# THE ROYAL SOCIETY PUBLISHING

# ROYAL SOCIETY OPEN SCIENCE

## Global relationships between tree-cavity excavators and forest bird richness

Yntze van der Hoek, Gabriel V. Gaona, Michał Ciach and Kathy Martin

**Review timeline**

| | |
|---|---|
| Original submission: | 27 May 2019 |
| 1st revised submission: | 13 December 2019 |
| 2nd revised submission: | 31 January 2020 |
| 3rd revised submission: | 14 March 2020 |
| 4th revised submission: | 15 June 2020 |
| Final acceptance: | 17 June 2020 |

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

# Review History

# RSOS-190962.R0 (Original submission)

## Review form: Reviewer 1

**Is the manuscript scientifically sound in its present form?**
Yes

**Are the interpretations and conclusions justified by the results?**
Yes

**Is the language acceptable?**
Yes

**Do you have any ethical concerns with this paper?**
No

**Have you any concerns about statistical analyses in this paper?**
No

**Recommendation?**
Major revision is needed (please make suggestions in comments)

**Comments to the Author(s)**
General comment:
The manuscript entitled "Global and universal relationships between tree-cavity excavators and forest bird richness." reports on an interesting exploratory study linking woodpeckers/other tree cavity excavators, secondary cavity users and other forest tree species at the global and bioregional levels. The results are useful and may inspire new studies exploring these relationships more in-depth. My main criticism concerns the quality of reasoning and how and to what extent different issues are introduced and discussed. Proposing the use of certain group of species as indicators or other type of indicator species shall rest on solid grounds as well as need of such indicators should be clearly put forward. I simply miss the delineation of the conservation/management problem why we need indicators. There are many articles published on the worldwide decline of primary/intact forests, their characteristics and, in my opinion, you do not use the opportunity to discuss the potential role of woodpeckers/other tree cavity excavators (with very intimate linkages to natural forest characteristics) to support your case. Also, even if you mention their usefulness in management, there is lacking information on the intensively managed forests as areas that lose both important characteristics linked to old-growth forests and forests with high level of naturalness and thereby lose most specialized forest species often being woodpeckers. Also use of woodpeckers/other excavators as indicators of successful forest restoration could be mentionaed. There is large body of literature on both above topics and I suggest that you should add paragraphs pertaining on these issues in both Introduction and Discussion sections. To limit the length of the article, you may get rid of several unnecessary repetitions. More suggestions below:
Detailed comments:
Line 99: Several species use smaller trees or snags too. Possibly add "often" or "usually".
Line 109: Woodpeckers (cavity excavators) are most often resident species what could additionally strengthen your reasoning on strong linkages to forest environments and their quality.
Lines 127-133: Please consult Wesolowski and Martin (2018) and extend the discussion on mechanism a bit more. I am lacking a clear statement on two possible, non-excluding each other mechanisms of expected relationships as very nicely stated way down in Discussion (Lines 312-314).
RESULTS: Could you add a summary table with numbers of species in different groups in different bioregions? It would provide some nice background for further discussions of results. You have those numbers already!
Lines 224-231: I do not understand how you can model the relationship between woodpeckers and the three other groups in Australasia, where, as you state below, there is no woodpeckers or even other strong excavators are largely lacking.
DISCUSSION: a bit confusing use of words "excavators/woodpeckers" (Line 244) and "excavators" (Line 275). Please check if necessary to use both of them!
Lines 239-243: Worthy to mention that forests in some bioregions supply decay-formed cavities in high numbers (particularly non-managed forests) and some other not (e.g. boreal forest in Europe – see Andersson et al. (2018): Andersson J., Domingo Gomez E., Michon S., Roberge J.-M. (2018) Tree cavity densities and characteristics in managed and unmanaged Swedish boreal forest. Scandinavian Journal of Forest Research, 33 (3), pp. 233-244. It would add the management angle in discussion about the role of woodpeckers/excavators for other species.
Lines 272-273: Please refer to studies on the global species richness of woodpeckers e.g. Mikusinski, G. 2006. Woodpeckers (Picidae) - distribution, conservation and research in a global perspective. Annales Zoologici Fennici 43: 86–95.
Lines 289-294: Refer also to the "primeval" Bialowieza Forest case in temperate zone being in stark contrast to managed forests (i.e. higher predation risk and subsequently preference for decay-formed cavities among secondary users. See: Wesolowski and Martin (2018) and references therein.

Lines 299-304: Please refer to papers by Wesolowski here: Wesolowski T. 2011."Lifespan" of woodpecker-made holes in a primeval temperate forest: A thirty year study. Forest Ecology and Management, 262 (9) , pp. 1846-1852.

## Review form: Reviewer 2

**Is the manuscript scientifically sound in its present form?**
No

**Are the interpretations and conclusions justified by the results?**
No

**Is the language acceptable?**
Yes

**Do you have any ethical concerns with this paper?**
No

**Have you any concerns about statistical analyses in this paper?**
Yes

**Recommendation?**
Major revision is needed (please make suggestions in comments)

**Comments to the Author(s)**
Many comments are made in the word file attached (Appendix A).

## Decision letter (RSOS-190962.R0)

31-Jul-2019

Dear Dr van der Hoek:

Manuscript ID RSOS-190962 entitled "Global and universal relationships between tree-cavity excavators and forest bird richness" which you submitted to Royal Society Open Science, has been reviewed.  The comments from reviewers are included at the bottom of this letter.

In view of the criticisms of the reviewers, the manuscript has been rejected in its current form. However, a new manuscript may be submitted which takes into consideration these comments.

Please note that resubmitting your manuscript does not guarantee eventual acceptance, and that your resubmission will be subject to peer review before a decision is made.

You will be unable to make your revisions on the originally submitted version of your manuscript. Instead, revise your manuscript and upload the files via your author centre.

Once you have revised your manuscript, go to https://mc.manuscriptcentral.com/rsos and login to your Author Center. Click on "Manuscripts with Decisions," and then click on "Create a Resubmission" located next to the manuscript number. Then, follow the steps for resubmitting your manuscript.

Your resubmitted manuscript should be submitted by 28-Jan-2020. If you are unable to submit by this date please contact the Editorial Office.

We look forward to receiving your resubmission.

Kind regards,
Alice Power
Editorial Coordinator
Royal Society Open Science
openscience@royalsociety.org

on behalf of Kevin Padian (Subject Editor)
openscience@royalsociety.org


Subject Editor Comments to Authors:

I am recommending a "reject/resub" decision because our "revision" turnaround time may be too short for the authors' needs in revising, and because the reviewers have raised extensive concerns, despite being encouraging overall about the manuscript.

They see issues with how the main problem of the study is set out, the methods, the evaluation, and the conclusions. They also note a geographic bias that may entail ecological biases in the relationships of excavators to their ecosystems.

If you elect to re-submit, please detail your responses to reviewers' comments and make clear how you have altered your re-submitted manuscript. Best wishes with your revisions.

Reviewers' Comments to Author:
Reviewer: 1

General comment:
The manuscript entitled "Global and universal relationships between tree-cavity excavators and forest bird richness." reports on an interesting exploratory study linking woodpeckers/other tree cavity excavators, secondary cavity users and other forest tree species at the global and bioregional levels. The results are useful and may inspire new studies exploring these relationships more in-depth. My main criticism concerns the quality of reasoning and how and to what extent different issues are introduced and discussed. Proposing the use of certain group of species as indicators or other type of indicator species shall rest on solid grounds as well as need of such indicators should be clearly put forward. I simply miss the delineation of the conservation/management problem why we need indicators. There are many articles published on the worldwide decline of primary/intact forests, their characteristics and, in my opinion, you do not use the opportunity to discuss the potential role of woodpeckers/other tree cavity excavators (with very intimate linkages to natural forest characteristics) to support your case. Also, even if you mention their usefulness in management, there is lacking information on the intensively managed forests as areas that lose both important characteristics linked to old-growth forests and forests with high level of naturalness and thereby lose most specialized forest species often being woodpeckers. Also use of woodpeckers/other excavators as indicators of successful forest restoration could be mentionaed. There is large body of literature on both above topics and I suggest that you should add paragraphs pertaining on these issues in both Introduction and Discussion sections. To limit the length of the article, you may get rid of several unnecessary repetitions. More suggestions below:
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Reviewer: 2
Comments to the Author(s)

Many comments are made in the word file attached

# Author's Response to Decision Letter for (RSOS-190962.R0)

See Appendix B.

# RSOS-192177.R0

## Review form: Reviewer 1

**Is the manuscript scientifically sound in its present form?**
Yes

**Are the interpretations and conclusions justified by the results?**
Yes

**Is the language acceptable?**
Yes

**Do you have any ethical concerns with this paper?**
No

**Have you any concerns about statistical analyses in this paper?**
No

**Recommendation?**
Accept with minor revision (please list in comments)

**Comments to the Author(s)**
Line 130: add a bracket at the end of the sentence

Lines 164-187: I opt for a very short explaination what do you mean by "universal" used in the title of the paper already here.

Lines 268-277: In contrast with added information about not analysing woodpeckers in Australasia (lines 236-238), you report it here and in Table 2. It is confusing to me.

Line 293: I have a hard time finding the paper by Tikkanen et al. 2006 as supporting your claim here. Possibly cite several paper based on single-species woodpecker studies or use some of those:
JM Roberge, P Angelstam, MA Villard. 2008. Specialised woodpeckers and naturalness in hemiboreal forests–deriving quantitative targets for conservation planning. Biological conservation, 2008
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Lines 392-394:  I suggest adding further argument here i.e. that woodpeckers are highly responsive to playbacks (both calls and particularly drumming) that, if applied in right season are very effective survey tool and cover relatively large areas. See e.g. Kumar, R. and Singh, P. (2010), Determining woodpecker diversity in the sub-Himalayan forests of northern India using call playbacks. Journal of Field Ornithology, 81: 215-222. doi:10.1111/j.1557-9263.2009.00267.x  or Jeremy A. Baumgardt, Joel D. Sauder, and Kerry L. Nicholson (2014) Occupancy Modeling of Woodpeckers: Maximizing Detections for Multiple Species With Multiple Spatial Scales. Journal of Fish and Wildlife Management: December 2014, Vol. 5, No. 2, pp. 198-207.

Table 2: remove data concerning the woodpeckers (see my comment above)

There is one important paper dealing with woodpeckers at the global scale that is relevant to your study but ommitted namely: Vergara-Tabares, D. L., M.Lammertink, E. G.Verga, A.Schaaf, and J.Nori (2018). Gone with the forest: Assessing global woodpecker conservation from land use patterns. Diversity and Distributions 24:640–651.
Please consider mentioning the results of this paper in the Introduction or Discussion. It is particularly interesting from the management perspective and the human influence on forest qualities.

# Review form: Reviewer 2

**Is the manuscript scientifically sound in its present form?**
No

**Are the interpretations and conclusions justified by the results?**
No

**Is the language acceptable?**
Yes

**Do you have any ethical concerns with this paper?**
No

**Have you any concerns about statistical analyses in this paper?**
Yes

**Recommendation?**
Major revision is needed (please make suggestions in comments)

**Comments to the Author(s)**
For the article to have the potential to be accepted, the authors must work, in my opinion, mainly on the following points:

1) work on the predictions, making them more precise, with more ecological language, and that revolve around the two main causes that the authors propose as the main drivers determining the relationships of excavators and forest birds: the sharing of habitat requirements, and the provision of excavated cavities. How these causes spatially vary based on geographic, climatic and historical characteristics in each region, will determine the predictions that will be tested.

2) rethink the overlapping of the bird categories, assessing which is the best option to determine which of the aforementioned factors (i.e. sharing of habitat requirements and cavity provisions), are the most likely drivers of the proposed relationships. As I comment in the text, the definition of the categories is inconsistent with the methodology used. And, if I understood well the methodology, I also have the impression that the overlapping of categories used may be influencing the results, inflating the relationships between excavators and forest birds, since in this last category are also included many SCNs and forest specialists. I have seen your response to a related comment I made in the previous version. I guess that a good possibility is that the only categories that overlap are 2 (SCN) and 3 (forest specialists). That way, you can see relationships that supposedly may be due more exclusively to provision of cavities (relationships of excavator with 2 would be stronger than with 3), or more related to sharing habitat requirements (relationships of excavator with 3 would be stronger than with 2). Also, leaving category 4 without overlapping can lead to different results and interpretations I think could be more interesting.

3) The discussion needs a lot of work. I would suggest that you focus on the differences between the zoogeographic regions, which is the main objective of the paper and what has been evaluated. The differences that may exist within each region should be minimized to the maximum, and only mentioned when strictly necessary. The discussion still has a great bias to try to explain the relationships between excavators and SCN, and there is a considerably smaller space in trying to explain the relationships with forest birds that do not nest in cavities. Finally, relationships in the Australasia region, which showed a different pattern from the rest (even in sign), were not explained, and these results are practically ignored when proposed, from the title, and the first and last paragraph of the discussion, that relationships are common to all zoogeographic regions.

Many other comments have been made in the attached file (Appendix C).

# Decision letter (RSOS-192177.R0)

08-Jan-2020

Dear Dr van der Hoek,

The Subject Editor assigned to your paper ("Global and universal relationships between tree-cavity excavators and forest bird richness") has now received comments from reviewers. We would like you to revise your paper in accordance with the referee and Associate Editor suggestions which can be found below (not including confidential reports to the Editor). Please note this decision does not guarantee eventual acceptance.

Please submit a copy of your revised paper before 31-Jan-2020. Please note that the revision deadline will expire at 00.00am on this date. If we do not hear from you within this time then it will be assumed that the paper has been withdrawn. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office in advance. We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Editors, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers.

To revise your manuscript, log into http://mc.manuscriptcentral.com/rsos and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Revision." Your manuscript number has been appended to denote a revision. Revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you must respond to the comments made by the referees and upload a file "Response to Referees" in "Section 6 - File Upload". Please use this to document how you have responded to each of the comments, and the adjustments you have made. In order to expedite the processing of the revised manuscript, please be as specific as possible in your response.

In addition to addressing all of the reviewers' and editor's comments please also ensure that your revised manuscript contains the following sections before the reference list:

• Ethics statement
If your study uses humans or animals please include details of the ethical approval received, including the name of the committee that granted approval. For human studies please also detail whether informed consent was obtained. For field studies on animals please include details of all permissions, licences and/or approvals granted to carry out the fieldwork.

• Data accessibility
It is a condition of publication that all supporting data are made available either as supplementary information or preferably in a suitable permanent repository. The data accessibility section should state where the article's supporting data can be accessed. This section should also include details, where possible of where to access other relevant research materials such as statistical tools, protocols, software etc can be accessed. If the data has been deposited in an external repository this section should list the database, accession number and link to the DOI for all data from the article that has been made publicly available. Data sets that have been

deposited in an external repository and have a DOI should also be appropriately cited in the manuscript and included in the reference list.

If you wish to submit your supporting data or code to Dryad (http://datadryad.org/), or modify your current submission to dryad, please use the following link:
http://datadryad.org/submit?journalID=RSOS&manu=RSOS-192177

• Competing interests
Please declare any financial or non-financial competing interests, or state that you have no competing interests.

• Authors' contributions
All submissions, other than those with a single author, must include an Authors' Contributions section which individually lists the specific contribution of each author. The list of Authors should meet all of the following criteria; 1) substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data; 2) drafting the article or revising it critically for important intellectual content; and 3) final approval of the version to be published.

All contributors who do not meet all of these criteria should be included in the acknowledgements.

We suggest the following format:
AB carried out the molecular lab work, participated in data analysis, carried out sequence alignments, participated in the design of the study and drafted the manuscript; CD carried out the statistical analyses; EF collected field data; GH conceived of the study, designed the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

• Acknowledgements
Please acknowledge anyone who contributed to the study but did not meet the authorship criteria.

• Funding statement
Please list the source of funding for each author.

Once again, thank you for submitting your manuscript to Royal Society Open Science and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Kind regards,
Andrew Dunn
Royal Society Open Science Editorial Office
Royal Society Open Science
openscience@royalsociety.org

on behalf of Prof Kevin Padian (Subject Editor)
openscience@royalsociety.org

Associate Editor Comments to Author:
The reviewers have provided further substantial feedback, but are broadly of the view that not only have you made efforts to improve the manuscript but that there is certainly merit in the general 'story' the manuscript is telling.
With this in mind, we'd like to invite you to submit a revised manuscript for further consideration. Bear in mind that we do not generally permit multiple rounds of revision, so

please do ensure that you incorporate the requested changes into the manuscript and provide an indication of how you've done so (using a tracked-changes version of the paper and a point-by-point response document).
Good luck!

