

Canopy functional composition as an indicator of bird traits, taxonomy, and vulnerability in tropical Peruvian forests

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This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)

I have reviewed the article entitled "Forest birds track canopy functional traits in the Peruvian Andes and Amazon" in which authors show how to integrate GIS that characterizes canopy proxies of tree traits with bird variables at the assemblage level. Although the topic is very appealing and interesting (and indeed needed), the manuscript does not match the expectations raised when reading the title. Based on the results and the reading the title should be changed since the authors did not address animal movement (or actual bird assemblage associations) in relation to canopy traits but how artificial bird assemblage variables relate with satellite-inferred canopy traits.

The article seems to be a tool-centered study in which authors tested how well a result from the GIS clustering based on proxies of tree traits is correlated with artificial bird assemblages' variables. In general, it shows nice results in which the inferred canopy traits are indeed correlated with bird assemblages' variables. The authors then highlight the usefulness of the satellite-based canopy description to infer things about the bird assemblages. Here is where I have my major concerns:

- Bird assemblages are artificial: overlapping polygons from Birdlife, may be ok, but taking that as the actual distribution and or the actual bird composition of a pixel should be taken with care. I know it is common usage, but that does not mean that it is exempt from errors or uncertainty that should be addressed at some point in the manuscript.
- Canopy traits are based on satellite images thus despite they are calibrated it is still a proximate inference of the actual trait value of the plant assemblage. In addition, the pixel size looks a bit big (1 ha) regarding the fine grain of the inferred traits (tree/plant/individual based). I know it's an integration of what the satellite/s can detect and thus is the result from the group of species in the pixel, nevertheless, it is dubious to make such an enormous extrapolation.
- The study is correlational while the authors insist on inferring causal associations between the variables. The association between the canopy and some bird variables exists regarding your results but it is not likely to find a causal association between them with a random forest procedure.
- Some of the bird assemblage variables used are redundant or are not clear how they represent different aspects of the bird assemblage (e.g. bird order and bird family).
- Why do you have first FFC and then FFG? Based on what are you over clustering that? The criteria are not informed and, as occurs in the bird variables, it is not clear how this is helping to understand the association between the canopy and bird assemblages.
- How much is enough explanation? Based on what are you saying that? We can agree that 90% is a lot but why 50? There is another 50 not explained that can be as likely as the 50% you are interpreting. In addition, don't you have a confidence/credibility/accuracy metric for the percentage estimations? It is not the same to have $90\% \pm 40$ that $90\% \pm 5$. It should be good to give the reader the decision to rely on your results based on a few more cues.

In addition to these points, I think the manuscript is highly driven by a conservation approach which is fine. The ecological questions that I would expect based on the title and some sentences of the introduction are missing. I felt that was not clear when authors tried to give ecological explanations to the results in which the readers can find sentences that come out of nothing with really strong statements with not even a reference (e.g. L119-120). I find that maybe the amount of space required by the journal is not helping to address the points I raised, obscuring the really cool findings of the study.

(Remarks on code availability)

Reviewer #2

(Remarks to the Author)

This manuscript aims to provide tools to aid conservation at the national scale. The scale of the analysis is impressive, covering 1492 bird species across the entire forested area of Peru. The results are compelling, with a 90 % correlation between canopy composition and bird taxonomic diversity. To caveat this review, I should point out that my expertise is on remote sensing of forest structure and composition, not on bird conservation. Nevertheless, some of the methods are unclear to me, and I am therefore unsure how robust the inferences are.

Major comments

1. The key finding of this study is that canopy functional composition predicts various bird diversity metrics. However, it is currently unclear how much information the canopy functional composition adds, since there is no null model to compare this against. For example, figure 1a suggests that some of the variation in bird diversity is simply explained by elevation, not canopy functional composition. Also, it would be really valuable to distinguish between variation explained by canopy structure metrics (which can be more easily measured) and canopy chemistry (which are unique to this proprietary data set and therefore hard to generalize). I would suggest that the authors provide three models for each metric of bird diversity. Model 1: bird diversity ~ topography + environment. Model 2: bird diversity ~ topography + environment + canopy structure. Model 3: bird diversity ~ topography + environment + canopy structure + canopy chemistry. The difference between these models represents the amount of additional variation explained by the unique data set in this study.
2. The ecological significance of the FFGs are not clearly explained in the manuscript. The interpretation of results relies heavily on the difference between these FFGs. I would suggest the authors add a table describing each of the FFGs in ecological terms, with some comment on how they are relevant for birds.
3. I think the FFCs could be removed from the main text. As far as I understand it, both the FFCs and FFGs represent clusters of forest functional composition. FFCs are in 36 groups while FFGs are in 6 groups. The authors show that FFGs are sufficient to explain bird diversity. However, the first paragraph of the results section focuses on the difference between FFCs and FFGs, which isn't particularly valuable for the reader.
4. I could not find the data on the links provided. The first link 'geoservidor.minam.gob.pe' opens a landing page without any reference to this study. Could you provide the specific link where the data is deposited? The second link (figshare) provides some summary data and R code. I would expect the rasters showing FFGs and polygons showing bird distributions to be provided, along with an R script which replicates the analysis from there.
5. I think the analysis may suffer from the statistical issues described here: Ploton, Pierre, et al. "Spatial validation reveals poor predictive performance of large-scale ecological mapping models." *Nature communications* 11.1 (2020): 4540. I would suggest you test the variance explained using a set of pixels which are (a) independent of the training data and (b) spatially distinct enough to avoid autocorrelation issues. I may have missed something in my recollection of the Ploton et al paper, so please check it.
6. No quantification of uncertainty. The abstract states that 90% of the variance was explained, but there is no uncertainty estimate on this number or on any others (or in the figures) in this manuscript.
7. I don't really understand how to interpret the colours in Fig 1b. The first bar tells me that 90% of the variance in taxonomic family is explained by FFGs. How did you then partition the variance explained between the different FFGs (the colours?). Could each bar be replaced by a single point?
8. The single figure is difficult to read / interpret. I'd suggest it is split into two separate figures. The map would be easiest to interpret alongside a map of elevation in Peru. Panels B and C could form their own figure and the size of the text increased. Figure 1C is missing labels / units on the x-axis. The colour scheme doesn't could be improved to make it more accessible, particularly the red-green contrast which is quite important in the southern half of Peru.

Comments on the writing

- Line 19-21. Please split this sentence in two. At present, it suggests that the 90% of variance explained applies to the other bird traits as well. Also, please add an uncertainty estimate to the 90%.
- Lines 25-55. This section could be re-structured. Currently, the results are reported in the first paragraph and the importance of the study is introduced in the second paragraph. I'd suggest these are swapped around to improve the flow.
- Line 119-120. 'Our results confirm that forests with different functional traits offer different cavity types and locations for nests'. I don't think this is supported by the results. This could be a possible explanation of the association between bird diversity and FFGs, but I don't think this study has any data on the different cavity types and location for nests.
- Methods section. This section introduces 11 acronyms which are not used elsewhere in the manuscript. Could you write these out in full?

(Remarks on code availability)

The main issue is that I cannot find the data on either of the links the authors provide. The figshare link provides summary data and the R code can reproduce the figures from this. However, to make this analysis reproducible the authors would need to provide the geographically explicit data and the code to reproduce the analysis from this. The code could also be much better commented to help the user understand what is going on.

Reviewer #3

(Remarks to the Author)

The study makes a substantial contribution to the fields of functional biogeography and conservation biology by providing a novel approach to linking forest canopy traits with bird diversity. While the research is methodologically rigorous and the

results are compelling, further work is needed to test the framework in other regions and incorporate broader ecological variables.

- The study demonstrates that 90% of the variance in bird taxonomic diversity in Peru can be explained by forest canopy functional diversity. This strong correlation highlights the importance of canopy functional traits, such as nutrient and water composition, in shaping bird diversity and their ecological traits.
- The findings suggest that mapping functional diversity can be a powerful tool for prioritizing conservation efforts, especially for forest-dependent birds with small geographic ranges and specialized habitat needs.
- The integration of remote sensing data with ecological modeling is a noteworthy methodological advance, enabling large-scale, high-resolution biodiversity assessments.

The study bridges a critical gap by connecting forest canopy functional traits with bird ecology and conservation, offering a framework for similar studies in other biodiverse regions.

- While previous research has addressed forest functional diversity (e.g., Asner et al., 2017), this study uniquely links these traits to bird functional and taxonomic diversity, expanding the scope of functional biogeography.
- The research is original in its use of a nationwide canopy functional diversity map to inform biodiversity conservation strategies. Relevant prior studies (e.g., Schneider et al., 2017) focused on forests' internal dynamics but did not explicitly relate them to animal communities.
- The conclusions are well-supported by:

- o Comprehensive data analysis using the Random Forest model, explaining a significant portion of variance in bird traits and taxonomy.
- o Robust methodological validation, including the use of established databases (e.g., BirdLife International) and cutting-edge remote sensing technologies.

While the study is methodologically sound, further research could verify the transferability of its findings to other tropical regions.

Data Analysis and Interpretation

- o Clear explanation of methods and statistical models.
- o Effective visualization of results through maps and variance explanation charts.
- o While the Random Forest model is powerful, its interpretability is limited. Additional sensitivity analyses or alternative models (e.g., generalized linear models) could strengthen causal inferences.
- o The study focuses on forest-dependent birds, potentially overlooking interactions with non-forest-dependent species. The methodology is robust, combining ecological data, high-resolution remote sensing, and machine learning.
- Sufficient detail is provided, including access to data repositories (e.g., FigShare). However, the dependence on specialized equipment (e.g., GAO) may limit replication by other researchers without similar resources in other parts of the world.

