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RESEARCH ARTICLE

Linking Spatial Patterns of Bird Diversity With Open Access Forest Height Models in a Biodiversity Hotspot

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ABSTRACT

Rapid environmental change is expected to cause lasting alterations in species abundance, richness, and distributions. Developing accessible tools to predict resulting biodiversity patterns and shifts is therefore crucial. Forest height is a key determinant of bird biodiversity and is usually modelled using LiDAR technology; however, high costs and limited accessibility hinder its broader use. As an alternative, open-access forest height layers could help overcome these barriers, but their application remains under-tested. We assessed whether four open-access forest height models (three globally available, and one locally available, calibrated with field measurements) could serve as useful predictors of species richness and foraging strata composition in bird assemblages within a Neotropical biodiversity hotspot, the Argentinian Atlantic Forest. We estimated overall and endemic bird species richness from 256 count points and extracted forest height values from the different models. Forest height was positively related to bird species richness. Models of endemic richness, rather than overall richness, showed greater explanatory and predictive power, likely reflecting stronger forest dependency. All models performed similarly but identified distinct areas of maximum predicted bird richness. Taller forests were associated with a greater proportion of canopy foragers across all species models; however, other relationships in foraging strata composition, for both all-species and endemic models, were not consistent among models. Our results indicate that canopy height models can serve as reliable predictors of bird species richness. We recommend this approach particularly in regions where LiDAR data are unavailable. We emphasize the importance of preserving taller forests to support diverse bird assemblages that include endemic species associated with mature forests.

1 | Introduction

Rapid environmental change, including global climate change (Salamin et al. 2010; Arneth et al. 2020) and accelerating rates of forest loss and habitat degradation (MapBiomas 2024), is driving dramatic shifts in biodiversity (Dirzo et al. 2014). Global monitored wildlife populations have declined by an alarming 73% over the last 50 years, and this situation is even more dramatic in South America, Central America and the Caribbean, where this decline reaches up to 95% (WWF Living Planet Report 2024). South American forest birds have been part of this rapid decline, yet some of the underlying ecological mechanisms remain poorly understood (Pollock et al. 2022). In view of this crisis, it is evident that there is a need for fast and accurate

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biodiversity metrics that are, importantly, accessible on a global scale (Schmeller et al. 2017).

One long-recognized determinant of bird diversity in forests is tree height (MacArthur and MacArthur 1961). This is a key component of forest structure as it usually enhances vertical heterogeneity. This, in turn, supports a variety of microhabitats and microclimates, providing birds with ecological niches for shelter, food, nesting sites and foraging opportunities (Schleuning et al. 2011). Higher forests hold a more complex vertical structure, fostering diverse foraging strategies among strata, thereby increasing guild and functional diversity (Walther 2002; Adamik et al. 2003). Moreover, the inclusion of vegetation structure in ecological analysis has improved the predictive power of richness models, suggesting that in forested ecosystems, vegetation structure is important for bird species (Culbert et al. 2013; Zellweger et al. 2016).

Studies that have demonstrated that forest height can serve as a robust predictor of avian richness often rely on LiDAR (Light Detection and Ranging) technologies, which offer precise environmental characterization, 3D modelling of topography, and detailed vegetative structure (Torresani et al. 2023). LiDAR's accuracy for metrics such as forest height, canopy cover, slope and visibility has provided invaluable insights into ecological studies (Vierling and Vierling 2026). Despite its potential, the high cost of LiDAR technology, coupled with limited availability in many regions (Hummel et al. 2011; OpenTopography 2026), presents significant barriers for widespread use (Potapov et al. 2021), especially in the Southern Hemisphere.

Recently, three global forest height models have been developed and have been made openly available: the high-resolution canopy height model of the Earth (hereafter, HRCH, Lang et al. 2023), the global forest canopy height map (hereafter, GFCH, Potapov et al. 2021), and the global map of tree canopy height (hereafter, GMTCH, Tolan et al. 2024). Furthermore, Silveira et al. (2023) produced a suite of spatial products describing forest structural attributes across the native forests of Argentina, including a forest height model derived from Sentinel-2 data and calibrated using 3788 plots (1000 m^2 each) from Argentina's Second Native Forest Inventory (2015–2020). They reported superior predictive performance of this model relative to GFCH. So far, the usefulness of tree height models for predicting species richness has been tested only using virtual species under simulated scenarios (Moudrý et al. 2024). Therefore, the forest height model layers hold potential, but their accuracy for biodiversity modelling remains unexplored.

One region where biodiversity measurement tools are essential is the Atlantic Forest, a biodiversity hotspot spanning Brazil, Paraguay and Argentina. It is considered one of the most threatened and important biomes for conservation in the world (Marques and Grelle 2021). This forest has been extensively cleared, modified and fragmented, with $<23\%$ of its original surface remaining, and only a fraction of that consists of mature, well-preserved forests (Vancine et al. 2024). The remaining forest is highly fragmented; 97% of fragments are smaller than 50 ha, and it is inadequately protected—$<10\%$ is under formal protection, of which 2.8% is in strictly protected areas (FVSA y WWF 2017; Vancine et al. 2024). In Misiones province (NE Argentina), the Atlantic Forest reaches its southwestern limit, delimited by an ecotone with savanna regions (Arana et al. 2021) and supports a high diversity of species, including many endemics. In contrast to neighbouring territories, in Misiones almost 57% of the original forest cover still remains (Vancine et al. 2024). Whereas Misiones represents only ~2% of the original global Atlantic Forest area (FVSA y WWF 2017), it now includes some of the largest and best-preserved Atlantic Forest areas. Even so, deforestation rates in Misiones have increased in the last decade (Mohebalian et al. 2022), raising serious concerns about the future of its biodiversity. Birds in the Atlantic Forest have been particularly affected, with a substantial loss of suitable environments (Zurita and Bellocq 2010). This situation is particularly concerning for endemic species of the Atlantic Forest, with over 30% now threatened or extinct (Vale et al. 2018) and projections indicating that the distributional ranges of some species will shrink even further (Souza et al. 2011).

In this study, we explore the potential of three global forest height models and the Argentina-wide forest height model, as predictors of overall and endemic bird species richness, using field bird survey data from the Atlantic Forest in Argentina. We hypothesize that the avian assemblages are influenced by the vertical structure of the forest, with forest height playing a key role in determining overall and endemic bird species richness. We predict a positive relationship between forest height and bird richness, as taller forests provide a greater diversity of niches that can support more diverse bird communities. Moreover, as previous studies have described that forest height affects bird foraging strategies (Batisteli et al. 2018), we additionally expect that forest height differently affects bird assemblages based on the foraging strata of species, thus shaping assemblage composition across the study region. We predict that taller forests will be positively correlated with assemblages with a high proportion of species dependent on canopy, as taller forests may provide greater vertical foraging space (Bakermans et al. 2012). Also, we expect a positive relationship with ground-foraging species, as taller forests may be associated with mature forests with more open ground conditions (Lesak et al. 2011).