Reviewer comments to Author:
Reviewer: 2

Comments to the Author(s)
For the article to have the potential to be accepted, the authors must work, in my opinion, mainly on the following points:

1) work on the predictions, making them more precise, with more ecological language, and that revolve around the two main causes that the authors propose as the main drivers determining the relationships of excavators and forest birds: the sharing of habitat requirements, and the provision of excavated cavities. How these causes spatially vary based on geographic, climatic and historical characteristics in each region, will determine the predictions that will be tested.

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Many other comments have been made in the attached file

Reviewer: 1

Comments to the Author(s)
Line 130: add a bracket at the end of the sentence

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Please consider mentioning the results of this paper in the Introduction or Discussion. It is particularly interesting from the management perspective and the human influence on forest qualities.

# Author's Response to Decision Letter for (RSOS-192177.R0)

See Appendix D.

# RSOS-192177.R1 (Revision)

## Review form: Reviewer 1

**Is the manuscript scientifically sound in its present form?**
Yes

**Are the interpretations and conclusions justified by the results?**
Yes

**Is the language acceptable?**
No

**Do you have any ethical concerns with this paper?**
No

**Have you any concerns about statistical analyses in this paper?**
No

**Recommendation?**
Accept with minor revision (please list in comments)

**Comments to the Author(s)**
Dear Authors,
Thanks for the new version of the manuscript that I find generally improved. I have some further suggestions (see below) and also think that the entire text should be thoroughly read by the native speaker; it is "sloppy" in several places.
Line 172: remove "comma" after "indicator"
Line 175: add "with" after "correlation"
Line 179: possibly, in global perspective, better to use broad-leaved since several coniferous trees may be "deciduous". Or change the classification to temperate, boreal, tropical etc.
Lines 185-190: poor English – check and re-write
Line 218: using "same species" is confusing here. What do you mean by "same species"?

Lines 219-220: provide names of the authors in the text
Line 292: add "i.e." before "between excavators…"
Line 295: was rho really 0.88 in both cases?
Line 355: higher temperature?
Line 363: "largely tropical" instead of "more tropical"?
Line 367: provide valid reference for this claim i.e. on high logging rates in Oriental Region
Line 373-377: it seems to be against your prediction. Whole sentence is a bit confusing.
Line 386: what dynamics do you mean? Fire dynamics?
Line 514-516: I would explicitly mention high detectability here

# Review form: Reviewer 2

**Is the manuscript scientifically sound in its present form?**
No

**Are the interpretations and conclusions justified by the results?**
No

**Is the language acceptable?**
Yes

**Do you have any ethical concerns with this paper?**
No

**Have you any concerns about statistical analyses in this paper?**
Yes

**Recommendation?**
Major revision is needed (please make suggestions in comments)

**Comments to the Author(s)**
See attached (Appendix E).

# Decision letter (RSOS-192177.R1)

04-Mar-2020

Dear Dr van der Hoek:

Manuscript ID RSOS-192177.R1 entitled "Global relationships between tree-cavity excavators and forest bird richness" which you submitted to Royal Society Open Science, has been reviewed. The comments of the reviewer(s) are included at the bottom of this letter.

Please submit a copy of your revised paper before 27-Mar-2020. Please note that the revision deadline will expire at 00.00am on this date. If we do not hear from you within this time then it will be assumed that the paper has been withdrawn. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office in advance. We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Editors, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers.

To revise your manuscript, log into http://mc.manuscriptcentral.com/rsos and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Revision." Your manuscript number has been appended to denote a revision. Revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you must respond to the comments made by the referees and upload a file "Response to Referees" in "Section 6 - File Upload". Please use this to document how you have responded to the comments, and the adjustments you have made. In order to expedite the processing of the revised manuscript, please be as specific as possible in your response.

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If your study uses humans or animals please include details of the ethical approval received, including the name of the committee that granted approval. For human studies please also detail whether informed consent was obtained. For field studies on animals please include details of all permissions, licences and/or approvals granted to carry out the fieldwork.

• Data accessibility
It is a condition of publication that all supporting data are made available either as supplementary information or preferably in a suitable permanent repository. The data accessibility section should state where the article's supporting data can be accessed. This section should also include details, where possible of where to access other relevant research materials such as statistical tools, protocols, software etc can be accessed. If the data have been deposited in an external repository this section should list the database, accession number and link to the DOI for all data from the article that have been made publicly available. Data sets that have been deposited in an external repository and have a DOI should also be appropriately cited in the manuscript and included in the reference list.

• Competing interests
Please declare any financial or non-financial competing interests, or state that you have no competing interests.

• Authors' contributions

All submissions, other than those with a single author, must include an Authors' Contributions section which individually lists the specific contribution of each author. The list of Authors should meet all of the following criteria; 1) substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data; 2) drafting the article or revising it critically for important intellectual content; and 3) final approval of the version to be published.

All contributors who do not meet all of these criteria should be included in the acknowledgements.

We suggest the following format:

AB carried out the molecular lab work, participated in data analysis, carried out sequence alignments, participated in the design of the study and drafted the manuscript; CD carried out the statistical analyses; EF collected field data; GH conceived of the study, designed the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

• Acknowledgements

Please acknowledge anyone who contributed to the study but did not meet the authorship criteria.

• Funding statement

Please list the source of funding for each author.

Once again, thank you for submitting your manuscript to Royal Society Open Science and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Kind regards,
Anita Kristiansen
Editorial Coordinator

Royal Society Open Science
openscience@royalsociety.org

on behalf of Kevin Padian (Subject Editor)
openscience@royalsociety.org

Associate Editor Comments to Author:
Associate Editor: 1
Comments to the Author:
As the reviewers acknowledge you've made 'good faith' efforts to improve your paper in response to their concerns, we'd like to offer you a final opportunity to revise your manuscript - this will be your last chance to persuade the reviewers that your manuscript is ready for acceptance: if you are unable to do so after revision, we may not be able to consider the paper further. We wish you every success in this revision, and look forward to receiving a new version of the paper in due course.

Reviewer comments to Author:
Reviewer: 2

Comments to the Author(s)
See attached. (RSOS-192177.R1_Proof_hi.pdf)

Reviewer: 1

Comments to the Author(s)
Dear Authors,
Thanks for the new version of the manuscript that I find generally improved. I have some further
suggestions (see below) and also think that the entire text should be thoroughly read by the
native speaker; it is "sloppy" in several places.
Line 172: remove "comma" after "indicator"
Line 175: add "with" after "correlation"
Line 179: possibly, in global perspective, better to use broad-leaved since several coniferous trees
may be "deciduous". Or change the classification to temperate, boreal, tropical etc.
Lines 185-190: poor English – check and re-write
Line 218: using "same species" is confusing here. What do you mean by "same species"?

Lines 219-220: provide names of the authors in the text
Line 292: add "i.e." before "between excavators…"
Line 295: was rho really 0.88 in both cases?
Line 355: higher temperature?
Line 363: "largely tropical" instead of "more tropical"?
Line 367: provide valid reference for this claim i.e. on high logging rates in Oriental Region
Line 373-377: it seems to be against your prediction. Whole sentence is a bit confusing.
Line 386: what dynamics do you mean? Fire dynamics?
Line 514-516: I would explicitly mention high detectability here

# Author's Response to Decision Letter for (RSOS-192177.R1)

See Appendix F.

# RSOS-192177.R2 (Revision)

## Review form: Reviewer 1

**Is the manuscript scientifically sound in its present form?**
Yes

**Are the interpretations and conclusions justified by the results?**
Yes

**Is the language acceptable?**
Yes

**Do you have any ethical concerns with this paper?**
No

**Have you any concerns about statistical analyses in this paper?**
No

**Recommendation?**
Accept with minor revision (please list in comments)

**Comments to the Author(s)**
I am generally pleased with changes included in this version of the manuscript. However, it would be great to carefully read some of the new sentences and improve them linguistically. For example check lines 312-319 and 363-368 (clean version) for missing words.

# Decision letter (RSOS-192177.R2)

We hope you are keeping well at this difficult and unusual time. We continue to value your support of the journal in these challenging circumstances. If Royal Society Open Science can assist you at all, please don't hesitate to let us know at the email address below.

Dear Dr van der Hoek:

On behalf of the Editors, I am pleased to inform you that your Manuscript RSOS-192177.R2 entitled "Global relationships between tree-cavity excavators and forest bird richness" has been accepted for publication in Royal Society Open Science subject to minor revision in accordance with the referee suggestions. Please find the referees' comments at the end of this email.

The reviewers and Subject Editor have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the comments and revise your manuscript.

• Ethics statement
If your study uses humans or animals please include details of the ethical approval received, including the name of the committee that granted approval. For human studies please also detail whether informed consent was obtained. For field studies on animals please include details of all permissions, licences and/or approvals granted to carry out the fieldwork.

• Data accessibility
It is a condition of publication that all supporting data are made available either as supplementary information or preferably in a suitable permanent repository. The data accessibility section should state where the article's supporting data can be accessed. This section should also include details, where possible of where to access other relevant research materials such as statistical tools, protocols, software etc can be accessed. If the data has been deposited in an external repository this section should list the database, accession number and link to the DOI for all data from the article that has been made publicly available. Data sets that have been deposited in an external repository and have a DOI should also be appropriately cited in the manuscript and included in the reference list.

If you wish to submit your supporting data or code to Dryad (http://datadryad.org/), or modify your current submission to dryad, please use the following link:
http://datadryad.org/submit?journalID=RSOS&manu=RSOS-192177.R2

• Competing interests
Please declare any financial or non-financial competing interests, or state that you have no competing interests.

• Authors' contributions
All submissions, other than those with a single author, must include an Authors' Contributions section which individually lists the specific contribution of each author. The list of Authors

should meet all of the following criteria; 1) substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data; 2) drafting the article or revising it critically for important intellectual content; and 3) final approval of the version to be published.

All contributors who do not meet all of these criteria should be included in the acknowledgements.

We suggest the following format:
AB carried out the molecular lab work, participated in data analysis, carried out sequence alignments, participated in the design of the study and drafted the manuscript; CD carried out the statistical analyses; EF collected field data; GH conceived of the study, designed the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

• Acknowledgements
Please acknowledge anyone who contributed to the study but did not meet the authorship criteria.

• Funding statement
Please list the source of funding for each author.

Please note that we cannot publish your manuscript without these end statements included. We have included a screenshot example of the end statements for reference. If you feel that a given heading is not relevant to your paper, please nevertheless include the heading and explicitly state that it is not relevant to your work.

Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript before  19-Jun-2020. Please note that the revision deadline will expire at 00.00am on this date. If you do not think you will be able to meet this date please let me know immediately.

To revise your manuscript, log into https://mc.manuscriptcentral.com/rsos and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions". Under "Actions," click on "Create a Revision."  You will be unable to make your revisions on the originally submitted version of the manuscript.  Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referees and upload a file "Response to Referees" in "Section 6 - File Upload".  You can use this to document any changes you make to the original manuscript.  In order to expedite the processing of the revised manuscript, please be as specific as possible in your response to the referees.

When uploading your revised files please make sure that you have:

1) A text file of the manuscript (tex, txt, rtf, docx or doc), references, tables (including captions) and figure captions. Do not upload a PDF as your "Main Document".
2) A separate electronic file of each figure (EPS or print-quality PDF preferred (either format should be produced directly from original creation package), or original software format)
3) Included a 100 word media summary of your paper when requested at submission.  Please ensure you have entered correct contact details (email, institution and telephone) in your user account
4) Included the raw data to support the claims made in your paper.  You can either include your data as electronic supplementary material or upload to a repository and include the relevant doi within your manuscript

5) All supplementary materials accompanying an accepted article will be treated as in their final form. Note that the Royal Society will neither edit nor typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details where possible (authors, article title, journal name).

Supplementary files will be published alongside the paper on the journal website and posted on the online figshare repository (https://figshare.com). The heading and legend provided for each supplementary file during the submission process will be used to create the figshare page, so please ensure these are accurate and informative so that your files can be found in searches. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Once again, thank you for submitting your manuscript to Royal Society Open Science and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Kind regards,
Andrew Dunn
Royal Society Open Science Editorial Office
Royal Society Open Science
openscience@royalsociety.org

on behalf of Prof Kevin Padian (Subject Editor)
openscience@royalsociety.org

Associate Editor Comments to Author :
The reviewer is broadly satisfied with the scientific content of the paper, though they would prefer that you seek further English language support. Examples of professional services providing such advice may be found at
https://royalsociety.org/journals/authors/benefits/language-editing/.

Reviewer comments to Author:
Reviewer: 1

Comments to the Author(s)
I am generally pleased with changes included in this version of the manuscript. However, it would be great to carefully read some of the new sentences and improve them linguistically. For example check lines 312-319 and 363-368 (clean version) for missing words.

# Author's Response to Decision Letter for (RSOS-192177.R2)

See Appendix G.

# Decision letter (RSOS-192177.R3)

We hope you are keeping well at this difficult and unusual time. We continue to value your support of the journal in these challenging circumstances. If Royal Society Open Science can assist you at all, please don't hesitate to let us know at the email address below.

Dear Dr van der Hoek,

It is a pleasure to accept your manuscript entitled "Global relationships between tree-cavity excavators and forest bird richness" in its current form for publication in Royal Society Open Science.

You can expect to receive a proof of your article in the near future. Please contact the editorial office (openscience_proofs@royalsociety.org) and the production office (openscience@royalsociety.org) to let us know if you are likely to be away from e-mail contact -- if you are going to be away, please nominate a co-author (if available) to manage the proofing process, and ensure they are copied into your email to the journal.

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Thank you for your fine contribution. On behalf of the Editors of Royal Society Open Science, we look forward to your continued contributions to the Journal.


Kind regards,
Andrew Dunn
Royal Society Open Science Editorial Office
Royal Society Open Science
openscience@royalsociety.org

on behalf of Prof Kevin Padian (Subject Editor)
openscience@royalsociety.org


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# Appendix A

**Global and universal** relationships between tree-cavity excavators and forest bird

richness

The overwhelming majority of tree-cavity excavators, among which woodpeckers are the most numerous group (van der Hoek, Gaona, & Martin, 2017), are forest or woodland birds. Indeed, general patterns of woodpecker richness correlate positively with amount of forest cover at the global scale (Ilsøe et al., 2017). However, many excavators are regarded as habitat specialists and have highly specific habitat requirements, among which the availability of dead wood is especially important (Hoyt & Hannon, 2002; Bütler, Angelstam, Ekelund, & Schlaepfer, 2004; Tikkanen et al., 2006). This group of birds utilizes large, live or decaying trees, or coarse woody debris, for nesting, roosting, and feeding. As a result, the prevalence of such attributes in a forest ecosystem may influence local richness and abundance of excavators (Martin & Eadie, 1999; Drever, Aitken, Norris, & Martin, 2008; Drever & Martin, 2010).

The strong attachment to specific forest elements, such as dead wood and large trees, makes excavators good indicators of the naturalness of ecosystems (Marchetti, 2004; Roberge & Angelstam, 2006; Virkkala, 2006; Drever et al., 2008; Drever & Martin, 2010), whereby their presence correlates strongly with other aspects of biodiversity (Mikusiński, Gromadzki, & Chylarecki, 2001; Nilsson, Hedin, & Niklasson, 2001; Angelstam et al. 2003). For example, studies in northern boreal and temperate regions revealed that many other forest birds respond similarly to habitat components required by woodpeckers, which leads to a strong correlation between woodpecker and forest bird richness and abundance at stand and landscape scales (Mikusiński et al., 2001; Roberge & Angelstam 2006; Drever et al., 2008). As a result, the responses of woodpeckers, and likely that of other tree-cavity-excavating birds (e.g.,

**Commented [MOU1]:** what is the difference between 'global' and 'universal'. There is nothing in the introduction, nor in the discussion, justifying the usage of these two words. I suggest to delete 'universal'

**Commented [MOU2]:** I see this paragraph as mostly unnecessary, with some of this information that can be fusioned with the second paragraph

**Commented [MOU3]:** you cited this article in the previous paragraph with the four authors, and here it is as 'et al.'. Please, correct where needed

**Commented [MOU4]:** you previously cited this article with the three authors, and here it is as 'et al.'. Please, correct where needed

26 barbets, trogons, nuthatches, and certain parrot species), to changes in forest habitats

27 may be indicative of responses of forest bird communities in general (Drever & Martin,

28 2010). Thus, excavators can be effective and efficient indicators at the forest ecosystem

29 scale, and thus useful as conservation and management targets (Roberge, Mikusiński, &

30 Svensson, 2008).

31     Excavators ~~are not only reliable indicators of other forest birds by means of their~~

32 ~~associations with forest characteristics, but correlations between both groups of birds~~

33 ~~are also partially determined by species interactions. Taken together, these~~and non-

34 excavator cavity nesters are linked into 'nest-webs' (sensu Martin and Eadie, 1999) ~~of~~

35 ~~interacting species,~~ which are structured by the availability and acquisition of tree-

36 cavities formed by two major processes: ~~'natural formation', in which fungi~~ decompose

37 wood by fungi over an extended period, or animal excavation (Cockle, Martin, &

38 Wesołowski, 2011; Cockle, Martin, & Robledo, 2012; Ruggera et al. 2016). Since most

39 excavators—at least the majority of woodpeckers— excavate a new nest cavity each

40 year, this mode of cavity creation steadily provides a large number of potential sheltered

41 roosting and nesting sites for secondary-users: both for vertebrates (Cockle et al., 2012)

42 and invertebrates (Tylianakis, Klein, Lozada, & Tscharntke, 2006; Powell, Costa,

43 Lopes, & Vasconcelos, 2011). As a result, cavity formation by excavation is the main

44 source of nest holes for species in many regions of the world (Cockle et al., 2011), and

45 richness of cavity excavators is likely to be indicative of the richness of a broad range of

46 non-excavating tree-cavity nesters. However, decay-formed cavities might be very

47 common in other regions, especially the tropics, and it is very likely that the relative

48 importance of both processes of cavity formation—and thus the strength of the

49 relationship between excavator richness and non-excavator richness—varies globally

50 (Cockle et al., 2011).