My recommendations:

1. The authors are advised to incorporate non-forest-dependent bird species to evaluate broader biodiversity patterns.
2. The authors are advised to supplement Random Forest analysis with models capable of testing specific causal hypotheses.
3. Perhaps consider global comparisons: Extend the framework to other biodiverse regions to assess its universality.
4. Include explicit modeling of anthropogenic threats (e.g., deforestation) to link functional diversity with conservation outcomes more directly.
5. The authors provide exemplary transparency, sharing both data and methods openly. However, the study would benefit from a detailed discussion on the limitations of remote sensing data and potential biases.

(Remarks on code availability)

To enhance the repeatability and reproducibility of the provided R code, the following recommendations can be implemented:

1. Provide Clear Documentation

Comments: Add detailed comments explaining the purpose of each code block and function.

Variable Descriptions: Include descriptions for each variable loaded (e.g., var1, var2) to clarify their role in the analysis.

2. Ensure Code Modularity

Function Encapsulation: Create reusable functions for repeated tasks, such as calculating variable importance or training Random Forest models. For instance:

```
run_random_forest <- function(data, formula, ntree=1000, seed=52) {  
  set.seed(seed)  
  model <- randomForest(formula, data=data, importance=TRUE, proximity=TRUE, ntree=ntree, na.action=na.omit)  
  return(model)  
}
```

Use this function throughout the script to ensure consistency.

3. Use Relative File Paths

Ensure file paths are relative and not system-dependent:

```
PEbirds <- read.csv("data/GAO_Peru_birds.csv")
```

Include a check for the existence of files with:

```
if (!file.exists("data/GAO_Peru_birds.csv")) stop("Data file not found!")
```

4. Add Input Validation

Validate the data before analysis to avoid runtime errors:

```
if (!all(c("FFG_1", "FFG_2") %in% colnames(PEbirds))) {  
  stop("Required columns are missing in the dataset.")  
}
```

5. Output Reproducible Results

Set Random Seeds: Use consistent random seeds across all analyses.

```
set.seed(123)
```

Save Results: Save model objects and intermediate results to files for easy inspection and re-use:

```
save(out.PEbirds, file="results/RandomForestModel.RData")
```

6. Enable Parameterization

Use configurable parameters at the start of the script for easy adjustments:

```
params <- list(  
  ntree = 1000,  
  seed = 52,  
  input_file = "data/GAO_Peru_birds.csv",  
  output_dir = "results/"  
)
```

7. Provide a Comprehensive README

Add a README file in the working directory with instructions on:

Required libraries and installation commands.

Input file formats and examples.

Steps to execute the script.

8. Version Control

Use a version control system like Git to track changes to the codebase. Include versioning in filenames to indicate script and data versions.

9. Include Data Integrity Checks

Ensure the input dataset matches the expected structure:

```
if (any(is.na(PEbirds$FFG_6))) warning("Missing data detected in FFG_6.")
```

10. Facilitate Dependency Management

Use renv or similar R package for dependency management to ensure all libraries are correctly installed:

```
library(renv)  
renv::init()
```

11. Add Tests

Include test cases for key functions to validate their performance with a minimal test dataset.

By implementing these steps, the code will be more reliable, understandable, and easier to reproduce by other researchers.

Version 1:

Reviewer comments:

Reviewer #2

(Remarks to the Author)

I was asked to check this manuscript again, with a focus specifically the authors response to reviewer 3. I think their response to reviewer 3 is very good, and I'm happy that they addressed all of the concerns that were raised in a reasonable way.

I've made this point before, but I still feel that the omission of the more basic variables we would expect to affect bird diversity is an substantial flaw in this analysis. Bird distributions are likely to be affected by temperature, particularly temperature extremes (e.g. coldest night time temperature, or hottest daytime temperature). Simultaneously, temperature is likely to covary with the forest function types used by the authors (everything covaries with elevation). We therefore cannot tell whether bird distributions are indeed driven by the forest functional types or simply temperature.

I do believe that canopy function types are likely to contain valuable information for the prediction of bird diversity. However, to demonstrate this the study would need to build a credible null model against which to test the value of canopy functional types.

(Remarks on code availability)

No

Reviewer #4

(Remarks to the Author)

I have read and reviewed a manuscript entitled "Canopy functional composition as an indicator of bird community traits and vulnerability in tropical Peruvian forests". I was invited to join the review process in a subsequent round, specifically replacing Reviewer #1. I was given the task of reviewing the author's response to reviewer's comments and checking if the main issues raised were solved.

Overall, I acknowledge the authors' substantial efforts in improving the manuscript. The analytical framework is both relevant and important, and the revisions have resolved most of the issues previously raised. Now, the analyses used are well described and fit well with the objective of the study and the tone of causality has been removed. However, although I have a very positive impression of the article, it is marred by an important theoretical issue of trait-based ecology. They used a refined method of obtaining plant functional traits with impressive resolution, but their way of relating them to bird functional traits is theoretically weak.

My main concern is that the authors introduce circularities in both parts of the analyses by defining some of the species observational (distributional) data as functional traits. In consequence, the study results are not overly meaningful in their current conditions.

But let me shortly explain the circularity issue. Functional traits are (in the strict sense) defined as morpho-physio-phenological traits (including social and behavioral traits for animals) that impact fitness via their effects on growth, reproduction, and survival of an individual (Violle et al. 2007 - <https://doi.org/10.1111/j.0030-1299.2007.15559.x>). This definition excludes information that is defined only at larger levels of aggregation, such as populations or species. Examples of the latter are habitat width, range size, or anything that relies on data obtained from species distributions across environmental gradients. A good example of this definition escape is defining a species as forest specialist/dependent or been migratory or not.

The authors introduced a few birds "functional traits" to their analysis that do not only not follow that definition but also, they use forest category that varied in vegetal structure like density and height to explain if a bird is forest dependent or not by living in those places. This approach introduces a form of circularity into the analysis, which undermines the interpretability of the results. For example, they use the FFG Amazon Swamp to explain a bird be low forest dependent. This is essentially equivalent to stating that a species has low forest dependence simply because it occurs in open habitats. The actual trait should be traits that allows birds individuals to live in that habitat.

Given the broad readership of Nature Communications, it is important that this misunderstanding of trait-based theory is addressed before publication, even though these traits did not show relevant relationships in this study. Furthermore, the presence of these nonfunctional traits only inflates the ordination technique with unconstrained variance.

This circularity concerns at least the following traits: Migratory Status, Forest Dependency and Distribution Size. These variables are derived from the observational study on species occurrence and not on independent measurements on the individuals/species. I would suggest the authors to redo the analysis including only those traits that are independent of the response variables. Regarding Mean generation length, I suggest not calling it a functional trait, but rather a life-history strategies trait, as it is calculated at the population level and reflects the rate of change of individuals in populations.

Previous reviewer #1 raised the limitation of using artificial bird assemblages, and I agree with their comment. Although the authors included a brief discussion of the limitations of this approach, I believe more needs to be done, such as making the ecological reliability of these communities transparent. Although the assessment is being made at the country level, it is still a very small area compared to the species' distribution areas, and there is likely no variation in species richness due to this. Therefore, I suggest that the authors provide a brief description of bird species richness across the raster cells under evaluation. Reporting the minimum, maximum, mean, and standard deviation of species richness would enhance transparency and allow readers to better assess the robustness of the results. Additionally, including a raster plot of bird species richness across Peru in the supplementary material would be highly valuable for readers, providing a clear visual complement to the descriptive statistics.

Besides these main points, I would also like to highlight some minor issues that require adjustment:

Lines 161–166: The authors state:

“High dependency on forest can influence conservation status of birds and other vertebrates 14,15. This dependency is especially important when forests are threatened by logging for timber or clearing for crops, plantations, and livestock farming 11, so predicting the extent of their forest dependency can have important conservation implications. Conserving functionally diverse forests could not only protect tree species but also diverse communities of birds depending on them.” However, the results clearly indicate that different levels of forest dependence were not associated with the PCA axes, and therefore showed no relationship with FFGs. As such, this part of the discussion is not supported by the results. Moreover, removing these variables from the set of functional traits would help ensure that the discussion remains fully grounded in the analyses presented.

Line 150 Are the avifaunas present in the Amazonian swamp forest (FFG5) said to have potentially low ecological resilience? Based on what results do the authors suggest this ecological condition? Ecological resilience refers to a community's capacity to maintain its functional roles in the face of environmental impacts and local extinctions, which is typically assessed through measures such as functional redundancy and the degree of niche packing. As these analyses were not conducted, this interpretation is not supported by the results and should be reconsidered or clarified.

Line 197 – 200 In my view, this approach does not provide a sufficiently “efficient” means to assess how forest changes may affect bird communities. The study relies on artificial communities, which limits the scope of inference; consequently, the results indicate potential patterns rather than demonstrated effects. Moreover, the authors imply impacts on bird community dynamics, but the study does not explicitly evaluate community dynamics. This point should be clarified to avoid overstating the conclusions.

Citation 28: This reference appears unusual, as it combines two data sources: the Lynx publisher's HBW and the BirdLife Datazone. I recommend that the authors separate these references clearly and specify in the supplementary material which traits were obtained from each source.

(Remarks on code availability)

The code <https://doi.org/10.6084/m9.figshare.12894230> directs to a figshare.com page with a 404 error (the page cannot be found/The page you are looking for does not exist or has been removed.)

Version 2:

Reviewer comments:

Reviewer #2

(Remarks to the Author)

Model selection

I appreciate the effort the authors have made to implement my previous suggestions on model selection. The results are now more believable. However, I still think this manuscript requires a better ‘null’ model to improve upon.

