Mostly Stable over 17 Years but Influenced by Forest Age

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Abstract: The effects of forest degradation, fragmentation, and climate change occur over long time periods, yet relatively few data are available to evaluate the long-term effects of these disturbances on tropical species occurrence. Here, we quantified changes in occupancy of 50 bird species over 17 years on Barro Colorado Island (BCI), Panama, a model system for the long-term effects of habitat fragmentation. The historical data set (2002–2005) was based on point counts, whereas the contemporary data set (2018) was based on acoustic monitoring. For most species, there was no significant change in occupancy; however, the occupancy of four species (*Tinamus major*, *Polioptila plumbea*, *Myiarchus tuberculifer*, and *Ceratopipra mentalis*) increased significantly, and the occupancy of three species (*Saltator grossus*, *Melanerpes pucherani*, and *Cyanoloxia cyanooides*) decreased significantly. Forest age explained the majority of occupancy variation and affected the occupancy of more bird species than survey period or elevation. Approximately 50% of the species seem to favor old-growth forest, and 15 species (30%) had a significantly higher occupancy in old-growth forest sites. Elevation had no significant impact on the occupancy of the majority of bird species. Although BCI has been a protected reserve for approximately 100 years, land-use legacies (i.e., forest age) continue to influence bird distribution.

Keywords: passive acoustic monitoring; occupancy; detectability; Barro Colorado Island; Panama; Arbimon neotropical birds



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1. Introduction

Changes in community composition continue long after initial isolation of habitat remnants [1]. Evidence and theoretical predictions indicate species losses occur for decades, even centuries, depending on the size of the remnant, characteristics of the surrounding habitat matrix, and species traits [2–5]. Predictors of which species are most at risk of decline and disappearance in fragmented landscapes are many, including initial local abundance at the time of habitat isolation, degree to which movements affect colonization dynamics, diet, and preferences for particular habitat characteristics [6,7]. Land-use change surrounding habitat remnants and successional dynamics within remnants (forest age) affect population dynamics and community structure as well. A naïve expectation is that remnants with mature forest surrounded by stable habitat matrix characteristics may be less likely to show evidence of community change or species' abundances through time. However, long-term studies have recently documented avian population declines and community shifts even in large tracts of undisturbed forests in Ecuador [8] and the Amazon [9]. Some bird species groups, such as terrestrial insectivores, appear to be more sensitive to habitat isolation and reduction in habitat area [10]. In undisturbed forests in the central Amazon, terrestrial and near-ground insectivorous bird species appear to be the most vulnerable, whereas some frugivorous species may increase in abundance [9]. Relatively few long-term studies of

population fluctuations exist for Neotropical sites, but the few available ones suggest fairly stable bird populations, especially in older forests [11]. Characterizing such long-term community shifts and the associated changes in population sizes of vulnerable species is needed for effective conservation and management.

Passive acoustic monitoring (PAM) offers a practical and inexpensive solution to assess population trends and community composition through time [12–14]. Autonomous recording technology is increasingly cheaper, smaller, and more efficient (e.g., AudioMoth–Open Acoustic Devices, UK [15]). Hundreds of these devices can be placed to cover extensive areas, and a large portion of the biota can be continuously and simultaneously recorded for months or even years. Extracting useful biological information from the audio recordings is becoming broadly accessible not only to the academic community, but also to wildlife managers and citizen scientists, thanks to online open- and user-friendly platforms (e.g., RFCx-ARBIMON and EcoSounds) and free statistical software and packages (e.g., R [16] and Unmarked [17]) that allow state-of-the-art automated species identification and ecological statistical analyses. In addition, recordings and species detections can be permanently stored, allowing anyone to review and use the data in future studies. PAM has been successfully used to detect and monitor rare and endemic species [18,19], to evaluate the impact of climate change on species distribution [20,21], to detect hunting of mammal species [22] and to document human impact on anurans and birds in the tropics [23–25].

In this study, we used PAM and occupancy models to understand shifting occupancy patterns and species persistence through time (17 years) on Barro Colorado Island (BCI), Panamá. BCI has been surveyed by ornithologists periodically since the 1920s [10,26–28], just after its isolation from nearby forests by rising waters of Gatun Lake, which forms part of the Panama Canal. This former hilltop, now a 1562-ha fragment and separated by water spanning as little as 250 m from adjacent forested parks, has lost 30% of its original forest-dwelling bird community, despite a century of protection from direct human disturbance [29,30]. Many of the lost forest-dwelling resident bird species are characteristic of the oldest and most humid forest on the island, which covers approximately half of the area. Disturbances more than 85 years ago have led to forest succession over time in the remaining area, to the point that today nearly the entire island is covered by tall forest [31]. Despite the loss of many species over the last century, the average rate at which species continue to disappear has declined only slightly [30]. The lost species are rarely replaced, so island-wide diversity continues to decline. To determine how the change in the distribution of forest age and the decline in species richness is affecting the distributions and population trends of the remaining species, we (1) compared bird occupancy between historical (2002–2005) and current (2018) periods and (2) evaluated the effect of environmental variables on bird occupancy.

2. Materials and Methods

2.1. Study site

Barro Colorado Island (BCI), Panamá, is the largest island (1562 ha) of the Barro Colorado Nature Monument reserve, which comprises forested islands and peninsulas in the Gatun Lake section of the Panama Canal. Part of the Panama Canal construction included damming of the Chagres River, which was initiated in 1914 and created the Gatun Lake. Before the damming, BCI was part of a continuous forest, but as the forest was flooded, only the highest areas remained as hilltop islands [32].

BCI receives ~2600 mm of rainfall annually and has a pronounced dry season between January and April. The vegetation is characterized as a semi-deciduous tropical moist forest. Since its establishment as a research station in 1920, BCI has been protected from human disturbance, such as logging and poaching, and most of the island is covered by old-growth forest (>500 years: Figure 1); most of the secondary forest on the island is also relatively old (>80 years) [32,33].