We predict that forest height derived from Silveira et al. (2023) will outperform the performance of other forest height models regarding richness and community composition predictions. We expect this because it was built with field forest height measurements from this study area, resulting in superior predictive performance compared to models based on GEDI data, as reported by Silveira et al. (2023). Finally, we discuss whether these open-access forest height models may serve as a basis for ecological modelling and biodiversity conservation through identifying areas of high biodiversity potential, especially in regions where LiDAR technologies are unattainable.

2 | Methods

2.1 | Study Area

This study was conducted in NE Argentina, in native forested areas of the Atlantic Forest (25° 37′-28° 21′ S, 53° 37′-55° 40′; Figure 1). This area is characterized by semi-deciduous



FIGURE 1 | The middle layer and understory of tall old-growth Atlantic Forest in the Yabotí Biosphere reserve, Misiones province, Argentina, with several tree species, epiphytes and different bamboo species. Photo Credit: M. Lammertink.

forests, with an annual precipitation range of 1000–2200 mm and a mean temperature range of 16°C–22°C. This is the southwestern limit of the Atlantic Forest, reaching an ecotone with the Campos district. This region features a mosaic of natural areas interspersed with urban zones and productive plantations, including pine (*Pinus* spp.), yerba mate (*Ilex paraguariensis*), and tobacco (*Nicotiana* spp.) (MapBiomas 2024). Two primary ecoregions are identified in this area (Arana et al. 2021; Marques and Grelle 2021): the interior mixed forest, characterized by a semi-deciduous forest with a tropical humid climate and no distinct dry season, and the Araucaria mixed forest, found at higher altitudes and typically experiencing colder weather, dominated by *Araucaria angustifolia* and featuring arborescent ferns.

2.2 | Study Design and Sampling Protocol

Field sampling was carried out between late June and mid-September in 2021–2023, during the mid to late austral winter. Although this period precedes the breeding season of most species (Marques-Santos et al. 2016), it is pair formation season in this subtropical region. Our field experience conducting vocalization-based surveys indicates this is the season with peak vocal activity, particularly of resident forest birds (Lammertink et al. 2020). We constructed species accumulation curves to evaluate whether our sampling effort was sufficient to adequately characterize community richness.

Each week during this period, we visited a different site with native forests, where we established eight bird-counting points (Figure 2). The selection of study sites was primarily guided by logistical feasibility and specific ecological criteria. Each site consisted of native forest patches with a minimum area of 2000 ha, large enough to accommodate eight count points spaced at least 830 m apart to avoid pseudoreplication and reduce the likelihood of recording the same individual birds at multiple locations. This distance was chosen based on known movement patterns of certain species and previous passive acoustic monitoring studies in the Atlantic Forest (Lammertink and Fernández 2022; De Araújo et al. 2024).

Points were located at least 300 m from roads to minimize edge effects and anthropogenic disturbance. Although some degree of surrounding fragmentation or deforestation was sometimes unavoidable, we ensured that selected points within each site were separated by no more than 1.5 km to maintain spatial independence and ecological comparability. Consequently, we prioritized areas with continuous forest cover. Sites required a central vehicular access route to allow the field team to efficiently reach the count points in low-light conditions before dawn. These combined criteria limited the number of suitable forest patches within the province. To ensure broad ecological representation, we distributed an equal number of sites in four major zones based on phytogeographic regions, river basins, and elevation. At each point, we deployed an autonomous recording unit (SM4, Wildlife Acoustics). Two methods, in-person point counts and listening to recordings, were used to detect and identify bird species and thus estimate species richness.

We placed a total of 256 points in 32 sites (Figure 2). We aimed to count bird species at each point twice, once in person using point counts and another by listening to autonomous recordings. Our point count surveys, both in-person and from recordings, covered areas with an approximate radius of 300–500 m, since we wanted to maximize the number of species detected (Matsuoka et al. 2014). Surveys lasted 85 min around dawn, starting 25 min before sunrise and ending one hour after, since this period corresponds to peak bird activity (De Araújo et al. 2021). We thus aimed for a sampling effort of 170 min per point to capture the majority of the assemblage during our work at each site. During this time, for both methods, every bird seen or heard was identified by four experienced observers (DZ, ML, Iván Ebrecht and Julián Márquez), and no automatic detection tools were used in the bird identification process.

When sampling areas of similar size, traditional point counts and analyses of autonomous recordings could yield similar estimates of species richness, although this may depend on the environment surveyed (Sedláček et al. 2015; Darras et al. 2018). The integration of both approaches is recommended for effective biodiversity monitoring (Drake et al. 2021). Since counts at the same point were conducted no more than three days apart, we merged them into a single presence/absence dataset per point for this analysis. All surveys were conducted under favourable weather conditions, avoiding days with rain or strong wind that could affect bird detection.

2.3 | Forest Height Models

Forest height data from the forest height models were derived as follows: from the HRCH model corresponding to the year 2020, with a spatial resolution of 10 m; from the GFCH model for the year 2019 with a spatial resolution of 30 m; from the GMTCH built from images belonging to the years 2017 to 2020, with a spatial resolution of 1 m (Tolan et al. 2024); and from Silveira et al. (2023), with a spatial resolution of 30 m.

Measuring individual trees, which is the most accessible and cost-effective way to obtain field-based height measurements,