The FFGs may well contain vital information that is not available elsewhere. However, I find the FFGs difficult to interpret and I don't think they are easily reproducible in other ecosystems (the discussion suggests they may be with satellite data, but this would also require a massive field campaign for calibration). In general, model selection should aim to find the simplest model which explains the data. I therefore think the analysis should test more of the common variables used to explain biodiversity before adding the FFGs. For example would suggest the authors include canopy height (separate from the FFGs) and distance to nearest road as predictors. In addition, the authors should check what variables other studies explaining large scale trends in biodiversity have used. In fact, I think there should be a discussion of previous ‘biodiversity models’ in the introduction. The claim of this study is that FFGs improve on previous ‘biodiversity models’, but this is not yet supported by the results.

I notice that the claim that FFGs explain 90% of bird diversity has been removed. Could the authors update this figure instead of removing it? At the moment, there is very little quantitative detail about how useful FFGs are. The manuscript states that (a) FFGs are informative for fewer bird traits than elevation and cloud cover but (b) when they are informative they are usually more important than elevation and cloud cover. This doesn't give me a clear answer on how important FFGs are.

In conclusion, the methods and results are such that all three scenarios below seem plausible to me:

Scenario 1: The variation in bird traits are explained by elevation (20%), cloud cover (20%) and FFGs (40%), with the remaining 20% unexplained.

Scenario 2: The variation in bird traits are explained by elevation (30%), cloud cover (30%) and FFGs (10%), with the remaining 30% unexplained.

Scenario 3: The variation in bird traits are explained by elevation (5%), cloud cover (5%) and FFGs (5%), with the remaining 85% unexplained.

Can you please improve the methods and clarify the results to ensure this is clearer.

Principal components of bird traits

The analysis of bird traits has completely changed in this version of the manuscript. The previous version directly used traits such as territoriality and nest placement, while the new version uses principal components of the bird traits. Can you explain the reason for this shift? This may well be a reasonable decision, but in my role as a sceptical reviewer I want to double check that the analysis was not changed because of a lack of significant results.

This new principal component analysis is also less interpretable. Apart from functional PC1, all PCs explain less than 30% of the variation in the trait space. A typical model result is therefore that, elevation and cloud cover explains 40 % of the variance in PC2, which itself explains 18 % of the variance in these traits. This is even more complicated when the FFGs are included, which are effectively principal components of another trait space!

I understand that this type of analysis may be necessary when comparing two multi-variate trait spaces and I don't think it is wrong in principle. However, if there are more easily interpretable results available (such as 'vulnerable bird species are mostly confined to high elevations with the tallest forests, suggesting that these are intact areas') I think these should be prioritized.

Conservation implications

The manuscript states that these results will be useful for conservation, but I am not sure how. Could you give some examples? The introduction states that: 'From a conservation perspective, it is critically important to understand how animals use remaining habitats and how they might respond to threats'. How can your results be used to help understand this latter question?

The final paragraph of the discussion states that 'While our goal was not to identify specific conservation areas, we demonstrated that remotely sensed data can be translated into important information concerning bird functional diversity'.

(Remarks on code availability)

Reviewer #4

(Remarks to the Author)

I have read and reviewed the manuscript now titled "Canopy functional composition as an indicator of bird traits, taxonomy, and vulnerability in tropical Peruvian forests." The authors significantly improved research reliability by adding data descriptions in the text and supplementary materials and by removing unsupported overstatements. They also eliminated circularity issues from the analysis. These changes enhanced transparency and ecological interpretability. The authors acknowledge that their results have limitations and should be used to complement assessments of real bird communities. The only suggestion I can offer now concerns line 339 of the current manuscript, which exhibits some character incompatibility in the model equations. Please pay attention to the ¶ symbols. Therefore, I believe that the manuscript is ready to be published.

(Remarks on code availability)

Now, the authors have provided access to the code and data in the link: <https://figshare.com/s/f84d0cdf27f96c850dcc>

Version 3:

Reviewer comments:

Reviewer #2

(Remarks to the Author)

Thank you for addressing my previous comments and improving the manuscript. I still have an important concern about the statistics.

In your response and in supplementary table 2, you state that you select the best model considering all potential factors including FFGs. You then remove the FFGs and test again to determine the contribution of the FFGs. I think this is the wrong way around and will artificially inflate the contribution of the FFGs.

Instead, I suggest you build the best null model possible using commonly used factors. Then, add the FFGs and determine how much additional variance they explain. This seems like a small change but I think it might significantly change the results.

To understand the difference between these two approaches, let's take an example. Let's assume (for the sake of argument) that bird trait A is correlated with elevation, canopy height and FFG1. If we assume that FFG1 is strongly correlated with canopy height, the most parsimonious model (model A) may include only elevation and FFG1. By your definition, the additional variance explained by FFG1 is given by the difference between model A and an elevation only model (model B). However, this erroneously assigns the variance that would be explained by canopy height to FFG1. In my approach you should build the best null model without any FFGs (bird trait A ~ elevation + canopy height, model C). You then add FFG1 to this model to determine the additional variance explained.

The key principle here is that we should build simple models wherever possible, and reserve more complex factors (FFGs) for cases where they are actually necessary.

(Remarks on code availability)

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Detailed response to reviewers
NCOMMS-24-56668-T

Reviewer #1

Comment:

I have reviewed the article entitled “Forest birds track canopy functional traits in the Peruvian Andes and Amazon” in which authors show how to integrate GIS that characterizes canopy proxies of tree traits with bird variables at the assemblage level. Although the topic is very appealing and interesting (and indeed needed), the manuscript does not match the expectations raised when reading the title. Based on the results and the reading the title should be changed since the authors did not address animal movement (or actual bird assemblage associations) in relation to canopy traits but how artificial bird assemblage variables relate with satellite-inferred canopy traits.

Response:

We thank the reviewer for their thoughtful and constructive feedback and time. As requested, we undertook a major revision of the manuscript, including substantial reanalysis of the data and updates to the statistical framework. We now use Bayesian multivariate models rather than Random Forest classification to more appropriately estimate the strength and uncertainty of associations between bird traits and remotely sensed forest functional groups. We agree that the title had to be changed to better reflect the findings of the study. Hence, we changed it to “Canopy functional composition as an indicator of bird community traits and vulnerability in tropical Peruvian forests”.

Comment: The article seems to be a tool-centered study in which authors tested how well a result from the GIS clustering based on proxies of tree traits is correlated with artificial bird assemblages’ variables. In general, it shows nice results in which the inferred canopy traits are indeed correlated with bird assemblages’ variables. The authors then highlight the usefulness of the satellite-based canopy description to infer things about the bird assemblages. Here is where I have my major concerns:

Bird assemblages are artificial: overlapping polygons from Birdlife, may be ok, but taking that as the actual distribution and or the actual bird composition of a pixel should be taken with care. I know it is common usage, but that does not mean that it is exempt from errors or uncertainty that should be addressed at some point in the manuscript.

Response: We agree with the reviewer that this approach involves uncertainty. However, at a country level analysis for all bird species in the given region, this is the best approximation we can use at this time. Nevertheless, in the revised manuscript, we now explicitly acknowledge the limitations of using BirdLife polygon ranges to infer species presence, including potential overestimation of local species richness and lack of local abundance data. While this is a widely used approach in broad-scale ecological modelling, we make clear that the resulting assemblages are inferred estimates and not direct observations. We also clarify that our aim was to test broad-scale patterns of trait structure in relation to canopy functional composition and not fine-scale assemblage composition per pixel.

Comment: Canopy traits are based on satellite images thus despite they are calibrated it is still a proximate inference of the actual trait value of the plant assemblage. In addition, the pixel size looks

a bit big (1ha) regarding the fine grain of the inferred traits (tree/plant/individual based). I know it's an integration of what the satellite/s can detect and thus is the result from the group of species in the pixel, nevertheless, it is dubious to make such an enormous extrapolation.

Response: We appreciate this important point. The satellite-based data used (from Asner *et al.* 2017) are mainly based on airborne imaging spectroscopy, not coarse-resolution satellite data, and represent some of the most detailed canopy trait estimates currently available at a national scale. The 1-ha pixel resolution balances the detectability of canopy traits with landscape-scale coverage, enabling national-scale analysis while capturing functional heterogeneity across forest types. We now explain this more clearly in the revised Methods, and discuss the aggregated nature of canopy traits and potential scale mismatches with bird traits in the Discussion. We emphasize that our results reflect associations at landscape and regional scales, which may not hold at finer local scales.

Comment: The study is correlational while the authors insist on inferring causal associations between the variables. The association between the canopy and some bird variables exists regarding your results but it is not likely to find a causal association between them with a random forest procedure.

Response: We agree and have removed any language implying causal inference. Additionally, we have replaced the previous Random Forest analysis with a Bayesian multivariate model that allows us to test associations between forest functional groups and bird trait PCs, while also estimating posterior distributions and credible intervals. This better communicates the strength and uncertainty of these associations and avoids implying causality.

Comment: Some of the bird assemblage variables used are redundant or are not clear how they represent different aspects of the bird assemblage (e.g. bird order and bird family).

Response: Thank you for this observation. In the revised analysis, we restructured the taxonomic variables using principal components analysis (PCA) on bird assemblage composition by taxonomic level. Rather than treating each taxonomic group as a separate response, we extracted major orthogonal axes of taxonomic structure. This approach avoids redundancy and better captures variation in community composition across FFGs. We now explain this revised framework in the Methods and justify how it reduces dimensionality while retaining interpretability.

