# **RESEARCH ARTICLE**



# Landscape scale effects of primary productivity on forest bird species occurrence and abundance in Argentina

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## Abstract

*Context* Approaches estimating landscape effects on biodiversity frequently focus on a single extent, finding one 'optimal' extent, or use narrow extents. However, species perceive the environment in different ways, select habitat hierarchically, and respond to multiple selection pressures at extents that best predict each pressure.

*Objective* We aimed to assess multi-scale relationships between primary productivity and species occurrences and abundances.

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Centro Austral de Investigaciones Científicas (CADIC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Houssay 200 (9410), Ushuaia, Tierra del Fuego, Argentina *Methods* We used a multi-scale approach, called 'scalograms', to assess landscape level effects of primary productivity, in the form of Dynamic Habitat Indices (DHIs) on the occurrences and abundances of 100 Argentinian forest bird species. We used average DHI values within multiple extents  $(3 \times 3 \text{ to } 101 \times$ 101 pixels; 30 m resolution), and 11 'scalogram' metrics as environmental inputs in occurrence and abundance models.

*Results* Average cumulative DHI values in extents  $81 \times 81$  to  $101 \times 101$  pixels (5.9 – 9.2 km<sup>2</sup>) and maximum cumulative DHI across extents were in the top three predictors of species occurrences (included in models for 41% and 18% of species, respectively). Average cumulative DHI values in various extents contributed~1.6 times more predictive power to occurrence models than expected. For species abundances, average DHI values and scalogram measures were in the top three predictors for <2% of species and contributed less model predictive power than expected, regardless of DHI type (cumulative, minimum, variation).

*Conclusions* Argentinian forest bird occurrences, but not abundances, respond to high levels of primary productivity at multiple, broad extents rather than a single 'optimal' extent. Factors other than primary productivity appear to be more important for predicting abundance.

**Keywords** Avian abundance · Avian occurrence · Dynamic Habitat Indices · Landsat · Landscape effect · Scalograms · Spatial scale

## Introduction

Understanding the scales at which species respond to their environment is important for advancing knowledge about habitat and resource selection, patterns of species occurrence and abundance, biodiversity patterns, and informing conservation and management strategies. Spatial scale (extent and resolution) has varying, often complex effects on the relationships between landscape patterns and biodiversity metrics such as species richness (Bar-Massada et al. 2012). The spatial scale at which environmental variables are summarized can greatly influence our ecological inferences about biological responses (Pease 2024). Species perceive the environment in different ways and select habitat in a hierarchical manner (Johnson 1980; Wiens and Rotenberry 1981; McGarigal et al. 2016). Geographic ranges are at the broadest scales, while home ranges, patches within home ranges, and specific resources within patches are increasingly narrower (Johnson 1980). Given that species interact with their environment in different ways and that habitat selection is hierarchical, the spatial scales of landscape effects likely differ between species, the biological response of interest, and environmental variables (Miguet et al. 2016; Stuber and Fontaine 2019; Pease 2024).

Theoretically, the spatial extent of landscape effects on species' responses increases in the following order: fecundity, abundance, occurrence, richness, and genetic diversity (McGarigal et al. 2016; Miguet et al. 2016). Resource availability in a population's breeding habitat influences fecundity, thus the landscape should affect fecundity at a small spatial extent. Abundance is often influenced by both local (births and deaths) and broader-scale (immigration and emigration) processes (Miguet et al. 2016), while occurrence depends on even broader spatial scales, because it is controlled by extinction and colonization events (Cushman and Mcgarigal 2004; Jackson and Fahrig 2014; Miguet et al. 2016). However, the scaleeffect (sensu Jackson & Fahrig 2012) may not follow the theoretical order of increasing scale-effect from fecundity to genetic diversity (Martin 2018; Moraga et al. 2019), such as when the scale-effect of the landscape variable indirectly depends on the scale at which the variable affects another variable, and that other variable strongly influences the biological response (Miguet et al. 2016). For example, if a species responds to water quality, but water quality is affected at the watershed scale, then the expected scale-effect of water quality on the species should be the size of watershed.

In the past, attempts to model species-environment relationships focused on a single extent which may oversimplify species-environment relationships (Stuber and Fontaine 2019; Pease 2024) or miss important spatial scales in species-environment relationships (McGarigal et al. 2016; Moraga et al. 2019). More recently, multi-scale models are used to identify scale-effects (Gabriel et al. 2010; Moraga et al. 2019; Stuber and Fontaine 2019), and often perform better than single-scale models (Hallman and Robinson 2020; Bergerot et al. 2022; Silveira et al. 2023). Some multi-scale analyses have focused on a few extents identified a priori in pursuit of a single optimal extent (Miguet et al. 2016), which can result in underestimation or misidentified landscape scaleeffects (Jackson & Fahrig 2015). Additionally, the true scale-effect may be outside of the few extents analyzed (Jackson and Fahrig 2015).

Assessing species-environment relationships across multiple extents resolves the dilemma of selecting a single extent a priori, facilitates describing the shape of species-environment relationships, identifying potential change points, and identifying multiple important extents (Stuber and Fontaine 2019; Pease 2024). For example, the impact of organic farming on biodiversity (Gabriel et al. 2010), and effects of natural habitat amount on parasitoid abundance (Marins et al. 2024) have been described at multiple scales.

One challenge of multi-scale analyses, is associated with methods using multiple buffers (Holland et al. 2004; Jackson and Fahrig 2015). In multiple buffer (or 'threshold') methods, landscape variables are measured across multiple concentric circles of different radii. However, the landscape elements within a buffer implicitly have equal impact on the biological response regardless of distance from the response location (Miguet et al. 2017; Stuber and Fontaine 2019; Lowe et al. 2022). This is biologically unrealistic, as distant landscape elements should have less impact than closer elements, and the impact of a landscape variable should decline continuously away from a focal site (Miguet et al. 2017; Lowe et al. 2022). One approach to avoid the problems presented by multiple buffers, is distance-weighting. In distance-weighting, a weighting function is used to define how a landscape variable's influence declines continuously with distance from a focal site (Miguet et al. 2017; Lowe et al. 2022).

A second challenge of multi-scale studies is that measuring landscape variables at multiple spatial extents results in autocorrelation and collinearity between predictors across scales (Silveira et al. 2023). In multiple buffer methods, there are few suitable methods for dealing with the autocorrelation of nested buffers (Lowe et al. 2022). Distance-weighting methods can offer ways to deal with multiple buffer assumptions, however until recently, distanceweighted methods relied on a priori decisions about extent and range values (Miguet et al. 2017), required custom computer coding, or did not allow for models that account for possible spatial autocorrelation in residual errors (Carpentier & Martin 2021). One distance-weighted method, 'scalescape' recent (Lowe et al. 2022), improves upon existing distanceweighted methods by offering a use-friendly way to perform distance weighting, that can be used with multiple types of models, and includes models that can account for spatial autocorrelation (Lowe et al. 2022). 'Scalescape', while useful for assessing landscape scale effects on pollinators (Bernhardsson et al. 2024; Lowe et al. 2024) and parasitoids (Marins et al. 2024) when local variables and categorical land cover variables were used in regional contexts, has proven to be computationally intensive at national scales, with large datasets (1000 - 32,000 locations per species; >100 species), and with continuous landscape variables.

