

Historical Occupancy of the Yellow-green Grosbeak *Caryothraustes canadensis* (Aves, Cardinalidae) in the Far North of the Atlantic Forest

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Determining how environmental factors and threats influence species occupancy patterns is essential to establish more efficient management strategies and policies for conserving natural populations and habitats. The Yellow-green Grosbeak (*Caryothraustes canadensis*) is a canopy specialist bird that occurs in the Atlantic Forest and represents a good model for evaluating how changes in regional scale characteristics can affect occupancy patterns of forest specialist species. Increasingly, occupancy models are being used to maximize these predictions because they are statistical methods that take imperfect detection into account, which strengthens inferences compared to other approaches. We evaluated how multiple environmental factors affected the large-scale occupancy of the *C. canadensis* over the last 30 years in the far north of the Brazilian Atlantic Forest, a recognized center of endemism and biodiversity. In this study, we collected secondary data from *C. canadensis* between 1991 and 2020. The occupancy of *C. canadensis* and several

environmental factors that explain the historical occupancy dynamics of the species in the northern Atlantic Forest region was determined, and analyses were conducted with single-season occupancy models. The daytime temperature range had the most significant impact on occupancy. The climate stability and the forest area were determining factors in the large-scale occupancy of *C. canadensis*. Other impacts on occupancy were noted as altitude and secondary effects due to the precipitation. Records of *C. canadensis* in the region are probably associated with multiple interaction factors. The preservation of forested and climatically stable habitats of the region should favor the establishment of forest specialist species such as *C. canadensis* along the studied stretch. Along the final portion of the São Francisco River, the more significant climatic instability, probably a consequence of the loss of forest cover, can be considered an area that requires more urgent action for the conservation of this forest specialist species. Thus, our data validate the importance of forest remnants and reinforce the adverse effects of habitat fragmentation and degradation on the requirements of endemic bird populations of the Atlantic Forest.

Key words: Altitude, Detection, Forest, Precipitation, Temperature

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BACKGROUND

Changes in species' current distribution patterns and regional extinctions in the Atlantic Forest are often attributed to habitat degradation (Joly et al. 2014; Diniz et al. 2022). Yet, there is evidence that other interacting factors, such as climate, topography, and forest cover, may also influence species distributions (Loiselle et al. 2010; Morante-Filho et al. 2021; Ribon et al. 2021). To establish more efficient conservation strategies and policies, it is paramount to investigate how multiple factors and threats influence the observed distributional patterns of natural populations, especially those considered endemic or threatened. These strategies tend to be quite expensive and require great effort in the field, which limits their results (Crouzeilles et al. 2020; Strassburg et al. 2020). To avoid wasting resources and efforts, therefore, conservation strategies must be based on the best available evidence and sound scientific analyses. Nonetheless, much of the information generated so far is not very robust when it comes to assessing environmental impacts (Bolton et al. 2019), discovering new populations (Allen and McMullin 2019), or describing poorly known ones

(Roberts et al. 2016) due to the inclusion of sampling biases, which can also limit the efficiency and success of many conservation strategies.

As a step forward, site-occupancy modeling approaches can reduce detection biases while estimating the values of species' habitat use (MacKenzie et al. 2002). These models are known as occupancy models and have become more and more used and popular over time (Del-Rio et al. 2015; Morante-Filho et al. 2021; Ribon et al. 2021). There are currently several occupancy modeling approaches, both in the context of populations and communities (MacKenzie et al. 2018). Whereas most distribution models do not consider the imperfect detection of species among their particularities, models that estimate occupancy based on population parameters that incorporate imperfect detection (MacKenzie et al. 2002, 2003) can reduce sampling biases due to errors in species detection (Bailey and Adams 2005). Two parameters are needed to generate more robust models and results: the occupancy probability and the detection probability (MacKenzie et al. 2002). Here, occupancy is conceptualized as the probability of species or taxonomic groups occupying a site (*e.g.*, forest, lake, geographic point, etc.) in each period (MacKenzie et al. 2002). Detection probability is the chance of registering the presence of the target species at a given time and location. In addition to occupancy and detection estimates, it is possible to include site covariates in the occupancy modeling (MacKenzie et al. 2002), which provides more adjusted models with high explanatory power and allows one to better understand what factors influence species distributions.

Efforts to generate these accurate occupancy models have been growing concomitantly with applications on different methods and taxa, which are linked to their ability to make more realistic predictions about the species occupancy (*e.g.*, Peterman et al. 2013; Vasudev et al. 2021; Vitekere et al. 2021). Recently, studies have explored occupancy with this predictive power for 68 birds in the southern portion of the Brazilian Atlantic rainforest and have shown that a reduced proportion of forest cover is negatively associated with the occupancy of the studied populations (Morante-Filho et al. 2021). Ribon et al. (2021) have shown how topography can also interfere with bird occupancy in the Atlantic Forest due to its interaction with the availability of microhabitats and local climate. Analyzed separately, these results can be controversial, but together they suggest that the inclusion or exclusion of certain information helps to explain the processes that act concomitantly on species occupancy. These types of results can provide important paths for management and conservation strategies.