Comment: Why do you have first FFC and then FFG? Based on what are you over clustering that? The criteria are not informed and, as occurs in the bird variables, it is not clear how this is helping to understand the association between the canopy and bird assemblages.

Response: We apologize for the earlier lack of clarity. FFCs (forest functional classes) refer to the original 36 canopy functional clusters identified via unsupervised clustering on multiple spectral and structural canopy traits. FFGs (forest functional groups) are broader aggregations of these classes into six ecologically interpretable groups, following previous work by Asner *et al.* (2017). We now clearly define these terms and justify the grouping based on their prior ecological validation, and their utility for reducing model complexity in trait-association testing.

Comment: How much is enough explanation? Based on what are you saying that? We can agree that 90% is a lot but why 50? There is another 50 not explained that can be as likely as the 50% you are interpreting. In addition, don't you have a confidence/credibility/accuracy metric for the percentage estimations? It is not the same to have $90\% \pm 40$ that $90\% \pm 5$. It should be good to give the reader the decision to rely on your results based on a few more cues.

Response: In the revised version, we no longer emphasize a specific percentage of "variation explained" as a definitive threshold. Instead, we present posterior means and 95% credible intervals from Bayesian models for all associations. These intervals are now reported in the tables and visualized in Fig. 2. We interpret these associations cautiously, highlighting where uncertainty spans zero. We also revised the language to avoid deterministic claims and instead emphasize the relative strength and direction of associations across forest types.

Comment: In addition to these points, I think the manuscript is highly driven by a conservation approach which is fine. The ecological questions that I would expect based on the title and some sentences of the introduction are missing. I felt that was not clear when authors tried to give ecological explanations to the results in which the readers can find sentences that come out of nothing with really strong statements with not even a reference (e.g. L119-120). I find that maybe the amount of space required by the journal is not helping to address the points I raised, obscuring the really cool findings of the study.

Response: Thank you for this thoughtful feedback. In our revision, we made several changes to better integrate ecological theory and interpretation. We now more clearly frame the study as a test of how canopy functional diversity relates to ecological and life-history traits in birds, which has implications for conservation, but is grounded in ecology. We also streamlined the conservation language in the Abstract and Results to give greater space to ecological insights emerging from the analyses. We agree that space constraints made full elaboration difficult, but we revised inline text to improve clarity without exceeding limits.

Reviewer #2

Comment:

This manuscript aims to provide tools to aid conservation at the national scale. The scale of the analysis is impressive, covering 1492 bird species across the entire forested area of Peru. The results are compelling, should point out that my expertise is on remote sensing of forest structure and composition, not on bird conservation. Nevertheless, some of the methods are unclear to me, and I am therefore unsure how robust the inferences are.

Response:

We thank the reviewer for their positive recognition of the scale and potential conservation relevance of our study. In response to the concern regarding methodological clarity and inference robustness, we undertook substantial revisions to improve transparency and interpretability. Specifically, we replaced our original Random Forest models with a Bayesian multivariate modelling framework, which offers clearer effect estimates and more robust statistical inference. We also added detailed explanations of our trait processing, model structure, and remote sensing inputs to improve accessibility for readers from both ecological and remote sensing backgrounds. We hope these revisions make the methods and conclusions more transparent and compelling, regardless of disciplinary expertise.

Comment: Major comments

1. The key finding of this study is that canopy functional composition predicts various bird diversity metrics. However, it is currently unclear how much information the canopy functional composition adds, since there is no null model to compare this against. For example, figure 1a suggests that some of the variation in bird diversity is simply explained by elevation, not canopy functional composition. Also, it would be really valuable to distinguish between variation explained by canopy structure metrics (which can be more easily measured) and canopy chemistry (which are unique to this proprietary data set and therefore hard to generalize). I would suggest that the authors provide three models for each metric of bird diversity. Model 1: bird diversity ~ topography + environment. Model 2: bird diversity ~ topography + environment + canopy structure. Model 3: bird diversity ~ topography + environment + canopy structure + canopy chemistry. The difference between these models represents the amount of additional variation explained by the unique data set in this study.

Response: We appreciate the reviewer's insightful suggestion to decompose the contribution of canopy structure and chemistry using nested models. Following major revision, we replaced the original Random Forest framework with a Bayesian multivariate modelling approach to more explicitly quantify how forest functional group (FFG) composition relates to species-level bird traits. In these revised models, we did not include additional covariates such as elevation, topography, or climate for the following conceptual and methodological reasons.

First, as described in Asner *et al.* (2017), the forest functional classes (FFCs) and groups (FFGs) used in our analysis were derived purely from airborne imaging spectroscopy and LiDAR data. These were constructed by clustering seven remotely-sensed canopy traits (including chemical and structural features) without the inclusion of topographic or environmental variables. Although canopy trait distributions are themselves shaped by underlying factors like geology, elevation, and slope, these covariates were only used post hoc in Asner *et al.* (2017) to interpret spatial patterns of FFGs, not as inputs to their creation. Thus, FFCs and FFGs implicitly capture broad-scale

environmental variation through their trait profiles (e.g., leaf nitrogen concentrations, LMA, canopy height), while remain rooted in direct biological measurements.

Second, including topographic or climatic covariates in our models would introduce a high degree of collinearity with the FFG predictors. Since FFG composition reflects ecological variation driven by environmental gradients, separating these effects statistically is problematic and could lead to misleading or circular interpretations. Including such predictors might also reduce the interpretability of the FFG effect sizes, which are our core interest in this study.

Finally, we believe our revised multivariate modelling approach provides stronger inference than the previous machine learning approach. Our framework explicitly quantifies the relationship between FFGs and bird functional, threat, and taxonomic traits, with full propagation of uncertainty, model diagnostics, and interpretable posterior estimates. Rather than focusing on model comparison or partitioning variance, our goal was to reveal how multidimensional forest functional composition relates to key axes of bird diversity, a question better addressed via our current approach.

Comment: 2. The ecological significance of the FFGs are not clearly explained in the manuscript. The interpretation of results relies heavily on the difference between these FFGs. I would suggest the authors add a table describing each of the FFGs in ecological terms, with some comment on how they are relevant for birds.

Response: Agreed and thank you for this helpful suggestion. We have now given each forest functional group (FFG) a short descriptive name and added a new table (Table 1) that summarizes the ecological characteristics of each FFG. This includes key canopy traits and observed associations with bird assemblages from our trait-based models. We believe this table greatly improves the interpretability of our findings and clarifies how forest functional composition relates to bird ecology and conservation.

Comment: 3. I think the FFCs could be removed from the main text. As far as I understand it, both the FFCs and FFGs represent clusters of forest functional composition. FFCs are in 36 groups while FFGs are in 6 groups. The authors show that FFGs are sufficient to explain bird diversity. However, the first paragraph of the results section focuses on the difference between FFCs and FFGs, which isn't particularly valuable for the reader.

Response: Thank you, we have now streamlined the Results to focus on the six FFGs used in modelling. Discussion of the FFCs (used for clustering input) is now confined to the Methods, and the first paragraph of the Results no longer emphasizes differences between FFCs and FFGs. This keeps focus on the more interpretable and actionable six-group classification.

Comment: 4. I could not find the data on the links provided. The first link 'geoservidor.minam.gob.pe' opens a landing page without any reference to this study. Could you provide the specific link where the data is deposited? The second link (figshare) provides some summary data and R code. I would expect the rasters showing FFGs and polygons showing bird distributions to be provided, along with an R script which replicates the analysis from there.

Response: We thank the reviewer for noting this oversight. The geoservidor.minam.gob.pe link refers to the national environmental portal where base forest layers are hosted, but we agree this is

not specific enough. We have now updated the Data Availability section with a direct link to the FFC and FFG maps in GeoTIFF format. We also updated the FigShare link hosting not only the trait matrix and the new (and better annotated) R-code, but also the bird distribution polygons used. These updates ensure full reproducibility of the results.

Comment: 5. I think the analysis may suffer from the statistical issues described here: Ploton, Pierre, et al. "Spatial validation reveals poor predictive performance of large-scale ecological mapping models." *Nature communications* 11.1 (2020): 4540. I would suggest you test the variance explained using a set of pixels which are (a) independent of the training data and (b) spatially distinct enough to avoid autocorrelation issues. I may have missed something in my recollection of the Ploton et al paper, so please check it.

Response: We thank the reviewer for highlighting the Ploton *et al.* (2020) study and the importance of accounting for spatial autocorrelation in ecological modelling. In our case, the forest functional classes (FFCs) and groups (FFGs) were not generated via supervised predictive modelling, but rather through clustering of field-calibrated canopy trait maps (Asner *et al.* 2017). These maps were built using imaging spectroscopy and LiDAR data, with trait retrieval models calibrated and validated using 79 one-hectare field plots spanning large environmental and spatial gradients (see: Asner *et al.* 2015. Quantifying forest canopy traits: Imaging spectroscopy versus field survey. *Remote Sensing of Environment* 158, 15–27. doi:10.1016/j.rse.2014.11.011). Because our functional diversity framework is based on direct measurements of canopy chemistry and structure, rather than predictive models fit to response data (e.g., biomass or bird diversity), it is less vulnerable to the overfitting risks raised by Ploton *et al.* (2020). We have clarified this in the revised Methods and cite the study to acknowledge this important issue.

Comment: 6. No quantification of uncertainty. The abstract states that 90% of the variance was explained, but there is no uncertainty estimate on this number or on any others (or in the figures) in this manuscript.

Response: We appreciate this important point. Unlike our earlier machine learning analysis, which quantified variance explained in a more deterministic framework, the Bayesian multivariate models used now offer a probabilistic perspective that incorporates uncertainty and better reflects the complexity of ecological systems. In our revision, we now include credible intervals (95% intervals) for all estimates based on posterior distributions from our Bayesian regression models. This change ensures greater transparency and allows readers to better assess model confidence.