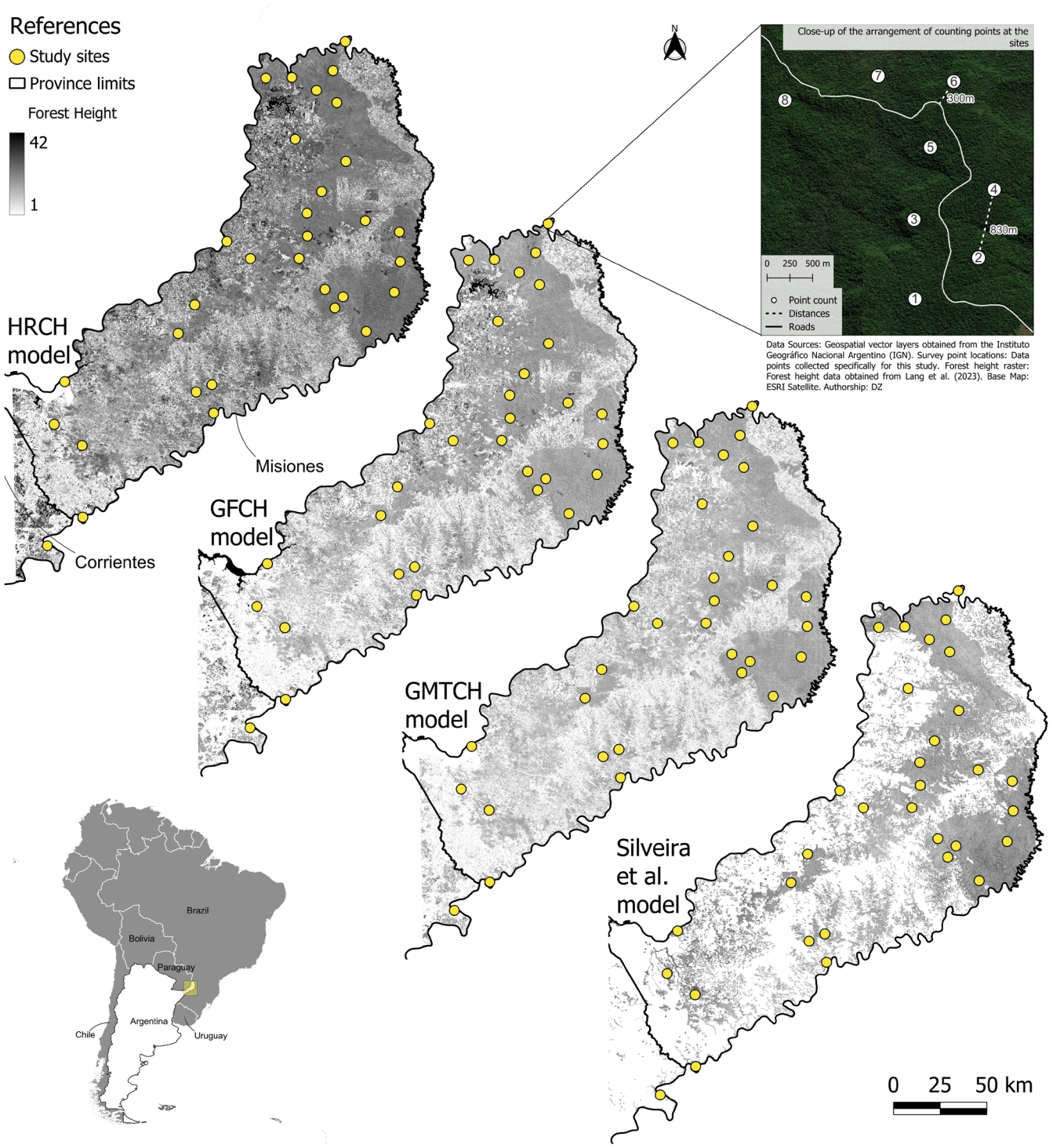


FIGURE 2 | Map of Misiones and Corrientes provinces, Argentina, with forest height retrieved from four forest height models, and our study sites, with the inset showing an example of the arrangement of count points at a site.

can be challenging in forested environments with multiple vegetation strata. In addition, the height of the tallest trees may sometimes be difficult or even impossible to measure accurately in the field. Even if individual trees were measured in the field, relating these measurements to remotely sensed forest-height models would not necessarily provide an accurate estimate of mean canopy height at the landscape scale. Moreover, no field measurement has proved to be fully effective, but laser scanning leads to better metric estimations (Larjavaara and Muller-Landau 2013; Wang et al. 2019). Thus, the most appropriate way to obtain direct measurements of average canopy height would probably be through LiDAR technology. Obtaining LiDAR measurements for 256 vegetation plots across three different years would require resources that were beyond our means. Considering this limitation, we aim to evaluate the usefulness of globally available open resources

for researchers and scientists facing similar difficulties. Since Silveira et al. (2023) proposed a previously validated model for estimating forest height, we considered these estimates sufficiently reliable to represent average forest height, even if some point-level estimates may not be perfectly accurate.

Since our point count surveys covered areas with an approximate radii of 300–500 m, we calculated the mean of the values of all cells inside a 400 m radius buffer around each count point, excluding values under 3 m height (i.e., non-forested and bushy areas). All variables described here, along with latitude, were tested for strong correlations. None showed significant correlations with one another ($r = -0.19–0.58$), except for two canopy height models, HRCH and GFCH, which were highly correlated.

2.4 | Data Analysis

2.4.1 | Overall and Endemic Avian Richness

In order to evaluate the effectiveness of the sampling effort, we calculated rarefaction curves (Gotelli and Colwell 2011). This indicates that the diurnal bird assemblage of our study area was adequately sampled, considering the diurnal species occurring in winter that we worked with. To compare the performance of the two survey methods—in-person and from acoustic recordings—we generated and compared separate individual-based rarefaction curves for each method.

To examine the association between forest height and bird diversity, we fitted generalized additive models (GAMs), which allow modelling complex, non-linear relationships between variables (Wood 2017; Pedersen et al. 2018). We modelled the response variables a priori as non-linear because bird diversity can peak at intermediate values of environmental covariates, based on our previous work in the study area (Zaffignani et al. 2026). Moreover, species often exhibit optimal environmental conditions for occurrence and abundance, resulting in nonlinear relationships with environmental variables (Anderson et al. 2022). To describe the non-linearity of the relationship between the model predictor and the response variables, we used effective degrees of freedom (edf). An edf equals to 1 is equivalent to a linear relationship, $1 < \text{edf} \leq 2$ is considered a weakly non-linear relationship, and $\text{edf} > 2$ implies a highly non-linear relationship (Wood 2017). We fitted models using overall and endemic species richness as response variables, and forest height, latitude, and sampling year as predictors.

We added latitude to account for a possible spatial autocorrelation in the sampling design (Legendre 1993). Longitude was not included as it was highly correlated with latitude ($r = 0.7$), as explained by the boot-like shape, inclined northeast, of the study area (Figure 1). By including latitude, we aimed to capture the environmental gradient across the study area, particularly the pronounced north–south variation in environmental conditions (e.g., precipitation and temperature). Including a spatial error term would instead account for spatial autocorrelation in the residuals, assuming that nearby sites are more similar to one another, which could partially absorb the environmental gradient of interest.

The sampling year was included to account for potential intra-year variations in species occurrences. We built simple GAMs for overall and endemic richness separately. In all models, we used a Poisson error structure with a log-link function, as there were no apparent issues of overdispersion (dispersion parameter = 1.09–1.78).