While distance-weighted methods may be better suited for multi-scales studies than multiple buffer methods, there are still some issues that need to be addressed. One approach that may bridge the gap between multiple buffer and distance-weighted methods is an adaptation of multiscale contextual spatial analysis (MCSPA). MCSPA is a multiscale pixelbased approach which summarizes the proportion of habitat found within increasing window sizes around each pixel, captures multiple extents simultaneously, and reflects the spatial context of each pixel in a landscape (Bar-Massada and Radeloff 2010). In MCSPA a scalogram is created (Fig. 1), which is a curve of changes in a response variable across nested scales (Frazier 2016; Sun et al. 2023; Zhang & Li 2013). The graph can be used to analyze the multiscale landscape patterns around pixels (Bar-Massada and Radeloff 2010).

Because the scalogram exhibits autocorrelation due to nested analysis extents, a third-order polynomial is fit, and the polynomial coefficients describe the spatial context (Bar-Massada and Radeloff 2010). The zero-order coefficient ( $\alpha_0$ ) relates to the landscape



**Fig. 1** The scalogram and the 1st derivative curves, measured from NDVI cumulative DHI (cDHI) at multiple spatial scales, for one focal pixel. On the scalogram curve five scalogram habitat measures are displayed: minimum, maximum and range of cumulative DHI values, and the extents at which cumulative DHI is minimum and maximum. Coefficient of variation, and intercept of cumulative DHI are not displayed. The first derivative curve shows the intercept of the 1st derivative, the 1.<sup>st</sup> derivative (maximum slope), and two critical points. X-axis = the size of the analysis window (size in pixels is above each scalogram point); y-axis = averaged cumulative DHI values (scalogram curve only)

variable value in the immediate neighborhood of the focal pixel. The first-order coefficient ( $\alpha_1$ ) defines the linear trend in increasing window sizes. The second-order coefficient ( $\alpha_2$ ) introduces a non-linear effect and denotes where the landscape variable values increase or decrease, allowing for inflection points (Bar-Massada & Radeloff 2010). The third-order coefficient ( $\alpha_3$ ) adds two more inflection points that describe situations where the landscape variable changes direction more than once (Bar-Massada & Radeloff 2010). While the scalogram averages the landscape variable in different extents, and thus assumes a constant effect within a given window, the fitting of a polynomial curve adds additional context beyond the constant effect within a window size.

MCSPA has only worked with categorical landscape variables, limiting its usefulness for assessing multi-scale species-environment relationships. Further, polynomial coefficients are not ecologically meaningful or easy to interpret (Silveira et al. in review). Recently, MCSPA has been modified to allow the use of continuous variables and to provide additional, ecological interpretable indices resulting from the scalograms (Silveira et al. in review). The ecologically interpretable measures are: the landscape value at the focal pixel, the minimum, maximum, range and coefficient of variation of landscape values among all extents, the extents at which the landscape variable is minimum and maximum, the maximum slope of the polynomial curve, how steep the slope is at the focal pixel, and two potential minimum or maximum points which provide information about major changes in the landscape variable. The modified approach is called 'scalograms' (Silveira et al. in review; Silveira et al. 2024), and was useful in explaining multi-scale relationships between primary productivity and abundances of several bird species and enhancing the performance of abundance models (Silveira et al. in review).

Spatial variation in global biodiversity gradients is explained by many forces including climate constraints (Santini et al. 2023), topography (McCain 2009; Perrigo et al. 2020), land cover (Basile et al.; 2021; Gábor et al. 2024) and land use (Newbold et al. 2015), and habitat structure (Gaston 2000; Willmer et al. 2022), however measures of energy, such as primary productivity, can better explain some biodiversity gradients (Gaston et al. 2000; Hawkins et al. 2003). Theoretically, areas of high productivity support more species and more individuals of species because these areas are associated with greater available energy in the form of food resources that can be partitioned among species than areas of low productivity (species-energy theory, or availableenergy theory; Hutchinson and MacArthur 1959; Wright 1983). The species energy theory is well supported. For example, primary productivity is positively associated with species distributions (Arenas-Castro et al. 2022), occurrences (Desrochers et al. 2010), abundances (Sarasola et al. 2008; Frixione & De Lamo 2017; Razenkova et al. 2023), densities (Santini et al. 2018), and species richness (Storch et al 2018; Di Cecco et al. 2022; Martínez-Núñez et al. 2023).

Vegetation productivity is easily captured in remotely sensed datasets (Pereira et al. 2013; Reddy, 2021), and many remotely sensed vegetation productivity indices are readily available for analyses. One such set of indices are the Dynamic Habitat Indices (DHIs), which summarize three measures of vegetation productivity (cumulative, minimum, and variation) over the course of a year (Mackey et al. 2004; Berry et al. 2007); useful indices of the energy available to organisms. DHIs are useful for understanding the species-primary productivity relationship, and support the species energy theory (Coops et al. 2009a, b; Michaud et al. 2014; Hobi et al. 2017; Radeloff et al. 2019; Suttidate et al. 2019). Species-primary productivity relationships are scale dependent, emerging at multiple spatial grains (Craven et al. 2022), but may be strongest at broader spatial scales (Storch et al. 2018). They may be stronger at broader spatial scales because the range of productivity is greater (Field et al. 2009; Cusen et al. 2012; Storch et al. 2018; Janousek et al. 2020).

Primary productivity has been strongly related to bird species occurrences worldwide (Pellissier et al. 2018; Dillon & Conway 2021; Arenas-Castro et al. 2022) and in Argentina (Pedrana et al. 2011; Apellaniz et al. 2012; Leveau et al. 2018; Micaela Rosas et al. 2023), but it's associations with abundances are less clear. Globally, primary productivity has inconsistently predicted species abundances (Santini et al. 2018, 2023), and in North America it has been positively (Mönkkönen et al. 2006), equivocally (Evans et.al 2006), and un-related to species abundances (Dobson et al. 2015). Similarly, in Argentina, primary productivity has been positively associated (Bellocq et al. 2011; Frixione & De Lamo 2017; Weyland et al. 2019), negatively associated (Haedo et al. 2017), and unrelated to bird species abundances (Calamari et al. 2018).