Comment: 7. I don't really understand how to interpret the colours in Fig 1b. The first bar tells me that 90% of the variance in taxonomic family is explained by FFGs. How did you then partition the variance explained between the different FFGs (the colours?). Could each bar be replaced by a single point?

Response: During the major revision of the manuscript, we have replaced this figure with new ones.

Comment: 8. The single figure is difficult to read / interpret. I'd suggest it is split into two separate figures. The map would be easiest to interpret alongside a map of elevation in Peru. Panels B and C could form their own figure and the size of the text increased. Figure 1C is missing labels / units on

the x-axis. The colour scheme doesn't could be improved to make it more accessible, particularly the red-green contrast which is quite important in the southern half of Peru.

Response: We have replaced this single figure and now split into different ones that plot the results of our new modelling approach.

Comment: Comments on the writing

• Line 19-21. Please split this sentence in two. At present, it suggests that the 90% of variance explained applies to the other bird traits as well. Also, please add an uncertainty estimate to the 90%.

Response: We have replaced this sentence considering the new results.

Comment: Lines 25-55. This section could be re-structured. Currently, the results are reported in the first paragraph and the importance of the study is introduced in the second paragraph. I'd suggest these are swapped around to improve the flow.

Response: Thank you for your suggestion. We have followed the journal's initial summary paragraph structure, but we agree and now re-structured the introduction for a better flow.

Comment: Line 119-120. 'Our results confirm that forests with different functional traits offer different cavity types and locations for nests'. I don't think this is supported by the results. This could be a possible explanation of the association between bird diversity and FFGs, but I don't think this study has any data on the different cavity types and location for nests.

Response: After rewriting the Discussion, we removed this sentence.

Comment: Methods section. This section introduces 11 acronyms which are not used elsewhere in the manuscript. Could you write these out in full?

Response: Thank you for this suggestion. We removed the unnecessary acronyms from the text and only kept the forest functional classes (FFC) and groups (FFG) as those are widely used in the manuscript.

Comment: Remarks on code availability

The main issue is that I cannot find the data on either of the links the authors provide. The figshare link provides summary data and the R code can reproduce the figures from this. However, to make this analysis reproducible the authors would need to provide the geographically explicit data and the code to reproduce the analysis from this. The code could also be much better commented to help the user understand what is going on.

Response: We updated the FigShare link that now contains the bird range polygons, trait database, and annotated R-script used in the study. We also added a direct link to the FFC and FFG maps in GeoTIFF format. We now better commented the new R-script used.

Reviewer #3

Comment:

The study makes a substantial contribution to the fields of functional biogeography and conservation biology by providing a novel approach to linking forest canopy traits with bird diversity. While the research is methodologically rigorous and the results are compelling, further work is needed to test the framework in other regions and incorporate broader ecological variables.

- The study demonstrates that 90% of the variance in bird taxonomic diversity in Peru can be explained by forest canopy functional diversity. This strong correlation highlights the importance of canopy functional traits, such as nutrient and water composition, in shaping bird diversity and their ecological traits.

- The findings suggest that mapping functional diversity can be a powerful tool for prioritizing conservation efforts, especially for forest-dependent birds with small geographic ranges and specialized habitat needs.

- The integration of remote sensing data with ecological modeling is a noteworthy methodological advance, enabling large-scale, high-resolution biodiversity assessments.

The study bridges a critical gap by connecting forest canopy functional traits with bird ecology and conservation, offering a framework for similar studies in other biodiverse regions.

- While previous research has addressed forest functional diversity (e.g., Asner et al., 2017), this study uniquely links these traits to bird functional and taxonomic diversity, expanding the scope of functional biogeography.

- The research is original in its use of a nationwide canopy functional diversity map to inform biodiversity conservation strategies. Relevant prior studies (e.g., Schneider et al., 2017) focused on forests' internal dynamics but did not explicitly relate them to animal communities.

- The conclusions are well-supported by:

- o Comprehensive data analysis using the Random Forest model, explaining a significant portion of variance in bird traits and taxonomy.

- o Robust methodological validation, including the use of established databases (e.g., BirdLife International) and cutting-edge remote sensing technologies.

While the study is methodologically sound, further research could verify the transferability of its findings to other tropical regions.

Data Analysis and Interpretation

- o Clear explanation of methods and statistical models.

- o Effective visualization of results through maps and variance explanation charts.

- o While the Random Forest model is powerful, its interpretability is limited. Additional sensitivity analyses or alternative models (e.g., generalized linear models) could strengthen causal inferences.

o The study focuses on forest-dependent birds, potentially overlooking interactions with non-forest-dependent species.

The methodology is robust, combining ecological data, high-resolution remote sensing, and machine learning.

- Sufficient detail is provided, including access to data repositories (e.g., FigShare). However, the dependence on specialized equipment (e.g., GAO) may limit replication by other researchers without similar resources in other parts of the world.

Response:

We thank the reviewer for their thoughtful and generous summary of our work. We fully agree that linking forest canopy traits to bird diversity at large spatial scales offers promising insights for functional biogeography and conservation. In response to multiple reviewer feedback, we undertook major revisions to strengthen the clarity and interpretability of our statistical approach. Specifically, we replaced the original Random Forest models with a Bayesian multivariate modelling framework that directly relates forest functional group (FFG) composition to multidimensional axes of bird traits, threat vulnerability, and taxonomic structure. This approach improves model transparency, accounts for uncertainty, and enables clearer ecological interpretation of effect sizes across trait groups. We hope that these revisions substantially improve the methodological rigor and interpretability of our study, while maintaining its core contribution: demonstrating how canopy functional diversity shapes avian diversity in tropical forests.

Comment: My recommendations: 1. The authors are advised to incorporate non-forest-dependent bird species to evaluate broader biodiversity patterns.

Response: We appreciate this suggestion and agree that including a broader range of bird species could offer additional insights. However, our study is explicitly focused on forest canopy functional diversity and its relationship to forest-dependent bird assemblages, which are directly tied to forest conditions. In an earlier review, we removed non-forest dependent bird species from our analysis because they confounded the ecological interpretations, as these species interact with different habitat variables (e.g., open land, edge, shores), of which we had no landscape models. We have clarified this rationale in the Methods and Discussion, and suggest this broader analysis as a valuable next step using similar approaches in future work.

Comment: 2. The authors are advised to supplement Random Forest analysis with models capable of testing specific causal hypotheses.

Response: Thank you for this crucial point. In response to this and other comments, we revised our statistical framework substantially. We replaced the Random Forest models with a Bayesian regression modelling approach, which (1) provides transparent parameter estimates with credible intervals, (2) supports variance partitioning across functional and environmental predictors, and (3) allows for explicit modelling of uncertainty and potential collinearity. This shift enables a more nuanced understanding of the relationships between forest traits and bird diversity, and helps avoid overfitting or black-box inference.

Comment: 3. Perhaps consider global comparisons: Extend the framework to other biodiverse regions to assess its universality.

Response: We agree that extending this framework more broadly is an important and exciting next step. In the revised Discussion, we now highlight the potential to expand this trait-based biodiversity approach across the full Amazon Basin. While our current study is limited to Peru due to the availability of high-resolution airborne LiDAR and imaging spectroscopy data, the framework could be extended to other regions as similar data become available. We also note that upcoming satellite-based imaging spectroscopy missions, such as ESA CHIME and NASA SBG, may complement airborne LiDAR by providing broader coverage of canopy chemical traits. When combined, these technologies could support large-scale, spatially continuous mapping of forest functional diversity and its links to animal traits and biodiversity.

Comment: 4. Include explicit modeling of anthropogenic threats (e.g., deforestation) to link functional diversity with conservation outcomes more directly.

Response: We appreciate the reviewer's suggestion. In our revised analysis, we incorporated a dedicated group of anthropogenic threat exposure variables at the species level, derived from BirdLife International. These include information on the presence of specific threats (e.g., agriculture, logging, hunting), IUCN Red List status, and population trends. We modelled these traits using a multivariate Bayesian framework to understand how forest functional composition relates to the conservation status and threat profiles of forest-dependent birds.

While we did not include landscape-scale metrics of anthropogenic pressure (e.g., forest loss or fragmentation), our species-level threat modelling directly links canopy functional diversity to conservation-relevant outcomes such as extinction risk and vulnerability. We believe this trait-based approach offers a complementary and generalizable framework that can be extended with spatial threat data in future work.

Comment: 5. The authors provide exemplary transparency, sharing both data and methods openly. However, the study would benefit from a detailed discussion on the limitations of remote sensing data and potential biases.

Response: Thank you for acknowledging our efforts toward transparency and open data. We now include a paragraph in the Discussion acknowledging several limitations of remote sensing, including scale mismatches, atmospheric noise, and uncertainty in spectroscopic trait inference. While a detailed treatment was not feasible within the scope of this manuscript, we highlight how our use of field-calibrated maps and spatial averaging helps to reduce these sources of error, and we advocate for continued integration with ground-based biodiversity observations.