Due to the clustering of points across sites, latitude showed gaps in their distribution. With sparse data, GAMs can be challenging to interpolate, sometimes producing biologically unreasonable fits (Edwards et al. 2023). We therefore fitted GAMs using penalized regression splines with smoothing parameters estimated by restricted maximum likelihood (REML), as implemented in mgcv. To limit the maximum flexibility of the latitude smoothing, we set the basis dimension to $k = 6$, based on visual inspection of the distribution of observations along the latitude gradient. The resulting effective degrees of freedom were estimated from the data through the REML smoothing procedure. We assessed the predictive ability of these models using a leave-one-out cross validation (LOOCV) approach (James et al. 2013). In this method, each observation in the dataset is used once as a test set while the remaining observations serve as the training set. This process is repeated n times, where n is the number of data, yielding n models.

Each model's performance is evaluated on the held-out observation, and these individual errors are then averaged to estimate the model's overall error. Leave-one-out cross validation (LOOCV) is particularly useful for small datasets (Wong 2015). We estimated the residual mean squared error (RMSE) and the predictive R^2 as metrics of prediction accuracy. To visualize the pattern between the explanatory and response variables, we used partial residual plots, which show the relationship between an explanatory variable and the response variable in a model while accounting for the effect of other predictors. To predict bird species richness for the entire study region, we applied the predict function using the forest height models resampled at 1 km resolution as a base. We predicted only for forest values present in the original dataset. We then masked the resulting predictions with the MapBiomas land cover map, in order to exclude all non-native forest areas. This ensured that predictions were not transferred to regions with planted forests, such as *Pinus* spp. and *Eucalyptus* spp. Along with the richness prediction maps, we report an uncertainty map represented as the standard error (SE) of predictions (Rocchini et al. 2011; Burns et al. 2020). We classified bird species as endemic or non-endemic to the Atlantic Forest following the database proposed by Vale et al. (2018).

2.4.2 | Foraging Strata

To assess the relationship between forest height and the foraging behaviour of birds in assemblages, we first sourced foraging stratum data from Wilman et al. (2014). Specifically, we obtained information on the proportion of each species' foraging activity at ground, understory, mid-height, aerial and canopy strata. We did this because field observations of foraging behaviour are highly challenging in forests such as those in our study area, where vegetation is dense and visibility is often limited to a few meters. Moreover, we wanted to estimate the average use of foraging strata for each species in order to identify general trends

rather than individual behaviours. Wilman's database accounts for the percentage of strata in which every species forages, summing 100% from one or multiple strata. Ten species that were aquatic or highly aerial foragers (≥ 70%) were excluded from the analyses.

Then, we applied a Correspondence Analysis (CA) to the species by foraging stratum matrix to characterize the composition of foraging stratum of individual species (Palacio et al. 2020). We assigned the resulting two CA scores of the main two axes to each species and computed the average for each bird assemblage at point level, so that each assemblage was now described by a foraging stratum composition variable. These average values represent the community-weighted means (CWM) on the CA axes used as traits, as is widely used in functional trait ecology (Gaüzère et al. 2019). We subsequently used these first two average scores as response variables (hereafter "foraging stratum composition") accounting for foraging stratum composition, relating each axis with forest height using GAMs (Gaussian error structure and identity link function, $k = 6$). This approach provides a quantitative measure of foraging behaviour composition, overcoming the limitation of relying on subjective and arbitrary species assignments to guilds (Jaksić 1981). With assemblages' foraging strata composition, we refer to how the assemblage is composed in terms of the frequency of every foraging stratum derived from the occurrences of species at each point.

All analyses and plots were performed in R 4.3.3 (R Core Team 2024) using the packages mgcv (Wood 2009), ggplot2 (Wickham 2016), and raster (Hijmans 2024). All maps (study area and richness predictions) were built using QGIS 3.36 (QGIS Development Team 2024).

3 | Results

3.1 | Taxonomic Diversity

We conducted 42 739 min of survey effort, both in the field (16 575 min) and from recorded audio (26 164 min). At 243 of the 256 count points, we achieved the target of 170 min survey effort. However, at 13 points, adverse weather conditions or equipment malfunctions during at least one count prevented reaching the target effort. In total, considering both methods, in person point counts and recordings, we recorded 24 763 bird occurrences, representing 31 199 individual birds across 253 species from 51 families (Appendix S1). After filtering out non-forest-dependent species and species that were aquatic or highly aerial foragers, we retained 15 957 occurrences, encompassing 235 species from 42 families, of which 61 species were endemic to the Atlantic Forest.

Bird species richness per point ranged from 27 to 92 species (mean = 62.3 ± 12.5). Regarding sampling method, species richness ranged from 24 to 75 species for in-person point counts (mean = 47.9 ± 11.8) and from 22 to 89 species for recordings (mean = 53.4 ± 12.7). Endemic species richness ranged from 5 to 35 species per point (mean = 18.8 ± 6.3). Overall richness and endemic richness were positively correlated ($r = 0.83$). There was no significant difference estimating species richness from recordings or from in-person surveys, as the confidence intervals for both methods substantially overlapped (Rarefaction curves are provided in Appendix S2, Figure S1).

3.2 | Forest Height Models

Among the 400 m radius plots, forest height derived from the HRCH model ranged from 12.1 to 25.3 m, with a mean of 21.2 ± 2.2 m. Measurements from the GFCH model ranged from 10.7 to 21.2 m, with a mean of 16.3 ± 1.7 m. Forest height derived from the GMTCH ranged from 10 to 16.5 m, with a mean of 13.2 ± 1.3 m. Finally, measurements from the Silveira forest height model ranged from 10.2 to 16.7 m, with a mean of 14.5 ± 1.1 m. In general terms, the HRCH model tended to estimate higher heights, while the GMTCH tended to estimate lower heights.

3.3 | Forest Height Models and Bird Richness

All GAMs for the different forest height models revealed distinct, linear and non-linear relationships between bird richness and forest height (Figure 3). Overall and endemic richness were positively related to forest height derived from all four models. Model performance for the four forest height models was better for the endemic bird richness models than for the overall bird richness model, resulting in higher explanatory power (Appendix S3).

Explanatory power was broadly similar among the forest height models (Table 1, R^2 for overall richness ranging from 0.3 to 0.38, and endemic richness from 0.45 to 0.49). However, for overall species richness, the Silveira model showed the best performance ($R^2 = 0.38$), whereas for endemic species richness the GFCH model performed best ($R^2 = 0.49$). In contrast, the HRCH model showed the lowest explanatory power for both overall and endemic richness ($R^2 = 0.30$ and 0.45, respectively). Regarding bird richness predictions, all models performed well in the Leave-one-out cross validation (LOOCV), but overall richness models had slightly worse performance than the endemic species richness model in all models (Appendix S3).