Species' traits play a role in their occupancy response to landscape elements, with larger-bodied and more mobile species responding at broader scales. Species' abundances may be lower in those with larger body mass, at higher trophic levels (Holland et al. 2004; Jackson and Fahrig 2015; Miguet et al. 2016; Pease 2024). In migratory species, precipitation and temperature may be associated with higher abundances (Santini et al. 2023), and climate may influence abundances of species with larger global ranges or smaller body mass as well (Howard et al. 2015).

We aimed to assess the multi-scale relationships between primary productivity derived from DHIs and bird species occurrence and abundance in Argentina, using scalograms (Silveira et al. in review; Silveira et al. 2024). Specifically, we wanted to 1) explore whether primary productivity is positively associated with probability of species occurrence and abundance, 2) to identify the spatial extents at which occurrence and abundance respond to primary productivity, and 3) to test the use of scalograms for characterizing multi-scale relationships. We analyzed these questions using a large, nation-wide dataset containing hundreds of species.

Following species-energy theory, we expected that high levels of primary productivity (high cumulative, high minimum, and low variation DHI; as well as maximum scalogram measures) would be associated with high probability of species occurrence and species abundances (our two measures of species response). Furthermore, if occurrence and abundance patterns behave according to the theoretical scale-effect of the landscape on species biological responses, we expected that DHI values at broader spatial extents would be more important for predicting species occurrences, while species' abundances would be more strongly predicted by DHI values at medium spatial extents (not the smallest nor broadest extents). However, for both occurrence and abundance, we expected that there would not be one single extent that was most important, and that the different DHIs (cumulative, variation, and minimum) may be influential at different extents. While the scalograms approach has been useful for explaining Page 5 of 22 68

the multi-scale relationships between environmental variables and abundance of three bird species in a small study area, it has not been tested with large datasets or across broad regions (Silveira et al. in review).

# Methods

## Study area

Our study area is the country of Argentina (Fig. 2), which  $covers \sim 2.8$  million  $km^2$  in southern South America, extending from 20° S to 60° S and 50° W to 80° W (Fig. 1). Argentina has many diverse climates and 15 terrestrial ecoregions (Burkart et al. 1999; Morello et al. 2012) due to the broad latitudinal and altitudinal gradients present in the country and the large ocean-to-land area that characterizes South America (Derguy et al. 2019). The northern part of the country is characterized by subtropical ecoregions while the southern part of the country has cold temperate to boreal systems, and altitudinally Argentina hosts sea level to nival regions (Derguy et al. 2019). Temperatures decrease from north to south, and there is a west-to-east precipitation gradient due to the topography of the Andes Mountains in the west and the flat lowlands of the east (Barros et al. 2015; Derguy et al. 2019).

## Data

# Bird data

We obtained bird occurrence data from the eBird Basic Dataset (eBird Basic Dataset 2023). eBird is a citizen science project, in which observers report observations of wild bird species from a single birding event. The list of observed birds is termed a 'checklist', and contains information about the number of individuals observed, the location, date, and time of observations, the type of survey, and measures of effort such as duration, number of observers, and distance traveled (Strimas-Mackey et al. 2023). eBird is semi-structured (Kelling et al. 2018), because it has flexible protocols that collect information on the observation process to allow for non-detections to be inferred (Strimas-Mackey et al. 2023).

Fig. 2 a Location of Argentina within South America. b Ecoregions of Argentina (Burkart et al. 1999; Morello et al. 2012): High Andes (HA), Andean-Patagonian forests (PAT), Mesopotamian grasslands (CAM), Humid Chaco (HC), Dry Chaco (DC), Delta and islands of Paraná River (DEL), Espinal forests (ESP), Patagonian steppe (PAS), Iberá Wetlands (IBW), Low Monte (LM), High Monte (HM), Pampas (PAM), Puna (PUN), Atlantic forests (AF), Yungas rainforests (YUN)



We downloaded data for all bird species occurring in Argentina from 2010–2022. We did not use eBird data from before 2010 because it did not launch globally until 2010 (Sullivan et al. 2014). We selected 2022 as our bird data endpoint so we would have 12 months of data for each year, as the full record for 2023 was not available at the time of our download.

We filtered the dataset to include only species which we considered to be forest affiliated. We used Birds of the World (Billerman et al. 2022), Avibase (Lepage et al. 2014; Lepage 2023), and AVONET (Tobias et al. 2022) to identify forest affiliated species. We utilized observations that were collected between August 1 of one year and March 31 of the following year, a period which encompasses when 94% of species of forest affiliated species (n=217) breed (Billerman et al. 2022). We excluded observations collected between April 1 and July 31 of the same year because we considered that to be the non-breeding period. We filtered our reduced dataset further, retaining complete, stationary or traveling checklists that were  $\leq 6$  h long,  $\leq 10$  km in length, speed  $\leq 100$ kmph, and had  $\leq 10$  observers because these thresholds reduce variation in detectability and effort in the context of eBird Status and Trends, and are recommended in 'Best Practices for using eBird Data' (Strimas-Mackey et al. 2023). By using these criteria, we imposed a more consistent structure on the data, and reduced variation in detectability and effort among eBird data (Strimas-Mackey et al. 2023).

Complete checklists are those in which an observer reports the counts of all individuals of each species they detected during their birding event. Because complete checklists include the number of individuals of all species observed, we can model a relative measure of abundance. We zero-filled checklistspecies matrices (i.e. assigned a count of zero) for checklists where a given species was not detected in a complete eBird checklist, allowing us to transform the data into detection/non-detection data (Strimas-Mackey et al. 2023). For each species we split the data into training and testing data (80% and 20% respectively).

We then subsampled the data to further reduce spatial and temporal biases. We spatially and temporally subsampled detections and non-detections separately within a  $3 \times 3$  km grid, randomly selecting one detection and one non-detection checklist from each grid cell for each week. We utilized a  $3 \times 3$  km grid because it has been sufficient to account for the spatial precision in eBird data when travelling counts are  $\leq 10$  km (Strimas-Mackey et al. 2023). eBird checklists provide a single latitude/longitude location, however, the location may not match that of a particularly observed bird because birds and observers may not overlap in space if the bird was detected at a distance, the location is considered a 'hotspot', or if the observer surveys an area while travelling rather than remaining stationary. 'Hotspots' are public locations used to aggregate data in eBird, which correspond to an area such as a park. If the hotspot coordinates are the park center and an observation is made at the park edge then the observation has spatial imprecision. Approximately 94% of checklists with a maximum distance travelled  $\leq 10$  km, are contained within a 1.5 km circle and 74% have a location error  $\leq$  500 m (Strimas-Mackey et al. 2023).