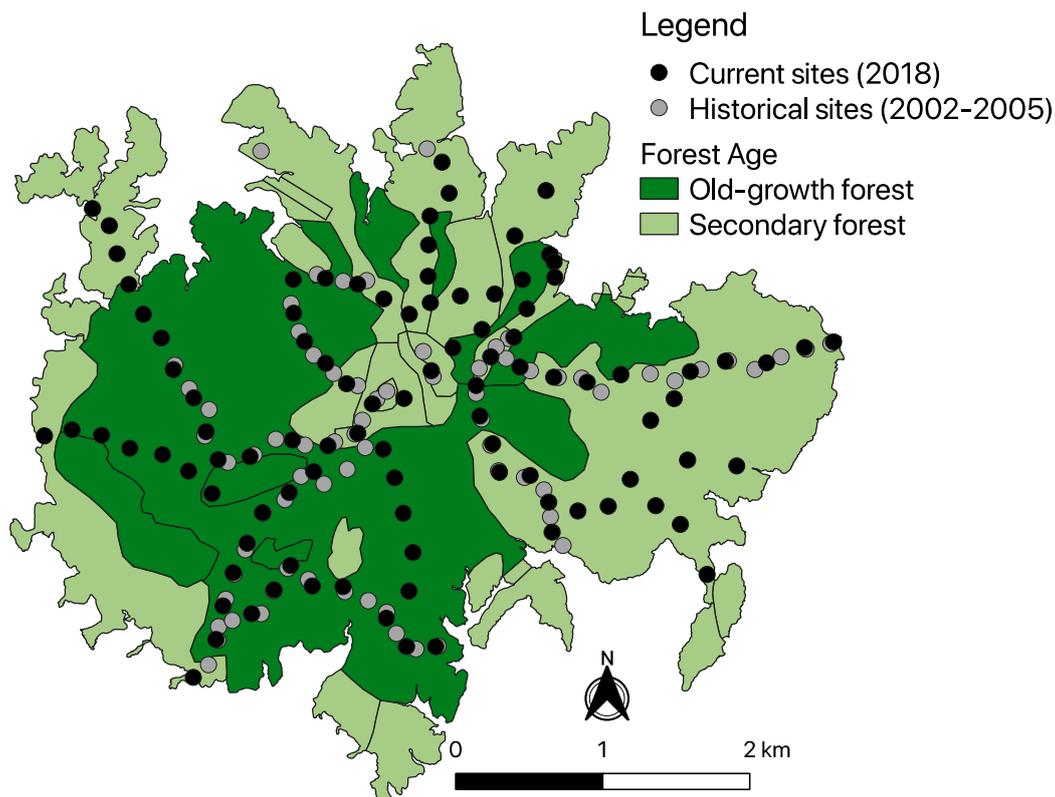


Figure 1. Map of Barro Colorado Island and distribution of forests of different ages (adaptation from [31]). The grey circles represent the historical sampling sites (2002–2005), and the black circles represent the most recent sampling sites (2018).

2.2. Survey and Resurvey Data

The historical distribution data were based on point counts from a long-term bird population study [2,29,30]. Point count locations were selected to sample the two major divisions of forest age on the island, old-growth and recovering second growth forests. We chose a subset of years (2002–2005) for the present study, because the sites aligned closely with the PAM sampling sites' locations. In the historical surveys, birds were identified during eight-minute visits to each location in March and April, which encompasses the best period to survey birds in central Panama (late March through mid-May), since singing activity for most bird species peaks just before the rainy season [34]. Prior work in this and adjacent bird communities revealed that greater than 85% of species present were detected during 8 min counts conducted between dawn and 10 a.m. [2,29]. Distances to all birds were measured or estimated. For the present study, we only used detections within 50 m to align with detection radii of recording units used in the recent surveys. Each point count ($n = 77$) was placed 200 m or more from its nearest neighbor (Figure 1). Approximately 98% of the detections in this and nearby studies were based on auditory cues [34].

The current distribution data were derived from recordings collected by Audiomoth recorders from 99 sampling sites in April and May 2018 (Figure 1). The locations of the recorders were selected to provide a rapid assessment of the occupancy of bird species across the island. Therefore, we took advantage of all existing trails to sample the island in a short time period. The recorders were placed at least 20 m away from trails and 200 m from each other. Recorders were placed on trees at a height of 1.5 m and were programmed to record one minute of audio every 10 min for a total of 144 one-minute recordings per day. The recording schedule of 1 min every 10 min was selected because it provides a good trade-off between our ability to detect different animal species, both diurnal and nocturnal, and the costs associated with the amount of data for storage, management, and analyses. The recorders remained in each sampling site for approximately one week. The gain was set as default/medium (30.6 dB). The recording

system used a 44.1 kHz/16-bit sampling rate, which recorded sounds between 0 and 24 kHz. The recorders' detection range will vary depending on the habitat and amplitude of each species' call, but on average, we estimated that most tropical forest bird species could be detected from up to approximately 50 m. Therefore, a site is defined as a three-dimensional hemisphere with a radius of 50 m around the recorder. All recordings were analyzed, permanently stored, and are available in the RFCx-ARBIMON project (<https://arbimon.rfcx.org/project/bci-panama-2018/dashboard>).

The detection history of species in the audio recordings was acquired through three steps. First, experts (MCC, GAL) manually searched for species in recordings from 5:00 to 9:00 a.m. from each site and created a call template for each species. Second, in the RFCx-ARBIMON platform, we used the template matching algorithm [35] by providing the system the species-call template, a playlist of all recordings, and a correlation threshold (0.1). All detections above the correlation threshold were cropped and displayed for posterior validation. Third, the experts reviewed the template matching results. In this step, we annotated the results as either positive or negative, indicating the corresponding species' presence or absence. In addition, we used species-call templates from Xeno-Canto (www.xeno-canto.org) to search for species not detected in the previous steps but detected in the historical data set.