Regarding spatial predictions, all four forest height models differed from each other (Figure 4). For the HRCH model, overall richness predictions ranged from 51 to 66 species per 1 × 1 km pixel, while endemic richness predictions ranged from 8 to 21. For overall species richness, GFCH predicted values ranging from 48 to 69 species, while predictions for endemic species richness ranged from 8 to 22 species. Predictions from the GMTCH model for overall richness ranged from 56 to 73, and for endemic richness predicted values were from 9 to 33 species. Regarding Silveira et al. model predictions, overall richness ranged from 46 to 68 and endemic richness from 7 to 21. In all models, predictions for overall richness generally exhibited higher levels of uncertainty compared to endemic richness. However, endemic richness displayed more localized peaks of uncertainty, particularly in areas with extreme richness values. These high-uncertainty regions often corresponded to pixels near diffuse forest boundaries.

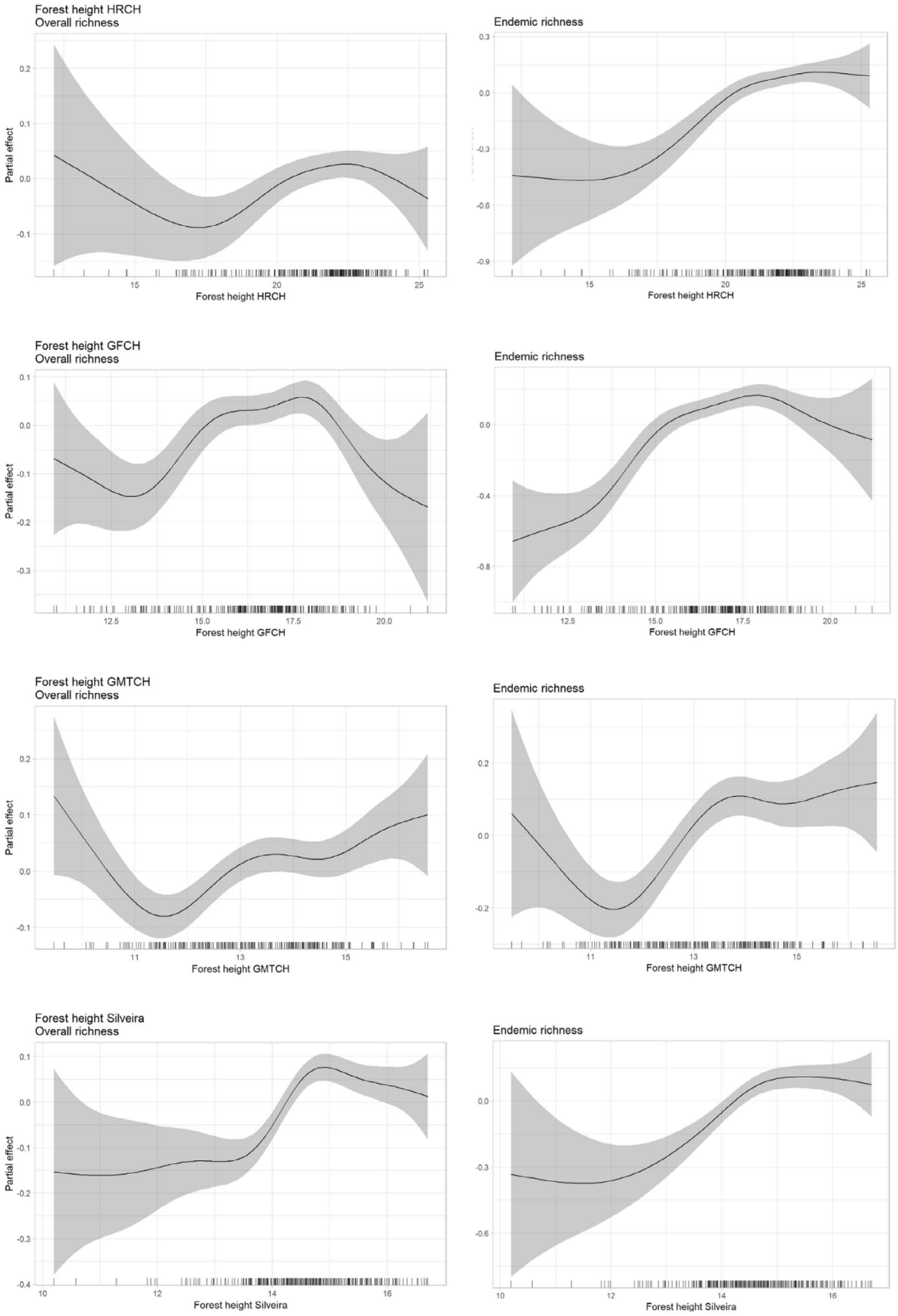


FIGURE 3 | Partial residual plots derived from the Generalized Additive Models, showing partial effects for bird richness in function of the four forest height models. The left column represents overall bird richness, while the right column represents endemic richness.

TABLE 1 | R^2 comparison among different forest height models, both for overall and endemic richness.

	Overall richness		Endemic richness	
Forest height model	R^2	p	R^2	p
HRCH	0.3	0.018	0.45	< 0.0001
GFCH	0.33	< 0.0001	0.49	< 0.0001
GMTCH	0.33	< 0.0001	0.47	< 0.0001
Silveira et al.	0.38	< 0.0001	0.47	< 0.0001

3.4 | Foraging Strata Composition

Regarding the foraging strata composition for overall and endemic species (Appendix S2, Figure S2), aerial foraging was the least represented stratum across all categories, particularly in endemic species (0.14%). In contrast, mid-height foraging strata was the most frequent stratum, particularly in endemic bird occurrences (36.1%). The proportion of canopy foraging across categories ranged from 11.6% to 17.9%, with the lowest representation in endemic bird occurrences but the highest in endemic richness.

In the Correspondence Analysis (CA), the first two dimensions accounted for 73.4% of total foraging stratum variation (Figure 5). The first axis (44.7% of variance explained) represented a gradient of ground-level foraging species (negative values, contribution = 63.0%) to mid-high stratum (contribution = 16.9%) and canopy foraging species (positive values, contribution = 19.6%). The second axis (28.7% of variance explained) was mainly related to canopy-level foraging species (positive values, contribution = 52.5%) and understory species (negative values, contribution = 36.7%).