**Commented [MOU5]:** I am not aware of this. I've seen some parrot species burrowing their own cavities in termitaria and cliffs, or 'arranging' cavities already done by woodpeckers or fungi. But I have not seen/heard about parrots excavating 'brand new' cavities in trees. Please, could you add a reference for that?

**Commented [MOU6]:** I see this extrapolation from responses of a very specific bird group (i.e. cavity nesters) to responses of the whole forest bird community, a bit pretentious. Drever & Martin did not find that association either, as can be seen in their summary: "Recent studies indicated that species richness of woodpeckers was correlated with richness of all forest birds, thus suggesting potential exists for management practices that can address needs of woodpeckers in particular and other forest birds in general… These results, combined with previously identified positive correlations between woodpecker and forest bird richness, indicate woodpeckers can be managed as a suite for the purpose of managing avian biodiversity as a whole."

Besides, most of these extrapolations were done in north temperate forests (NA and Europe), which are structurally simpler than tropical forests. For example, excavators and understory birds might have similar responses to logging in north temperate forests, but different responses in tropical and subtropcial forests. If the article is focused at a global scale, these considerations need to be taken into account.

So, unless you have a better argumentation for this association at a global scale, I suggest to delete this part

**Commented [MOU7]:** This is not what Cockle et al. (2011) found. According to the map in the Figure 2a, you can see that the pattern that you mention (excavated cavities as main source for non-excavator birds) is only strong in North America, very weak in Europe (only 1 out of 4 studies showed that pattern), and opposite in South America and Australia, this is, non-excavator birds mainly used decay-formed cavities (there is no study in Africa). After Cockle et al. (2011), Ruggera et al. (2016) quoted "Therefore, in the PF woodpeckers do not seem to play a key role in provisioning cavities to the nest-web, a pattern also shown for other South American and some European forests, and contrary to the findings in North America (Cockle et al., 2011a,b; Pereira et al., 2009; Wesołowski, 2007)."

Please, be careful when citing other authors, and put strictly what they have found

51    Finally, it is worth noting that ~~the diversity of excavators can be indicative of other~~

52    ~~groups of species as~~ excavators can ~~be habitat engineers which~~ facilitate foraging of

53    other bird species by perforating the bark of trees to expose insects or sap (Bull &

54    Jackson, 1995; Montellano, Blendinger, & Macchi, 2013) and ~~which~~ play a role in the

55    dispersal of fungi which leads to wood softening, thus further aiding in the provision of

56    potential nest-cavities (Jusino et al., 2016).

57    Local studies of cavity-nesting birds and their ~~community~~ interactions are largely

58    biased towards temperate zones, and only a few authors have explored global variation

59    in nest-web characteristics or addressed how such variation should be taken into

60    account when considering cavity-nester communities in forest conservation or

61    management (e.g., Cockle et al., 2011; Ruggera et al. 2016). Given the significant role

62    that woodpeckers and other excavators play in forest ecosystems across most of the

63    world, we might predict that these birds could be reliable indicators of avian diversity

64    and richness not only at local and regional scales (Mikusiński et al., 2001; Martin,

65    Ibarra, & Drever, 2015), but also at a global scale. Therefore, the aim of the present

66    study is to investigate whether there are consistent patterns in the relationships between

67    avian tree-cavity excavators (hereafter: excavators) and species richness of non-

68    excavating tree-cavity nesters (hereafter: non-excavators), forest specialist species, and

69    forest birds in general, across the globe. Given the important role of excavators in forest

70    ecosystems, we expect that non-excavator, forest specialist, and forest bird richness will

71    generally increase with the number of excavators present in the ecosystem, regardless of

72    the ecosystem or location. However, we also predict that the strength of the relationship

73    between excavators and richness of other forest birds will vary across zoogeographic

74    regions, following indications that the richness of different groups of tree-cavity nesting

75    birds (excavators, non-excavators) varies substantially across the world (van der Hoek

et al., 2017). If previously observed relationships between cavity-excavators and other

forest birds scale up from local forest stands or ecosystems to zoogeographic or global

levels, then this strengthens the potential of tree cavity-excavators as both indicators and

management surrogates.

**Material and Methods**

We used published global distribution maps of tree-cavity nesting birds (van der Hoek

et al., 2017) and forest birds (Betts et al., 2017) to extract richness estimates per 10×10

km grid cell. Maps for both tree-cavity nesters and forest birds were based on the same

species range maps provided by BirdLife International and NatureServe (2015). Bird

species were classified in: 1) excavators: XXXXXX; 2) non-excavators: all birds known

to nest in tree cavities but which do not excavate their cavities, most of which are forest

birds; 3) forest specialists: birds that make exclusive use of forest; and 4) forest birds in

general: birds that use forest habitat and at least one other type of habitat. We used only

range polygons where a species' presence was classified as 'Extant' or 'Probably

extant', and assigned 'presence' to all grid cells that overlapped with range polygons.

Next, we created generalized least squares (gls) models to assess the linear relationships

between excavators and the other bird categories excavators and all forest birds (birds

classified as using forest exclusively and those using forest habitat and at least one other

type of habitat; hereafter: forest birds), all forest specialists (birds classified as making

exclusive use of forest by Betts et al. (2017)), or all non-excavating cavity-nesters (all

birds known to nest in tree cavities but which do not excavate their cavities, most of

which are forest birds; hereafter: non- excavators). To take biogeographical differences

into account, we proceeded to separate trends across the globe, and created gls models

100 for the six zoographic regions separately ( : Nearctic, Palearctic, Neotropical,

101 Afrotropical, Oriental, and Australasia ).

102     As our data were spatially structured, we followed similar protocols to adjust for

103 spatial autocorrelation as per Storch et al. (2006). This implied the use gls models with

104 an exponential spatial covariance structure, as these models had the best fit in

105 preliminary tests, which reduced—rather than eliminated—the influence of spatial

106 autocorrelation on our models. In these tests, exponential gls models consistently had

107 the lowest Akaike's Information Criterion (AIC) value compared to a set of models,

108 including an ordinary least squares model with no spatial structure, and gls models with

109 Gaussian, linear, rational quadratics and spherical spatial covariance structures.

110     Even though gls models work well with large datasets, we found that gls models

111 fitted on all data failed to converge (using the R package "nlme" (Pinheiro et al., 2016)).

112 To circumvent this computational problem, we first grouped grid cells by

113 zoogeographic region. We thereafter ran 1000 models on bootstrap permutations of

114 1000 randomly selected grid cells (see Kissling, Sekercioğlu, & Jetz, 2012; Ilsøe et al.,

115 2017). Of these 1000 model iterations, we subsequently calculated the mean (±SD),

116 minimum and maximum coefficients of the regression slope. Next, we obtained a

117 measure of the strength of each correlation by fitting each exponential gls model to a

118 different, non-overlapping, test data set of 1000 randomly selected grid cells. We then

119 proceeded to calculate the Spearman rho coefficient of the correlation between

120 predicted and observed data, for all 1000 models per zoogeographic region. Finally, we

121 calculated the mean Spearman rho of all significant models per zoogeographic region.

122 We repeated all of these analyses for woodpeckers as a subset of the excavators. All

123 data, R scripts, and initial results needed to reproduce our analyses presented here are

124 deposited online (Appendix S1).

**Commented [MOU18]:** I find necessary to clarify some 'ecological' issues (i.e. not statistical) in methods. 1) Did you include the whole area of each biogeographic zone? or 2) only the forest areas in each one of them?
If (1): How do you think the different amount of area/forest area of each biographic zone can influence your results? How non-forest excavators (as some woodpeckers) can incluence your results? or did you exclude them?
Another question: given the cnsideration of Palearctic and Oriental regions, what does the AUSTRALASIA region includes? what part of Asia?

**Commented [MOU19]:** What did you specifically model? which were the variables?

**Commented [MOU20]:** I am not an especialist in this kind of analyses, and I could not fully understand it. Given that many readers of this kind of papers are not especialists either, I find very important to better explain this methodological part. What are the predicted and what the observed data? What does tell us the regression slopes and what the mean spearman rho?

Nevertheless, at this point, I have the impression that you modeled the richness of non-excavators and forest birds, relative the presence of excavators (explanatory variable), i.e. in a causal manner (= gls models). However, in the introduction this relationship was mostly raised in a correlational manner, this is, that both excavators and the other forest bird groups show similar responses to forest structure and disturbances. Exceptions to this correlational relationship are, for example, the FEW cases (in terms of global areas) in which excavators are essential for non-excavators by providing new cavities or food resources (sap and insects in excavator perforations). In short, you are analysing a relationship that you mostly posted as correlational, with regression models. Please, if my reasoning is incorrect, just ignore it, but explain better the methodology.

125

**Results**

~~We distilled global patterns in the r~~Relationships between excavator richness and that of non-excavators, all forest birds, and forest specialists ~~(Fig. 1), though relationships~~ differed in relative strength and regression slope, and also according to ~~depending on the group of birds and~~ the zoogeographic region analysed (Fig. 2, Table 1). ~~For example, the R~~relationships between excavators and non-excavators and forest-associated birds were typified by particularly steep regression slopes in the ~~Neotropics and the other~~ predominantly tropical regions ~~(~~: Neotropical Afrotropical and Oriental~~)~~. In the Neotropics, the presence of one additional excavator species in a grid cell implied an increase of more than two additional non-excavators, ten forest bird species, or four forest specialists. In contrast, regression slopes were less steep in predominantly temperate and boreal regions such as the Nearctic and Palearctic, where an increase of one excavator species signified an increase of approximately one non-excavator species, four to five forest birds, or one forest specialist. Similar to variation in the slopes of the regressions, we found differences in the strength (as represented by Spearman's rho) of these relationships, with again stronger relationships in the predominantly tropical Afrotropical, Oriental, and Neotropical regions than in the comparably more temperate/boreal Nearctic and Palearctic regions (Table 1).

Although the relationships between excavators and the other three bird groups ~~of cavity-nesting and forest-associated birds~~ were generally ~~similar in nature (~~positive~~)~~, there were some differences in the relative strength of these relationships across zoogeographic regions. For example, excavator richness was a particularly strong predictor of non-excavator richness and of all forest birds in the Oriental region (rho = 0.88 and 0.86, respectively), and slightly less so for forest specialists (rho = 0.77),

---

**Commented [MOU21]:** I find Figures 1 and 2 redundant, given that in Fig. 1 you detailed ellipses for each of the six zoogeographic region. I'd say that you can leave only the figure 2 and nothing will be lost.

**Commented [MOU22]:** what does mean this category? specialists? all forest birds? both? you should be consistent with category names

**Commented [MOU23]:** I wouldn't say that Afrotropical and Oriental zones have also 'particularly steep slopes'. For example, in Table 1 can be seen that Australasian slopes are all steeper than Afrotropical and Oriental slopes. Also, Nearctic and Palearctic slopes of non-excavator are equal or steeper than that of Oriental, respectively; and that of forest specialist birds are also steeper or equal than that of Afrotropical, respectively. SO, the pattern you wrote is not as clear as you suggest.

**Commented [MOU24]:** It's hard to follow yourreasoning. It seems like sometimes your reasoning is associative/correlative (e.g. both excavators and other groups of forest birds have similar responses to disturbances), other times it is explanatory (e.g. theexcavator richness determines the richness of other non-excavator cavity-users by providing new cavities), and here it is predictive: the addition of 1 excavator species implies the addition of X forest bird species, ignoring any other type of causes, such as phylogenetic, biogeographical, etc. You must decide which of these visions you are going to explore, or clearly establish that all of them will be analysed, with their respective methodologies and theoretical support

**Commented [MOU25]:** What exactly does the Rho (=strength) mean in this context? low values of Rho mean that the relationships are not very reliable? for example in australasian region. And more important, what would be the joint interpretation of the slopes, the percentage of models with p greater than 0.5 and the rho?

150  whereas excavator richness in the Afrotropics showed a strong relationship with all

151  forest birds (rho = 0.94) and with forest specialists (rho = 0.88), but a somewhat weaker

152  association with non-excavators (rho = 0.79).

153  We repeated all analyses for woodpeckers as a subset of excavators and found nearly

154  identical results, with again significant positive relationships between woodpeckers and

155  other groups of cavity-nesting or forest-associated birds in all regions but Australasia,

156  and with steeper regression slopes and stronger relationships in the predominantly

157  tropical Neotropical, Oriental and Afrotropical regions as compared to more shallow

158  slopes and weaker associations in the Nearctic and Palearctic (Table 2). The relative

159  strength of the relationships between woodpeckers and the three other groups of cavity-

160  nesting and forest-associated birds did again depend on the zoogeographic region (in

161  similar ways as for excavators), and woodpeckers were equally strong predictors of the

162  richness of other birds as excavators in general, with the notable exception of

163  Australasia. In this region, excavators showed a weak (rho = 0.69) but often significant

164  (p < 0.05 in 97 percent of model iterations) positive relationship with forest specialists,

165  whereas no clear relationship emerged between woodpeckers and forest specialists (rho

166  = -0.08).

167

168  **Discussion**

169  We found strong positive relationships between excavators/woodpeckers and non-

170  excavators, forest birds and forest specialists at global and zoogeographic scales,

171  although these relationships differed in both strength and characteristics (regression

172  slopes) across zoogeographic regions. Our results imply that excavators and

173  woodpeckers (a predominant subset of excavators) hold potential as indicators and

174  management surrogates across most of the world (Hunter Jr et al., 2016), but also that

**Commented [MOU26]:** I did not understand the difference between the global and the zoogeographic scale of analysis. That is why I suggested that figures 1 and 2 are redundant. Furthermore, there are not numerical results for the global scale of analysis. So, I'd suggest to better clarify these results

175 we have to take differences among zoogeographic regions into account if we are going

176 to adopt these surrogates for conservation or management. Furthermore, the

Commented [MOU27]: I would like to read what are those differences to take into account from a practical point of view

177 zoogeographic variation among nest-web assemblages hints at underlying differences in

178 factors ranging from broad-scale patterns in evolutionary history (e.g., speciation) to

179 more local-scale variation in ecosystem characteristics and species traits (e.g., tree

180 cavity availability and a species' level of habitat specialization).

Commented [MOU28]: The comment on nest-webs here, in the first paragraph of Discussion, is out of context. Besides, variation among nestwebs... in relation to what? Are you trying to relate the association of excavators and other forest birds with variations in nestweb characteristics? it's far from clear, and you are leaving out a key aspect: the diversity, persistence and characteristics of trees with cavities

181     Many excavators, woodpeckers included (hereafter excavators/woodpeckers), have

182 strong preferences for specific forest elements, such as dead and decaying trees or

183 particularly large trees (e.g., Tikkanen et al. 2006). In turn, these elements, and the

184 processes that drive their presence and abundance, are of great importance to habitat

185 formation and create additional niche space to support many groups of organisms

186 (Stokland, Siitonen, & Jonsson, 2012). Therefore, we can expect that forests that meet

187 the habitat requirements of excavators (e.g., certain levels of availability of decaying

188 and dead wood) provide high quality habitat for many other organisms. This may

189 explain higher richness of forest birds (especially forest specialists) in areas occupied by

190 high numbers of excavators/woodpeckers. For non-excavating species that utilize tree-

191 cavities for their nests, this relationship may be enhanced by the fact that

192 excavators/woodpeckers create or facilitate potential nest substrates (Martin & Eadie,

193 1999). In other words, the strong habitat preferences of many excavators/woodpeckers,

194 as well as the facilitatory role excavators play in providing nest substrates, make these

195 birds potential indicators of many forest-associated species and, by extension, of high-

196 quality forests (i.e., natural, old growth; Drever et al. 2008).