2.3. Species Data Set

Although there was considerable overlap in the species detected in both periods, we focused our occupancy analyses on a subset of 50 bird species with at least two detections in each sampling period. In addition, we selected species that could provide a mix of responses (i.e., declining, stable, increasing) based on temporal patterns in abundance data (Robinson 2001) (Table S1). Moreover, the selected species cover a variety of guilds, sizes, and rarity (Table S1) and thus provide a good representation of the BCI bird community.

2.4. Occupancy Analyses

The data acquired from the post-validation of the recordings were used to create single-season occupancy models [36] to compare species distributions between historical (2002–2005) and current (2018) survey periods using the package Unmarked [17], and AICmodavg [37] in R [16]. The structure of each matrix included rows as the number of sites and columns as the number of sampling days per site. For each day, we assigned one of two states: 0—no detections in any of the recordings, or 1—if 1 or more recordings had a validated presence. Because the contemporary surveys were not conducted at the exact same sampling sites as the historical surveys, we used an unpaired-site model [38] where data from all sites from both periods are used in a single-season occupancy model, and Era is used as a covariate influencing both occupancy and detection parameters. Because within-year replicate surveys were unavailable for the historical data, we treated each year in the historical data as a replicate visit. Consequently, we may overestimate occupancy probability in the historical time, and thus, our results may tend to overestimate the declines and underestimate increases in occupancy. One advantage of our occupancy approach is that it can control for differences in methodologies [39]. This means that species detectability was estimated for each sampling period/method, providing an unbiased estimation of species absences in both periods/methods. Our models contain a sampling level describing the probability of detection conditioned on occupancy (p) and an underlying biological level describing the probability (ψ) that a site is occupied. An example equation of the unpaired occupancy model can be described as:

$$\begin{array}{l} \text{Biological level—Occupancy } (\psi) \\ \text{logit}(\psi) = \beta_0 + \beta_1 \text{era} + \beta_2 \text{ForestAge} + \beta_3 \text{elevation} \end{array} \quad (1)$$

$$\begin{array}{l} \text{Sampling level—Detectability } (p) \\ \text{logit}(p) = \beta_4 + \beta_5 \text{era} \end{array} \quad (2)$$

To estimate the distribution (ψ) for each species, we constructed a set of competing hypotheses of how occupancy changed over Era, Elevation, and Forest age (Table S2). Era and Forest age were covariate factors indicating the time of surveys (historical era and contemporary era) and the dominance of primary or secondary forest, whereas Elevation was a standardized continuous covariate represented by a linear function. Forest age data were based on Mascaro et al. (2011). Since old-growth forest and relatively old secondary forest dominate the landscape in BCI, we simplified the four forest age categories into two: old-growth forest (>400 years) and old secondary forest (100–150 years). We extracted the percent of forest cover in a buffer of 50 m around each sampling site and assigned one of the forest age categories when more than 50% of the buffer include one forest age. We tested eight parameterizations of (ψ) by combining these covariates along with additive terms and a null model (intercept-only) (Table S2). Combinations of the covariates along with interaction terms were considered for the detection function, but exploratory analyses indicated problems with model convergence, so we opted to include only Era in the detection term to reduce model set complexity [40]. We compared models using AICc, and we estimated occupancy by model-averaging all models with $\Delta\text{AICc} < 2.0$ using the function *modavgPred* from the *AICmodavg* package.

To determine the effect of Era on species detectability, we computed the model average effect size between historical and current surveys, using the function *modavgEffect* from the *AICmodavg* package. Similarly, to determine the effect of Era and Forest Age on species occupancy, we computed the model average effect size between historical and current surveys, and between old-growth and secondary forest using the function *modavgEffect*. To determine the effect of Era, the Elevation covariate was held constant (i.e., mean = 0), whereas each one of the forest age groups were fixed. In that way, we have the effect of Era on the occupancy parameter for old-growth forest sites and for secondary forest sites. To determine the effect of Forest Age, the Elevation covariate was held constant, whereas each one of the Era groups was fixed. The model average effect size of the Era and Forest Age was based on all models with $\Delta\text{AICc} < 2.0$. We used a similar approach to determine the effect of elevation on species occupancy by computing the model-average parameter estimates with the shrinkage method based on all fitted models using the function *modavgShrink*. We used 85% confidence intervals to make model-selection and parameter-evaluation criteria more congruent [41]. Therefore, we considered a significant effect of a variable to occur when the 85% confidence interval did not include zero.

3. Results

Detection probability varied greatly among species, and more than half of the species had greater detectability in one particular period (Figure 2, Table S3), suggesting that failures to account for detection probability could negatively affect occupancy estimates and our inference regarding the effect of Era on species occupancy. Of the 50 species included in the occupancy models, only three species had significantly higher detectability in the historical period, whereas 22 species had similar detectability among historical and current periods, and 25 species had significantly higher detectability in the current period (Figure 2, Table S4).

Although occupancy point estimates showed that about half of the species ($n = 22$) expanded their distributions, both in old-growth and secondary forest, on the island since the historical period (Table S5), only four showed a significant increase (i.e., 85% CI did not overlap with zero) (Figure 3). These species were a large terrestrial species (*Tinamus major*), two under- and mid-story species (*Ceratopipra mentalis* and *Myiarchus tuberculifer*), and one canopy species (*Poliophtila plumbea*). *Tinamus major* (0.30–0.98, historical–current occupancy probabilities in old-growth forest) and *Poliophtila plumbea* (0.39–0.72) had the greatest changes in occupancy, whereas *Ceratopipra mentalis* (0.77–0.96) and *Myiarchus tuberculifer* (0.71–0.95) had the smallest change in occupancy. Ten other species also showed a substantial increase in occupancy between 2002–2005 and 2018 (change in occupancy > 0.10), although with imprecise estimates of the effect of Era.