In Brazil, we have seen an increase in studies that use occupancy models to address issues related to bird ecology and conservation. For instance, studies that have considered biogeographic factors have primarily emphasized vegetation (Del-Rio et al. 2015; Bhakti et al. 2018; Morante-Filho et al. 2021) and topography (Ribon et al. 2021) as predictors of bird occupancy in the Atlantic

Forest. Thus, considering the most relevant factors that are commonly related to the distribution patterns of forest birds at local scales, we tested their potential to also predict the occupancy of the Yellow-green Grosbeak (*Caryothraustes canadensis*) at relatively larger scales and over the last 30 years in the highly threatened northernmost portion of the Atlantic Forest. Based on the species' habitat requirements and the climate properties of the current taxon's distributional records, we expected higher occupancy rates in moderate to highly forested and rainy areas. Additionally, we also evaluated the contribution of other environmental factors that might help explain the historical occupancy dynamics of the species in the northern Atlantic Forest region.

MATERIALS AND METHODS

Study area and spatial design

We carried out the study in the far north of the Atlantic Forest, Northeastern Brazil, in the states of Alagoas, Pernambuco, Paraíba, and Rio Grande do Norte (Fig. 1). Historically, the region is considered the most degraded portion of the Atlantic Forest, due to the conversion of native forest into agricultural land (*e.g.*, sugarcane matrix) since the 16th century when European peoples colonized Brazil (Joly et al. 2014). It is estimated that more than 85% of the original cover of this forest has already been removed and that most of the small remnants are highly isolated from each other and remain under constant anthropogenic pressures (see Ribeiro et al. 2009). This area contains the largest number of threatened and endemic birds in the Atlantic Forest (ICMBio 2018) and is where the first extinctions of bird taxa in the Atlantic Forest occurred (Lees and Pimm 2015).

As the limits of this ecosystem vary according to the literature and adopted criteria, we considered the Atlantic Forest integrative limit provided by Muylaert et al. (2018) to delimit our study area. Then, we established a continuous grid with 204 cells ($\sim 17 \times 17$ km) within this established boundary to study species occupancy in the region (Fig. 1). Our sampling unit is represented by each grid cell.

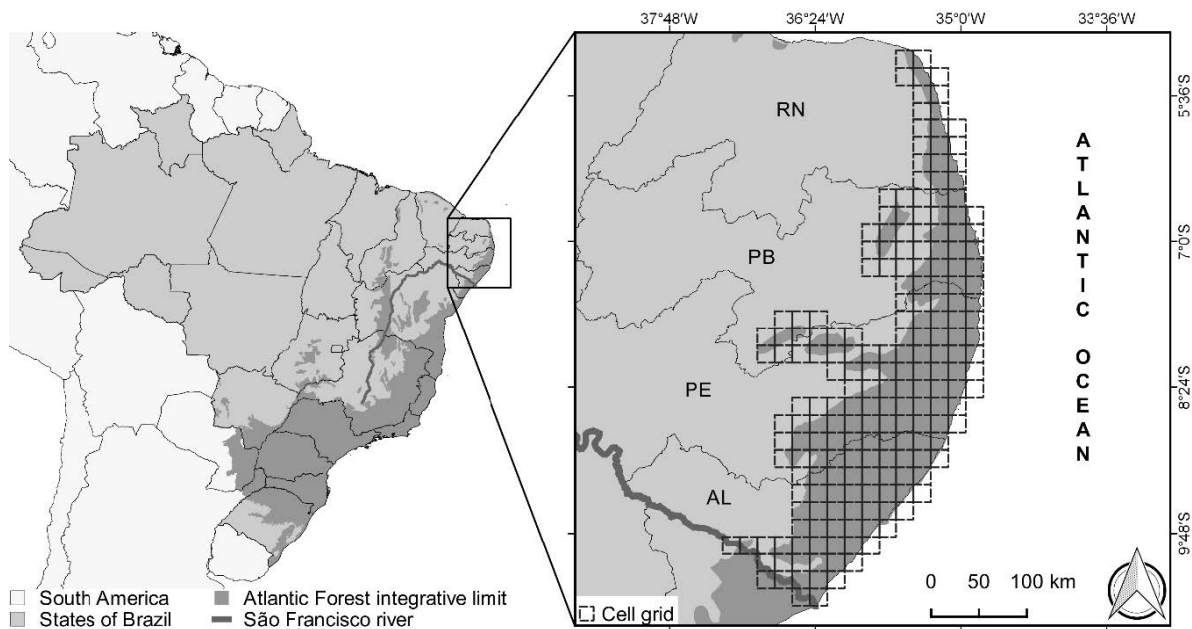


Fig. 1. Study area and spatial design in the far north of the Atlantic Forest, Brazil. The 204 grid cells, designed around the Atlantic Forest integrative limit (Muylaert et al. 2018), were used to collect occurrence data of *Caryothraustes canadensis* between 1991–2020.