Commented [MOU29]: However, in several other nestwebs (for example in South America [Cockle et al. 2012, Ruggera et al. 2016] and India [Manikandan & Balasubramanian 2018]), most non excavator birds mainly use decay-formed cavities in living trees. Only 10-25% of interactions (including excavator interactions) are made with snags. So, the evidence to date (even in the Neotropics, where your results showed the strongest association between excavators and non-excavators), would not be explained by the number of snags or the amount of woodpecker-excavated cavities. Also, you need to better explain why forest especialist birds would benefit from the presence of 'certain levels (how much?) of availability of decaying and dead wood'

197     The steep slopes we found for correlations between excavators/woodpeckers and

198 other forest birds in the predominantly tropical regions (Neotropics, Oriental,

199 Afrotropical) contrast to more shallow slopes in the temperate/boreal regions

200 (Palearctic, Nearctic). Macro-scale processes (e.g., as outlined by Gaston, 2000), such

201 as speciation events, are likely to account for some of these differences among

202 zoogeographic regions. First, overall species richness, of birds (Blackburn & Gaston,

203 1996), including cavity-nesting birds (van der Hoek et al., 2017), and also of trees as

204 potential substrates for cavities (Currie & Paquin, 1987), differs both among and within

205 zoogeographic regions, likely inducing differences in nest-web assemblages (see e.g.

206 Cockle et al. (2012) for global differences in nest-web characteristics). However,

207 variation in species composition and associated variation in functional richness (i.e.

208 variety of functional traits), more than richness per se, is likely to contribute most to

209 spatial variation in nest-web assemblages across global scales. For example, the

210 Australasian region lacks the presence of Piciformes, the Order to which nearly 75% of

211 excavators belong (van der Hoek et al., 2017), whereas speciation processes have led to

212 a relatively high diversity of Piciformes in southeast Asia (Benz, Robbins, & Peterson,

213 2006). ~~Given that we found nearly similar results for woodpeckers and excavators as a~~

214 ~~larger group that includes e.g., barbets, except for in Australasia, we hereafter discuss~~

215 ~~these jointly as 'excavators'.~~

216     We hypothesize that observed spatial variation in the relationships between

217 excavators and other forest birds within zoogeographic regions stems more from local

218 differences in habitat and vegetation characteristics (e.g. tree species composition and

219 climatic variables (Huston, 1999), as well as o tree cavity availability and their

220 formation agents (Remm & Lõhmus 2011)) rather than from speciation processes. Such

221 differences would for example explain how in the Neotropics, cavity-nesting

222 assemblages studied in the temperate mountain forests of Chile had a 1:6 ratio of

223 excavators (4 species) to non-excavators (25 species; Altamirano, Ibarra, Martin, &

224 Bonacic, 2017) whereas a subtropical Atlantic moist forest supported relatively higher

**Commented [MOU30]:** differences in relation to what of the nestwebs? you need to be more specific

**Commented [MOU31]:** You need to better explain this: how speciation and other macro-scale processes across the globe influence on the results you found. Explanations generally are biased to nestwebs. However, you have other bird groups that not necessarily are cavity-nesters. Also, you don't necessarily have to invoke networks (of which there are relatively few reports worldwide) to talk about cavity-nesters (of which there are comparatively many more reports around the world)

**Commented [MOU32]:** Again, 1) variation in relation to what of the nestwebs? you need to be more specific. And 2) Explanations generally are biased to nestwebs, you don't need to invoke networks to talk about cavity-nesters

**Commented [MOU33]:** Astralasia region doesn't lack Piciformes. As you say a few words later, SE Asia has a high diversity of Piciformes. So, be careful when you explain Australasia results as a unique region (see comment also about AUSTRALASIA in methods). In fact, I would like to find a better explanation of the results of the Australasian region, since it had the most contrasting results with the rest of the regions.

**Commented [MOU34]:** I honestly lost the point of the paragraph. I do not see a concrete explanation or discussion of some aspect of the reported results. I did not understand why the tropical regions had deeper slopes (although, see comment on results on the criticism of this pattern), I did not understand how to explain the flatter slopes of the temperate / cold regions of the north, nor did I find a convincing explanation of the contrasting results of the Australasian region

**Commented [MOU35]:** What are these 'within' variations? In results, you have always emphasized differences 'between' zoogeographic regions. Please, explain better

225 numbers of excavators with a 1:3 ratio of excavators (9) to non-excavators (25) (Cockle

226 et al., 2012). Similarly, we can hypothesize that at least some variation at regional

227 scales stems from differences in the propensities for re-use of excavated cavities by

228 non-excavators. For example, proportions of decay-formed cavities used are particularly

229 high in parts of the world with high amounts of precipitation (e.g., most of the wet

230 tropics), a reflection of fungal growth, and lower in anthropogenically disturbed

231 landscapes than in primary forests (Remm & Lõhmus, 2011). In turn, a high availability

232 of decay-formed cavities might allow for a relatively high non-excavator richness, with

233 fewer species dependent on excavators for the supply of nest-cavities. For example,

234 even woodpeckers, commonly considered primary excavators, occasionally use decay-

235 formed cavities in Neotropical temperate rainforests where tree decay is the key driver

236 of nest-web structure (Altamirano et al., 2017). Finally, we find that relatively higher

237 numbers of non-excavators, or cavity-nesters in general, may occur in regions where

238 many species are habitat generalists that utilize other nest substrates than tree-cavities

239 (e.g., 40% of cavity nesters in Neotropical temperate forests are facultative users of tree

240 cavities for nesting; Altamirano et al., 2017), as compared to regions where most cavity

241 nesters are obligate tree-cavity users (e.g., over 85% of cavity nesters in temperate

242 Nearctic forests; Wesołowski & Martin, 2018). Finally, it is worth noting that cavity

243 availability and use are also likely to be influenced by cavity persistence (longevity), a

244 characteristic that can have considerable spatial variation due to factors such as land use

245 patterns (e.g., logging), climatic factors (e.g., rainfall), and cavity characteristics (e.g.,

246 whether they are located in live or dead trees; e.g., Edworthy, Wiebe, & Martin, 2012;

247 Cockle, Martin, & Bodrati, 2017).

248     We detected relative differences in strengths among the relationships between

249 excavators/woodpeckers and non-excavators, forest birds, and forest specialists across

**Commented [MOU36]:** what differences? you have not established what are the differences along the neotropical region in terms of climatic variables, tree species composition, tree availability and their formation agents. Also, include in this comparison the work by Ruggera et al. 2016, how their results fit in the explanation your trying to develop?

**Commented [MOU37]:** variation of what?

**Commented [MOU38]:** then, if non-excavators do not 'need' excavators as cavity-forming agents, why did they show the greatest association in richness in the Neotropics?

**Commented [MOU39]:** Also, Lammertink et al. 2019. Helmeted Woodpeckers roost in decay-formed cavities in large living trees: a clue to an old-growth forest association. Condor 121:1-10 DOI: 10.1093/condor/duy016

**Commented [MOU40]:** Altamirano et al. 2017 wrote: 'Among SCNs, ten species (40%) were obligate and 15 (60%) were non obligate cavity nesters. Non obligate cavity nesters included six (24%) facultative, five (20%) marginal, and four (16%) incidental SCN'. If we include also PCN, facultative cavity nesters are 20%.

**Commented [MOU41]:** how are they influenced? Again, I lost the point. You began talking about 'spatial variation in the relationships between excavators and other forest birds within zoogeographic regions', but then you focused (again) only on excavators and non-excavators, especially in the Neotropics.

250    zoogeographic regions. These differences were most likely to stem from the same

251    variation among species and ecosystem characteristics discussed above (e.g., the

252    distribution and relative importance of cavity forming agents), and indicate that richness

253    of excavators/woodpeckers may be a better indicator of richness of other cavity and

254    forest-associated species in one region than in another. In addition, the relative strength

255    of relationships between excavators and other forest birds might reflect whether

256    excavators are indicative of the richness of other species due to shared associations with

257    particular forest elements (indirect association), due to their direct facilitation of nest

258    cavities (direct facilitation), or whether both factors play a role. For example, we found

259    that relationships between excavator and forest bird or forest specialist richness in the

260    Afrotropics are relatively strong, whereas the relationship between excavators and non-

261    excavators is comparatively weaker. This might indicate that, in the Afrotropics,

262    excavators are especially strong predictors of other groups of forest-associated birds

263    through their mutual habitat requirements, rather than through their direct facilitation of

264    tree-cavities. In contrast, excavators are relatively stronger predictors of non-excavators

265    in the Oriental region, which might lead to hypotheses that excavators play a more

266    direct, nest-web structuring role through the provision of cavities in the Oriental region.

267       Some non-excavators might use cavities created by multiple excavator species,

268    whereas others predominantly use cavities formed by processes of degradation, damage

269    or insect activity (Martin & Eadie 1999; Cockle et al., 2012; Ruggera et al., 2016). In

270    addition, certain excavators might be especially abundant or provide cavities that are

271    very commonly reused by several species, whereas others are scarce and leave only a

272    few short-lived cavities that would not be generally available for use by non-excavators.

273    Given such complexities among nest-web interactions, it is important to emphasize that

274    we present general global patterns in the composition of tree-cavity-using assemblages

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**Commented [MOU42]:** in which ones?

**Commented [MOU43]:** I believe that this is a central point, that it should be better developed in the introduction, and that the methodology should be chosen according to that. It is not the same to analyze something in a correlative way, that in an explanatory or predictive way

**Commented [MOU44]:** This does not make sense to me. The relationship is weak, and you argue that it is because they have similar requirements. However, if they have similar habitat requirements, it would not be logical to think that their richness should vary in a similar way?

**Commented [MOU45]:** however, see Manikandan & Balasubramanian 2018. Sequential Use of Tree Cavities by Birds and Nest Web in a Riparian Forest in Southwest India. Acta Ornithologica, 53(1):49-60.

**Commented [MOU46]:** All this is vague and inconclusive: it may be this but it may also be the other

275 (i.e., communities of linked species that often interact within networks), and do not

276 provide evidence for direct causal links between the presence of one group of species

277 and another or direct evidence of species interactions at the zoogeographic regional

278 scale.

> **Commented [MOU47]:** I do not see an important point in this paragraph. I suggest to erase it completely

279     Excavators, of which woodpeckers are an important subset, appear to be useful

280 indicator species for forest bird diversity at multiple spatial scales, across the world.

> **Commented [MOU48]:** which ones? you only analysed at the zoogeographic scale

281 They form a small and fairly easy to identify (even by citizen scientists) subset of the a

282 larger group of species (forest birds) . often studied to understand the effects of

283 anthropogenic disturbances. Studies of excavators (or woodpeckers specifically),

284 especially in high biodiversity tropical regions, might provide quick measures of forest

285 quality and biodiversity. A comprehensive study of all forest birds in some regions like

286 Amazon or Congo basin would require considerable local expertise and training, which

287 is often difficult to achieve due to social and monetary limitations. Thus, we conclude,

288 excavators have excellent potential as study subjects for conservation monitoring and

289 planning initiatives, in comparative research, and to guide the establishment of region-

290 wide forest conservation strategies, especially in the largely understudied tropical

291 regions of the world.

292

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294 We would like to thank Lisa Manne, and Kristina Cockle for their critical remarks on

295 drafts of this article.

296

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**Commented [MOU49]:** Sometimes, there's a –, and sometimes there's a -. Please, use only one

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419    **Table 1. Results of generalized least square models of possible correlations**

420    **between (1) excavator and non-excavator richness, (2) excavator and forest bird**

421    **richness, (3) excavator and forest specialist richness.** Each result reflects the mean

422    outcome of 1000 models build with 1000 randomly selected grid cell data points that

423    include an exponential spatial covariance structure. The mean Spearman rho was

424    calculated over the fit of each of 1000 models to a test data set.

| Zoogeographic region | Correlation | Mean Slope (Min. – Max.; SD) | % of models with $P < 0.05$ | Mean Spearman rho |
|---|---|---|---|---|
| Nearctic | 1 | 0.8 (0.4 - 1.3; 0.1) | 60 | 0.73 |
| | 2 | 4.3 (3.3 - 5.9; 0.4) | 63 | 0.84 |
| | 3 | 1.4 (1.2 - 1.6; 0.1) | 71 | 0.71 |
| Palearctic | 1 | 1.1 (0.7 - 1.4; 0.1) | 84 | 0.78 |
| | 2 | 4.9 (4.0 - 6.7; 0.4) | 73 | 0.85 |
| | 3 | 1.1 (0.8 - 1.7; 0.1) | 83 | 0.79 |
| Oriental | 1 | 0.7 (0.6 - 0.9; 0.0) | 100 | 0.88 |
| | 2 | 5.7 (4.9 - 6.6; 0.3) | 100 | 0.86 |
| | 3 | 1.6 (1.3 - 1.9; 0.1) | 100 | 0.77 |
| Neotropical | 1 | 2.4 (1.9 – 3.0; 0.2) | 83 | 0.95 |
| | 2 | 10.8 (9.1 - 14.0; 0.7) | 72 | 0.97 |
| | 3 | 4.2 (3.4 - 5.2; 0.2) | 72 | 0.96 |
| Afrotropical | 1 | 1.1 (0.7 - 1.9; 0.2) | 76 | 0.79 |
| | 2 | 6.8 (5.0 - 9.8; 0.9) | 73 | 0.94 |
| | 3 | 0.9 (0.6 - 1.5; 0.1) | 79 | 0.88 |
| Australasian | 1 | 1.8 (1.4 - 2.2; 0.1) | 88 | -0.14 |
| | 2 | 7.5 (2.3 - 11.2; 1.3) | 100 | 0.31 |
| | 3 | 1.0 (-0.1 – 2.0; 0.3) | 97 | 0.69 |

425

426

427 **Table 2. Results of generalized least square models of possible correlations**

428 **between (1) woodpecker and non-excavator richness, (2) woodpecker and forest**

429 **bird richness, and (3) woodpecker and forest specialist richness.** Each result reflects

430 the mean outcome of 1000 models build with 1000 randomly selected grid cell data

431 points that include an exponential spatial covariance structure. The mean Spearman rho

432 was calculated over the fit of each of 1000 models to a test data set.

| Zoogeographic region | Correlation | Mean Slope (Min. – Max.; SD) | % of models with *P* < 0.05 | Mean Spearman rho |
|---|---|---|---|---|
| Nearctic | 1 | 1.0 (0.5 - 1.6; 0.2) | 61 | 0.70 |
| | 2 | 5.3 (3.7 - 8.0; 0.7) | 67 | 0.79 |
| | 3 | 1.7 (1.1 - 2.2; 0.1) | 70 | 0.63 |
| Palearctic | 1 | 1.2 (0.9 - 2.3; 0.1) | 81 | 0.79 |
| | 2 | 5.6 (4.3 - 8.1; 0.6) | 73 | 0.83 |
| | 3 | 1.3 (0.9 - 2.0; 0.2) | 82 | 0.73 |
| Oriental | 1 | 1.0 (0.8 - 1.3; 0.1) | 100 | 0.88 |
| | 2 | 7.9 (6.6 - 9.8; 0.5) | 100 | 0.88 |
| | 3 | 2.2 (1.7 - 2.6; 0.1) | 100 | 0.80 |
| Neotropical | 1 | 3.3 (2.4 - 4.9; 0.4) | 68 | 0.94 |
| | 2 | 14.3 (10.8 - 20.5; 1.6) | 67 | 0.93 |
| | 3 | 5.2 (3.9 - 6.6; 0.5) | 73 | 0.88 |
| Afrotropical | 1 | 1.6 (0.9 - 3.5; 0.4) | 72 | 0.74 |
| | 2 | 9.9 (6.4 - 19.6; 1.9) | 69 | 0.86 |
| | 3 | 1.3 (0.7 - 3.2; 0.3) | 80 | 0.81 |
| Australasian | 1 | 1.9 (-0.1 - 4.4; 0.6) | 81 | -0.33 |
| | 2 | 8.6 (1.2 - 21.8; 2.4) | 75 | -0.30 |
| | 3 | 3.9 (-0.2 – 9.0; 1.2) | 96 | -0.08 |