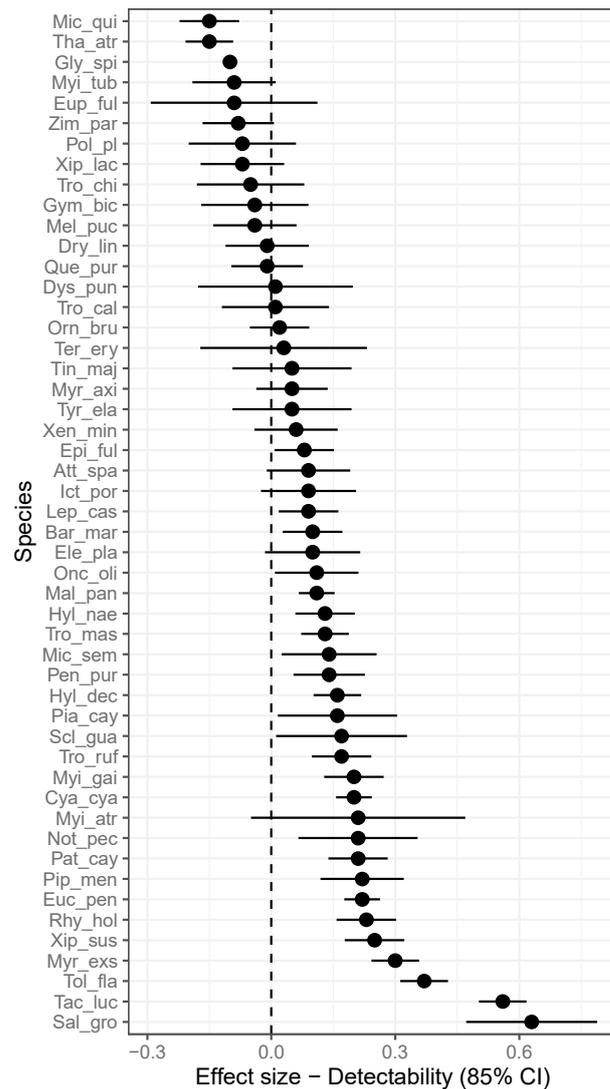


Figure 2. Model-averaged estimates of effect sizes of Era on bird detectability. Error bars are 85% confidence intervals. The dot line represents no change in detectability between Eras; species to the left of the line had higher detectability in the historical era, whereas species to the right of the line had higher detectability in the current era. For more information on species code and names, see Table S1.

In contrast, 14 species showed a decrease in occupancy point estimates (Table S5). Two species had a significant and negative effect of Era on occupancy on both old-growth (Figure 3A) and secondary forest (Figure 3B): *Cyanoloxia cyanooides* (1.0–0.16), an understory omnivore, and *Melanerpes pucherani* (0.59–0.11), an omnivorous woodpecker species. Whereas one species *Saltator grossus* (1.0–0.02) had a significant and negative effect of Era only on old-growth forest (Figure 3A). Four other species also showed a substantial decrease in occupancy between 2002–2005 and 2018 (change in occupancy > 0.10), although with imprecise estimates of Era’s effect. Despite the large occupancy decline detected for *Cyanoloxia cyanooides* and *Saltator grossus*, these species occurred in few sites in the historical period ($n = 7$ and $n = 3$) and were never detected in the same site twice in the historical period. Low occupancy associated with low detectability can often lead to occupancy probabilities close to one with no reliable uncertainty measures [36]; therefore, we interpret the change in occupancy by *Cyanoloxia* and *Saltator* with caution. Among the species with no significant change in occupancy ($n = 43$), 24% ($n = 5$) were relatively rare ($\psi < 0.30$) in the old-growth forest, and ($n = 10$) were rare in the secondary forest, occurring only in a few sites on the island. In contrast, 24 species are very common and

widespread in the old-growth forest ($\psi > 0.70$), and 17 species are very common and widespread in the secondary forest (Table S5).