3.5 | Forest Height Models and Foraging Strata Composition

GAMs showed linear and non-linear relationships between foraging composition (CA axes) and forest height from all models (Figure 6). Overall, the four height models showed comparable performance across most variables (Appendix S4). Nonetheless, the HRCH and the GMTCH models exhibited more similar responses to each other, while the GFCH model aligned more closely with the Silveira et al. model. The clearest relationship with foraging strata composition and forest height was regarding the first CA axis. In all models of all-species and the HRCH and GMTH of endemic species model the first CA axis had positive, significant relationship with forest height, suggesting higher canopy forager representation at greater forest heights. These relationships exhibited a unimodal pattern, reaching a peak and then either declining or levelling off at higher canopy heights (> 20 m for the HRCH model and > 15 m for the GMTCH model). The second CA axis showed no significant relationship with forest height in any of the four all-species models, nor in the HRCH and GMTCH endemic species models. However, the GFCH and the Silveira et al. model, showed a significant relationship between the second axis and forest height in the endemic species model, suggesting an increase of mid-height foragers with taller forests.

4 | Discussion

Our results show a significant, positive association between tree height derived from forest height models and bird species richness, with a stronger association for endemic birds than for overall birds in the southern Atlantic Forest. We also found patterns in bird foraging strata composition related to forest height, though these patterns varied depending on the forest height model used. Again, differences between overall and endemic species were found. These results indicate that the open-access forest height models can serve as a valuable variable for estimating bird species richness. Applying GAMs, which have demonstrated strong predictive capabilities for bird species richness (Kosicki 2020), we achieved substantial predictive performance with only two variables, forest height and latitude, accounting for 30%–38% of the variance in overall richness and 45%–49% in endemic richness, depending on the forest height model.

Roll et al. (2015) found that tree height was not a strong predictor of amphibians, mammals and bird diversity at the global scale, but its importance increased within biogeographic realms, particularly in the Neotropics, highlighting the value of local studies. In contrast, Feng et al. (2020) found that forest height was a strong predictor of bird richness across both global and regional scales. Consistent with this, our results show a positive relationship between forest height and bird richness, supporting the use of forest height models to explain and predict bird diversity at regional scales.

Endemic species richness consistently showed a stronger association with forest height than overall richness, likely reflecting the close ecological association of endemic species with forested habitats (Vale et al. 2018). This underscores the importance of incorporating subgroups, such as endemics, and species identities into ecological studies to better understand species composition and responses to environmental changes (De Lima et al. 2013). Differences among forest height estimates were evident across models. Overall, HRCH tended to produce the highest height values, whereas GMTCH generally yielded the lowest estimates, consistent with findings reported by Moudrý et al. (2024). Despite their differences estimating forest height among sampling points, the explanatory power for bird richness was similar. We suggest that local-scale inaccuracies are likely to be attenuated when predictions are aggregated across larger areas. In our analyses, the Silveira et al. height model showed the best performance for overall species richness and ranked second for endemic richness. However, the applicability of this model is currently limited to Argentina. Although all three global models showed similar performance, for bird species richness predictions we recommend the GFCH model of Potapov et al. (2021), based on its higher R^2 values, its consistency with results reported by

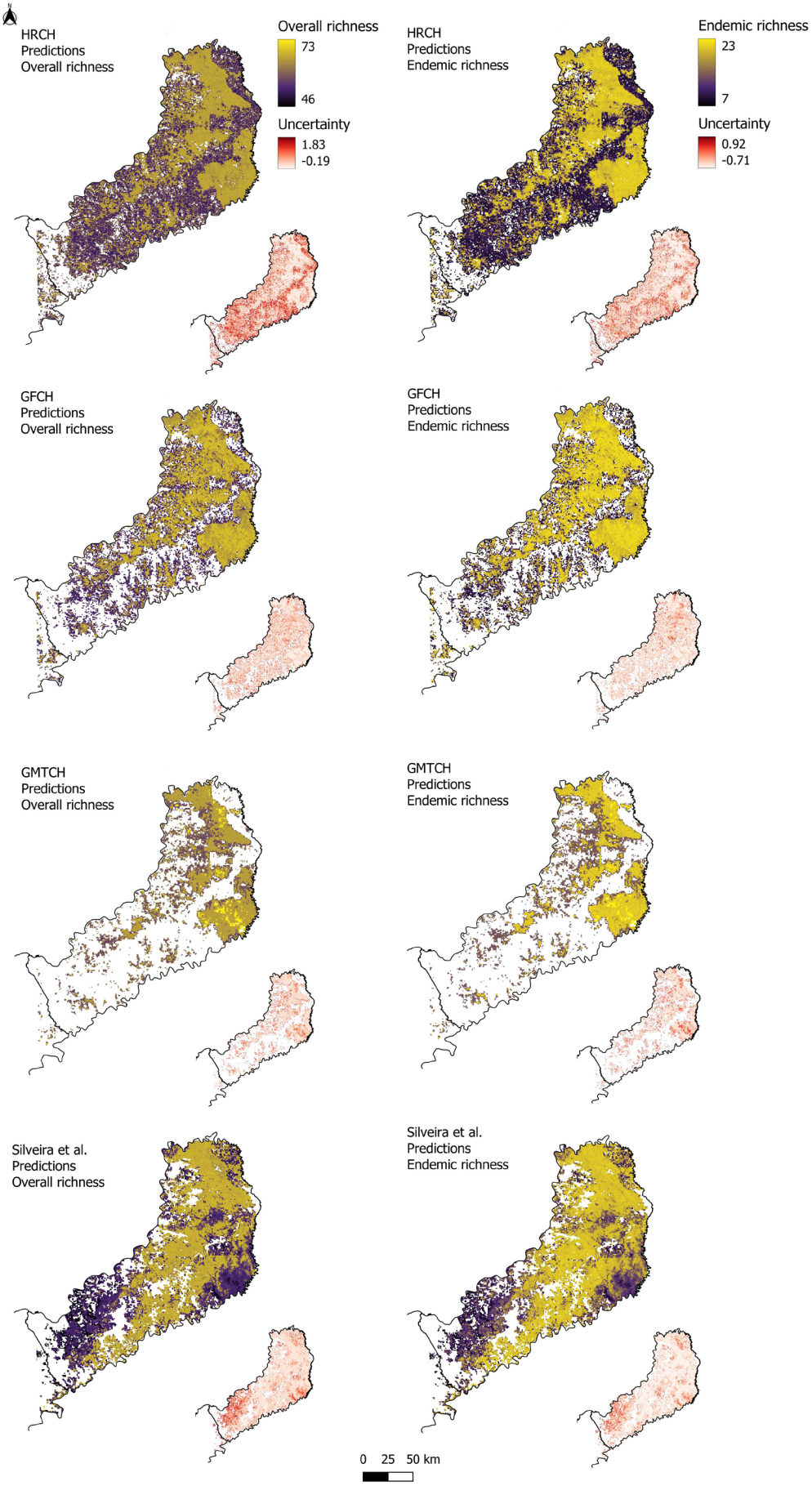


FIGURE 4 | Legend on next page.