Comment: Remarks on code availability:

To enhance the repeatability and reproducibility of the provided R code, the following recommendations can be implemented:

1. Provide Clear Documentation

477 Comments: Add detailed comments explaining the purpose of each code block and function.
 478 Variable Descriptions: Include descriptions for each variable loaded (e.g., var1, var2) to clarify their
 479 role in the analysis.
 480

481 2. Ensure Code Modularity

482

483 Function Encapsulation: Create reusable functions for repeated tasks, such as calculating variable 484 importance or training Random Forest models. For instance:

485

```
486 run_random_forest <- function(data, formula, ntree=1000, seed=52) {
487   set.seed(seed)
488   model <- randomForest(formula, data=data, importance=TRUE, proximity=TRUE, ntree=ntree,
489     na.action=na.omit)
490   return(model)
491 }
```

492

493 Use this function throughout the script to ensure consistency.
 494

495 3. Use Relative File Paths

496

497 Ensure file paths are relative and not system-dependent:

498

```
499 PEBirds <- read.csv("data/GAO_Peru_birds.csv")
500
```

501 Include a check for the existence of files with:

502

```
503 if (!file.exists("data/GAO_Peru_birds.csv")) stop("Data file not found!")
504
```

505 4. Add Input Validation

506

507 Validate the data before analysis to avoid runtime errors:

508

```
509 if (!all(c("FFG_1", "FFG_2") %in% colnames(PEBirds))) {
510   stop("Required columns are missing in the dataset.")
511 }
```

512

513 5. Output Reproducible Results

514

515 Set Random Seeds: Use consistent random seeds across all analyses.

516

```
517 set.seed(123)
518
```

519 Save Results: Save model objects and intermediate results to files for easy inspection and re-use:

520

```
521 save(out.PEBirds, file="results/RandomForestModel.RData")
522
```

523 6. Enable Parameterization

524

525 Use configurable parameters at the start of the script for easy adjustments:
 526

```

527 params <- list(
528   ntree = 1000,
529   seed = 52,
530   input_file = "data/GAO_Peru_birds.csv",
531   output_dir = "results/"
532 )
533
534 7. Provide a Comprehensive README
535
536 Add a README file in the working directory with instructions on:
537 Required libraries and installation commands.
538 Input file formats and examples.
539 Steps to execute the script.
540
541 8. Version Control
542
543 Use a version control system like Git to track changes to the codebase. Include versioning in
544 filenames to indicate script and data versions.
545
546 9. Include Data Integrity Checks
547
548 Ensure the input dataset matches the expected structure:
549
550 if (any(is.na(PEbirds$FFG_6))) warning("Missing data detected in FFG_6.")
551
552 10. Facilitate Dependency Management
553
554 Use renv or similar R package for dependency management to ensure all libraries are correctly
555 installed:
556
557 library(renv)
558 renv::init()
559
560 11. Add Tests
561
562 Include test cases for key functions to validate their performance with a minimal test dataset.
563
564 By implementing these steps, the code will be more reliable, understandable, and easier to reproduce
565 by other researchers.
566
567 Response: Thank you for this very useful guide of how to make our model script more
568 understandable and reproducible. We have implemented these changes and updated the script
569 accordingly.

```

Reviewer #2

Thanks for addressing the reviewer comments. I think that the manuscript is now much clearer and easier to follow. However, I still think that the lack of a null model is a fundamental flaw in this analysis. The central finding is that bird diversity is predictable by canopy functional types, which has not been shown previously. However, previous studies on bird diversity have demonstrated that it is also predictable by other, simpler variables such as elevation and temperature. This study does not test whether the canopy functional types add any new information to the predictability of bird diversity. In your response you state that you cannot include elevation and temperature in the model because they are so strongly correlated with the canopy functional types. I would argue that this study therefore cannot disentangle these drivers of bird diversity, whether using Random Forest models or a bayesian approach.

I was asked to check this manuscript again, with a focus specifically the authors response to reviewer 3. I think their response to reviewer 3 is very good, and I'm happy that they addressed all of the concerns that were raised in a reasonable way.

I've made this point before, but I still feel that the omission of the more basic variables we would expect to affect bird diversity is an substantial flaw in this analysis. Bird distributions are likely to be affected by temperature, particularly temperature extremes (e.g. coldest night time temperature, or hottest daytime temperature). Simultaneously, temperature is likely to covary with the forest function types used by the authors (everything covaries with elevation). We therefore cannot tell whether bird distributions are indeed driven by the forest functional types or simply temperature.

I do believe that canopy function types are likely to contain valuable information for the prediction of bird diversity. However, to demonstrate this the study would need to build a credible null model against which to test the value of canopy functional types.

We appreciate the reviewer's continued engagement and apologise for not addressing these concerns fully in the previous iteration. We agree that demonstrating the added value of canopy functional types required explicit comparison against simpler baseline predictors and a null model. We have now endeavoured to address this directly with competing hypotheses that species trait distributions can be predicted by forest functional groups, environmental predictors (in our case cloud cover and elevation), or a combination of these variables.

We now use an information-theoretic model selection framework (AICc) that evaluates all possible subset combinations of predictors, including an intercept-only null model. Crucially, we incorporated elevation and cloud cover as competing predictors alongside the six forest functional group (FFG) variables. This allows the data to determine whether FFGs provide information beyond these simpler environmental variables that previous studies have shown to predict bird diversity.

Our results demonstrate the value of this approach. Across 16 PC axes analysed as responses, the majority of the best-fit models (10 out of 16) contained one or more of the FFG predictors. Cloud cover and elevation appeared in 13 of the models, but eight of these also contained FFG variables. That is, that eight of the PC axes responses were best explained by combinations of both FFG and simple environmental variables, demonstrating that FFGs provide complementary information beyond traditional predictors. Additionally, the null model was selected for 2 axes (Life PC3: clutch size/nest placement; Functional PC3: body

proportions with only marginal elevation effect), indicating our predictors did not meaningfully explain variation in those dimensions.

For example:

Functional PC1 (body size, 58% variance): Best model included 4 FFGs + elevation + cloud (6 predictors)

Threats PC2 (human impacts, 17% variance): Best model included 2 FFGs + elevation + cloud (4 predictors)

Taxonomy PC1 (taxonomic order, 28% variance): Best model included 4 FFGs + elevation + cloud (6 predictors)

These results directly address the reviewer's concern by showing that: (1) we explicitly tested whether FFGs, environmental variables, or neither best explain trait variation; (2) when FFGs are selected, they often complement rather than substitute for traditional environmental predictors; and (3) we transparently report when the null model or simpler models are most parsimonious.

This information-theoretic approach provides a robust framework for demonstrating that canopy functional types contain valuable, non-redundant information for predicting bird trait diversity. We believe this substantially strengthens the manuscript and directly addresses the reviewer's fundamental concern about disentangling drivers of bird diversity.

Reviewer #4

I have read and reviewed a manuscript entitled "Canopy functional composition as an indicator of bird community traits and vulnerability in tropical Peruvian forests". I was invited to join the review process in a subsequent round, specifically replacing Reviewer #1. I was given the task of reviewing the author's response to reviewer's comments and checking if the main issues raised were solved.

Overall, I acknowledge the authors' substantial efforts in improving the manuscript. The analytical framework is both relevant and important, and the revisions have resolved most of the issues previously raised. Now, the analyses used are well described and fit well with the objective of the study and the tone of causality has been removed. However, although I have a very positive impression of the article, it is marred by an important theoretical issue of trait-based ecology. They used a refined method of obtaining plant functional traits with impressive resolution, but their way of relating them to bird functional traits is theoretically weak.

My main concern is that the authors introduce circularities in both parts of the analyses by defining some of the species observational (distributional) data as functional traits. In consequence, the study results are not overly meaningful in their current conditions. But let me shortly explain the circularity issue. Functional traits are (in the strict sense) defined as morpho-physio-phenological traits (including social and behavioral traits for animals) that impact fitness via their effects on growth, reproduction, and survival of an individual (Violle et al. 2007 - <https://doi.org/10.1111/j.0030-1299.2007.15559.x>). This definition excludes information that is defined only at larger levels of aggregation, such as populations or species. Examples of the latter are habitat width, range size, or anything that relies on data obtained from species distributions across environmental gradients. A good

example of this definition escape is defining a species as forest specialist/dependent or been migratory or not.

The authors introduced a few birds "functional traits" to their analysis that do not only not follow that definition but also, they use forest category that varied in vegetal structure like density and height to explain if a bird is forest dependent or not by living in those places. This approach introduces a form of circularity into the analysis, which undermines the interpretability of the results. For example, they use the FFG Amazon Swamp to explain a bird be low forest dependent. This is essentially equivalent to stating that a species has low forest dependence simply because it occurs in open habitats. The actual trait should be traits that allows birds individuals to live in that habitat.

Given the broad readership of Nature Communications, it is important that this misunderstanding of trait-based theory is addressed before publication, even though these traits did not show relevant relationships in this study. Furthermore, the presence of these nonfunctional traits only inflates the ordination technique with unconstrained variance.

This circularity concerns at least the following traits: Migratory Status, Forest Dependency and Distribution Size. These variables are derived from the observational study on species occurrence and not on independent measurements on the individuals/species. I would suggest the authors to redo the analysis including only those traits that are independent of the response variables. Regarding Mean generation length, I suggest not calling it a functional trait, but rather a life-history strategies trait, as it is calculated at the population level and reflects the rate of change of individuals in populations.

We thank the reviewer for highlighting this theoretical concern about circularity. We revised our trait dataset to exclude migratory status, forest dependency, and distribution size from our analysis to avoid circularity issues.

Following the reviewer's guidance, we now classify traits into four conceptually distinct groups:

1. Functional traits – strictly morphological, physiological, or behavioural attributes measured at the individual level (e.g., body mass, beak width, wing length, tail length, etc.), primarily sourced from the AVONET database (Tobias et al. 2022; Ecology Letters, doi:10.1111/ele.13898), which compiles direct measurements from over 90,000 individual birds worldwide.
2. Life history traits – traits reflecting species-level demographic strategies (e.g., mean generation length, clutch size, diet, etc.).
3. Conservation status – categorical variables derived from IUCN Red List assessments.
4. Taxonomic identity – order and family, used for phylogenetic structure analysis.