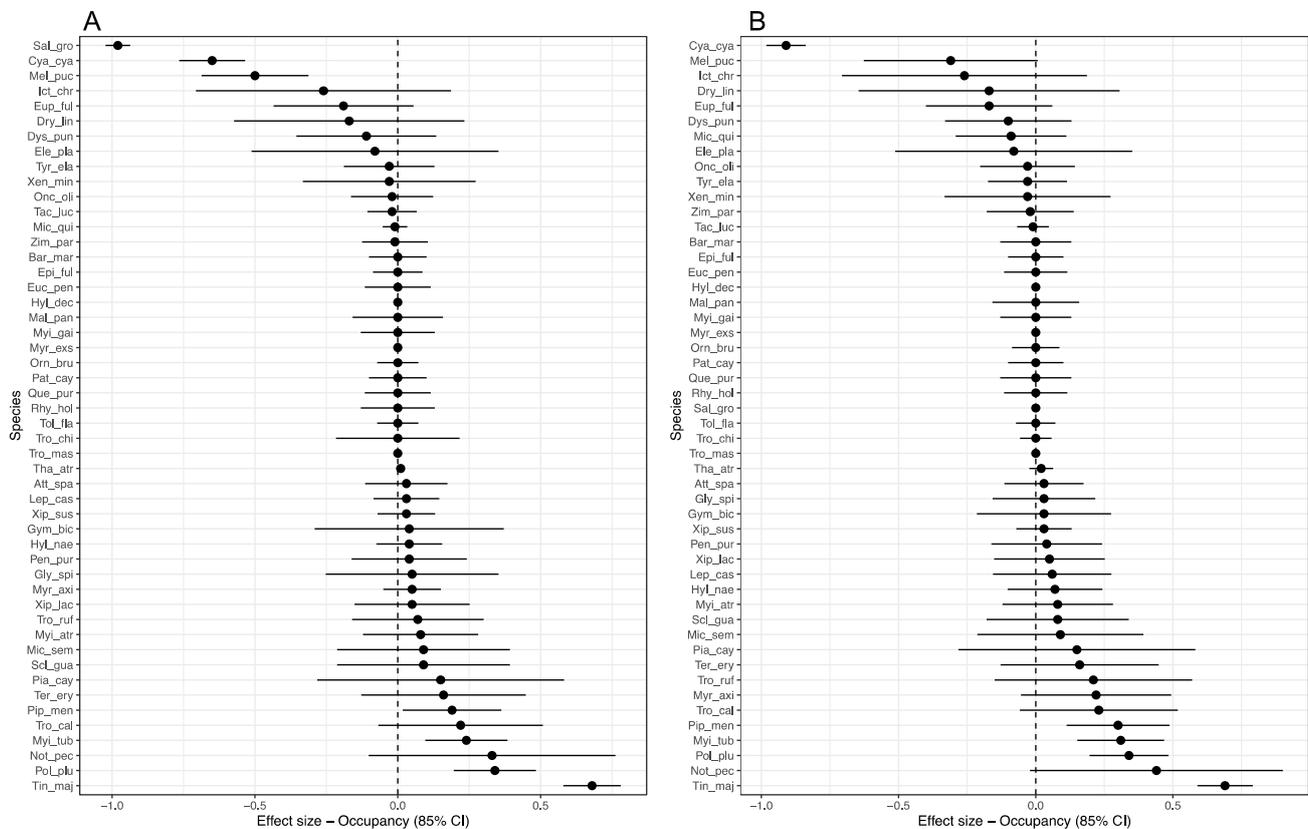


Figure 3. Model-averaged estimates of effect sizes of Era on bird occupancy in (A) old-growth forest and (B) secondary forest. Error bars are 85% confidence intervals. The dot line represents no change in occupancy between Eras; species to the left of the line had higher occupancy in the historical era, whereas species to the right of the line had higher occupancy in the current era. For more information on species code and names, see Table S1.

Forest age had a significant effect on occupancy of more bird species than Era and elevation, and overall, birds had higher occupancy estimates in the oldest forest sites (Figure 4). Occupancy is significantly higher in old-growth forest sites for 30% of bird species ($n = 15$) (Figure 4A), which comprise a mix of understory and canopy insectivores along with understory and canopy omnivores. Two of these 15 species had higher occupancy in old growth forest only in the current period (*Cyanoloxia cyanoides*, *Dryocopus lineatus*) (Figure 4B) whereas *Saltator grossus* had higher occupancy in old growth sites only in the historical period (Figure 4A).

Only three of the 15 birds associated with old-growth forest sites had significant occupancy changes between historical and current periods (*Melanerpes pucherani*, *Cyanoloxia cyanoides*, and *Saltator grossus*), in which the occupancy declined in all three species. Another 17 species also showed a substantial higher occupancy in old-growth forest sites in the current period (occupancy change > 0.10), although with imprecise estimates of the effect of forest age. Elevation had no significant impact on the occupancy of the majority of bird species (Figure 5). Nevertheless, five bird species (*Glyphorynchus spirurus*, *Microrhopias quixensis*, *Myrmotherula axillaris*, *Poliocrania exsul*, and *Penelope purpurascens*) showed a positive relationship between elevation and occupancy. Another five species showed a negative relationship between elevation and occupancy (*Patagioenas cayennensis*, *Icterus chrysater*, *Trogon chionurus*, *Cyanoloxia cyanoides*, *Tyrannulus elatus*). Among the species with a significant elevation effect on occupancy, only *Cyanoloxia cyanoides* showed a decline in occupancy between periods.