FIGURE 4 | Spatial predictions for the HRCH, GFCH, GMTCH and Silveira et al. models. Overall bird species richness (left) and endemic bird species richness (right) across the study region, as predicted from the canopy height models. Uncertainty of the mean prediction for each map is shown as the range of the standard error confidence interval, with the posterior transformation to a logarithmic scale. Predictions were constrained to the range of forest height values sampled in our plots, and no extrapolation beyond this range was performed to prevent unreliable estimates.

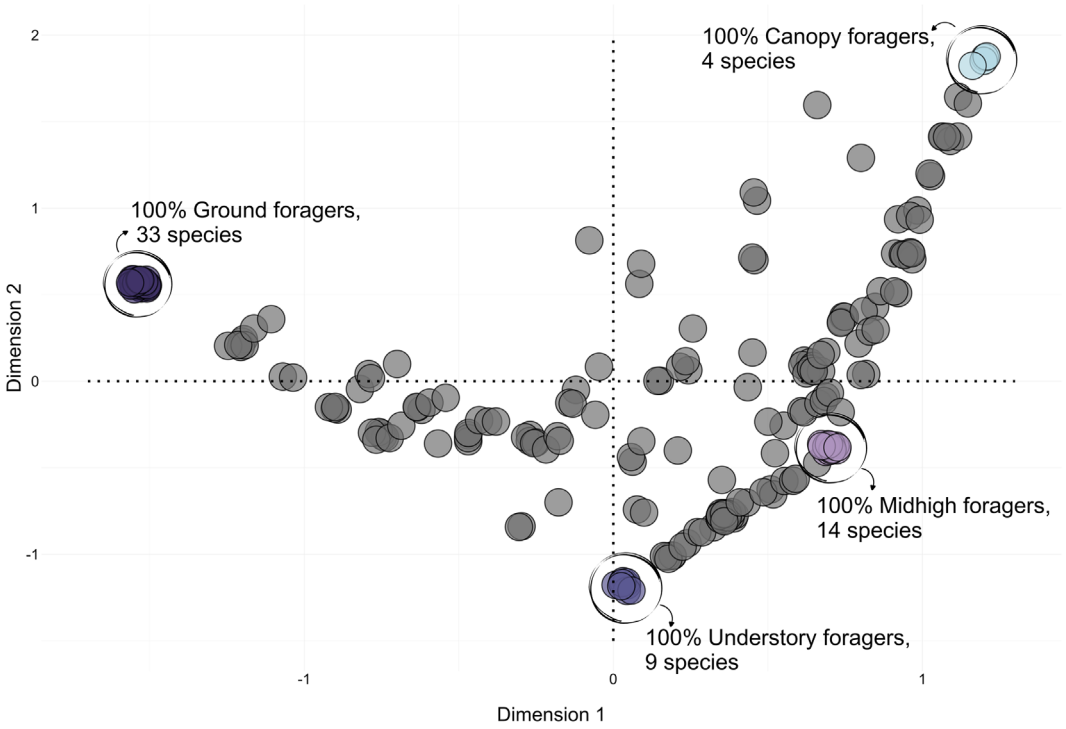


FIGURE 5 | Distribution of species along the two principal Correspondence Analysis axes. Species that exclusively rely on a single foraging stratum are highlighted in colour. Lower values on the first dimension correspond to ground-foraging behaviour, while higher values on the second dimension indicate greater reliance on the canopy stratum.

Silveira et al. (2023), and its stronger statistical support across multiple models.

Despite small discrepancies regarding predicted richness hotspots among models, most revealed consistent spatial patterns, including lower predicted richness in the southwestern portion of the study area and within more isolated forest patches. Also, all models identified peak richness in the north–central region, corresponding to one of the largest biological corridors of the southern Atlantic Forest, the 'Corredor Verde' (Di Bitetti et al. 2006), which includes the largest protected area in the Argentine Atlantic Forest, Urugua-í Provincial Park. With the exception of Silveira et al. (2023), all models also highlighted areas of maximum overall and endemic richness within the Yabotí Biosphere Reserve, located in the southeastern limit of the study area.

Besides the effect that forest structure may have on bird richness, the influence of forest structure on avian diversity can vary considerably between different bird taxonomic groups and guilds (Camprodon and Brotons 2006; Vogeler et al. 2014). Differences in the vertical structure of forests do not affect all species or guilds equally (Lesak et al. 2011; Castaño-Villa et al. 2019). Our results from the four forest height models indicate that taller forests support assemblages with a greater proportion of canopy foragers when considering all species and endemic species according to the HRCH and GMTCH models. Without directly measuring each stratum, forest height can serve as a useful indicator of subcanopy structure and its potential for supporting specific groups.

Our results highlight the potential of forest height models for ecological applications such as Ecological Niche Modelling (ENM) and Species Distribution Modelling (SDM), fields that have increasingly incorporated remote sensing data in recent years (Sillero et al. 2021; Bonthoux et al. 2018). Also, canopy structure variables derived from LiDAR data have been shown to improve model performance in predicting bird species' occurrence probabilities (Burns et al. 2020). Among these variables, forest height has proven especially valuable, enhancing the accuracy of niche models for birds (Ficetola et al. 2014). We therefore recommend the use of forest height models in ENMs and SDMs. Moreover, given the positive relationship we observed between foraging stratum composition and forest height, forest height models could also be applied in more complex SDM that incorporate species traits, such as joint Species Distribution Models (jSDMs; Ovaskainen and Abrego 2020).