Spatial subsampling as outlined above, reduces spatial bias that occurs due to participants surveying near their homes (Luck et al. 2004), in easily accessible locations (Kadmon et al. 2004), or in areas known to have species of interest (Prendergast et al. 1993). Temporal subsampling reduces biases such as participants preferentially sampling when they are available (Courter et al. 2013), or at times when more birds may be observed (Sullivan et al. 2014). The spatial and temporal subsampling also increases the prevalence of occurrences in our data, which reduced class imbalances (Robinson et al. 2018). When classes are imbalanced (many non-detections and few detections), models which predict that a species is absent everywhere will have high accuracy but will be ecologically uninformative (Strimas-Mackey et al. 2023). While we reduced biases in the data prior to modelling, we further accounted for the observation process by including effort variables in our models, described in the 'Analysis' section below.

We conducted all eBird data preparations outlined above using the 'auk' (Strimas-Mackey et al. 2018) and 'ebirdst' packages (Strimas-Mackey et al. 2022) in R (R Core Team 2023). After the preparation above, we retained species with a minimum of 1000 occurrence records in the final dataset (n=124)species; Online Resource 1). While the spatial and temporal subsampling of the data reduced class imbalances (Robinson et al. 2018), we used 1000 occurrences as our cut-off because species distribution model accuracy tends to increase with the number of presences in the training set and we felt 1000 occurrences provided a good balance between species' sample sizes, data prevalence, and a sufficiently large list of species for analyses (Wisz et al. 2008; Fukuda and De Baets 2016; Liu et al. 2019).

## Environmental data

We used three composite dynamic habitat indices (DHIs; Berry et al. 2007; Coops et al. 2009a, b) representing median conditions from 2010 to 2022; cumulative, variation, and minimum, that we calculated from Normalized Difference Vegetation Index (NDVI; 30 m resolution) as landscape variables in our analyses. We used NDVI-based DHIs because NDVI is solely derived from reflectance measures (as is the case for gross primary productivity-based

DHIs, which risks error propagation), it provides values in low productivity environments where other vegetation measures are not estimated and set to 0, and there is a larger range of variability in minimum values (Radeloff et al. 2019). We chose the DHIs over other primary productivity measures because they provide integrated measures of primary productivity that directly relate to different aspects of the species-energy relationships (Radeloff et al. 2019). Of the three DHIs, cumulative DHI reflects the productive capacity of a landscape across a year, and higher levels of cumulative primary productivity should support more species or more individuals (Coops et al. 2009a, b). Variation DHI reflects primary productivity seasonality within a year. Areas with less seasonality in primary productivity should support more species or individuals than areas which are more seasonal (Hurlbert and Haskell 2003; Rahbek et al. 2007). Minimum DHI reflects the lowest primary productivity levels in a year, capturing periods of low resources or environmental stress. High minimum productivity should support more species or individuals because energy availability remains high (Schwartz et al. 2006).

The three DHIs were calculated for the entire country of Argentina plus a buffer of 200 km around the country's border (Online Resource 2). We included this buffer to capture broad-scale landscape scale effects around bird occurrence points near the border of Argentina. To create the three DHIs we first selected the highest NDVI Landsat value (available in Google Earth Engine-GEE: Gorelick et al. 2017) in each month of each year from 2010 to 2022. Because Landsat has a return interval of 16 days, and cloud cover can affect image quality, monthly image acquisitions for a given pixel are often sparse. Thus, we selected the highest NDVI value because that represented the maximum level of productivity, and thus energy available to organisms in that month. We aggregated the monthly values over all years, and then selected the median monthly values to generate a composite monthly time series. To generate the final cumulative DHI we summed the monthly time series values. To generate the minimum DHI we selected the minimum monthly time series value. To generate the variation DHI we calculated the coefficient of variation of the monthly time series values. We set pixels classified as snow (zero productivity) to zero. We scaled the three DHIs from 0 to 100%.

## Scalogram habitat measures

We used scalogram habitat measures as environmental inputs in our occurrence and abundance models. We calculated scalogram habitat measures centered on the focal pixel, i.e. the pixel containing each eBird checklist in our testing and training datasets (after cleaning, filtering, and subsampling the eBird data) using the following procedure. We first computed minimum, cumulative, and variation DHIs at multiple spatial extents. To do so, we used moving windows centered on a focal pixel ranging from  $3 \times 3$  to  $101 \times$ 101 pixels  $(3 \times 3, 5 \times 5, 7 \times 7, 9 \times 9, 11 \times 11, 21 \times 21, 100)$  $31 \times 31, 41 \times 41, 51 \times 51, 61 \times 61, 71 \times 71, 81 \times 81,$  $91 \times 91$ ,  $101 \times 101$  pixels) corresponding to windows ranging from 0.0081 km<sup>2</sup> to 9.18 km<sup>2</sup>, to calculate the average minimum, cumulative, and variation DHIs within each extent, across the entire study area. The corresponding window lengths were: 90 m, 150 m, 210 m, 270 m, 330 m, 630 m, 930 m, 1230 m, 1530 m, 1830 m, 2130 m, 2430 m, 2730 m, 3030 m. Pearson's correlations between average DHI values within extents can be found in Figure 1 of Online Resource 3. After calculating the DHI values within each window, we generated scalograms for each DHI by plotting the average DHI values against the size of the analysis window around each focal pixel (Fig. 1; Online Resource 4).

scalograms were plotted, we fitted After polynomial curves and calculated seven measures based on the fitted curve (Fig. 1). Measures derived from the fitted polynomial curve are: the intercept (the value at the focal pixel), minimum, maximum, range, and coefficient of variation of landscape variable among all extents, and the extents at which the landscape variable has minimum and maximum values. The measures derived from the fitted polynomial curve describe two general aspects about the landscape variable. The intercept, minimum, maximum, range, and coefficient of variation provide information on how the variable changes in relation to focal pixel changes across the full range of extents. The minimum and maximum extent describe at which extents the variable is at its minimum or maximum values.

In addition to the seven measures calculated from the fitted curves, we calculated the 1st derivative of the polynomial curve to obtain four more measures, which characterize how rapidly the landscape variable changes as extent changes (Fig. 1). Measures derived from the 1st derivative of the polynomial curve are: the first derivative (maximum slope of the polynomial curve), the intercept of the first derivative (how steep the slope is at the focal pixel), and the first and second critical points of the first derivative (the extents at which the first derivative is 0, potential minimum or maximum, information about major changes in the landscape variable). The measures derived from the 1st derivative capture how rapidly the landscape variable changes as analysis extent size changes. Throughout the manuscript we call this collection of 11 measures 'scalogram habitat measures' (descriptions can be found in Online Resource 5; Silveira et al. 2024). Pearson's correlations between the scalogram habitat measures for each DHI can be found in Figure 2 of Online Resource 3, and correlations between scalogram habitat measures and average DHI values within extents can be found in Figures. 3–5 in Online Resource 3.