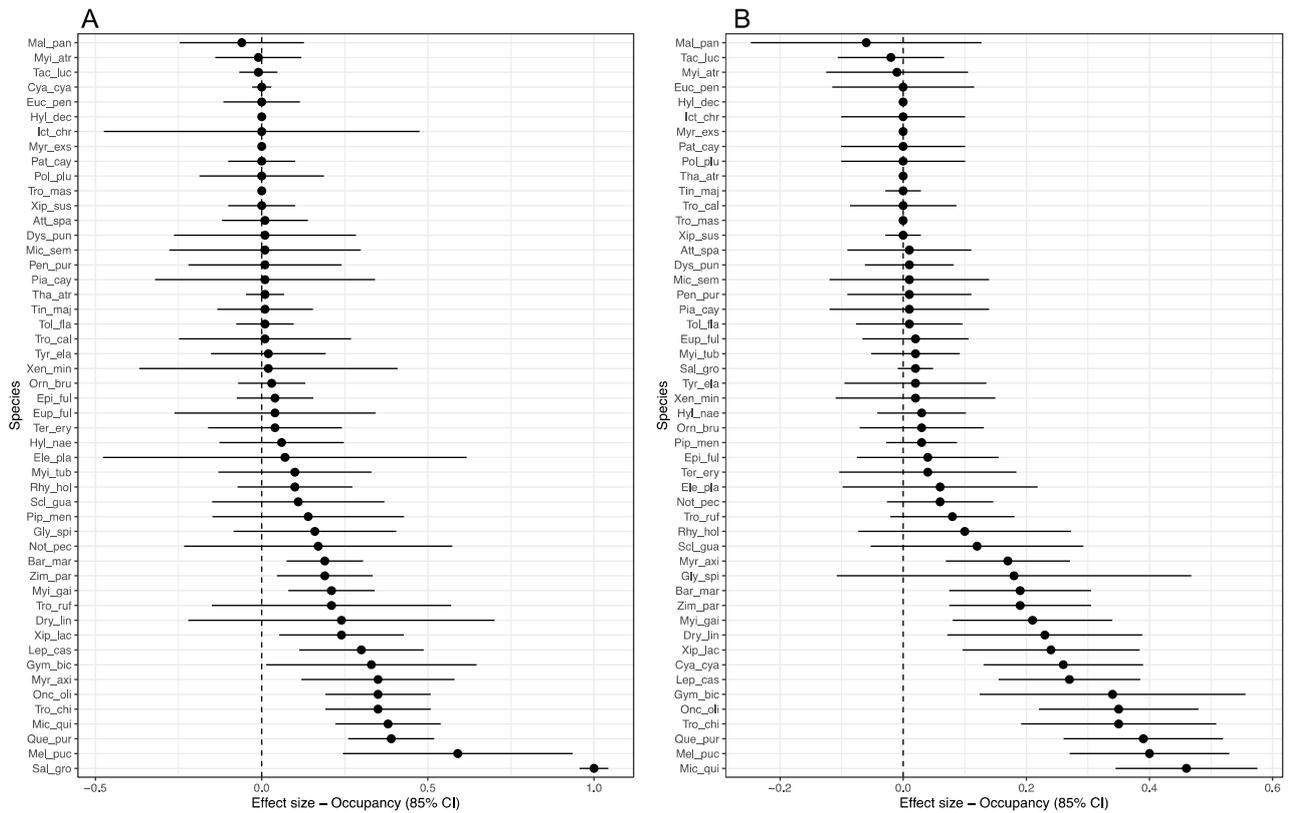


Figure 4. Model-averaged estimates of effect sizes of Forest Age on bird occupancy in (A) the historical era and (B) current era. Error bars are 85% confidence intervals. The dot line represents no change in occupancy between old-growth and secondary forest; species to the left of the line had higher occupancy in the secondary forest, whereas species to the right of the line had higher occupancy in old-growth forest. For more information on species code and names, see Table S1.

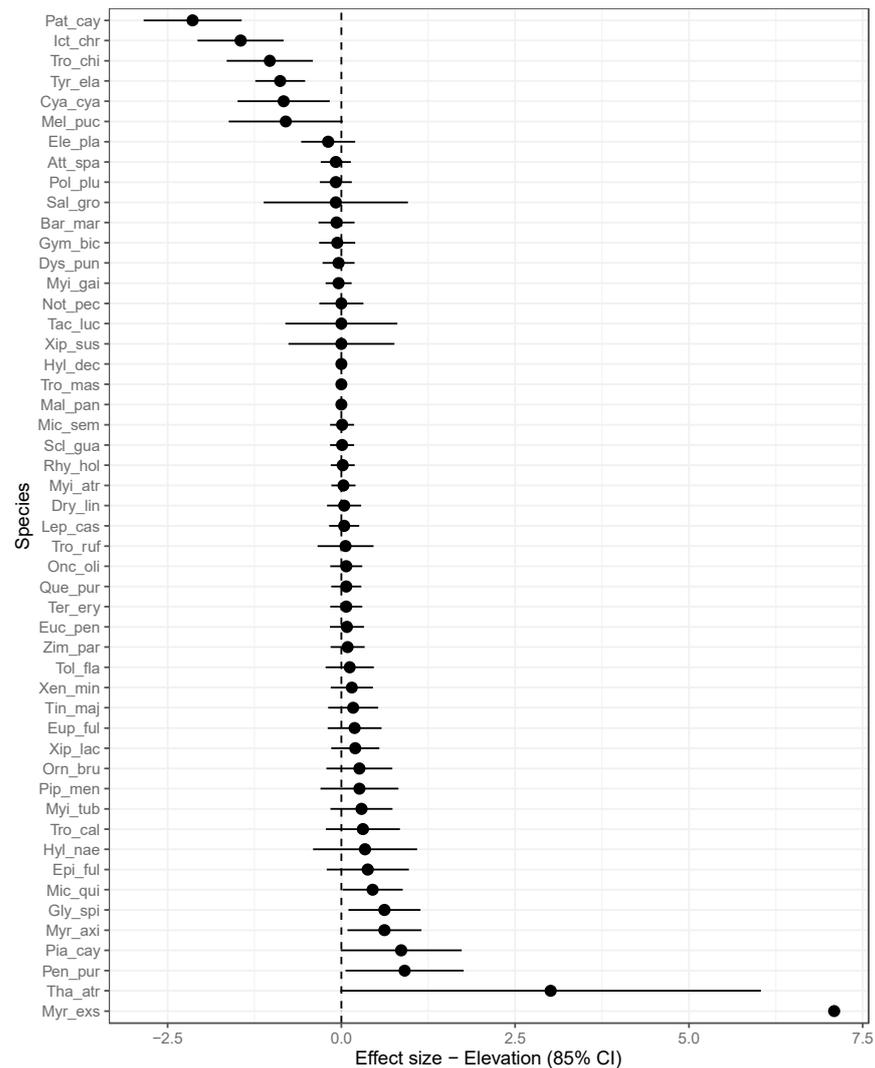


Figure 5. Model-averaged estimates of effect sizes of elevation on bird occupancy. Error bars are 85% confidence intervals.