Target species

We studied the occupancy of Yellow-green Grosbeak (*Caryothraustes canadensis frontalis*) (Hellmayr, 1830), an endemic Cardinalidae taxon from the Brazilian Atlantic Forest (Silveira et al. 2022). This subspecies exhibits a strong dependence on forested environments and is characterized by a geographically restricted distribution in the far north of the Atlantic Forest domain (Brewer 2020; Silveira et al. 2022). Notably, it and *C. c. brasiliensis* have been proposed as distinct species, separate from other populations based on genetic, vocal, and morphological attributes (Tonetti et al. 2017). This taxonomic proposal was accepted by the Brazilian Committee of Ornithological Records (CBRO), which officially designates both lineages within the Atlantic Forest as a single species, denoted as *C. brasiliensis* (Pacheco et al. 2021). Nevertheless, recently, *C. c. frontalis* was recognized as a valid terminal taxon by Lima (2022). Besides, this population is recognized by its geographically disjunct distribution, primarily inhabiting the region north of the São Francisco River, in the states of Pernambuco and Alagoas (Silveira et al. 2022). Therefore, in the following sections of the text, when we use the nomenclature *Caryothraustes canadensis* we are referring to the population *C. c. frontalis*. Until recently, this population had been classified as Endangered on the Brazilian National Red List (MMA 2014), but it has now been downlisted and classified as Least Concern (MMA 2022). However, if further studies confirm the species status of this population, it likely faces greater conservation challenges, given its notably limited and highly fragmented distribution range (Lima 2022; França et al. 2023). The main threats that influence the

persistence of the Atlantic Forest populations of this species are deforestation and the illegal capture of wild individuals (Roda 2008).

Data collection

We collected occurrence data for *C. canadensis* in the studied region from 1991 to 2020. This period encompasses the highest number of occurrence records of the species, thereby mitigating potential issues arising from an excess of genuine absences that could impact detection estimates (Boyd et al. 2023). Detection probability is influenced by sampling effort, meaning that including additional years may increase the likelihood of sampling error. Therefore, we deemed years before 1991 irrelevant for records and recognized their potential to introduce bias into the analysis.

The records information was obtained from several sources, such as online citizen science platforms (ebird.org, gbif.org, specieslink.net, wikiaves.com.br, and xeno-canto.org), ornithological collections (UFPA, UFRN, UFPB, UFPE, UFAL, UEFS, and UFRJ), specialized researchers, and literature (scholar.google.com and ara.cemave.gov.br). On the Scholar Google website, we used the following keywords to obtain occurrence records, considering the study area and the species nomenclature: “*Caryothraustes canadensis*” AND (“Atlantic Forest” OR “Mata Atlântica”). After compiling all occurrence data, we conducted a thorough review and corrected the geographical coordinates that seemed to be incorrect ($n = 10$), such as those located in urban centers or other areas not consistent with the species’ habitat. These points were relocated to within the largest forest area corresponding to the same grid cell. The same procedure was applied when we only had information from the municipality of occurrence, adjusting the geographic points to the cell that represented the largest proportion of forest area available in the municipality or considering some other coordinate where the species has already been recorded. This careful process ensured an accurate analysis of the data. Thus, we considered the detection of the species in the grid cells for each year sampled, which allowed us to move forward with the data analysis.

We selected and collected information from five environmental covariates mentioned in the literature (altitude, forest area, annual precipitation, and diurnal temperature range), which may be potential influencers in the occupancy of *C. canadensis* (Table 1). We extracted the values of the covariates in each cell of the grid, from georeferenced files from different databases (see Table 1). No environmental covariate exhibited correlation values $\geq |0.7|$ (Pearson’s r) (Table S1). Consequently, we decided to retain all covariates for the subsequent analyses.

Table 1. Description of the four environmental covariates used to estimate the occupancy probability of *Caryothraustes canadensis* in the far north of the Atlantic Forest, Brazil

Covariate	Description	Category	Source
Altitude (m)	Five random elevation values collected on a raster	Topography	AMBDATA platform (www.dpi.inpe.br/Ambdata/download.php)
Forest area (ha)	Forest cover in the Atlantic Forest (forest, mangrove, and restinga), estimated between 2018 and 2019	Vegetation cover	SOS Mata Atlântica platform (mapas.sosma.org.br) (SOS Mata Atlântica & INPE 2020)
Annual precipitation (mm)	The sum of all total monthly precipitation values estimated between 1970 and 2000	Climate	WorldClim platform (worldclim.org) (Fick & Hijmans, 2017)
Diurnal temperature range (°C)	Mean of the monthly temperature ranges (monthly maximum minus monthly minimum), estimated between 1970 and 2000	Climate	WorldClim platform (worldclim.org) (Fick & Hijmans, 2017)

Data Analysis

We used single-season occupancy modeling to estimate occupancy rates and how they are influenced by environmental factors (MacKenzie et al. 2002). A special feature of these models is their ability to predict the occupancy probability of species between 0 and 1 (*i.e.*, <1). This model assumes that the occupancy of the species is static (closed) along the time (*i.e.*, occupancy does not change in a cell within the sampling season) and the detection of the target species in a cell is independent of other cells (Bailey and Adams 2005). Our models do not consider occupancy at the individual level, which assumes the occurrence of births, deaths, immigration, and emigration. Within this context, we considered that the species' occupancy in the grid cells would be influenced by detection at the population level at the spatial scale defined (MacKenzie et al. 2002).