433

**Figure legends**

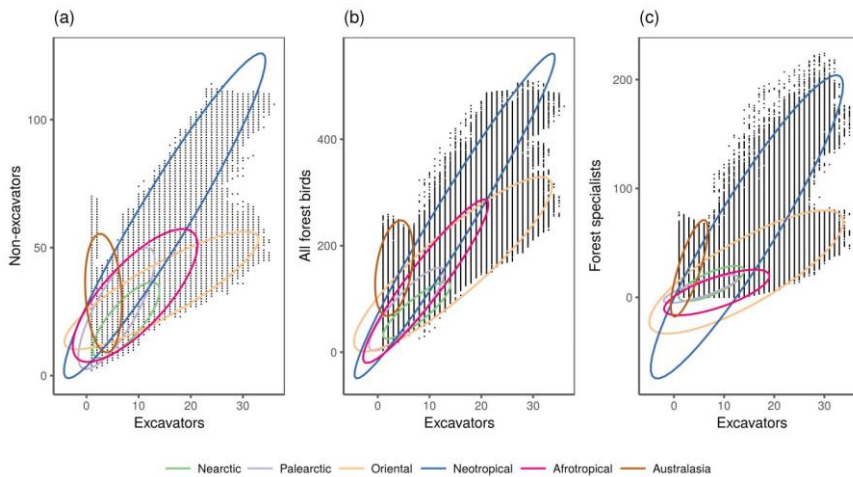**Figure 1. Scatterplots indicating potential correlations between excavators and non-excavators (a), excavators and all forest birds (b), and excavators and ~~all~~ forest specialist birds (c).** Circular polygons represent the distribution of 95% of grid cells pertaining to each of six zoogeographic regions. Points represent richness values in 10x10 km grid cells.
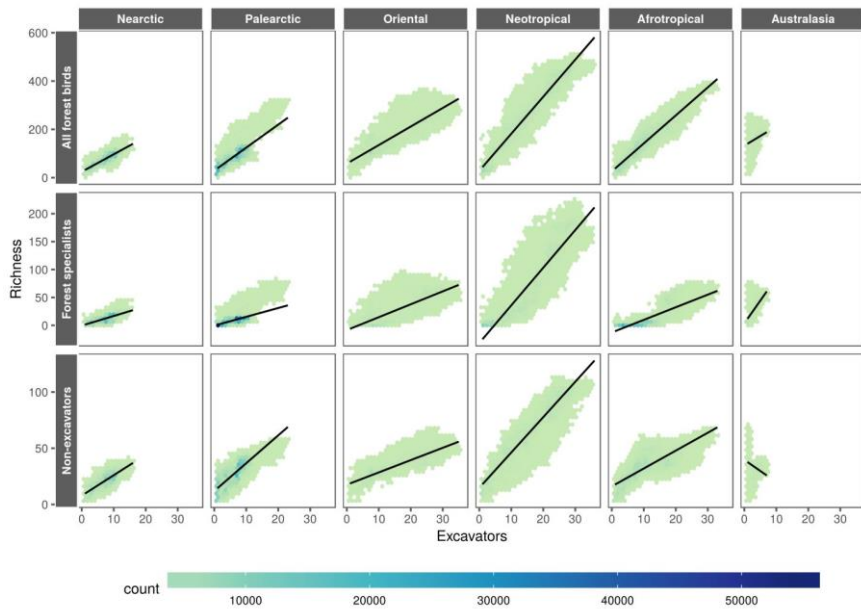
**Commented [MOU50]:** if something is 'circular', it cannot be a 'polygon'

**Figure 1.**

443 **Figure 2. Scatter plots of the correlation between the richness (number of species)**

444 **of excavators and all forest birds (upper row), all forest specialists (middle row),**

445 **and all non- excavating cavity-nesters (bottom row) in six zoogeographic regions.**

446 Points represent species richness values in 10x10 km grid cells, and the solid line

447 represents the fit of a linear regression model, created using all grid cell values.

448



449 **Figure 2.**

# Appendix B

I am recommending a "reject/resub" decision because our "revision" turnaround time may be too short for the authors' needs in revising, and because the reviewers have raised extensive concerns, despite being encouraging overall about the manuscript.

They see issues with how the main problem of the study is set out, the methods, the evaluation, and the conclusions. They also note a geographic bias that may entail ecological biases in the relationships of excavators to their ecosystems.

If you elect to re-submit, please detail your responses to reviewers' comments and make clear how you have altered your re-submitted manuscript. Best wishes with your revisions.

Reviewers' Comments to Author:
Reviewer: 1

General comment:
The manuscript entitled "Global and universal relationships between tree-cavity excavators and forest bird richness." reports on an interesting exploratory study linking woodpeckers/other tree cavity excavators, secondary cavity users and other forest tree species at the global and bioregional levels. The results are useful and may inspire new studies exploring these relationships more in-depth.

**RESPONSE: We thank the reviewer for their supportive comments.**

My main criticism concerns the quality of reasoning and how and to what extent different issues are introduced and discussed. Proposing the use of certain group of species as indicators or other type of indicator species shall rest on solid grounds as well as need of such indicators should be clearly put forward. I simply miss the delineation of the conservation/management problem why we need indicators. There are many articles published on the worldwide decline of primary/intact forests, their characteristics and, in my opinion, you do not use the opportunity to discuss the potential role of woodpeckers/other tree cavity excavators (with very intimate linkages to natural forest characteristics) to support your case. Also, even if you mention their usefulness in management, there is lacking information on the intensively managed forests as areas that lose both important characteristics linked to old-growth forests and forests with high level of naturalness and thereby lose most specialized forest species often being woodpeckers.

**RESPONSE: We thank the reviewer for pointing out these ways to strengthen our text. We have added arguments and citations to strengthen these points throughout the Introduction (e.g., lines 96-98).**

Also use of woodpeckers/other excavators as indicators of successful forest restoration could be mentionaed. There is large body of literature on both above topics and I suggest that you should add paragraphs pertaining on these issues in both Introduction and Discussion sections. To limit the length of the article, you may get rid of several unnecessary repetitions. More suggestions below:

Detailed comments:

Line 99: Several species use smaller trees or snags too. Possibly add "often" or "usually".

**RESPONSE: We agree with the reviewer that there are many exceptions, for which we followed the suggestion to add 'often' to soften the generalization.**

Line 109: Woodpeckers (cavity excavators) are most often resident species what could additionally strengthen your reasoning on strong linkages to forest environments and their quality.

**RESPONSE: We thank the reviewer for this valid point, and have incorporated a sentence to illustrate this in the second paragraph of our introduction.**

Lines 127-133: Please consult Wesolowski and Martin (2018) and extend the discussion on mechanism a bit more. I am lacking a clear statement on two possible, non-excluding each other mechanisms of expected relationships as very nicely stated way down in Discussion (Lines 312-314).

**RESPONSE: We thank the reviewer for this valid point. We agree that this is a key element of our manuscript that should be clarified much earlier in the text, and have a such included lines to address this topic in the very beginning of the Introduction.**

RESULTS: Could you add a summary table with numbers of species in different groups in different bioregions? It would provide some nice background for further discussions of results. You have those numbers already!

**RESPONSE: We understand that this might make it much easier to follow some of the reasoning, plus it would benefit authors who would like to build on our analyses. We have therefore followed your advice and added a supplementary table (Table S1) summarizing these data.**

Lines 224-231: I do not understand how you can model the relationship between woodpeckers and the three other groups in Australasia, where, as you state below, there is no woodpeckers or even other strong excavators are largely lacking.

**RESPONSE: Thank you for pointing this out, this is indeed a mistake. We have removed the 'woodpecker part' for Australasia and have added text to make this clear in methods as well ('We repeated all of these analyses for woodpeckers as a**

**subset of the excavators, with the notable exception of Australasia where woodpeckers are absent.')**

DISCUSSION: a bit confusing use of words "excavators/woodpeckers" (Line 244) and "excavators" (Line 275). Please check if necessary to use both of them!

**RESPONSE: We agree that this is a bit confusing and have simplified this, by simply using excavator/woodpecker when an argument or explanation concerns both groups equally and 'excavator' or 'woodpecker' by itself if it is particular to only one of these groups (e.g., when evidence does not extend beyond woodpeckers or when discussing specific results (e.g., ratios)).**

Lines 239-243: Worthy to mention that forests in some bioregions supply decay-formed cavities in high numbers (particularly non-managed forests) and some other not (e.g. boreal forest in Europe – see Andersson et al. (2018): Andersson J., Domingo Gomez E., Michon S., Roberge J.-M. (2018) Tree cavity densities and characteristics in managed and unmanaged Swedish boreal forest. Scandinavian Journal of Forest Research, 33 (3), pp. 233-244. It would add the management angle in discussion about the role of woodpeckers/excavators for other species.

**RESPONSE: We have added more text on this (esp. lines 304-309) including the reference suggested. We absolutely agree that this is a key element of the story, yet we aimed not to add too much to an already rather lengthy manuscript.**

Lines 272-273: Please refer to studies on the global species richness of woodpeckers e.g. Mikusinski, G. 2006. Woodpeckers (Picidae) - distribution, conservation and research in a global perspective. Annales Zoologici Fennici 43: 86–95.

**RESPONSE: We have added this reference.**

Lines 289-294: Refer also to the "primeval" Bialowieza Forest case in temperate zone being in stark contrast to managed forests (i.e. higher predation risk and subsequently preference for decay-formed cavities among secondary users. See: Wesolowski and Martin (2018) and references therein.


**RESPONSE: We have added a section on this, including additional references.**

Lines 299-304: Please refer to papers by Wesolowski here: Wesolowski T. 2011."Lifespan" of woodpecker-made holes in a primeval temperate forest: A thirty year study. Forest Ecology and Management, 262 (9) , pp. 1846-1852.

**RESPONSE: We added this reference.**

Reviewer 2:

What is the difference between 'global' and 'universal'. There is nothing in the introduction, nor in the discussion, justifying the usage of these two words. I suggest to delete 'universal'

**RESPONSE: We thank the reviewer for this remark, it made it clear to us that we needed to clarify these terms. When we use the term 'global' we imply that these relationships can be found in nearly every region of the world, with 'universal' we mean that they are of similar nature (strong and positive).**

**We clarify these terms in both the Introduction and the Discussion (e.g., by adding that 'Around the world, we can find relationships of a universal nature (strong and positive) between excavator and forest bird richness.').**

I see this paragraph as mostly unnecessary, with some of this information that can be fusioned with the second paragraph

**RESPONSE: We understand that this start of the Introduction could be stronger, highlighting both the problem (need for indicators) and the opportunity (excavators/woodpeckers could make great indicators). We have reworked the introduction to accommodate these changes.**

**The reviewer mentions multiple inconsistencies in citations/references, we have now adopted the 'Open Biology/Royal Society Open Science' style and all issues should be resolved.**

I am not aware of this. I've seen some parrot species burrowing their own cavities in termitaria and cliffs, or 'arranging' cavities already done by woodpeckers or fungi. But I have not seen/heard about parrots excavating 'brand new' cavities in trees. Please, could you add a reference for that?


**RESPONSE: Although not common, parrots especially in Australasia may excavate in trunks that are in advanced stages of decay, without there having been a previous cavity, see e.g., Courtney, J. 2010. An Observation of Nesting Behaviour in Marshall's Fig-Parrot 'Cyclopsitta diophthalma marshalli'. Australian Field Ornithology, Vol. 27, No. 4, Dec 149-152.**

…..So, unless you have a better argumentation for this association at a global scale, I suggest to delete this part.

**RESPONSE: We have, in this new version, followed up on your suggestion and removed this statement that the response of woodpeckers can be indicative of that of forest birds in general.**

This is not what Cockle et al. (2011) found. According to the map in the Figure 2a, you can see that the pattern that you mention (excavated cavities as main source for non-excavator birds) is only strong in North America, very weak in Europe (only 1 out of 4 studies showed that pattern), and opposite in South America and Australia, this is, non-excavator birds mainly used decay formed cavities (there is no study in Africa). After Cockle et al. (2011), Ruggera et al. (2016) quoted "Therefore, in the PF woodpeckers do not seem to play a key role in provisioning cavities to the nest-web, a pattern also shown for other South American and some European forests, and contrary to the findings in North America (Cockle et al., 2011a,b; Pereira et al., 2009; Wesołowski, 2007)." Please, be careful when citing other authors, and put strictly what they have found.

**RESPONSE: We agree that we may have overstated the importance of excavators for the provision of cavities, and have altered our language accordingly (e.g., stating that 'cavity formation by excavation is an importance source of nest holes for species in many regions of the world'). However, Cockle et al. has shown that woodpeckers are an important provider of cavities in farmlands and altered forests in Argentina. Thus, even in South America, woodpeckers may provide a larger role in the provisioning of tree cavities than currently recognized.**

- Please, see the previous comment on this pattern. Actually, it seems that woodpeckers play a considerably smaller role than that you stated, as cavity providers in many non-disturbed ecosystems. If my previous comment is correct, how is this prediction held?

**RESPONSE: We think this new version of our manuscript does a better job at highlighting the two mechanisms by which excavators are indicators: due to their associations with particular forest elements and their role in facilitating the presence of other species through the provision of nest cavities. We therefore think this prediction is still valid, but we did alter the text to recognize this point:**

**"Nevertheless, we might predict that these birds could be reliable indicators of avian diversity and richness not only at stand or landscape-levels (8, 17), but also across large regions at a global scale, not only for the cavities that excavators supply but also due to excavators' associations with forest elements that are indicative of heterogeneous forests with a high degree of naturalness."**

I see necessary to call to this group with something that recalls that are cavity users, because both forest specialist species and forest birds in general include also non-excavator bird species. An option can be 'secondary cavity-nesters'

**RESPONSE: We have followed this useful suggestion and have changed non-excavator to 'secondary cavity-nester' throughout the text.**

Here or in Methods: it's necessary to clarify if these categories are mutually exclusive. For example, some secondary cavity-nesters are forest specialists, and of course, are also forest birds in general. These species are considered in the three categories or only in the 'non-excavator' category? How this nested data set would eventually influence your results?

**RESPONSE: We added a sentence in the Methods to explain that some of these numbers are indeed nested, with for example a forest specialist also being counted as a forest bird. We can see how it could be interesting to know (for example) details on the relationship between excavators and forest specialists that do not nest in cavities, which we do not provide at this point. One reason for this is that sample size for many grid cells would become too low for our models to converge, particularly when we would count forest specialists that do not breed in cavities as a separate group (e.g., there are relatively few forest specialists in the Nearctic that are not also cavity-nesters).**

**Another reason is that we aimed to know whether excavators make useful indicators and management surrogates. For this we wanted to know how indicative excavators are of larger and more inclusive suites of forest-associated birds, not of very specific subgroups (e.g., forest-associated species that do not breed in cavities and that do not exclusively use forest habitat).**

What about the other two bird groups?

**RESPONSE: We have altered this text to make clear we predict that spatial variation in forest characteristics, management regimes, and bird communities will lead to differences in relationships between excavators and forest birds.**

- I suggest to deeply restructure the introduction: 1) a first paragraph that talks in general about the relationship of excavators with other birds (fusion of the first two paragraphs); 2) Exclusive paragraphs for each excavator relationship with each of the other 3 groups of birds. In each paragraph express what is known and what is the relationship predicted by the authors, and how they think that these relationships may vary in relation to the biogeographic regions considered. Another option is that the geographical variations of the relationships are expressed together in a separate paragraph. On the other hand, I think that it must necessarily be emphasized and made clear, what is the novelty provided by this study, in comparison with other studies cited in the same introduction and that address comparisons very similar to those of this study (eg Drever et al. 2008, Mikusinski et al 2001, Virkkala 2006).

**RESPONSE: We thank both Reviewer 1 and 2 for this suggestion for restructuring, and have adopted these suggestions. We have given more attention to the novelty of our study in the very first paragraph of our new version (Larger scale, testing for general patterns across all major biogeographic areas), and have further regrouped and organized the paragraphs in the introduction.**

- I find necessary to clearly define the categories of bird groups you use. I tried to do this by copy-and-paste some information you wrote below. However, I don't know if I did it correct, and the definition of 'excavator' group is missing. Please, check it and correct it. Yet, something is not clear to me, Can a given bird species be part of more than one group? If the answer is yes, how that influences on results?

**RESPONSE: We have added some text to clarify this in the methods and provided clear definitions of all bird groups used (see also our response to an earlier query above.**

- I find necessary to clarify some 'ecological' issues (i.e. not statistical) in methods. 1) Did you include the whole area of each biogeographic zone? or 2) only the forest areas in each one of them? If (1): How do you think the different amount of area/forest area of each biographic zone can influence your results? How non-forest excavators (as some woodpeckers) can inclue your results? or did you exclude them? Another question: given the cnsideration of Paleartic and Oriental regions, what does the AUSTRALASIA region includes? what part of Asia?