4. Discussion

4.1. Occupancy Stability

Occupancy by the 50 bird species was mostly stable over 17 years. Given that BCI has been losing species since its isolation nearly 100 years ago [27,29], we would expect only a few species to be disappearing so long after the initial isolating event; therefore, stable occupancy patterns should be generally anticipated. However, the island continues to lose two to four species per decade and, based on associating traits of lost species with species still extant and possessing those same traits, a few more are predicted to disappear in the coming decades [30]. Rare species with restricted occurrence in BCI, even with stable populations, can still be prone to extinction, since population fluctuation or stability is not necessarily strongly related with extinction probabilities [42,43]. Extinction probabilities may be instead related to habitat alterations, such as isolation owing to fragmentation, that limit dispersal between local populations.

We detected no new colonizations, and rare species continued to be rare. Species that disappeared from BCI just prior to initiation of our historical surveys (2002–2005 data), including *Celeus loricatus*, *Lipaugus unirufus*, *Vireolanius pulchellus*, *Notharcus tectus*, and *Colonia colonus*, were not detected. One of the few understory forest species predicted to disappear but still maintaining a small population size [30], *Platyrinchus coronatus*, was not detected during PAM surveys in 2018 but does persist in very small numbers (WDR,

personal observation). Three other species detected in both survey periods exhibit stable but highly restricted occupancy, including *Sclerurus guatemalensis*, *Dysithamnus puncticeps*, and *Euphonia fulvicrissa*. Two of the three species (not *Euphonia*) have been predicted to be likely to disappear in the near future [30]. The overall pattern of continued absence of previously missing species reinforces the idea that either habitat suitability has changed for some species or isolation of the island by water restricts immigration by certain species [44]. Of the few previously missing species that occasionally re-appear on BCI, all are excellent fliers (e.g., Pheasant Cuckoo *Dromococcyx phasianellus*), yet extremely few establish new persistent breeding populations [30]. Despite the dominant pattern of stable occupancy, we documented substantial dynamism in spatial distributions across the island.

4.2. Changes in Occupancy

Occupancy point estimates suggest an overall trend of increasing species distributions over the 17 years, with four species markedly increasing their distributions. These four species, including a tinamou (*Tinamus major*), manakin (*Ceratopipa mentalis*), flycatcher (*Myiarchus tuberculifer*) and gnatcatcher (*Poliophtila plumbea*), are among the most common species on BCI [2]. The expansion in spatial occupancy is a strong indicator of overall habitat suitability for these species. The expansion was predicted by Robinson (2001) in only one of these four species (the tinamou). One of the species (*Ceratopipa mentalis*) was predicted to be in decline based on comparisons with Willis' (1974) island-wide population estimates, but the inexact nature of Willis' method may have led to inflated population size estimates [2]. In contrast, of 14 species with lower occupancy in the current time, only three showed marked decreases in their distributions. Two of those, *Cyanoloxia cyanoides* and *Saltator grossus* of moist forest understory, were characterized by low occupancy and also low detectability in the historical period, a combination of results limiting interpretability [36]. *Cyanoloxia cyanoides* is known to wander widely across the island, moving from one wet drainage to another. Because its vocalizations are loud and distinctive, it is easy to hear, but it rarely stays in one place long enough to be detected regularly. In fact, in the historical surveys, it was never detected in the same place twice. The PAM data revealed an association of its occurrence with older forest and lower elevation sites, which are the streamside habitats on BCI. The other species showing a strong reduction in spatial occupancy was the Black-cheeked Woodpecker (*Melanerpes pulcherani*), a species associated with wetter forests in central Panama [34].

Tinamus major had the highest increases in occupancy. *Tinamus major* is a relatively large terrestrial species that is protected from hunting on BCI. This species was considered uncommon ($n = 200$; Willis 1980) in the 1970s and estimated to have a declining population during the 1990s ($n = 100$; Robinson 2001). Our observation of an expanding distribution since the early 2000s may be related to possible declines in predators of adult tinamous as well as their nests. Predators of adult tinamous include cats and raptors. BCI has relatively low densities of large raptors [2] and large cats (pumas), but has high numbers of small cats, especially ocelots [45]. Yet ocelot diets on BCI appear to be dominated by small mammals [46]. Predation of tinamou ground nests, however, may be strongly influenced by numbers of coatimundis, capuchin monkeys, and even peccaries [47], which are known to have experienced severe population crashes through time on BCI. In particular, periods of famine, leading to die-offs of mammals, have been documented periodically (1930, 1958, 1970, 1983, 1989, and 2010) [48–51]. The most recent die-off of coatis resulted in a severe decline of coati numbers, coincident with our observation of expanded tinamou occupancy and distribution. We hypothesize that fluctuations in tinamou populations could be directly related to the population dynamics of their nest predators.

Another possible explanation for the observed expansion of *Tinamus major* in BCI may be related with a higher detection range from the acoustic recorders. The tinamou species can likely be detected with the recorders at distances greater than 50 m. Therefore, the current estimates for the tinamou should be interpreted in terms of the proportion of the habitat used rather than the proportion covered by territorial birds of that

species [52]. Nevertheless, we find this alternative scenario unlikely given our field impressions. In addition, if louder calls were expected to overestimate occupancy estimates in the current time, we would expect a similar result for other species, such as the crested guan (*Penelope purpuracens*), black-breasted puffbirds (*Notharchus pectoralis*), and woodcreepers (*Xiphorhynchus* sp), which was not the case.

4.3. Forest Age and Elevation Effects on Occupancy

The positive association between occupancy and old-growth forest sites in this study may also explain past extinctions and the general stability in occupancy between survey periods for most species. The relationship between forest age and species richness, composition, and abundance have been extensively documented in the tropics [53,54]. Species richness may be similar in forests of different ages, but the composition is often dissimilar because of a lack of old-growth forest specialists and some functional groups in the secondary forests [53]. On BCI, secondary forests are now relatively old (>100 years) and connected to the oldest forest (>500 years). Seven of the extinct species in the 1990s in BCI were mainly associated with the young secondary forest, and their disappearance was likely related to the forest's successional maturation [29]. Another seven species extinct on BCI were forest-dwelling resident bird species associated with the oldest and the most humid forest on the island [29]. Given that most of the young secondary-forest species have disappeared and that secondary forest is all relatively old now (>100 years), it is likely that forest-dwelling species whose populations persisted on the island now have even more appropriate habitat [29,30]. Nevertheless, our occupancy results show that many species still favor the oldest forests on the island, and the few species that declined in occupancy over the last 17 years have been largely associated with the oldest forests. The apparent lack of an elevation effect on species occupancy is likely related to the small variation in elevation change in the island (150 m).