## Analysis

To model relative species abundance, we used a twostep hurdle model, following Strimas-Mackey et al. (2023) and Keyser et al. (2023), in which we estimated encounter rates (hereafter called 'occurrence') in the first step, and then estimated the expected count of individuals on eBird checklists where the species was detected in the second step (hereafter called 'abundance models'). With eBird data we cannot estimate absolute detectability, but by accounting for variation in detectability by including effort variables in our models, unaccounted detectability is more consistent across sites (Guiller-Arroita et al. 2015). Therefore, our estimated encounter rates are proportional to occupancy, but at a consistently lower value (Strimas-Mackey et al. 2023). Similarly, abundance models produce estimates of relative abundance, i.e. an index of the counts of individuals present in the search area, because the models account for variation in detection rates but do not directly estimate the absolute detection probability (Strimas-Mackey et al. 2023). In both steps of this hurdle model, we used a random forest algorithm, implemented with the 'ranger' package in R (Wright and Ziegler 2017). We describe the first step of the hurdle model in the 'occurrence models' section, and the second step of the hurdle model in the 'abundance models' section, below. Detailed instructions on eBird occurrence and abundance model fitting in R can be found in Strimas-Mackey et al. (2023).

# Occurrence models

In our occurrence models, we used a balanced random forest approach to relate species detections and nondetections to average DHI values within each extent  $(3 \times 3 \text{ to } 101 \times 101 \text{ pixels})$ , 11 scalogram habitat measures, and effort covariates. Our seven effort variables (checklist duration, distance traveled, speed during observation period, number of observers, day of year, hour of day, year; Online Resource 5) were included to account for variation in detectability and observer effort. The response variable was binary (species observed; 1 or 0). We used a balanced random forest approach because while we partially addressed class imbalances in our data with the spatial and temporal subsampling described in the 'Bird data' section of our Methods, there were still many more non-detections than detections. With the balanced random forest approach the model grows each tree based on a random sample of the data that has an equal number of detections and non-detections, using a bootstrap sample, and predicts probabilities instead of the most probable class. To do this we specified that the model sample all detections (the rarer class), and an equally sized, randomly-selected subset of the non-detections (the common class).

Because the predicted probabilities from the initial balanced random forest models do not always align well with the observed detection frequencies (Strimas-Mackey et al. 2023), we trained calibration models as a diagnostic tool to better understand the predictions from our models. To conduct a calibration of the continuous predictions from our random forest models, we fitted a binomial generalized additive model that was constrained to increase monotonically, with the observed occurrence as the response and the continuous occurrence probability as the predictor. We visually verified that the relative ranking of predictions was generally good by plotting observed encounter rates against estimated encounter rates and seeing where points fell relative to an x = y line (calibration plots can be found in Online Resource 6), such that sites with estimated higher encounter rates generally have higher observed encounter rates (Strimas-Mackey et al. 2023). We assessed calibration model performance, which produced continuous occurrence probabilities, with mean square error (MSE) as a measure of the differences between estimated and true values, root mean square error (RMSE). In the context of continuous probability of species occurrences, which range from zero to one, we expected good MSE and RMSE scores to be numbers close to zero. Calibration model performance metrics can be found in Table 1 of Online Resource 7.

After checking that our initial estimated probabilities of occurrences align with observed occurrences using the calibration process, we used thresholding to reclassify the continuous probabilities to binary presence/absence before further assessing model performance. We reclassified the continuous probability of occurrence into binary presence/ absence because our abundance models (described in the next section) are conditioned on the species being present at a location. Because eBird data is class-imbalanced, we used the MCC-F1 curve to set the threshold for each species (Strimas-Mackey et al. 2023) because traditional thresholding methods (ex: Kappa statistic, area under the receiveroperator curve) can over-weight the common class (Cao et al. 2020). This method plots the Matthews correlation coefficient against the F1 score for a range of thresholds, and the threshold where the curve is closest to the point of perfect performance is selected (Strimas-Mackey et al. 2023). We assessed binary occurrence model quality using our testing data and the following performance metrics: area under the precision-recall curve (prAUC), Matthew's correlation coefficient (MCC; also known as phi or mean square contingency coefficient), and F1 score (Strimas-Mackey et al. 2023). We used prAUC instead of area under the receiver operating characteristic curve (AUC-ROC) because classimbalanced data impacts the interpretation of measures like AUC-ROC that incorporate the true negative rate. Precision-recall AUC varies on a scale from zero to one, with scores greater than the prevalence of presences in the dataset indicating better than random performance (Boyd et al. 2012; Sofaer et al. 2019). We considered models with prAUC values that were 0.1 greater than prevalence to be better than random, however higher values are better as they represent the trade-off between false negative and false positive classifications in imbalanced datasets. MCC is a balanced measure that can be used with class imbalanced data and is a correlation coefficient between the observed and predicted binary classifications, measured on a -1 to 1 scale (1 = perfect prediction, 0 = random)-1 = total disagreement). We considered models with MCC  $\geq 0.3$  to have suitable performance. F1 is the harmonic mean of precision and recall, with 1 indicating perfect precision and recall, and 0 indicating a complete lack of precision and recall. We prioritized evaluating model performance with prAUC and MCC over F1 because prAUC can be adjusted for class imbalances while F1 cannot (Boyd et al. 2012; Sofaer et al. 2019), and MCC is more reliable than F1 (Chicco & Jurman 2020, 2023). Occurrence model performance metrics can be found in Table 2 of Online Resource 7.

# Abundance models

Our relative abundance models are an extension of our occurrence models. We first trained regression random forests models to estimate the expected count of individuals on eBird checklists where a species was detected or predicted to be detected by our occurrence models. Observation count was the response variable in our abundance models, and the predictors were effort variables, average DHI values in each extent, scalogram metrics, and predicted occurrence (Online Resource 5). We included predicted occurrence because it improves the predictive performance of abundance models (Johnson et al. 2015; Fink et al. 2020; Strimas-Mackey et al. 2023; Keyser et al. 2023). Conditioning the prediction of expected counts on occurrence helps account for the high number of zero counts when modelling abundance over broad extents (Johnston et al. 2015). High numbers of zero counts can be generated from observations in unsuitable habitat, when individuals were present but not detected, or when individuals were not present and not detected (Johnson et al. 2015). Thus, in the first step of the two-step hurdle model (described in the 'occurrence model' section above), the occurrence model distinguishes between suitable and unsuitable habitat. In the second step, the abundance models estimate the expected count on checklists within suitable habitat locations identified in the first step, thereby reducing the number of zero counts in unsuitable habitats (Johnson et al. 2015).