We also clarify that generation length has been reclassified as a life history trait rather than a functional trait, consistent with the reviewer's definition.

As before, our analyses focus exclusively on forest-dependent bird species, ensuring that our comparisons reflect variation within forest assemblages rather than between forested and non-forested habitats.

Finally, we note that the revised model set now uses an information-theoretic model selection framework (AICc) incorporating a null model to evaluate predictor contributions (see

response to Reviewer #2). Together, these changes eliminate potential circularity, align our trait framework with core principles of trait-based ecology, and improve the interpretability and theoretical rigor of the study.

Previous reviewer #1 raised the limitation of using artificial bird assemblages, and I agree with their comment. Although the authors included a brief discussion of the limitations of this approach, I believe more needs to be done, such as making the ecological reliability of these communities transparent. Although the assessment is being made at the country level, it is still a very small area compared to the species' distribution areas, and there is likely no variation in species richness due to this. Therefore, I suggest that the authors provide a brief description of bird species richness across the raster cells under evaluation. Reporting the minimum, maximum, mean, and standard deviation of species richness would enhance transparency and allow readers to better assess the robustness of the results. Additionally, including a raster plot of bird species richness across Peru in the supplementary material would be highly valuable for readers, providing a clear visual complement to the descriptive statistics.

We thank the reviewer for this valuable suggestion to improve transparency regarding the use of polygon-based bird assemblages. We agree that reporting the variation in estimated species richness across Peru helps assess the ecological reliability of the assemblages derived from BirdLife International range data.

We have now quantified and reported descriptive statistics of species richness by forest functional group (minimum, maximum, mean, and standard deviation). To visually complement these statistics, we have added a new Supplementary Figure 2, which maps forest-dependent bird species richness across Peru (all, threatened, non-threatened). This addition enhances the ecological interpretability and transparency of our analytical framework, as suggested.

Besides these main points, I would also like to highlight some minor issues that require adjustment:

Lines 161–166: The authors state:

“High dependency on forest can influence conservation status of birds and other vertebrates 14,15. This dependency is especially important when forests are threatened by logging for timber or clearing for crops, plantations, and livestock farming 11, so predicting the extent of their forest dependency can have important conservation implications. Conserving functionally diverse forests could not only protect tree species but also diverse communities of birds depending on them.”

However, the results clearly indicate that different levels of forest dependence were not associated with the PCA axes, and therefore showed no relationship with FFGs. As such, this part of the discussion is not supported by the results. Moreover, removing these variables from the set of functional traits would help ensure that the discussion remains fully grounded in the analyses presented.

We agree with the reviewer and have removed discussion statements referring to variation in forest dependency, as this variable has now been excluded from our trait dataset to avoid circularity. The revised text now focuses on the demonstrated relationships between canopy functional composition and bird ecological and life-history traits, which remain highly relevant for conservation.

Line 150 Are the avifaunas present in the Amazonian swamp forest (FFG5) said to have potentially low ecological resilience? Based on what results do the authors suggest this ecological condition? Ecological resilience refers to a community's capacity to maintain its functional roles in the face of environmental impacts and local extinctions, which is typically assessed through measures such as functional redundancy and the degree of niche packing. As these analyses were not conducted, this interpretation is not supported by the results and should be reconsidered or clarified.

We agree that our phrasing implied an interpretation of community-level ecological resilience, which we did not directly assess. We have therefore revised the sentence to focus on the individual-level life-history implications supported by our data, removing the speculative reference to ecological resilience. The revised sentence now reads: "Birds inhabiting northern Amazonian swamp forests (FFG5) tended to be larger-bodied and longer-lived species, traits associated with slower reproductive strategies and increased vulnerability to environmental disturbance." This revision accurately reflects the observed trait associations without overextending their ecological interpretation.

Line 197 – 200 In my view, this approach does not provide a sufficiently "efficient" means to assess how forest changes may affect bird communities. The study relies on artificial communities, which limits the scope of inference; consequently, the results indicate potential patterns rather than demonstrated effects. Moreover, the authors imply impacts on bird community dynamics, but the study does not explicitly evaluate community dynamics. This point should be clarified to avoid overstating the conclusions.

We agree that our approach does not model community dynamics directly, but rather identifies broad-scale associations between canopy functional composition and the trait structure of bird assemblages derived from range-based distributions. To avoid overstating inference, we have revised the discussion to emphasize that our results highlight potential patterns and mechanisms linking forest functional composition to avian traits, rather than demonstrated dynamic responses. The revised text now presents the framework as a scalable, hypothesis-generating approach for anticipating how changes in canopy function may influence community structure, pending validation with local abundance and temporal data.

Citation 28: This reference appears unusual, as it combines two data sources: the Lynx publisher's HBW and the BirdLife Datazone. I recommend that the authors separate these references clearly and specify in the supplementary material which traits were obtained from each source.

The "HBW and BirdLife International Digital Checklist of the Birds of the World" is a single, jointly maintained resource that integrates taxonomy from the Handbook of the Birds of the World series (Lynx) with BirdLife International's global taxonomy and IUCN Red List assessments. Our citation follows BirdLife International's official format for this checklist (see <https://datazone.birdlife.org/species/taxonomy>). To enhance clarity, we have explicitly noted in the Methods that this checklist provides taxonomy, IUCN Red List category, and vulnerability data used in our analyses (see Supplementary Table 1 for details).

Remarks on code availability:

The code <https://doi.org/10.6084/m9.figshare.12894230> directs to a figshare.com page with a 404 error (the page cannot be found/The page you are looking for does not exist or has been removed.)

Sorry for the confusion, the DOI link of Figshare only works once it has been released (accepted for publication). During the review process, please use this direct link accessing the same data: <https://figshare.com/s/f84d0cdf27f96c850dcc>

Detailed response to Reviewers
Manuscript ID: NCOMMS-24-56668B
Title: Canopy functional composition as an indicator of bird traits, taxonomy, and vulnerability in tropical Peruvian forests

We thank the Reviewers for the continued engagement with our manuscript and for the opportunity to revise. We have addressed all remaining concerns in full and outline our responses below. In particular, we have substantially strengthened the quantitative framing of our results in response to Reviewer #2's core concern about the magnitude of Forest Functional Group (FFG) effects and have explicitly expanded our environmental predictor set to address the null model critique.

We recognise that combining remote sensing, high-dimensional trait data, and multivariate modelling creates a dense methodology that can be difficult to parse. To improve accessibility for the broad readership of Nature Communications, we have created a modelling framework table (new Supplementary Table 2). This table breaks down our analysis into plain-English steps, clearly defining the inputs (bird PCs, FFGs), the environmental controls, and the interpretative goal of each analytical step. We believe this will serve as a vital guide for readers to navigate the statistical results.

Reviewer #2

(1) Model selection

I appreciate the effort the authors have made to implement my previous suggestions on model selection. The results are now more believable. However, I still think this manuscript requires a better 'null' model to improve upon.

The FFGs may well contain vital information that is not available elsewhere. However, I find the FFGs difficult to interpret and I don't think they are easily reproducible in other

ecosystems (the discussion suggests they may be with satellite data, but this would also require a massive field campaign for calibration). In general, model selection should aim to find the simplest model which explains the data. I therefore think the analysis should test more of the common variables used to explain biodiversity before adding the FFGs. For example would suggest the authors include canopy height (separate from the FFGs) and distance to nearest road as predictors. In addition, the authors should check what variables other studies explaining large scale trends in biodiversity have used. In fact, I think there should be a discussion of previous ‘biodiversity models’ in the introduction. The claim of this study is that FFGs improve on previous ‘biodiversity models’, but this is not yet supported by the results.

We thank the reviewer for this important feedback. In our revision, we have substantially expanded the null model beyond elevation and cloud cover to incorporate seven environmental predictors: elevation, cloud cover, aboveground carbon density (a measure of canopy biomass), urbanisation (night-light emissions), bare substrate cover, photosynthetically active vegetation cover, and total solar insolation. This broad environmental baseline captures the major structural, climatic, and anthropogenic gradients most likely to covary with both forest functional composition and bird trait variation.

Our approach goes beyond the reviewer’s specific suggestion of canopy height (which is closely related to ACD) and distance to roads (proxied here by urbanisation). Against this expanded baseline, FFGs remained informative for 12 of 16 trait axes, contributing between 12% and 62% of explained variance where present (Supplementary Data 10). On four axes (nocturnality, aerial foraging specialisation, and two others), FFG contribution was negligible, and we report this transparently. Where FFGs were informative, their standardised effect sizes were generally substantially larger than those of the environmental predictors. We believe this directly addresses the reviewer’s three scenarios below: our results most closely resemble Scenario 1, with FFGs making meaningful and often dominant contributions to explained variance on the majority of trait dimensions.

We also wish to be fully transparent regarding the absolute variance explained by these models. As is typical in macroecological studies linking highly aggregated, polygon-based species ranges to continuous environmental rasters, the total R^2 values for our models are generally modest (often < 0.1). This reflects the inherent noise of broad-scale ecological data, where much of the total variance is driven by unmeasured local factors such as biotic interactions, historical biogeography, and micro-habitat selection (e.g., see Møller & Jennions 2002). However, our focus in this study is not to build a predictive model of bird traits, but to test whether canopy chemistry provides a unique signal amidst that noise. The fact that FFGs consistently emerge as top predictors and account for a substantial proportion of the explainable variance demonstrates their robust ecological relevance at the landscape scale.

Furthermore, as requested, we have expanded the Introduction mentioning standard biodiversity models to better contextualize how canopy functional data builds upon and improves these traditional frameworks.