4.4. Alternative Scenarios and Caveats

Given the high number of species with estimates of more than 50% population declines between the 1970s and 1990s ($n = 37$; [2]), the overall stable occupancy found in our study may seem counterintuitive. One possible explanation is that a decrease in bird abundance does not translate into a decrease in occupancy. Sites could remain occupied over time while the total number of individuals occupying those sites may be decreasing. Although this may help explain the minimal occupancy changes between 2002 and 2018, we consider this scenario unlikely for two reasons. First, with some exceptions (e.g., *Ceratopipra mentalis*), most of the species we studied have relatively small home ranges (<16 ha) [34]. Given the recorders' detection radius (~50 m) and the distance between sampling sites (~200 m), we were most likely detecting one to two individuals of most species at each site. Second, there is a large body of literature across different taxonomical groups and ecosystems, showing a strong and positive relationship between occupancy and abundance [55–57].

Although only seven species had a significant change in occupancy between the historical and current period, occupancy point estimates suggest an overall trend of increasing species distributions. Therefore, bird species that still persist in BCI may be benefiting from forest maturation and currently expanding in distribution. This alternative scenario in which many species are actually expanding distributions is not unlikely, since our results may be biased against the detection of an increase in occupancy.

Because the historical data lack replicate visits in the same year, we considered four consecutive years (2002, 2003, 2004, and 2005) as replicate visits in the occupancy models. In this case, some species' populations may not be closed for site colonization and extinctions during the four years in the historical data set. The violation of this assumption may overestimate occupancy probability in the historical time, and consequently, our results will tend to overestimate the declines and underestimate increases in occupancy [58]. Only two species had significant population declines, and there was no declining pattern of the occupancy point estimates. In contrast, four species had a significant increase in occupancy,

and about half of the occupancy point estimates increased from historical to the current period. Therefore, an additional 17 species may actually have expanded their distribution through time.

Another potential limitation of our study and many other studies evaluating long-term population changes via two “snapshots” in time [21,59–61] is that the relative fluctuations in the intervening years remain unknown, and these are important for accurate interpretation of population trends. The importance is more pronounced, however, when populations fluctuate strongly. It is clear that some species on BCI have declined and disappeared, but many other forest-dwelling species in the region have been characterized as having stable populations [2,11]. To improve our understanding of temporal changes in occupancy, abundance, and distributions across BCI, detailed analyses of annual or near-annual surveys will be required.

We do not know if the overall stable occupancy pattern observed on BCI is similar in the nearby mainland forest because of a lack of similar studies. Only a few studies have compared the avifauna of BCI and adjacent forest, and these studies showed that: (1) avifauna on BCI had reduced species richness and abundance related to a nearby mainland forest [62] and (2) that connectivity with the extensive primary forest is a more critical determinant of avian species richness and community structure than forest age [63].

4.5. Species Detectability

Despite a stable occupancy found for the majority of the species, detectability was higher in 2018 than in 2002–2005 for most species. The lack of correlation between occupancy and detectability highlights the challenges of using unadjusted point counts to estimate species distributions. Unadjusted point counts can produce biased estimates of change in occupancy affecting inferences about population dynamics [36,64]. The increase in detectability in the current period may have at least two non-exclusive explanations. First, passive acoustic monitoring (PAM) gathers more data and outperforms traditional point-counts. Several studies have shown that PAM can detect similar or more species than traditional survey techniques [65–67], which is not surprising given that hundreds of recorders can be left in the field continuously recording the soundscape for weeks and months. In addition, recordings allow identifications to be revisited at any time and are not missed or lost as they might be during ephemeral point counts. Some species that do not vocalize much may be difficult to detect using PAM, but PAM’s use does not preclude the use of combinations of different techniques (using PAM devices and observational surveys by humans). Second, the increase in detectability may be related to an increase in bird abundance in occupied sites, resulting in more vocalizations and more detections. We consider this explanation to be unlikely given that most of the sampled species occur at low enough densities that only one or two territories at most would be within range of any PAM device.

5. Conclusions

In this study, we have provided a quantitative description of occupancy changes for 50 species over 17 years in a neotropical forest fragment, evaluated the effect of forest age and elevation on bird species, and quantified degree of occupancy change in the 50 species. Our results add to the body of empirical findings regarding the positive effect of old-growth forest on bird occurrence and support the general conclusion that populations of most bird species in older forests on BCI are currently stable. Further, we found that passive acoustic monitoring provides higher detectability for most bird species than traditional point counts. Our results further illustrate how acoustic monitoring provides an easy and powerful way to monitor animal populations along elevational gradients. We encourage studies that will test potential mechanisms influencing population stability, and we encourage the establishment of long-term monitoring projects around the globe to improve information on species distributions given the threat of climate change.

Supplementary Materials: The following are available online at <https://www.mdpi.com/1424-2818/13/2/50/s1>: Table S1: List of the 50 bird species selected for occupancy analyses, Table S2: List of occupancy models used in the analyses, Table S3: Estimated detectability for each species per Era, Table S4: Model average effects for Era, Elevation and Forest Age variables on occupancy and detection parameters, Table S5: Estimated occupancy for each species per Era and Forest Age, Table S6: Model selection results for each species.

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