After estimating the expected count, we produced an estimate of relative abundance by multiplying the predicted occurrence probability by the expected count. We consider this to be an estimate of relative abundance (an index of the count of individuals present in the search area of an observer) because we cannot directly estimate absolute detection probabilities from eBird data. We assessed count and abundance predictions using our testing data and mean squared error (MSE), root mean square error (RMSE), Spearman's rank correlation coefficient and Pearson correlation coefficient (Strimas-Mackey et al. 2023). We considered correlations < 0.2 to be very weak, 0.2 to 0.39 to be weak, 0.4 - 0.59 to be moderate, and  $\geq 0.6$  to be strong. Spearman's correlations assess the ability of the model to estimate the rank order of counts or abundances. Pearson correlations assess the ability to estimate counts or abundances on the log scale, which is beneficial when dealing with data spanning a large range of values, such as flocking species with high counts. Correlation on counts measure within-range performance, such that observed and estimated counts are compared for locations in which the species was predicted to occur. Correlations on relative abundance assesses predictive performance based on all locations and not just where a species was predicted to occur. We interpreted MSE and RMSE in the context of species count, such that smaller numbers that are closer to zero are better. Most observations consist of counts of zero or very few individuals therefore we expected a good prediction would have MSE and RMSE values close to zero. Abundance model performance metrics can be found in Table 3 of Online Resource 7.

#### Variable importance

For both occurrence and abundance models, we used predictor importance (average Gini index), and partial dependence to identify associations between predictors and our dependent variables (either occurrence or species abundance). We standardized predictor importance scores to compare among species by calculating the proportion of the total scores contributed by each predictor (Keyser et al. 2023). We used partial dependence plots to estimate the marginal effect of a single predictor on the dependent variable when all others were held constant, to identify the direction and magnitude of effect that each predictor had on the dependent variable (either occurrence or species abundance). To estimate the directionality (positive or negative) of each predictor's effect on the dependent variable, we fit simple linear models to the partial dependence plots and extracted the beta coefficient (Keyser et al. 2023).

# Results

# Model validation

We considered 100 species to have suitable occurrence models; these had an average prAUC of 0.26 (sd=0.1), a difference between prAUC and prevalence of 0.21 (sd=0.08), MCC of 0.44 (sd 0.07), and an F1 value of 0.46 (sd=0.09) (Online resource 7). Calibrated occurrence models, which we used to validate our original random forest models before thresholding, had an average MSE of 0.03 (sd=0.03), and an RMSE of 0.16 (sd=0.07; Online resource 7).

On average, resulting abundance models had Spearman correlations of 0.37 (sd=0.08) for counts, and 0.39 (sd=0.07) for relative abundance (Online resource 7). Pearson's correlations for counts were on average 0.41 (sd=0.08), and for relative abundance 0.43 (sd=0.08). Average MSE for counts was 24.73 (sd=83.48) and for abundances was 2.98 (sd=9.65), while count RMSE was 3.3 (sd=3.84) and abundance RMSE was 1 (sd=1.41; Online resource 7).

## Effort variables

In occurrence models, four of our seven effort variables (day of year, checklist distance, checklist duration, and hour of day) were important for predicting occurrences of some species (Fig. 3). In particular, checklist duration was within the top three predictors for 45% of species and was positively associated with predicted occurrences. Hour of day was also important for 22% of species and was mainly negatively associated with predicted occurrences. Day of year and checklist distance were in the top three predictors for 9% and 10% of species respectively. Checklist speed was important for 7% of species. In occurrence models, effort variables explained  $\sim 1.3$  times more predictive power than expected if all



Fig. 3 Magnitude and direction of responses of predicted bird species occurrence and relative abundance to the top three most important variables in the predictive models. Magnitude, on the x-axis, is represented by proportional variable importance values (scale -1 to +1), and direction of response is based on the beta coefficient for a given variable in a univariate model of the probability of occurrence as a function of the explanatory variable. Positive relationships are shown in orange and negative relationships are shown in blue, and the center of the plot is 0. The number of species that respond to a variable is captured by the number of bars (y-axis). Each bar represents the response of one species to a variable. More bars indicate that a variable was in the top three most important variables for many species. Cumulative, minimum, and variation DHIs are abbreviated to cDHI, mDHI, and vDHI respectively. a predicted occurrence responses (from occurrence models), and b predicted species' abundance response (from abundance models)

variables contributed to model predictive power equally (Fig. 4).

In models of relative abundance, four of our seven effort variables were important for predicting relative abundance for many species, however predicted occurrence was by far the most important (Fig. 3), and was in the top three predictors of relative abundance for 98% of species. Day of year was important for predicting relative abundance of 30% species, and had more negative associations than positive associations with relative abundance. Checklist distance was important for 14% of species and was positively associated with relative abundance. Checklist duration was important for 71% of species and was positively associated with relative abundance. Year was only important for five species (5%) and was negatively associated with relative abundance. Hour of day was important for 64% of species and was mainly negatively associated with relative abundance. Effort variables and predicted occurrence explained 2.9 times and 10.4 times more predictive power in models than expected if all variables contributed to model predictive power equally (Fig. 4).

#### Scalogram habitat measures

Of the 33 possible scalogram habitat measures (11 measures for each of three DHIs) included in occurrence models, only four were important for predicting many species occurrences: variation DHI minimum value, variation DHI range, minimum DHI maximum value, and cumulative DHI maximum value (Fig. 3). Cumulative DHI maximum value was

in the top three predictors for 18% of species and had a positive relationship with predicted occurrence for > 70% of species. Variation DHI minimum value was in the top three predictors for six species (6%), and had a negative relationship with occurrences of three species, and a positive relationship with occurrences of three species. Variation DHI range was in the top three predictors for eight species, having a negative relationship with occurrences of two species, and a positive relationship with occurrence of six species. Minimum DHI maximum value was important for seven species, being negatively associated with occurrences of one species and positively associated with occurrences of six species. In occurrence models, scalogram habitat measures contributed less than expected to model predictive power (Fig. 4).

Scalogram habitat measures were not important in our abundance models (Fig. 3) and were only in the top three predictors for < 2% of species each. Scalogram measures also explained less variation in abundance models than expected (Fig. 4).

#### Spatial extents

We found that cumulative primary productivity (cumulative DHI) was generally important in species occurrence models and was positively related to the predicted occurrence of species. Average cumulative DHI values within any extent were in the top three predictors for 51% of species and had positive relationships with predicted occurrence for >70% of species (Fig. 3). We found that cumulative DHI values at broad spatial extents were particularly important and that cumulative DHI values within extents  $81 \times 81$  pixels (5.90 km<sup>2</sup>),  $91 \times 91$  pixels (7.45  $km^2$ ), and  $101 \times 101$  pixels (9.18  $km^2$ ) were in the top three predictors in occurrence models for 18%, 23%, and 37% of species respectively, and were positively related to occurrences of 93% of species (Fig. 3). Cumulative DHI within our smallest analysis extent  $(3 \times 3 \text{ pixels}; 0.01 \text{ km}^2)$  and the  $7 \times 7 \text{ pixel extent}$  $(0.04 \text{ km}^2)$  were never in the top three predictors for any species, while cumulative DHI within the 5  $\times$  5 pixel extent (0.02 km<sup>2</sup>) was important for one species. As a group, cumulative DHI values within extents explained~1.6 times more variation within occurrence models than expected (Fig. 4).