**RESPONSE: We thank the reviewer for this question. We have added text to explain this in the Methods: "We did not restrict our analyses to forested regions, wanting to avoid making subjective decisions on the classification of a grid cell to a specific vegetation/habitat type. Yet, to make sure we did look for possible relationships between these forest-associated species in regions they actually occur, we did remove cells with zero excavators/woodpeckers and cells where the numbers of secondary cavity-nesters, forest specialists, or all forest birds were lower than that of excavators/woodpeckers from further analyses. "**

**That said, we are not sure how the amount of area/forest area would influence our results, but we have aimed to circumvent that issue as much as possible by randomly selecting (1000 times) 1000 grid**

cells per region, thereby comparing similar surface (though not necessarily forest, but see above) areas per region.

Australasia encompasses the following regions, following our adaptation of the classification of van der Hoek et al. 2017. Diversity and Distributions, which is in turn based on that of the Handbook of the Birds of the World (Del Hoyo et al.): American Samoa, Australia, Bismarck Archipelago, Admiralty Islands, Cook Islands, Easter Island, Federated States Micronesia, Fiji, French Polynesia, Guam and the Marianas, Johnston Island, Kiribati, Macquarie Island, Marshall Islands, Nauru, New Caledonia, New Guinea, New Zealand, Niue, Norfolk Island, Papua New Guinea, Pitcairn Islands, Samoa, Solomon Archipelago, Tokelau, Tonga, Tuvalu, Vanuatu, Wake Island, Wallis and Futuna. Practically, we can say that most excavators in this region are from (Papua) New Guinea and surrounding islands.

- What did you specifically model? which were the variables?

RESPONSE: The gls models are more clearly explained now: " This implied the use of gls models with excavator richness as a predictor variable, the richness of one of the categories of forest-associated birds as a response variable, and a variable exponential spatial covariance structure…"

- I am not an especialist in this kind of analyses, and I could not fully understand it. Given that many readers of this kind of papers are not especialists either, I find very important to better explain this methodological part. What are the predicted and what the observed data? What does tell us the regression slopes and what the mean spearman rho? Nevertheless, at this point, I have the impression that you modeled the richness of non-excavators and forest birds, relative the presence of excavators (explanatory variable), i.e. in a causal manner (= gls models). However, in the introduction this relationship was mostly raised in a correlational manner, this is, that both excavators and the other forest bird groups show similar responses to forest structure and disturbances. Exceptions to this correlational relationship are, for example, the FEW cases (in terms of global areas) in which excavators are essential for nonexcavators by providing new cavities or food resources (sap and insects in excavator perforations). In short, you are analysing a relationship that you mostly posted as correlational, with regression models. Please, if my reasoning is incorrect, just ignore it, but explain better the methodology.

RESPONSE: We have added some clarification (see e.g., the answer above) that may help understand these methods better.

That said, it is correct that a gls model is basically an ordinary linear regression model with some different assumptions (or some assumptions not met; in this case related to spatial autocorrelation). However, whereas the reasoning behind a correlation vs. a regression differ, the statistics are, in this particular case, the same. A correlation can indeed encompass any relationship between two variables, without assuming cause and effect, whereas a linear regression can only be that: a linear relationship where we assume that X predicts Y. When the correlation is linear though, this becomes one and the same in terms of output (though not interpretation, which we therefore have been careful with, see our Discussion). In other words, when in this particular case both tests address the 'null hypothesis that the two variables are not linearly related. If run on the same data, a correlation

**test and slope test provide the same test statistic and p-value.' (see e.g., http://sites.utexas.edu/sos/guided/inferential/numeric/bivariate/cor/).**

**So why then this regression and not a correlation, if they provide the same outcome but correlations are easier to interpret? Largely because we would be unable to incorporate a measure to address spatial autocorrelation into a correlation test.**

- given that in Fig. 1 you detailed ellipses for each of the six zoogeographic region. I'd say that you can leave only the figure 2 and nothing would be lost

**RESPONSE: We have followed this suggestion and removed the first of the two figures, leaving only the multi-paneled one. That said, we opted to add one map that shows global distributions of excavators relative to secondary cavity-nesters, a map which we deem to be illustrative of the spatial variation and clustering (e.g., between zoogeographic regions) that we discuss in our manuscript.**

- It seems like sometimes your reasoning is associative/correlative (e.g. both excavators and other groups of forest birds have similar responses to disturbances), other times it is explanatory (e.g. the excavator richness determines the richness of other non excavator cavity-users by providing new cavities), and here it is predictive: the addition of 1 excavator species implies the addition of X forest bird species, ignoring any other type of causes, such as phylogenetic, biogeographical, etc. You must decide which of these visions you are going to explore, or clearly establish that all of them will be analysed, with their respective methodologies and theoretical support.

**RESPONSE: Although regressions provide both explanatory and predictive outcomes we understand that our language here is confusing, and our statements may be misinterpreted as meaning one can simply predict from a given number of excavators how many other forest birds there are at that location (which is, of course, not that simple as you rightly point out). Yet, whether the tested relationships are associative (similar habitat needs etc.) or causative (birds use the cavities created by excavators), the fact of the matter is that they are linear. But, in some regions, this relationship is stronger than in others. We should have focused on this and not the steepness of the slopes; and we have therefore removed these parts from the Results and Discussion sections.**

**That said, we explore whether there are relationships between excavators and other forest birds (the gls models themselves), but also aimed to see if this could then be used to determine to what extent excavator richness is indicative of that of other species (the matching with the test data set and derivation of Spearman rho's). We hope that this approach is clearer from our revised manuscript.**

- Commented [MOU25]: What exactly does the Rho (=strength) mean in this context? low values of Rho mean that the relationships are not very reliable? for example in australasian region. And more important, what would be the joint interpretation of the slopes, the percentage of models with p greater than 0.5 and the rho?

**RESPONSE: Rho would here give us an idea how 'perfect' the linear relationships are (with rho = 1 being perfect with all grid cells falling on one line), whereas the slope (which we now removed from further discussion (see above) but present in the Results section to be complete in our presentation of model statistics) would tell us how many other forest birds (other than excavators) there are likely to be in a given location (grid cell) relative to the number of excavators (this does thus present an idea of**

'what richness' a certain number of excavators would possibly indicate). The % of models with a p < 0.05 gives us an idea whether these relationships are significant or not, given we had to iterate over many (1000) models, this would be a measure of reliability of the relationships given the combination of both the correlation coefficient and the sample size (which here is always 1000).

Low values of rho do not necessarily mean that that the relationships are not very reliable, but rather that they would not be strong enough to be able to 'use richness of excavators' to predict how many other forest birds are in a given location (here grid cell). Thus low values of rho would, in this case, show that excavators are rather poor indicators of other forest birds, even though the relationships might be real and significant.

- Commented [MOU27]: I would like to read what are those differences to take into account from a practical point of view and Commented [MOU28]: The comment on nest-webs here, in the first paragraph of Discussion, is out of context. Besides, variation among nestwebs… in relation to what? Are you trying to relate the association of excavators and other forest birds with variations in nestweb characteristics? it's far from clear, and you are leaving out a key aspect: the diversity, persistence and characteristics of trees with cavities

RESPONSE: We have made some substantial changes to our text and hope to now provide a clearer line of argumentation.

- However, in several other nestwebs (for example in South America [Cockle et al. 2012, Ruggera et al. 2016] and India [Manikandan & Balasubramanian 2018]), most non excavator birds mainly use decay-formed cavities in living trees. Only 10-25% of interactions (including excavator interactions) are made with snags. So, the evidence to date (even in the Neotropics, where your results showed the strongest association between excavators and non-excavators), would not be explained by the number of snags or the amount of woodpecker-excavated cavities. Also, you need to better explain why forest especialist birds would benefit from the presence of 'certain levels (how much?) of availability of decaying and dead wood'

RESPONSE: We have made substantial changes to the text in the Discussion, incorporating suggestions by both reviewers, which means that we now provide a clearer insight in the differences in the importance of decay vs. excavated cavities in the different regions. With that, we anticipate to have resolved these issues as well.

- differences in relation to what of the nestwebs? you need to be more specific. You need to better explain this: how speciation and other macro-scale processes across the globe influence on the results you found. Explanations generally are biased to nestwebs. However, you have other bird groups that not necessarily are cavity-nesters. Also, you don't necessarily have to invoke networks (of which there are relatively few reports worldwide) to talk about cavitynesters (of which there are comparatively many more reports around the world)

RESPONSE: We thank the reviewer for this comment. We have made substantial changes to our text, reflecting better that both direct facilitation through nest-webs and indirect associations play a role in shaping the observed relationships. As a result of these changes, we have also paid more attention to the role of differences in community composition etc. in shaping these relationships.

- Australasia region doesn't lack Piciformes. As you say a few words later, SE Asia has a high diversity of Piciformes. So, be careful when you explain Australasia results as a unique region (see comment also about AUSTRALASIA in methods). In fact, I would like to find a better explanation of the results of the Australasian region, since it had the most contrasting results with the rest of the regions.

**RESPONSE: There is a difference between the Oriental and Australasian zoogeographic regions that may have gone unnoticed to the reviewer. Most of Indonesia and other SE Asian countries falls within the Oriental region, with the Wallace line separating this region from the Australasian region (e.g., Papua/New Guinea) where some excavators exist but Piciformes are notably absent (see also e.g., Mikusiński, G. (2006, January). Woodpeckers: distribution, conservation, and research in a global perspective. In Annales Zoologici Fennici (pp. 86-95). Finnish Zoological and Botanical Publishing Board.). That said, we do agree that the results we found for the Australasian region deserved more attention, and have thus extended on this in the text.**

- what differences? you have not established what are the differences along the neotropical region in terms of climatic variables, tree species composition, tree availability and their formation agents. Also, include in this comparison the work by Ruggera et al. 2016, how their results fit in the explanation your trying to develop?

**RESPONSE: In our revised version you will find references to Ruggera et al. as well as more comprehensive explanation of the differences found across and within regions.**

- then, if non-excavators do not 'need' excavators as cavity-forming agents, why did they show the greatest association in richness in the Neotropics?

**RESPONSE: We anticipate that we have now explained this better, focusing on the fact that indirect associations (shared forest elements etc.) are more important than direct facilitation (cavities) in explaining these relationships.**

- Commented [MOU40]: Altamirano et al. 2017 wrote: 'Among SCNs, ten species (40%) were obligate and 15 (60%) were non obligate cavity nesters. Non obligate cavity nesters included six (24%) facultative, five (20%) marginal, and four (16%) incidental SCN'. If we include also PCN, facultative cavity nesters are 20%. Commented [MOU41]: how are they influenced? Again, I lost the point. You began talking about 'spatial variation in the relationships between excavators and other forest birds within zoogeographic regions', but then you focused (again) only on excavators and non-excavators, especially in the Neotropics.

**RESPONSE: We have changed these parts of text substantially, hopefully addressing these issues and providing more clarity.**

- I believe that this is a central point, that it should be better developed in the introduction, and that the methodology should be chosen according to that. It is not the same to analyze something in a correlative way, that in an explanatory or predictive way

**RESPONSE: Yes, we agree. We have made an effort to provide more attention to these two different mechanisms (direct facilitation and indirect association) by which relationships between excavators and other forest birds may be formed.**

## Appendix C

# ROYAL SOCIETY
# OPEN SCIENCE

## Global and universal relationships between tree-cavity excavators and forest bird richness

| | |
|---:|:---|
| Journal: | *Royal Society Open Science* |
| Manuscript ID | RSOS-192177 |
| Article Type: | Research |
| Date Submitted by the Author: | 13-Dec-2019 |
| Complete List of Authors: | van der Hoek, Yntze; The Dian Fossey Gorilla Fund International, Karisoke Research Center<br>Gaona, Gabriel; Justus Liebig Universität Giessen Graduiertenzentrum<br>Ciach, Michal; University of Agriculture in Krakow<br>Martin, Kathy; University of British Columbia, |
| Subject: | ecology < BIOLOGY |
| Keywords: | Facilitator species, Indicator species, Species interactions, Picidae, Management surrogates, Woodpeckers |
| Subject Category: | Biology (whole organism) |
| | |

# SCHOLARONE™
# Manuscripts

**Author-supplied statements**

Relevant information will appear here if provided.

*Ethics*

*Does your article include research that required ethical approval or permits?:*
This article does not present research with ethical considerations

*Statement (if applicable):*
CUST_IF_YES_ETHICS :No data available.

*Data*

*It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:*
Yes

*Statement (if applicable):*
Links to the data and R scripts to reproduce analyses presented in Global and universal relationships between tree-cavity excavators and forest bird richness can be found in Appendix S1.

*Conflict of interest*

I/We declare we have no competing interests

*Statement (if applicable):*
CUST_STATE_CONFLICT :No data available.

*Authors' contributions*

This paper has multiple authors and our individual contributions were as below

*Statement (if applicable):*
YH and GVG carried out the data analysis, and led the design of the study and writing of the manuscript; MC and KM critically revised the manuscript. All authors contribute to the writing of the final manuscript, gave final approval for publication and agree to be held accountable for the work performed therein.

Title: Global and universal relationships between tree-cavity excavators and forest bird richness

Running title: Excavator and forest bird relationships

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47  **Abstract**
48  Global monitoring of biodiversity and ecosystem change can be aided by the effective use of
49  indicators. Tree-cavity excavators, the majority of which are woodpeckers (Picidae), are known
50  to be useful indicators of the health or naturalness of forest ecosystems and by the diversity of
51  forest birds. They are indicators of the latter due to their associations with particular forest
52  elements and because of their role in facilitating other species through the provision of nest
53  cavities. Here, we investigated whether these positive correlations between excavators and other
54  forest birds are also found at global scales. We used global distribution maps to extract richness
55  estimates of tree-cavity nesting and forest-associated birds, which we grouped by zoogeographic
56  regions. We then created generalized least squares (gls) models to assess the relationships
57  between these groups of birds. We show that richness of tree-cavity excavating birds correlates
58  positively with that of cavity-nesters and forest birds at global scales, but with variation across
59  zoogeographic regions. As many excavators are relatively easy to detect, play keystone roles at
60  local scales, and are effective management targets, we propose that excavators are useful for
61  biodiversity monitoring across multiple spatial scales and geographic regions, especially in the
62  tropics.
63
64  **Keywords**
65  Facilitator species, Indicator species, Management surrogates, Picidae, Species interactions,
66  Woodpeckers

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**Introduction**

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94 Forests worldwide are facing increasing anthropogenic pressures, with both a rapid decline in the
95 surface area of natural forests and a decrease in the naturalness of forests as a result [1, 2]. In
96 turn, these reductions of high-quality forest habitats have led to a loss of forest-associated
97 biodiversity [3-5]. To monitor these changes in forest ecosystems and their denizens, we often
98 look at specialized animals that require the availability of specific habitat structures and
99 processes across long temporal and large spatial scales [6], such as birds that respond not only to
100 a loss in overall forest cover but also to a change in forest health, quality, and integrity [7-10].
101 Excavators such as woodpeckers, barbets, nuthatches, trogons and certain parrot species—among
102 which woodpeckers are the most numerous group [11]—may be especially effective indicators
103 due to their associations with particular forest elements and their role in facilitating the presence
104 of other species through the provision of nest cavities. Indeed, there is empirical evidence that
105 their presence can be indicative of the state of both the forest (e.g., the presence of large trees
106 [12], heterogeneous forest structure [13], or a high level of naturalness [14-18]) as well as the
107 richness and abundance of other forest-associated species [19-21]. However, we may question
108 whether excavators are universally effective indicators, at least of biodiversity, in all geographic
109 regions or forest types. For example, excavators are better predictors of richness and abundance
110 of other forest resident birds in deciduous versus coniferous forests of certain parts of hemiboreal
111 Europe [15].
112     If relationships between excavators and other forest-associated biota are universally
113 positive in nature, and common not only at stand- and landscape-scales but hold across large
114 geographic regions, then excavators could form a unique group of indicators that may be
115 effective across multiple locations and spatial scales [22]. To find species that are effective as
116 both indicator and management surrogates across multiple regions would be especially useful in
117 the largely understudied tropics where comprehensive biodiversity assessments are costly and
118 logistically challenging [23]. The first signs are promising as the overwhelming majority of tree-
119 cavity excavators are forest or woodland birds and general patterns of woodpecker richness
120 correlate positively with the amount of forest cover at the global scale [24]. Moreover, many
121 excavators are regarded as habitat specialists and tend to have highly specific habitat
122 requirements, ~~requirements~~ which are usually only met in forests with high degrees of
123 naturalness and low levels of disturbances (e.g., logging). In fact, restoration efforts have
124 effectively made use of woodpeckers to indicate that restoration has successfully reached a
125 certain level of naturalness [25, 26]. This group of birds often utilizes large, live or decaying
126 trees, or coarse woody debris, for nesting, roosting, and feeding, and the availability of dead
127 wood is in particular found to be important [27-29]. This role of excavators as indicators of the
128 naturalness of ecosystems, whereby their presence correlates strongly with other aspects of
129 biodiversity, is enhanced by the fact that the majority of species are forest residents, which
130 arguably makes them more responsive to local changes in habitat quality (see e.g., [30].
131     Excavators are not only reliable indicators of other forest birds by means of their mutual
132 associations with forest characteristics, but correlations between both groups of birds are also
133 partially determined by species interactions. Taken together, these 'nest-webs' [31] of interacting
134 species are structured by the availability and acquisition of tree-cavities formed by two major
135 processes: 'natural formation', in which fungi decompose wood over an extended period, or
136 animal excavation [32, 33]. Since most excavators—at least the majority of woodpeckers—
137 excavate a new nest cavity each year, this mode of cavity creation steadily provides a large
138 number of potential sheltered roosting and nesting sites for secondary-users: both for vertebrates

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[33] and invertebrates [34, 35]. As a result, cavity formation by excavation is an important source of nest holes for species in many regions of the world, especially North America [33]. However, decay-formed cavities are likely to be more important nest sites in other regions, especially the tropics, and it is very likely that the relative importance of both processes of cavity formation—and thus the strength of the relationship between excavator richness and secondary cavity-nester richness—varies globally [33]. Finally, it is worth noting that excavators play additional roles (beyond the direct provision of cavities) that may facilitate other species. For example, as excavators perforate the bark of trees they may expose insects or sap for other species to forage on [36, 37]. In addition, excavators can aid in the dispersal of fungi, which in turn enhances processes of wood softening and the formation of decay-formed cavities [38].