We organized the detection history as a binary matrix of detection (1) and non-detection (0), considering species occurrence data for each of the 204 cells (Fig. 1; Table S2) and years (1991–2020) (Table S2). Next, we performed the modeling in two stages. First, with the occupancy

probability (ψ) fully parametrized (all environmental covariates), we tested the best structure for detection probability (ρ). In this stage, we compared three models, the full temporal with different detection over the years [$\rho(t)$, model 1], a linear trend in detection rates over the years [$\rho(trend)$, model 2], and constant detection [$\rho(.)$, model 3]. In the second stage, we selected the best-ranked model from the first stage and performed all possible combinations of the environmental covariates on ψ .

$$\begin{aligned} &\psi (alt + for + pre + tem) \rho (t) \text{ (model 1)} \\ &\psi (alt + for + pre + tem) \rho (trend) \text{ (model 2)} \\ &\psi (alt + for + pre + tem) \rho (.) \text{ (model 3)} \end{aligned}$$

where, (*alt*) is the altitude, (*for*) is the forest area, (*pre*) is the annual precipitation, (*tem*) is the diurnal temperature range, (*trend*) is the linear trend in detection rates over the years, (*t*) is the different detection over the years, and (*.*) is the constant detection.

To select the best-ranked models, we used the Akaike Information Criterion for small samples (AIC_c) and associated metrics (ΔAIC_c , difference in AIC_c of model *i* about the best-ranked model; w_i , model weight). Models ranked with $\Delta AIC_c \leq 2$ were considered to perform well (Burnham and Anderson 2002). The importance of the final set of models was represented by those best-ranked and with the lower number of associated parameters (Arnold 2010).

The occupancy modeling allowed us to obtain the estimated occupancy values per cell and generate a map, from the mean of the occupancy probability rates for each model with $\Delta AIC_c \leq 2$. In this map, we pointed out the cells with $\psi > 0.50$ that included protected areas, from information provided by Ministério do Meio Ambiente (MMA 2021) and Instituto Socioambiental (ISA 2023).

We performed occupancy models using MARK software version 10.0 (White and Burnham 1999). To build the graphs, we used the ggplot2 package of the R software (R Core Team 2021), crossing the occupancy information obtained about each covariate. We used QGIS software version 2.18.19 (QGIS Development Team 2018) to process all geographic information and produce maps.

RESULTS

We gathered 192 occurrence records of *C. canadensis* within 15 spatial grid cells (7% of the total cells). Among these records, 142 were collected from citizen science platforms (74%) and 50 from scientific publications and provided by researchers and ornithological collections (26%) (Fig. 2). The highest concentration of data was associated with the cell that covers most of the protected area Murici Ecological Station, in Alagoas (Fig. 2).