◄Fig. 4 Violin plots and boxplots showing the relative variable importance scores for grouped effort variables, DHI scalogram metrics, and DHI values at various extents for the 100 bird species, in (a) occurrence models, and (b) abundance models. Outliers are represented by black dots. Dashed horizontal lines indicate the expected variable importance value of the variable group (ex: all seven effort variables) if all variables (seven effort +33 scalograms +42 extents) in the model contributed an equal amount of variable importance (i.e. 100%). Model predictive power is represented by relative variable importance scores, which is the quotient of the importance value of an individual variable divided by the sum of all importance values for all variables in the model

High minimum levels of primary productivity (minimum DHI) was important in fewer occurrence models than cumulative primary productivity. Average minimum DHI at various extents were among the top three predictors of probability of occurrence for 16% of species, and mainly had a positive relationship with species occurrences (Fig. 3). Minimum DHI values at various extents contributed approximately the expected amount of predictive power in occurrence models (Fig. 4). As with cumulative DHI, minimum DHI values at broad extents— $81 \times 81$  pixels (5.90 km<sup>2</sup>),  $91 \times 91$ pixels (7.45 km<sup>2</sup>), and  $101 \times 101$  pixels (9.18 km<sup>2</sup>) were important for more species (7%, 7%, and 6% respectively) than minimum DHI within smaller extents.

Low variation in primary productivity (variation DHI) was important for predicting occurrences of fewer species than cumulative and minimum primary productivity, with average variation DHI values in various extents being included in the top three predictors of occurrence for 8% of species. Variation DHI values in  $71 \times 71$  (4.54 km<sup>2</sup>),  $81 \times 81$  pixels  $(5.90 \text{ km}^2)$ ,  $91 \times 91$  pixels  $(7.45 \text{ km}^2)$ , and  $101 \times 101$ pixels  $(9.18 \text{ km}^2)$  extents were in the top three predictors for the occurrence  $\leq 6\%$  of species for each extent. For species in which variation DHI values in extents  $\geq$  71 × 71 pixels were important in occurrence models, occurrence was mainly negatively associated with variation DHI (Fig. 3). Variation DHI values contributed approximately the expected amount of predictive power in occurrence models (Fig. 4).

Species abundances were not explained well by any DHI values within the analysis extents; DHI within various extents and scalogram measures were in the top three predictors for < 2% of species each (Fig. 3). When we considered which extents were important for predicting these species abundances, cumulative DHI values in  $101 \times 101$  pixel extent (9.18 km<sup>2</sup>), and variation DHI within 5 × 5 pixels (0.02 km<sup>2</sup>), and 91 × 91 (7.45 km<sup>2</sup>) pixel extents were important for only one species each (1% of modelled species). DHI values within extents explained less variation in abundance models than expected (Fig. 4).

# Discussion

In this study we examined the usefulness of scalogram-based metrics describing primary productivity in a nested set of spatial extents for predicting two aspects of forest bird populations, occurrence and abundance. These metrics identify the spatial extents at which primary productivity influences bird spatial patterns, while avoiding conflation with spatial autocorrelation. We found that high levels of primary productivity supported greater probability of species occurrence but not abundance, and that species occurrences responded to primary productivity at multiple broad spatial extents. We found limited support for the idea that species respond at different scales to different environmental variables, and that occurrence responds at broader scales than abundance, however we only explored different facets of primary productivity, and our abundance models did not predict relative abundance well.

We expected that high levels of primary productivity would support many species and many individuals, however we found that only higher probability of occurrence (i.e., many species) was associated with high primary productivity. Most species responded to cumulative primary productivity, rather than to minimum levels or variation in primary productivity. When species occurrences were influenced by minimum primary productivity or variation in primary productivity they were associated with high levels of minimum productivity and low levels of variation. This finding is in line with expectations that as productivity increases in an area (e.g. annual and minimum productivity), that area should support more species, and that one is more likely to encounter a species in areas with high productivity (Currie et al. 2004; Radeloff et al. 2019). Occupancy of most forest birds in Argentina was not strongly tied to variation in primary productivity, but when it was, they were responding positively to low variation in productivity (i.e. more stable environments), which is in line with findings that areas with stable primary productivity across the annual cycle can support more species (Rahbek et al. 2007; Williams and Middleton 2008; Radeloff et al. 2019).

When we considered at which spatial extents species occurrences responded to primary productivity, we found it responded at broad spatial extents, but that there was not a single characteristic extent at which occurrences responded to primary productivity. Cumulative DHI values at broad extents ( $\geq$  81 × 81 pixels; 5.90 km<sup>2</sup>) were important predictors in 40% of species occurrence models, and minimum and variation DHIs values within extents  $\geq 81 \times 81$  (5.90 km<sup>2</sup>) and  $\geq 71 \times 71$  (4.54 km<sup>2</sup>) were important for fewer species. This suggests that after accounting for observer effort, high cumulative and minimum primary productivity (i.e. available energy), and low variation in primary productivity, at broader spatial extents is important for predicting forest bird species occupancy across Argentina. The finding that primary productivity at multiple broad extents was important in predicting species occurrences supports the idea that species respond to environmental variables at multiple scales because species select habitat in a hierarchical manner (Wiens and Rotenberry 1981; McGarigal et al. 2016).

Our findings that species occurrences responded to primary productivity also align with findings from other areas, where species-primary productivity relationships are scale-dependent, and are stronger at broader spatial extents than at smaller spatial extents (Desrochers et al. 2010; Storch et al 2018; Di Cecco et al. 2022). We expected that our analysis extents encompassed areas orders of magnitude larger than territory sizes of the vast majority of birds we studied, which would be sufficient to assess broad-scale habitat selection. While we did not identify territory sizes of each species we studied, territory size estimates from birds in the same genera, similar habitats, or with similar traits as those we studied are generally < 0.2km<sup>2</sup> (Stouffer 2007; Kikuchi 2009; Ribon & Marini 2016; Guppy et al. 2023; Zammarelli et al. 2024). However, we realize that our largest analyzed extent  $(9.2 \text{ km}^2)$  However, we realize that our largest analyzed extent (9.2 km2) may not have fully encompassed areas used by some species, particularly for those that are area sensitive. For example, in other regions species responded to areas as small as 0.03  $km^2$  or as large as 1809  $km^2$  (Dardanelli et al. 2006; Desrochers et al. 2010; Shake et al. 2012; Anderle et al. 2022). However, area sensitivity often responds to patch or habitat size and not necessarily to primary productivity variation within the patch, and further, not all species are area sensitive. In North America, bird species richness and primary productivity were more strongly related at broad extents ( $\sim 25 \text{ km}^2$ ) than small extents ( $<1 \text{ km}^2$ ; Di Cecco et al. 2022). Even at the very broad extent of 12,364 km<sup>2</sup>, primary productivity influenced species richness (Hurlbert and Jetz 2010). Thus, evidence from the literature suggests that we could greatly increase analysis window sizes and still find relationships with primary productivity. However, species richness and species occurrence, while related (a species must be present at a site to contribute to richness), may have different relationships with primary productivity. Species richness overlooks species-specific responses, and areas with similar species richness may have different species compositions.