Local studies of cavity-nesting birds and their interactions are largely biased towards temperate zones, and only a few authors have explored global variation in nest-web characteristics or addressed how such variation should be taken into account when considering cavity-nester communities in forest conservation or management (e.g., [33, 39]). Nevertheless, we might predict that these birds could be reliable indicators of avian diversity and richness not only at stand or landscape-levels [9, 19], but also across large regions at a global scale, if not for the cavities that excavators supply but for the associations of excavators with forest elements that are indicative of heterogeneous forests with a high degree of naturalness. Therefore, the aim of the present study is to investigate whether there are consistent patterns in the relationships between avian tree-cavity excavators (hereafter: excavators) and species richness of non-excavating tree-cavity nesters (hereafter: secondary cavity-nesters), forest specialist species, and forest birds in general, across the globe. If previously observed relationships between cavity-excavators and other forest birds scale up from local forest stands [17] or ecosystems [19] to zoogeographic or global levels, then this strengthens the potential of tree cavity-excavators as both indicators and management surrogates.

Given the important role of excavators in forest ecosystems, we predicted that secondary cavity-nester, forest specialist, and forest bird richness generally will increase with the number of excavators present in the ecosystem, regardless of the ecosystem or location. However, we also predicted that the nature (e.g., the strength and slope of correlations) of the relationships between excavators and richness of other forest birds will vary across zoogeographic regions, reflecting differences in forest characteristics (e.g., deciduous vs. coniferous forests), forest management practices (e.g., forests being more or less intensively managed), and bird communities (e.g., the relative richness of different groups of forest-associated birds), as previously discussed in e.g., [33]. In particular, we predicted that correlations between excavators and other birds would be particularly strong, but with relatively shallow regression slopes, in regions with relatively high intensities of forest management (vs. unmanaged natural forests) and low overall diversity. In these predominantly temperate and boreal regions, such as the Nearctic and Palearctic, relationships between excavators and other forest birds that are driven by mutual associations with particular forest elements would be enhanced by direct interactions through the provision of nest cavities, as a lack of available decay-formed cavities may increase the dependence of secondary-cavity nesters on excavated cavities. We predicted relatively shallow regression slopes in these regions (Nearctic, Palearctic), as there is a relatively low ratio between the numbers of excavators and secondary-cavity nesters [11]. For regions that largely span the tropics, such as the Neotropics, we also predicted positive correlations between excavators and other forest birds, but as these relationships would be driven mainly by mutual associations with particular forest elements and less by direct interactions through the provision of nest cavities—

185  decay-formed cavities being more prevalent here—we predicted these correlations to be weaker.
186  However, as these regions are more diverse, we also predicted that there would be relatively
187  higher numbers of forest birds per excavator, resulting in steeper regression slopes.

188

189  **Material and Methods**
190  We used published global distribution maps of tree-cavity nesting birds [11] and forest birds [40]
191  to extract richness estimates per 10×10 km grid cell. Maps for both tree-cavity nesters and forest
192  birds were based on the same species range maps provided by BirdLife International and
193  NatureServe [41]. We selected and classified focal bird species following [11, 40] as 1)
194  excavators (species that are known to often or always excavate their own nesting cavities),
195  secondary cavity-nesters: birds which are known to nest in tree cavity but which never or rarely
196  excavate their own cavity, 3) forest specialists: birds that exclusively use forest habitat, and 4)
197  forest birds: birds that use forest habitat but also at least one other type of habitat. We note that
198  some species were counted in more than one category (e.g., a species that is a 'forest specialist'
199  is per definition also counted as a 'forest bird'). However, excavators were never counted in any
200  other category.
201       We used only range polygons where a species' presence was classified as 'Extant' or
202  'Probably extant', and assigned 'presence' to all grid cells that overlapped with range polygons.
203  Next, we created generalized least squares (gls) models to assess the linear relationships between
204  excavators and other categories of forest-associated birds. To take biogeographical differences
205  into account, we proceeded to separate trends across the globe, and created gls models for the six
206  zoographic regions separately: Nearctic, Palearctic, Neotropical, Afrotropical, Oriental, and
207  Australasia. We did not restrict our analyses to forested regions, wanting to avoid making
208  subjective decisions on the classification of a grid cell to a specific vegetation/habitat type. Yet,
209  to make sure we did look for possible relationships between these forest-associated species in
210  regions they actually occur, we removed cells with zero excavators/~~woodpeckers~~ and cells where
211  the numbers of secondary cavity-nesters, forest specialists, or all forest birds were lower than
212  that of excavators/~~woodpeckers~~ from further analyses.
213       Our data were spatially structured (i.e., high and low richness of birds in different
214  categories (excavators etc.) was spatially clustered) across and within zoogeographic regions, as
215  demonstrated by the global distribution of the relative number of cavity excavators to non-
216  excavating cavity-nesting birds (expressed as the ratio of excavator / non-excavating cavity-
217  nester; Fig. 1). Thus, we followed similar protocols to adjust for spatial autocorrelation as per
218  Storch et al. [42]. This implied the use of gls models with excavator richness as a predictor
219  variable, the richness of one of the categories of forest-associated birds as a response variable,
220  and a variable exponential spatial covariance structure, as these models had the best fit in
221  preliminary tests, which reduced—rather than eliminated—the influence of spatial
222  autocorrelation on our models. In these tests, exponential gls models consistently had the lowest
223  Akaike's Information Criterion (AIC) value compared to a set of models, including an ordinary
224  least squares model with no spatial structure, and gls models with Gaussian, linear, rational
225  quadratics and spherical spatial covariance structures.
226       Even though gls models work well with large datasets, we found that gls models fitted on
227  all data failed to converge (using the R package "nlme" [43]). To circumvent this computational
228  problem, we first grouped grid cells by zoogeographic region. We thereafter ran 1000 models on
229  bootstrap permutations of 1000 randomly selected grid cells (see [24, 44]). Of these 1000 model
230  iterations, we subsequently calculated the mean (±SD), minimum and maximum coefficients of

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231  the regression slope. As gls models do not provide a measure of the strength of relationships, we
232  proceeded with a different measure of the strength of each correlation: fitting each exponential
233  gls model to a different, non-overlapping, test data set of 1000 randomly selected grid cells. We
234  then proceeded to calculate the Spearman rho coefficient of the correlation between predicted
235  and observed data, for all 1000 models per zoogeographic region. Finally, we calculated the
236  mean Spearman rho of all significant models per zoogeographic region. We repeated all of these
237  analyses for woodpeckers as a subset of the excavators, with the notable exception of Australasia
238  where woodpeckers are absent. All data, R scripts, and initial results needed to reproduce our
239  analyses presented here are deposited online (Appendix S1).
240

241  **Results**
242  Using gls modelling to assess the global patterns for the relationships between excavator richness
243  and that of secondary cavity-nesters, forest specialists, and all forest birds, we found positive
244  relationships between all pairs of comparisons.  However, these relationships differed in relative
245  strength and regression slope depending on the group of birds and zoogeographic region
246  analysed (Fig. 2, Table 1; see Table S1 for an overview of the number of species per group per
247  region).
248       In terms of variation across zoogeographic regions, the relationships between excavators
249  and all other groups of forest-associated birds were typified by particularly steep regression
250  slopes in the Neotropics, where the presence of one additional excavator species in a grid cell
251  implied an increase of more than two additional secondary cavity-nesters, ten forest bird species,
252  or four forest specialists. In contrast, regression slopes were less steep in predominantly
253  temperate and boreal regions such as the Nearctic and Palearctic, where an increase of one
254  excavator species signified an increase of approximately one secondary cavity-nester species,
255  four to five forest birds, or one forest specialist. More importantly, and similar to variation in the
256  slopes of the regressions, we found differences in the strength (as represented by Spearman's
257  rho) of these relationships, with again stronger relationships in the predominantly tropical
258  Afrotropical, Oriental, and Neotropical regions than in the comparably more temperate/boreal
259  Nearctic and Palearctic regions (Table 1).
260       Although the relationships between excavators and the other three groups of cavity-
261  nesting and forest-associated birds were generally similar in nature (positive), there were some
262  differences in the relative strength of these relationships across zoogeographic regions. For
263  example, excavator richness was a particularly strong predictor of secondary cavity-nester
264  richness and of all forest birds in the Oriental region (rho = 0.88 and 0.86, respectively), and
265  slightly less so for forest specialists (rho = 0.77), whereas excavator richness in the Afrotropics
266  showed a strong relationship with all forest birds (rho = 0.94) and with forest specialists (rho =
267  0.88), but a somewhat weaker association with secondary cavity-nesters (rho = 0.79).
268       We repeated all analyses for woodpeckers as a subset of excavators and found nearly
269  identical results, with again significant positive relationships between woodpeckers and other
270  groups of cavity-nesting or forest-associated birds in all regions but Australasia, and with steeper
271  regression slopes and stronger relationships in the predominantly tropical Neotropical, Oriental
272  and Afrotropical regions as compared to more shallow slopes and weaker associations in the
273  Nearctic and Palearctic (Table 2). The relative strength of the relationships between
274  woodpeckers and the three other groups of cavity-nesting and forest-associated birds again
275  depended on the zoogeographic region (in similar ways as for entire group of excavators) such
276  that woodpeckers were strong predictors of the richness of other birds as excavators in general,

277 with the notable exception of Australasia. Nevertheless, despite the complete absence of
278 woodpeckers from this region, we did find a weak (rho = 0.69) but often significant ($p < 0.05$ in
279 97 percent of model iterations) positive relationship between richness of excavators and forest
280 specialists.

## Discussion

283 We found strong positive relationships between excavators/woodpeckers and secondary cavity-
284 nesters, forest birds and forest specialists at global and zoogeographic scales, although these
285 relationships differed in both strength and characteristics (regression slopes) across
286 zoogeographic regions. Our results imply that excavators and woodpeckers (a predominant
287 subset of excavators) hold potential as indicators and management surrogates across most of the
288 world [ ], but also that we need to take differences among zoogeographic regions (e.g., in the
289 composition of local and regional nest-webs with regards to the relative numbers of excavators
290 and secondary cavity-nesters as seen in Fig. 1) into account if we are to adopt these as surrogates
291 for conservation or management.

292     Many excavators, woodpeckers included, have strong preferences for specific forest
293 elements, such as dead and decaying trees or particularly large trees (see e.g., [28]). In turn, these
294 elements, and the processes that drive their presence and abundance, are of great importance to
295 habitat formation and create additional niche space to support many groups of organisms [46].
296 Therefore, we can expect that forests that meet the habitat requirements of excavators (e.g.,
297 certain levels of availability of decaying and dead wood) provide high-quality habitat for many
298 other wildlife species. This may explain the higher richness of forest birds in areas occupied by
299 high numbers of excavators/woodpeckers. For non-excavating species that utilize tree-cavities
300 for their nests, this relationship may be enhanced by the fact that excavators/woodpeckers create
301 or facilitate potential nest substrates [2 ]. In other words, the strong habitat preferences of many
302 excavators/woodpeckers, as well as the facilitatory role excavators play in providing nest
303 substrates, make these birds potentially effective indicators of many forest-associated species
304 and, by extension, of high-quality forests (i.e., natural, old-growth; [17, 18].

305     The steep slopes we found for correlations between excavators/woodpeckers and other
306 forest birds in the predominantly tropical regions (Neotropics, Oriental, Afrotropical) contrast to
307 more shallow slopes in the temperate/boreal regions (Palearctic, Nearctic). Macro-scale
308 processes (e.g., as outlined by Gaston [47]), such as speciation events, are likely to account for
309 some of these differences among zoogeographic regions. First, the overall richness of birds [48],
310 including cavity-nesting birds [11], and also of trees as potential substrates for cavities [49],
311 differs both among and within zoogeographic regions, likely inducing differences in tree-cavity-
312 nesting assemblages [33]. However, variation in species composition and associated variation in
313 functional richness (i.e., the variety of functional traits varies across spatial and environmental
314 gradients, as has been shown, for example, for dietary guilds [44]), is likely to contribute most to
315 spatial variation in nest-web assemblages across global scales. Specifically, with regards to nest-
316 webs, species with the ability to excavate cavities are not randomly distributed across the world.
317 For example, the Australasian region lacks the presence of Piciformes, the Order to which nearly
318 75% of excavators belong [11], whereas speciation processes have led to a relatively high
319 diversity of Piciformes in Southeast Asia [50, 51].

320     The observed spatial variation in the relationships between excavators and other forest
321 birds within zoogeographic regions may stem mainly from local differences in habitat and
322 vegetation characteristics (e.g., tree species composition and climatic variables [52]) as well as

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spatial variation in tree cavity availability and their formation agents [53], rather than from speciation processes.  Such differences would, for example, explain how in the Neotropics, cavity-nesting assemblages studied in the temperate mountain forests of Chile [54] had a 1:6 ratio of excavators (4 species) to secondary cavity-nesters (25 species) whereas a subtropical Atlantic moist forest [32] supported relatively higher numbers of excavators with a 1:3 ratio of excavators (9 species) to secondary cavity-nesters (25 species). An important factor to consider here is the potential for regional variation in cavity substrate availability (e.g., large trees) and the supply of decay-formed cavities due to differences in the onset and rate of decay processes as well as forest management (e.g., [55-57]). For example, retention of large trees can, in many forests, provide nesting and roosting opportunities for additional species as both opportunities for excavation and processes of decay become more prevalent.

In addition, we can hypothesize that at least some variation at regional scales stems from differences in the propensities for re-use of excavated cavities by secondary cavity-nesters. For example, there are signs that non-excavating cavity-nesters may experience higher predation risk in excavated versus decay-formed cavities, which may induce a preference for decay-formed cavities among secondary users if decay-formed cavities are in sufficient supply (e.g., a pattern found in some of the few unmanaged temperate forests in the European parts of the Palearctic; [58, 59]). In turn, the availability of decay-formed cavities may correspond to the aforementioned historical or current forest management practices as well as spatial patterns in climatic factors. For example, proportions of decay-formed cavities used are particularly high in parts of the world with high amounts of precipitation and more active regimes of fungal growth (e.g., most of the wet tropics), with both being lower in anthropogenically-disturbed landscapes than in primary forests [53]. In turn, high availability of decay-formed cavities might allow for a relatively high richness of secondary cavity-nesters, with fewer species dependent on excavators for the supply of nest-cavities. For example, even woodpeckers, commonly considered primary excavators, occasionally use decay-formed cavities in Neotropical temperate rainforests where tree decay is the key driver of nest-web structure [54].