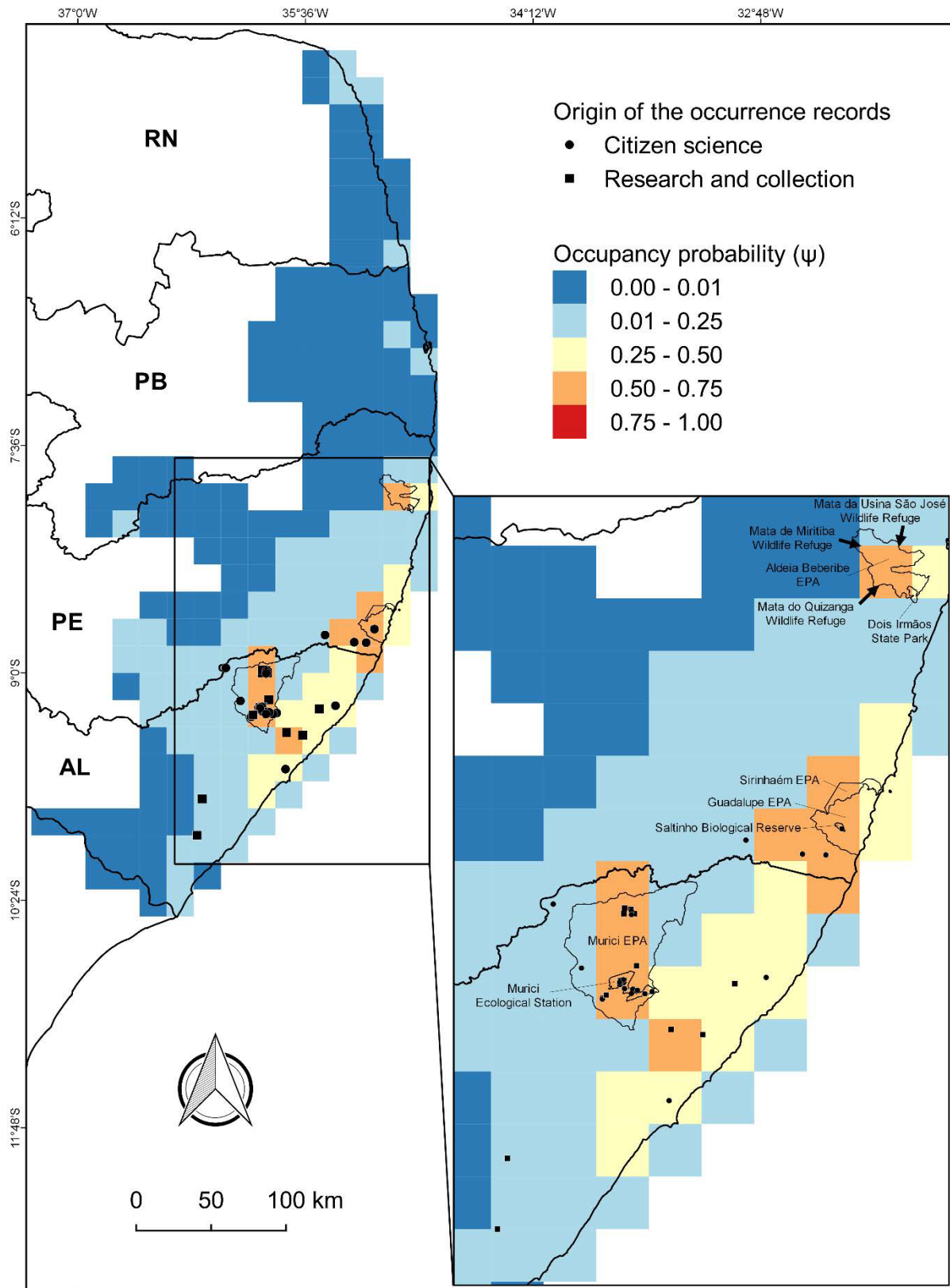


Fig. 2. Occurrence records and historical occupancy estimates of *Caryothraustes canadensis* (1991–2020) in the far north of the Atlantic Forest, Brazil. The lower inset highlights moderate to high estimated occupancy ($\psi = 0.50-0.75$), including the protected areas.

Occupancy models

We obtained one model with good performance (Model 2) in the first modeling stage from the three models analyzed. The difference in ΔAIC_c from this to the second-ranked model was 3.25 and the weight of the best-ranked model was 84% ($w_i = 0.84$). Then, in the second modeling stage, three of the 16 models generated were classified as good performance models and corresponded to 73% ($w_i = 0.73$) of the total weight (Table 2). In general, we observed that the linear trend in detection rates over the years (*trend*) was the most important temporal covariate in ρ (first and second stage), and all environmental covariates included in the modeling were important in ψ (second stage). All three best-ranked models had the additive effect of forest area (*for*) and diurnal temperature range (*tem*) on ψ (Table 2). However, there is uncertainty regarding the hypothesis that best explains ψ . The importance of ρ (*trend*) shows that, for historic constructions that are based on information present in different bases, the sampling effort directly affects ρ .

Table 2. Single-season occupancy models for 30 years (1991–2020) of *Caryothraustes canadensis*. Models are in rank order, and those with good performance ($\Delta AIC_c \leq 2$) are shown: models 1, 2, and 3. Legend: ψ = occupancy probability; ρ = detection probability; (*alt*) = altitude; (*for*) = forest area; (*pre*) = annual precipitation; (*tem*) = diurnal temperature range; (*trend*) = linear trend in detection rates over the years; (*t*) = different detection over the years; (.) = null effect

# ^a	Models	AIC _c ^b	ΔAIC_c ^c	w_i ^d	K ^e
1°	ψ (<i>alt</i> + <i>for</i> + <i>pre</i> + <i>tem</i>) ρ (<i>trend</i>) ^f	357.30	0	0.33	7
2°	ψ (<i>alt</i> + <i>for</i> + <i>tem</i>) ρ (<i>trend</i>)	358.02	0.71	0.23	6
3°	ψ (<i>for</i> + <i>tem</i>) ρ (<i>trend</i>)	359.23	1.92	0.13	5
5°	ψ (<i>alt</i> + <i>for</i> + <i>pre</i> + <i>tem</i>) ρ (.) ^g	360.55	3.25	0.07	6
30°	ψ (<i>alt</i> + <i>for</i> + <i>pre</i> + <i>tem</i>) ρ (<i>t</i>) ^h	387.79	30.49	0	35
33°	ψ (.) ρ (.) ⁱ	398.69	41.39	0	2

^aModel ranking order. ^bAkaike Information Criterion adjusted for small samples. ^cDifference of AIC_c of model *i* relative to the best-ranked model. ^dModel weight. ^eNumber of parameters. ^fModel 2 (selected for the second stage). ^gModel 3 (not selected for the second stage). ^hModel 1 (not selected for the second stage). ⁱNull model.

Weight and effect of covariates

The individual weight of the four environmental covariates of occupancy probability in the set of models was greater than 0.50 in all cases (Table 3). The occupancy of *C. canadensis* was negatively influenced by diurnal temperature range ($\beta = -1.7062$; SE = 0.70988) and positively by forest area ($\beta = 0.0003$; SE = 0.00009), altitude ($\beta = 0.0061$; SE = 0.00276), and annual precipitation ($\beta = 0.0033$; SE = 0.00199) (Fig. 3).

The linear trend in detection rates over the years presented a weight equal to 0.84 in the set of models and presented greater explanatory power on detection (Table 3). This temporal covariate was present in all the best-ranked models and positively affected the detection probability ($\beta = 0.04$; $SE = 0.02$) (Fig. 4).