We found little support for the idea that species respond to different environmental variables at different scales. Species occurrences were explained by all three DHIs (variation, minimum, cumulative) at extents  $\geq$  71 × 71 pixels (4.54 km<sup>2</sup>), but were most strongly influenced by cumulative DHI. The three DHIs characterize different aspects of the same phenomena – primary productivity, and thus likely exert similar selective pressures on species. We may have found different responses at a variety of scales if we had included variables capturing other important habitat characteristics such as temperature, habitat heterogeneity, or topography.

While we found that occurrence responded to primary productivity at broad extents, following our expectations, we did not find that abundance responded to primary productivity at any extent, which was counter to our expectations. We expected that primary productivity would be a good predictor of bird species abundances in Argentina because climate predictors such as rainfall, while important, are often indirect influences on birds in Argentina through effects on resources such as vegetation productivity, fruit abundance (Mendoza et al. 2017), or arthropod abundance (Pinheiro et al. 2002; Jahn et al. 2010; Mendoza and Araujo 2022). Additionally, while climate explained ~97% of variance in primary productivity globally, primary productivity was more important in explaining global community trophic structures of birds when combined with climate (Mendoza and Araujo 2022). It is likely that we didn't find strong support because our abundance model performance was low. Our abundance models were weakly to moderately able to rank the order of relative abundance at all locations and had moderate to weak ability to rank estimated counts in line with observed counts at locations where species were predicted to occur. Abundance models further had a moderate ability to estimate relative abundance on a log scale, indicating they did not model abundances of flocking species well.

Globally (Santini et al. 2018, 2023), and regionally (Mönkkönen et al. 2006; Evans et al. 2006; Dobson et al. 2015) primary productivity has been an inconsistent predictor of bird species abundances while precipitation (Williams et al. 2008; Niedziałlkowska et al. 2010; McCain et al. 2018; Yapu-Alcazar and Naoki 2022) and temperature (Ralph 1985; Githaiga-Mwicigi et al. 2002; de la Fuente et al. 2023) have been positively related to abundances. In Argentina, primary productivity has been associated with increases (Frixione & De Lamo 2017; Haedo et al. 2017; Weyland et al. 2019) and decreases (Haedo et al. 2017) in abundance for bird species, but sometimes climate or land use were more important (Sarasola et al. 2008; Bellocq et al. 2011; Calamari et al. 2018). Approximately 60% of the species we analyzed were insectivores, 32% of which were in Tyrannidae, a family which may have stronger correlations with precipitation and temperature than to primary productivity in South America (MacPherson et al. 2018). Other factors such as resource limitation or patchiness, population density, competition, reproduction, dispersal, and behavioral or social constraints may affect abundance as well (Nielsen et al. 2005). Some of the species we modelled rely on habitat features not directly related to primary productivity. For example, woodpeckers, parrots, and a handful of other species included in our study rely on cavities in large mature, or dead trees for nesting (Politi et al. 2009; Rivera et al. 2022).

The lack of landscape scale effect of DHIs on abundance may also have occurred if the location imprecision of eBird data masked the effects. More than 95% of eBird checklists with a 10 km distance cutoff (as used in this study) are contained within a 1.5 km radius circle, and ~75% are contained within a 0.5 km radius circle (Strimas-Mackey et al. 2023). A 1.5 km radius circle (7.1 km<sup>2</sup>) is smaller than our two largest extents  $(91 \times 91 \text{ and } 101 \times 101 \text{ pixels})$ ; 7.45  $\text{km}^2$  and 9.18  $\text{km}^2$ ), while a 0.5 km radius circle (0.79 km<sup>2</sup>) is smaller than all extents  $\geq$  31  $\times$  31 pixels (0.86 km<sup>2</sup>). Thus, any extent  $\geq$  31  $\times$  31 pixels should encompass the area surveyed by  $\sim 75\%$ of checklists. We expected DHI landscape level effects on abundance to have been revealed at these intermediate extents, in line with the theory that landscape level effects on abundance should appear at intermediate spatial extents (broader than effects on fecundity but less broad than effects on occurrence; Miguet et al. 2016).

There are numerous ways to assess landscape scale effects of environmental variables on species biological responses, and landscape scale effects may operate differently across different extents, biological responses, and environmental variables. We used a recently developed multi-scale approach, scalograms, to model landscape scale effects of primary productivity on two different biological responses, bird species occurrence and abundance. Scalograms can be utilized with a variety of environmental variables and in a variety of modelling frameworks, but variable correlations should be considered, particularly in modelling frameworks which are sensitive to highly correlated variables. Primary productivity values calculated within various extents, and several scalogram habitat metrics were useful for predicting bird species occurrences but not abundances. The scalogram approach (Silveira et al. in review), which has been applied to small sets of point count data previously (Silveira et al. in review), was easily applied to a large, nation-wide, semi-structured dataset. Scalograms are a promising new approach in the toolbox of techniques for understanding landscape level effects of a variety of environmental and habitat conditions on biodiversity, across multiple scales simultaneously, while accounting for spatial autocorrelation. The identification of the most relevant environmental or habitat characteristics that predict species occurrences or abundances, and the scales at which they act, are important for developing and implementing conservation actions that best protect biodiversity.

Author contributions Ashley M. Olah performed data analysis and led the writing. Natalia Politi, Guillermo Martínez Pastur, and Luis Rivera contributed expert knowledge for identifying forest affiliated bird species. Anna M. Pidgeon and Volker C. Radeloff supervised the project and obtained funding. Akash Anand and Eduarda M. O. Silveira produced the 'scalograms' package and assisted with package troubleshooting and parallelization. Eduarda M. O. Silveira processed Landsat DHIs for use in analyses. All authors contributed to the research strategy and methodology, commented on drafts of the manuscript, and gave final approval for publication.

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**Data availability** eBird data used in this study are freely available online at https://ebird.org/science/download-ebird-data-products. Landsat DHIs generated and used in analyses during the current study are available from the corresponding author on reasonable request.

#### Declarations

**Conflict of interest** The authors declare no financial or non-financial interests to disclose.

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