I notice that the claim that FFGs explain 90% of bird diversity has been removed. Could the authors update this figure instead of removing it? At the moment, there is very little quantitative detail about how useful FFGs are. The manuscript states that (a) FFGs are informative for fewer bird traits than elevation and cloud cover but (b) when they are

informative they are usually more important than elevation and cloud cover. This doesn't give me a clear answer on how important FFGs are.

In conclusion, the methods and results are such that all three scenarios below seem plausible to me:

Scenario 1: The variation in bird traits are explained by elevation (20%), cloud cover (20%) and FFGs (40%), with the remaining 20% unexplained.

Scenario 2: The variation in bird traits are explained by elevation (30%), cloud cover (30%) and FFGs (10%), with the remaining 30% unexplained.

Scenario 3: The variation in bird traits are explained by elevation (5%), cloud cover (5%) and FFGs (5%), with the remaining 85% unexplained.

Can you please improve the methods and clarify the results to ensure this is clearer.

We agree that the previous manuscript was insufficiently explicit about the magnitude of FFG effects, and we have addressed this in two ways.

First, we have added a formal variance partitioning analysis to directly quantify the unique contribution of FFGs. For each of the 16 PC axes, we compared the R^2 of the top-ranked model (containing both FFGs and environmental predictors) to that of an equivalent model with FFG terms excluded, retaining only the environmental predictors that appeared in the top-ranked model. The difference (ΔR^2) expressed as a proportion of the full model R^2 provides a standardised measure of the variance uniquely attributable to FFGs, independent of the environmental baseline.

The results are reported in full in Supplementary Table 12, and the key numbers are now stated explicitly in both the Results and Discussion. FFGs were informative for 12 of 16 trait axes, contributing between 12% and 62% of explained variance on those axes (with the single most important case being body size, Functional PC1, where FFGs account for 33% of explained variance on top of the environmental baseline). On four axes, most notably nocturnality (Functional PC2) and aerial foraging specialisation (Life History PC4), FFG contribution was negligible, and we report this transparently.

(2) Principal components of bird traits

The analysis of bird traits has completely changed in this version of the manuscript. The previous version directly used traits such as territoriality and nest placement, while the new version uses principal components of the bird traits. Can you explain the reason for this shift? This may well be a reasonable decision, but in my role as a sceptical reviewer I want to double check that the analysis was not changed because of a lack of significant results.

This new principal component analysis is also less interpretable. Apart from functional PC1, all PCs explain less than 30% of the variation in the trait space. A typical model result is therefore that, elevation and cloud cover explains 40 % of the variance in PC2, which itself explains 18 % of the variance in these traits. This is even more complicated when the FFGs are included, which are effectively principal components of another trait space!

I understand that this type of analysis may be necessary when comparing two multi-variate trait spaces and I don't think it is wrong in principle. However, if there are more easily interpretable results available (such as 'vulnerable bird species are mostly confined to high

elevations with the tallest forests, suggesting that these are intact areas’) I think these should be prioritized.

The shift to Principal Component Analysis (PCA) was driven by the significant expansion of our trait database, not by the results of the initial analysis. As detailed in our revised Methods, we now utilize the AVONET database, which allowed us to incorporate 32 distinct morphological and ecological variables (up from the smaller set used previously). Testing 32 variables individually would introduce severe issues with: (1) multiple testing: running 30+ separate models dramatically increases the risk of spurious significant results (Type I errors); and (2) multicollinearity: traits in AVONET (e.g., wing length, Kipp’s distance, and dispersal ability) are highly correlated. Analysing them separately violates the assumption of independence and obscures the true drivers of community structure.

By using PCA, we condensed these covarying traits into independent axes representing integrated ecological strategies (or “syndromes”), such as the trade-off between dispersal capacity and sedentariness. This is a standard and robust approach in modern functional trait ecology (e.g., Tobias et al. 2022, Ecology Letters) to ensure that results reflect broad evolutionary patterns rather than isolated trait correlations.

We agree that PCA axes can be abstract and that interpreting nested variances (e.g., environmental variance within a PC’s trait variance) is mathematically complex. To improve interpretability and directly address the reviewer’s request for accessible conclusions, we have:

- restricted our interpretation to the leading PC axes that map onto clear biological gradients (e.g., “for functional traits, PC1 separated large-bodied from small-bodied species across all morphological measurements”);
- provided clear Factor Loading Tables (Supplementary Data 1–4) so readers can see exactly which raw traits drive each axis;
- visualization: while the statistical tests are multivariate, we have ensured that the visualization of results (e.g., Fig. 2b) clearly illustrates the directionality of these relationships (e.g., showing that specific Forest Groups favour large-bodied, slow-reproducing communities);
- added a new modelling framework table (Supplementary Table 2) that explicitly translates our multivariate analytical steps into plain English ecological interpretations, bridging the gap between statistical complexity and practical conservation insights.

We believe this strikes the right balance between statistical rigor (handling high-dimensional data) and biological clarity.

(3) Conservation implications

The manuscript states that these results will be useful for conservation, but I am not sure how. Could you give some examples? The introduction states that: ‘From a conservation perspective, it is critically important to understand how animals use remaining habitats and how they might respond to threats’. How can your results be used to help understand this latter question?

The final paragraph of the discussion states that ‘While our goal was not to identify specific conservation areas, we demonstrated that remotely sensed data can be translated into important information concerning bird functional diversity’.

We thank the reviewer for prompting us to clarify the practical application of our findings. We agree that the previous text was somewhat generic.

The core conservation implication is that FFGs act as proxies for resource landscapes. Because distinct FFGs support distinct avian functional strategies, conservation strategies that focus only on forest cover or species richness might inadvertently fail to protect specific ecological functions.

As an example, conservation plan might protect a large area of Floodplain Forest (FFG3) and assume the region's biodiversity is secure. However, our results show that FFG3 is dominated by small-bodied, fast-reproducing passerines that are exposed to pollution and disturbance. Without explicitly protecting the chemically distinct Swamp Forests (FFG5), the region would lose the specific functional syndrome of very large-bodied, evolutionarily distinct non-passerines (which have slow life-histories), potentially leading to a collapse in seed dispersal services despite total forest cover remaining high.

We have revised the Introduction and Discussion to explicitly articulate this mechanism: mapping canopy function allows managers to stratify protected areas by functional potential rather than just structural habitat, ensuring the persistence of vulnerable life-history strategies.

Reviewer #4

I have read and reviewed the manuscript now titled “Canopy functional composition as an indicator of bird traits, taxonomy, and vulnerability in tropical Peruvian forests.” The authors significantly improved research reliability by adding data descriptions in the text and supplementary materials and by removing unsupported overstatements. They also eliminated circularity issues from the analysis. These changes enhanced transparency and ecological interpretability. The authors acknowledge that their results have limitations and should be used to complement assessments of real bird communities.

The only suggestion I can offer now concerns line 339 of the current manuscript, which exhibits some character incompatibility in the model equations. Please pay attention to the [?] symbols.

Therefore, I believe that the manuscript is ready to be published.

Remarks on code availability:

Now, the authors have provided access to the code and data in the link:
<https://figshare.com/s/f84d0cdf27f96c850dcc>

We thank the reviewer for their careful re-evaluation of the manuscript. We appreciate the positive assessment that the revisions have resolved the earlier concerns.

Regarding the remaining technical issue, we have corrected the character incompatibility affecting the model equations caused by a formatting/encoding issue during PDF transformation. We thank the reviewer for identifying this issue and are pleased that they consider the manuscript ready for publication.

Reviewer #2

Thank you for addressing my previous comments and improving the manuscript. I still have an important concern about the statistics.

In your response and in supplementary table 2, you state that you select the best model considering all potential factors including FFGs. You then remove the FFGs and test again to determine the contribution of the FFGs. I think this is the wrong way around and will artificially inflate the contribution of the FFGs.

Instead, I suggest you build the best null model possible using commonly used factors. Then, add the FFGs and determine how much additional variance they explain. This seems like a small change but I think it might significantly change the results.

To understand the difference between these two approaches, let's take an example. Let's assume (for the sake of argument) that bird trait A is correlated with elevation, canopy height and FFG1. If we assume that FFG1 is strongly correlated with canopy height, the most parsimonious model (model A) may include only elevation and FFG1. By your definition, the additional variance explained by FFG1 is given by the difference between model A and an elevation only model (model B). However, this erroneously assigns the variance that would be explained by canopy height to FFG1. In my approach you should build the best null model without any FFGs (bird trait A ~ elevation + canopy height, model C). You then add FFG1 to this model to determine the additional variance explained.

The key principle here is that we should build simple models wherever possible, and reserve more complex factors (FFGs) for cases where they are actually necessary.

We agree with the reviewer's principle of parsimony and appreciate the suggestion to use a more conservative statistical baseline. To address this, we have re-run our variance partitioning analysis using a strict hierarchical modelling framework:

For each bird trait axis, we first conducted model selection using only standard environmental and structural predictors (e.g., elevation, canopy height, cloud cover). This established the most parsimonious optimal 'null' model.

We then introduced the FFG variables to these established optimal baseline models.

We calculated the change in explanatory power (ΔR^2) between the baseline model and the FFG-inclusive model.

This conservative approach guarantees that canopy function (FFGs) is only credited with explaining unique variance that cannot be accounted for by simpler, traditional metrics. We have updated our Methods section, the Results, and all relevant supplementary tables to transparently report these new ΔR^2 values. As expected under this stricter framework, while the absolute variance attributed to FFGs shifted slightly, their role as robust, independent predictors of avian trait diversity remains clear.