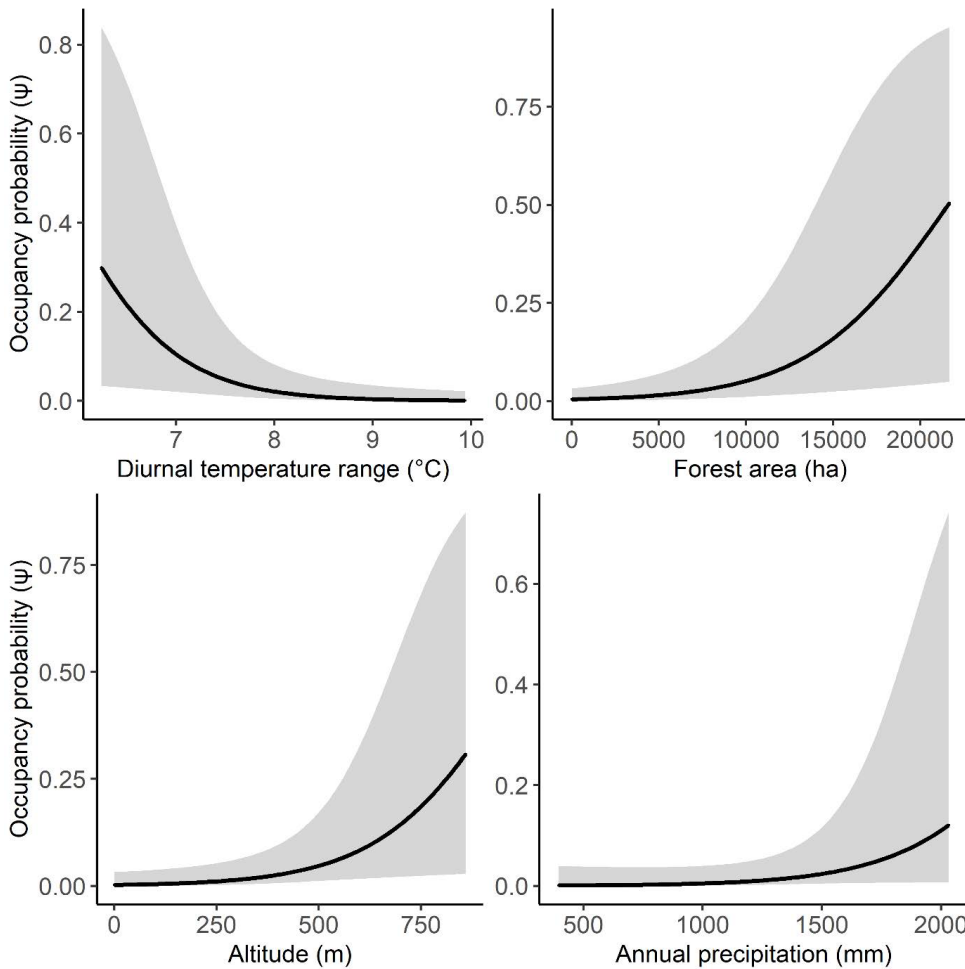


Fig. 3. Predicted effect of environmental covariates on the historical occupancy of *Caryothraustes canadensis* in the far north of the Atlantic Forest, Brazil, based on the best-ranked model of occupancy modeling.

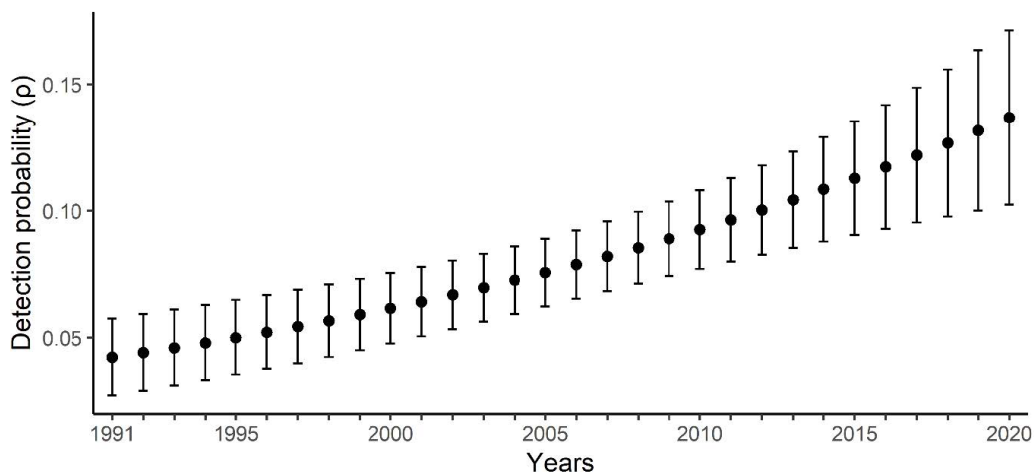


Fig. 4. Linear trend in detection rates over the years (1991–2020) and its relationship to the detection probability (estimates \pm standard error) of *Caryothraustes canadensis* in the far north of the Atlantic Forest, Brazil.

Table 3. Individual weight and the number of models for each covariate in the model set. Legend: ψ = occupancy probability; ρ = detection probability; (*alt*) = altitude; (*for*) = forest area; (*pre*) = annual precipitation; (*tem*) = diurnal temperature range; (*trend*) = linear trend of sampling effort over the years

Parameters (covariates)	Weight	Number of models present
ψ (<i>tem</i>)	0.98	16
ψ (<i>for</i>)	0.97	16
ψ (<i>alt</i>)	0.75	16
ψ (<i>pre</i>)	0.54	16
ρ (<i>se</i>)	0.84	16

Occupancy in the cell grid

All the records found for the species in the period studied (1991–2020) are limited to the states of Pernambuco and Alagoas (Fig. 2). The occupancy prediction map of *C. canadensis* includes nine cells with moderate to high occupancy probabilities ($\psi > 0.50$) (Fig. 2). Six of these cells overlap legally protected areas and are occupied according to our occurrence records. Three new cells were identified with a considerable probability of occupancy (>50%) in which there are no known *C. canadensis* occurrence records. Low to moderate occupancy grid cells ($\psi = 0.25$ – 0.50) were also indicated in the northern and southern coasts of Pernambuco and northeastern Alagoas. Furthermore, there are four cells with this occupancy rate where *C. canadensis* was recorded in Alagoas. Finally, cells with low occupancy ($\psi = 0.01$ – 0.25) were located on the northern and southern coasts of Rio Grande do Norte, on the intermediate coast of Paraíba, in the Agreste region of Paraíba, Pernambuco, and Alagoas, and along much of the Forest Zone of Pernambuco and Alagoas.