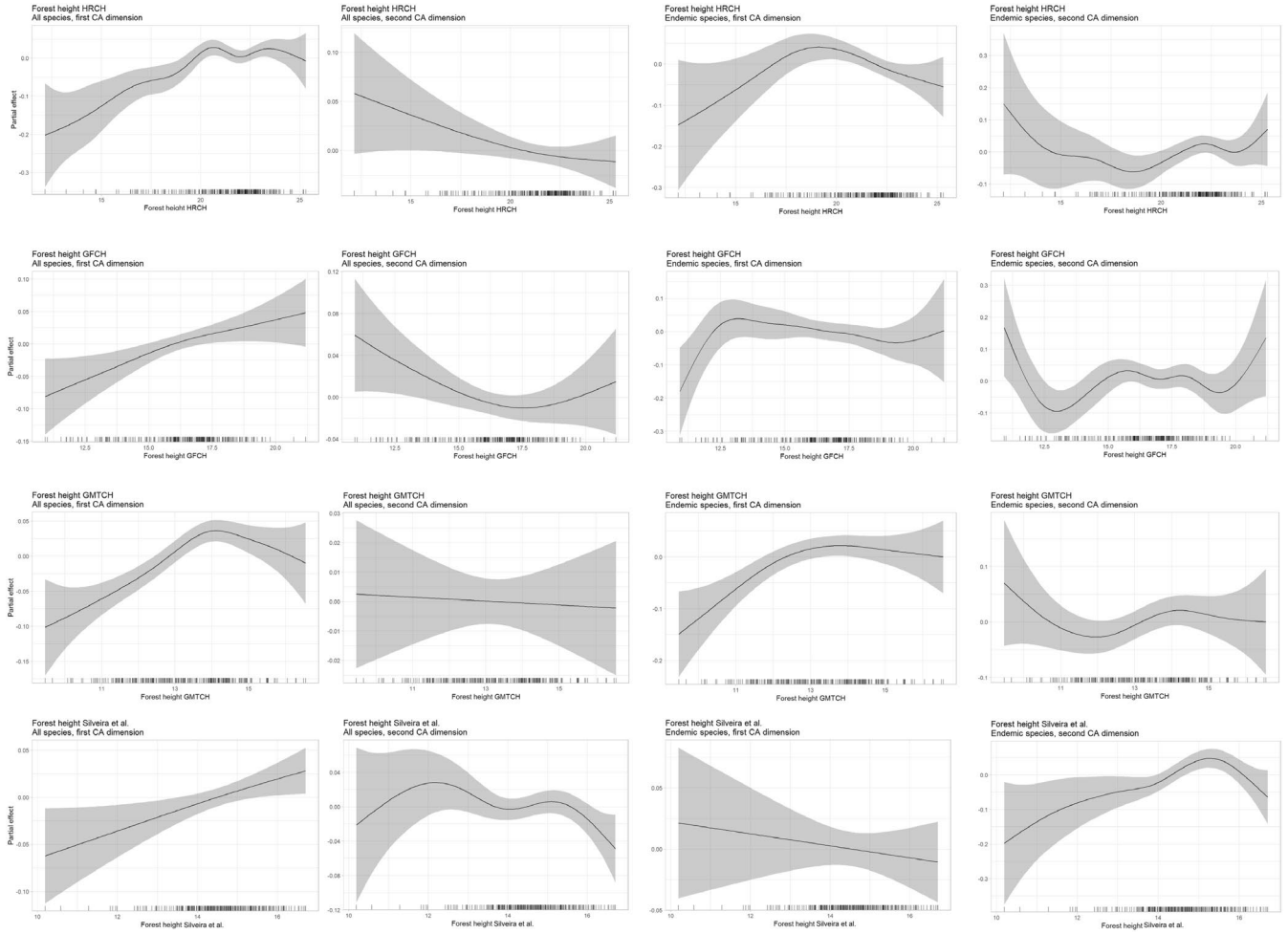


FIGURE 6 | Partial residual plots derived from the Generalized Additive Models, showing partial effects for bird strata composition (X and Y axis from the CA analysis) in function of forest height. The first row shows results from the HRCH model, the second row shows results from the GFCH model, the third row corresponds to the GMTCH, while the fourth row corresponds to the Silveira et al. model. The first and second columns represent the all-species models (X and Y axis), while the third and fourth columns correspond to the endemic species models (X and Y axis). Shaded areas indicate 95% confidence intervals.

Given the context of rapid environmental change, which is expected to intensify and lead to lasting alterations in species abundance, richness, and distribution patterns (Sala et al. 2000), it is necessary to develop and test different data and techniques that serve as effective tools for predicting biodiversity patterns and shifts. Moudrý et al. (2024) analysed the performance of forest height measurements for ecological modelling using both LiDAR and three different open-access forest height models, applied on a virtual species. LiDAR data emerged as the most reliable predictor in these models. However, LiDAR requires specialized equipment and expertise, limiting its accessibility to researchers worldwide. Considering these constraints, especially in remote and unprotected areas, open-access alternatives like the forest height models we used are crucial for expanding research opportunities where LiDAR is inaccessible. We encourage researchers to test these open-access canopy height layers in other regions worldwide to build broader evidence based on their performance and ecological relevance across different forest types and biogeographic contexts. We find these actions imperative, particularly in light of the ongoing disparities between countries and world regions in terms of funding, participation, locally-based studies, and the underrepresentation of research from the Global South (Haelewaters et al. 2021, Soares et al. 2023).

Considering the positive relationship between taller forests and higher bird richness—especially among endemic species, of which many are tied to mature forest—we recommend forest management practices that prioritize maintaining and enhancing forest height. Efforts should specifically focus on preserving taller forests with large trees, including regulating selective logging practices due to their detrimental effects, such as concentrated damage and increased tree mortality (Bedrij et al. 2024). Maintaining and restoring tall forests not only supports greater biodiversity but also aligns with the habitat needs of species closely associated with mature forests. Our findings suggest that remote sensing tools, integrated with literature information and field-collected data, can help identify new areas with suitable forest height conditions to support high-richness bird communities, particularly those with endemic and highly forest-dependent species that currently lack protection.

Author Contributions

Daniela Zaffignani: investigation, conceptualization, funding acquisition, writing – original draft, methodology, visualization, writing – review and editing, software, formal analysis, data curation, validation. **Martjan Lammertink:** conceptualization, investigation, supervision, funding acquisition, project administration, writing – original draft, writing – review and editing, methodology, resources. **Juan Manuel Fernández:** writing – original draft, writing – review and editing, conceptualization. **Luciano N. Segura:** conceptualization, supervision, writing – review and editing, writing – original draft, validation. **Facundo X. Palacio:** conceptualization, formal analysis, writing – original draft, writing – review and editing, validation, methodology, software, supervision.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available from the authors on reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Species list from the bird sampling, their families and foraging strata composition. Values from each category represent the estimated percentage use of each stratum by each bird species. **Appendix S2: Figure S1.** Rarefaction curves for both sampling methods. The confidence intervals for both methods substantially overlapped, indicating similar patterns of species richness rate detections. **Figure S2.** Differential proportion of foraging strata behavior, for total bird occurrences, overall richness, endemic bird occurrences and endemic richness. **Appendix S3:** Relationships between bird richness, forest height (from the four models) and latitude. Results from Generalized Additive Models are shown. **Appendix S4:** Results of the GAMs for the CA axis, for all forest height models.