DISCUSSION

Population distribution

Here, we present the first distribution information and update the actual occupancy estimates for *C. canadensis* on a large scale. The few studies on this species include restricted information related to occurrence records and censuses carried out almost 20 years ago in forest fragments of the

state of Alagoas (Silveira et al. 2003). Most of the biology information mentioned for *C. canadensis* is based on the subspecies *C. c. canadensis* (Banks-Leite and Cintra 2008; Martínez-Ortega et al. 2014; Guallar et al. 2020). New research aimed at searching for other populations in the region studied and gathering more information on the species occurrence should be included in future analyses, which should improve the performance forecasts. To supply the information deficits for the species, we also suggest that efforts of species population estimates be employed to evaluate the persistence of this species in its localities in the extreme northern portion of the Atlantic Forest.

The species populations located north of the São Francisco River remain poorly known (Silveira et al. 2003; Farias and Pereira 2009; Lobo-Araújo et al. 2013) and are more endangered when compared to those located in the southern portion (Silveira et al. 2022). In general, populations of *C. canadensis* in the Atlantic Forest are commonly associated with the few well-preserved rainforests in the region (Silveira et al. 2003; Lobo-Araújo et al. 2013). In turn, populations that occur in Bahia and other states in southeastern Brazil are more abundant and distributed in the landscapes they occupy, including areas of secondary forest (Cavarzere et al. 2022).

Environmental factors operating on a large scale

In general, our study has revealed a strong correlation between environmental factors and the large-scale occupancy patterns of *C. canadensis*. These findings support the hypothesis that non-climatic factors should also be considered when evaluating areas that are important for species that depend to some degree on forested landscapes (Oliveira-Silva et al. 2022). The addition of non-climatic factors improves distribution models by breeding more realistic scenarios for forest-dependent bird assessments. Species ecological requirements predicted suitable climatic areas within native vegetation landscapes (Rajão et al. 2010; Giorgi et al. 2014; Oliveira-Silva et al. 2022) and became part of these predictors for mitigation more efficient of anthropogenic impacts and climate change.

Three environmental factors contributed the most to explaining the species occupancy estimates we found. The most favorable conditions for occupancy of *C. canadensis* in the far north of the Brazilian Atlantic Forest combine the stability in diurnal temperature ranges throughout the years with species requirements that are mainly related to topography and landscape composition. As expected for a species with restricted geographic distribution and dependent on preserved forested landscapes (Silveira et al. 2022; Oliveira-Silva et al. 2022), we confirmed the strong and positive relationship between forest area extension within the grid cells and *C. canadensis* occupancy rates. Furthermore, we found that certain intervals at higher altitudes tend to be better

occupied than those at lower altitudes. These results contrast bounded by broad and fine scales with those observed by other authors in the same region, where *C. canadensis* occurrence was more common in flat-top and low-altitude forest fragments (Lobo-Araújo et al. 2013). Ribon et al. (2021) found that in other properties of the topography, such as relief type (e.g., lowlands, ravines, hillsides, and hilltops), there is a partitioning in the occupancy of bird assemblages. However, these topographic aspects were also pointed out as dependent on better clarification (Cavarzere et al. 2021). We lack further clarification on how these multiple factors interact with the observed patterns of these populations and different scales.

Previous studies have already reported the importance of climate on bird distribution predictions in tropical rainforests (Williams and Middleton 2008; Oliveira-Silva et al. 2022; Jirinec et al. 2022). This is especially concerning due to the context of global climate change (Mantyka-Pringle et al. 2015). Only recently have studies been including the role of multiple factors, including topography and forest cover for conservation strategies on a broader scale (Ribon et al. 2021; Oliveira-Silva et al. 2022). Therefore, it remains unclear how such factors will interact with a changing climate. Although the role of climatic factors in predicting changes in biodiversity patterns is well studied (Souza et al. 2011; Mota et al. 2022; Oliveira-Silva et al. 2022), changes in environmental pressures that accelerate their intensity and speed are difficult to measure and are very unstable. It is known that many species have other non-climatic specific habitat requirements that may be determinants for their actual occupancy. In the same way that habitat structure is important to determine bird occupancy at small scales (Morante-Filho et al. 2021; Ribon et al. 2021), we suggest that habitat structural factors, such as the proportion of forest cover, should be considered at a landscape scale to more accurately predict the areas where the species could potentially occupy, especially when evaluating species restricted to forested habitats.

Temperature affected occupancy estimates for *C. canadensis*. Our results show that the areas with high climatic stability can act as important refuges for the species. This finding strongly suggests that the populations of *C. canadensis* that occur in the studied area might be one of the most susceptible to the effects of climate change, which agrees with a previous study in the same region (Tonetti et al. 2022). How increasing temperature may affect patterns of local abundance as well as the structure and distribution of endemic and forest populations are still unclear and may be considered as the next frontier to mitigate these effects and the most important challenge for their conservation in this decade (Souza et al. 2011; Mota et al. 2022).

As expected, the representativeness of forest areas within the established squares showed a positive relationship with the occupancy estimates of *C. canadensis*. This pattern is expected and found in other studies with birds from humid tropical forests (Lees and Peres 2010; Benchimol and Peres 2015; Morante-Filho et al. 2021). The conservation of forest fragments, even on a large scale,

is essential for their presence due to the specificity of *C. canadensis* due to its specific habitat requirements. The occupancy probability of the species is very low when associated with the forest area for a rate of 0.50 when there are about 20000 ha of forest. Morante-Filho et al. (2021) found similar results for *C. canadensis* in the southern portion of the São Francisco River, where 67.6% forest cover is required for a 60% occupancy probability. In this way, we emphasize the warning about the integrity and maintenance of forest landscapes, which must be a prerequisite for any strategy aimed at directing the target species of this study. Protecting and restoring forest fragments through the creation of conservation units represent the most promising measure for the persistence of the species, mainly for populations in the far north of the Atlantic Forest.

Finally, the positive effect of the altitude on the occupancy probability of *C. canadensis* is poorly understood. Anjos et al. (2022) found that the diversity of birds that occur in valley bottoms tends to be greater than in plateaus. The patterns found for *Caryothraustes sp.* in a study in the Amazon region agree with our findings. For canopy birds, evidence of occupancy of the genus more frequently in the hills than in the valleys is expected (Banks-Leite and Cintra 2008). Differently, our study can indicate an indirect effect of other environmental factors where topographic features are likely to lead to relevant microclimate variations for the bird in the hill-tops than on lowlands (Banks-Leite and Cintra 2008; Anderle et al. 2022). One of these may be related to differences between habitats, where higher areas would be more connected and preserved compared to lower elevations (Poulsen and Lambert 2000).

Temporal effects on detection

The linear trend of sampling effort over the years was the most important temporal covariate for detection. This indicates that for species with low detectability, the increase in data sampling enhances the chances of detection and, consequently, a better performance of the estimates. In Brazil, birdwatchers began to become popular in the last decade, which resulted in the acquisition of large amounts of data over large spatiotemporal scales (Klemann-Junior et al. 2017; Alexandrino et al. 2019; Tubelis 2023). The use of citizen science data was essential to closing gaps in knowledge about the occurrence and distribution of species studied and to improve the performance of occupancy models. If validated with traditional scientific references, this data contributes to biogeography knowledge and conservation policies by increasing the relevant number of records about the geographic areas where species occur (Klemann-Junior et al. 2017; Alexandrino et al. 2019; Tubelis 2023).

For rare species, it is common that, despite great efforts, few records are obtained due to their restricted distribution, low abundance, and low detection probability. The integration of

Academic and birdwatchers' efforts can be an important strategy to promote this biogeography knowledge (Alexandrino et al. 2019), but this requires conscious and ethical practices that guarantee the well-being of natural populations, especially about threatened species. For example, bird detections in the breeding season increased slightly, although they did not find relevant differences in estimates between sampling methods (Zamora-Marín et al. 2021). Targeting well-planned campaigns and initiatives at these key periods can be crucial to reducing biases due to low detection of threatened, endemic, and rare species. Although there is a growth in the use of occupancy models for application to conclusions or large-scale management strategies, the use of temporal factors and citizen science for birds is still quite restricted and deserves caveats. About the use of different sources and methods applied in the detections, we suggest that future studies better assess their influence, since the hypothesis lacks better clarification on the occupancy observed on the use of historical data and different sources.

CONCLUSIONS

This is the first published study to assess the role of multiple environmental factors in the historical large-scale occupancy of birds in the most threatened region of the Atlantic Forest, taking imperfect detection into account. We established reliable benchmark data on the *C. canadensis* distribution in the far north of the Atlantic Forest by modeling occupancy while accounting for species imperfect detection. This study also identified factors that limit species distributions in the northern portion of the Atlantic Forest, which environmental managers can then target to expand *C. canadensis* distribution and guide recovery of population and landscape elsewhere in the Atlantic Forest.

For canopy birds such as *C. canadensis*, strong differences between occupied and non-occupied areas may be related to forest area, which should be a proxy for the availability of microhabitat necessary for the species occurrence. We expected that the large-scale occupancy of *C. canadensis* would increase with the increase of the forest area per cell, but we also found the importance of the temperature for the canopy bird occupancy. Now, we need to understand to what extent the fragments in the northern portion of the Atlantic Forest can maintain their viable populations and sustain their abundance in these occupied sites. We emphasize that future strategies for the conservation of the studied birds must strongly integrate the maintenance of large areas with the recovery of microhabitats in the indicated places but consider whether they correspond to climatically suitable areas.

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Supplementary materials

Table S1. Results of environmental covariate dependency. (download)

Table S2. History detection of *Caryothraustes canadensis* based on occurrence data compiled between 1991–2020 across 204 grid cells delimited in the far north of the Atlantic Forest. (download)