Finally, we feel that relatively higher numbers of secondary cavity-nesters, or cavity-nesters in general, may occur in regions where many species are habitat generalists that utilize other nest substrates than tree-cavities (e.g., 40% of cavity nesters in Neotropical temperate forests are facultative users of tree cavities for nesting [54]), as compared to regions where most cavity nesters are obligate tree-cavity users (e.g., over 85% of cavity nesters in temperate Nearctic forests [59]). Finally, it is worth noting that cavity availability and use are also likely to be influenced by cavity persistence (longevity) a characteristic that can have considerable spatial variation due to factors such as land-use patterns (e.g., logging), climatic factors (e.g., rainfall), and cavity characteristics (e.g., whether they are located in live or dead trees [60-62]).

We detected relative differences in strengths among the relationships between excavators/woodpeckers and secondary cavity-nesters, forest birds, and forest specialists across zoogeographic regions. These differences were most likely to stem from the same variation among species and ecosystem characteristics discussed above (e.g., the distribution and relative importance of cavity-forming agents), and indicate that richness of excavators/woodpeckers may be a better indicator of richness of other cavity and forest-associated species in one region than in another. In addition, the relative strength of relationships between excavators and other forest birds might reflect whether excavators are indicative of the richness of other species due to shared associations with particular forest elements (indirect association), due to their direct facilitation of nest cavities (direct facilitation), or whether both factors play a role. For example,

8

369 we found that relationships between excavator and forest bird or forest specialist richness in the
370 Afrotropics are relatively strong, whereas the relationship between excavators and secondary
371 cavity-nesters is comparatively weaker. This might indicate that, in the Afrotropics, excavators
372 are especially strong predictors of other groups of forest-associated birds through their mutual
373 habitat requirements, rather than through their direct facilitation of tree-cavities. In contrast,
374 excavators are relatively stronger predictors of secondary cavity-nesters in the Oriental region,
375 which might lead to hypotheses that excavators play a more direct, nest-web structuring role
376 through the provision of cavities in the Oriental region.

377     Some secondary cavity-nesters might use cavities created by multiple excavator species,
378 whereas others predominantly use cavities formed by processes of degradation, damage or insect
379 activity [31, 32, 39]. In addition, certain excavators might be especially abundant or provide
380 cavities that are very commonly reused by several species, whereas others are scarce and leave
381 only a few short-lived cavities that would not be generally available for use by secondary cavity-
382 nesters. Given such complexities among nest-web interactions, it is important to emphasize that
383 we present general global patterns in the composition of tree-cavity-using assemblages (i.e.,
384 communities of linked species that often interact within networks). We lack evidence for direct
385 causal links between the presence of one species group with another, as well as direct evidence
386 of species interactions at the zoogeographic regional scale.

387     Around the world, we found relationships of a universal nature (strong and positive)
388 between excavator and forest bird richness. As such, we deem excavators, of which woodpeckers
389 are an important subset, to be useful indicator species for forest bird diversity at multiple spatial
390 scales. They form a small and fairly easy to identify (even by citizen scientists) subset of a larger
391 group of species (forest birds) often studied to understand the effects of anthropogenic
392 disturbances. Studies of excavators (or woodpeckers specifically), especially in high biodiversity
393 tropical regions, might provide quick measures of forest quality and biodiversity, which may in
394 turn guide forest management decisions (e.g., improving the retention of large trees). A
395 comprehensive study of all forest birds in some regions like the Amazon or Congo basin would
396 require considerable local expertise and training, which is often difficult to achieve due to social
397 and monetary limitations. Thus, we conclude, excavators have excellent potential as study
398 subjects for conservation monitoring and planning initiatives, in comparative research, and to
399 guide the establishment of region-wide forest conservation strategies, especially in the largely
400 understudied tropical regions of the world.

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402 **Acknowledgments**
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550    year study. *Forest ecology and management*. **262**, 1846-1852.

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552 **Table 1. Results of generalized least square models of possible correlations between (1)**
553 **excavator and secondary cavity-nester richness, (2) excavator and forest bird richness, (3)**
554 **excavator and forest specialist richness.** Each result reflects the mean outcome of 1000 models
555 build with 1000 randomly selected grid cell data points that include an exponential spatial
556 covariance structure. The mean Spearman rho was calculated over the fit of each of 1000 models
557 to a test data set.

| Zoogeographic region | Correlation | Mean Slope (Min. – Max.; SD) | % of models with $P < 0.05$ | Mean Spearman rho |
|---|---|---|---|---|
| Nearctic | 1 | 0.8 (0.4 - 1.3; 0.1) | 60 | 0.73 |
|  | 2 | 4.3 (3.3 - 5.9; 0.4) | 63 | 0.84 |
|  | 3 | 1.4 (1.2 - 1.6; 0.1) | 71 | 0.71 |
| Palearctic | 1 | 1.1 (0.7 - 1.4; 0.1) | 84 | 0.78 |
|  | 2 | 4.9 (4.0 - 6.7; 0.4) | 73 | 0.85 |
|  | 3 | 1.1 (0.8 - 1.7; 0.1) | 83 | 0.79 |
| Oriental | 1 | 0.7 (0.6 - 0.9; 0.0) | 100 | 0.88 |
|  | 2 | 5.7 (4.9 - 6.6; 0.3) | 100 | 0.86 |
|  | 3 | 1.6 (1.3 - 1.9; 0.1) | 100 | 0.77 |
| Neotropical | 1 | 2.4 (1.9 – 3.0; 0.2) | 83 | 0.95 |
|  | 2 | 10.8 (9.1 - 14.0; 0.7) | 72 | 0.97 |
|  | 3 | 4.2 (3.4 - 5.2; 0.2) | 72 | 0.96 |
| Afrotropical | 1 | 1.1 (0.7 - 1.9; 0.2) | 76 | 0.79 |
|  | 2 | 6.8 (5.0 - 9.8; 0.9) | 73 | 0.94 |
|  | 3 | 0.9 (0.6 - 1.5; 0.1) | 79 | 0.88 |
| Australasian | 1 | 1.8 (1.4 - 2.2; 0.1) | 88 | -0.14 |
|  | 2 | 7.5 (2.3 - 11.2; 1.3) | 100 | 0.31 |
|  | 3 | 1.0 (-0.1 – 2.0; 0.3) | 97 | 0.69 |

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576 **Table 2. Results of generalized least square models of possible correlations between (1)**
577 **woodpecker and secondary cavity-nester richness, (2) woodpecker and forest bird richness,**
578 **and (3) woodpecker and forest specialist richness.** Each result reflects the mean outcome of
579 1000 models build with 1000 randomly selected grid cell data points that include an exponential
580 spatial covariance structure. The mean Spearman rho was calculated over the fit of each of 1000
581 models to a test data set.

| Zoogeographic region | Correlation | Mean Slope (Min. – Max.; SD) | % of models with $P <$ 0.05 | Mean Spearman rho |
|---|---|---|---|---|
| Nearctic | 1 | 1.0 (0.5 - 1.6; 0.2) | 61 | 0.70 |
| | 2 | 5.3 (3.7 - 8.0; 0.7) | 67 | 0.79 |
| | 3 | 1.7 (1.1 - 2.2; 0.1) | 70 | 0.63 |
| Palearctic | 1 | 1.2 (0.9 - 2.3; 0.1) | 81 | 0.79 |
| | 2 | 5.6 (4.3 - 8.1; 0.6) | 73 | 0.83 |
| | 3 | 1.3 (0.9 - 2.0; 0.2) | 82 | 0.73 |
| Oriental | 1 | 1.0 (0.8 - 1.3; 0.1) | 100 | 0.88 |
| | 2 | 7.9 (6.6 - 9.8; 0.5) | 100 | 0.88 |
| | 3 | 2.2 (1.7 - 2.6; 0.1) | 100 | 0.80 |
| Neotropical | 1 | 3.3 (2.4 - 4.9; 0.4) | 68 | 0.94 |
| | 2 | 14.3 (10.8 - 20.5; 1.6) | 67 | 0.93 |
| | 3 | 5.2 (3.9 - 6.6; 0.5) | 73 | 0.88 |
| Afrotropical | 1 | 1.6 (0.9 - 3.5; 0.4) | 72 | 0.74 |
| | 2 | 9.9 (6.4 - 19.6; 1.9) | 69 | 0.86 |
| | 3 | 1.3 (0.7 - 3.2; 0.3) | 80 | 0.81 |
| Australasian | 1 | 1.9 (-0.1 - 4.4; 0.6) | 81 | -0.33 |
| | 2 | 8.6 (1.2 - 21.8; 2.4) | 75 | -0.30 |
| | 3 | 3.9 (-0.2 – 9.0; 1.2) | 96 | -0.08 |

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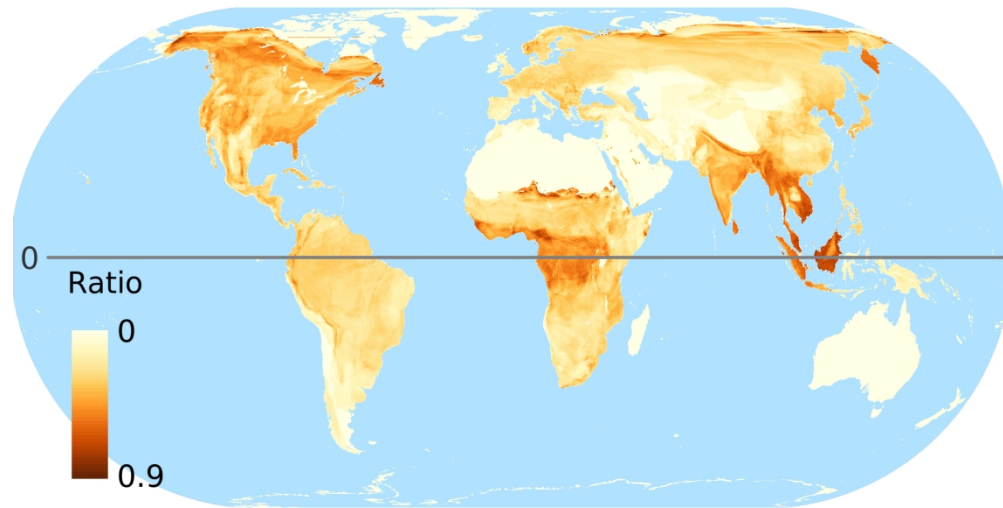596
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**Figure legends**

**Figure 1.  Global map of the relative richness of tree cavity excavators versus secondary cavity-nesting birds (expressed as the ratio excavator / secondary cavity-nester) in 10x10 km grid cells**.  Low values (light colors) indicate relatively low numbers of excavators as compared to secondary cavity-nesters (~~or, inversely, relatively high numbers of secondary cavity-nesters~~) while high values (dark colors) indicate a relatively higher proportion of excavators to secondary cavity-nesters.
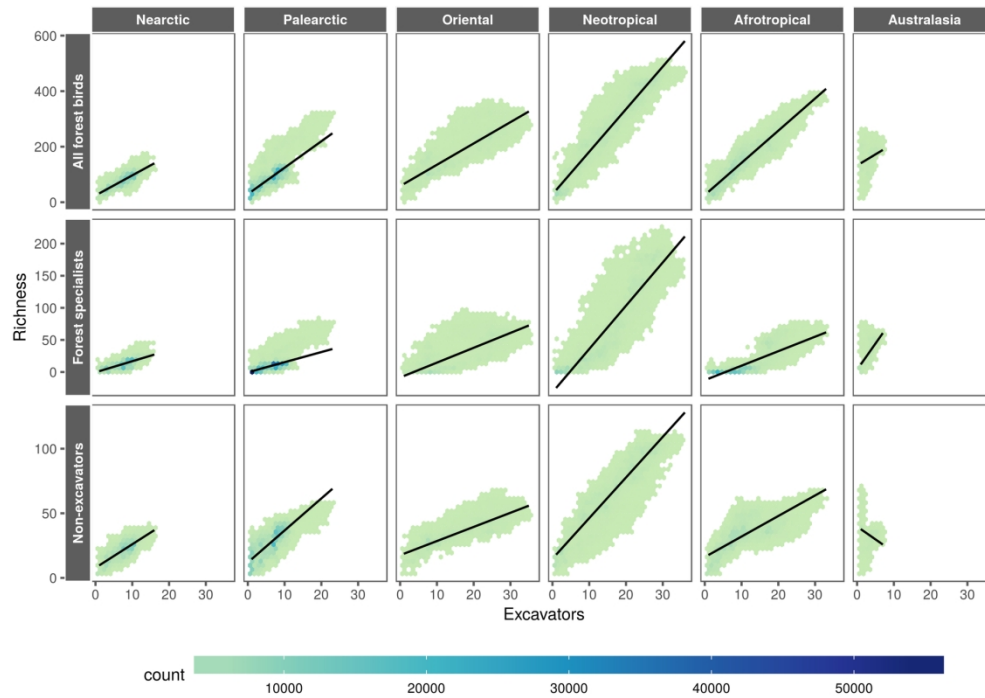
**Figure 2. Scatter plots of the correlation between the richness (number of species) of excavators and all forest birds (upper row), all forest specialists (middle row), and all non-excavating cavity-nesters (bottom row) in six zoogeographic regions.** Points represent species richness values in 10x10 km grid cells, and the solid line represents the fit of a linear regression model, created using all grid cell values.

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**Figure 1.**

**Figure 2.**

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Figure 1. Global map of the relative richness of tree cavity excavators versus secondary cavity-nesting birds (expressed as the ratio excavator / secondary cavity-nester) in 10x10 km grid cells. Low values (light colors) indicate relatively low numbers of excavators as compared to secondary cavity-nesters (or, inversely, relatively high numbers of secondary cavity-nesters) while high values (dark colors) indicate a relatively higher proportion of excavators to secondary cavity-nesters.

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Figure 2. Scatter plots of the correlation between the richness (number of species) of excavators and all forest birds (upper row), all forest specialists (middle row), and all non-excavating cavity-nesters (bottom row) in six zoogeographic regions. Points represent species richness values in 10x10 km grid cells, and the solid line represents the fit of a linear regression model, created using all grid cell values.

167x119mm (300 x 300 DPI)

Authors Response letter to editor:

I am recommending a "reject/resub" decision because our "revision" turnaround time may be too short for the authors' needs in revising, and because the reviewers have raised extensive concerns, despite being encouraging overall about the manuscript.

They see issues with how the main problem of the study is set out, the methods, the evaluation, and the conclusions. They also note a geographic bias that may entail ecological biases in the relationships of excavators to their ecosystems.

If you elect to re-submit, please detail your responses to reviewers' comments and make clear how you have altered your re-submitted manuscript. Best wishes with your revisions.

Reviewers' Comments to Author:
Reviewer: 1

General comment:
The manuscript entitled "Global and universal relationships between tree-cavity excavators and forest bird richness." reports on an interesting exploratory study linking woodpeckers/other tree cavity excavators, secondary cavity users and other forest tree species at the global and bioregional levels. The results are useful and may inspire new studies exploring these relationships more in-depth.

**RESPONSE: We thank the reviewer for their supportive comments.**

My main criticism concerns the quality of reasoning and how and to what extent different issues are introduced and discussed. Proposing the use of certain group of species as indicators or other type of indicator species shall rest on solid grounds as well as need of such indicators should be clearly put forward. I simply miss the delineation of the conservation/management problem why we need indicators. There are many articles published on the worldwide decline of primary/intact forests, their characteristics and, in my opinion, you do not use the opportunity to discuss the potential role of woodpeckers/other tree cavity excavators (with very intimate linkages to natural forest characteristics) to support your case. Also, even if you mention their usefulness in management, there is lacking information on the intensively managed forests as areas that lose both important characteristics linked to old-growth forests and forests with high level of naturalness and thereby lose most specialized forest species often being woodpeckers.

**RESPONSE: We thank the reviewer for pointing out these ways to strengthen our text. We have added arguments and citations to strengthen these points throughout the Introduction (e.g., lines 96-98).**

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Also use of woodpeckers/other excavators as indicators of successful forest restoration could be mentionaed. There is large body of literature on both above topics and I suggest that you should add paragraphs pertaining on these issues in both Introduction and Discussion sections. To limit the length of the article, you may get rid of several unnecessary repetitions. More suggestions below:

Detailed comments:

Line 99: Several species use smaller trees or snags too. Possibly add "often" or "usually".

**RESPONSE: We agree with the reviewer that there are many exceptions, for which we followed the suggestion to add 'often' to soften the generalization.**

Line 109: Woodpeckers (cavity excavators) are most often resident species what could additionally strengthen your reasoning on strong linkages to forest environments and their quality.

**RESPONSE: We thank the reviewer for this valid point, and have incorporated a sentence to illustrate this in the second paragraph of our introduction.**

Lines 127-133: Please consult Wesolowski and Martin (2018) and extend the discussion on mechanism a bit more. I am lacking a clear statement on two possible, non-excluding each other mechanisms of expected relationships as very nicely stated way down in Discussion (Lines 312-314).

**RESPONSE: We thank the reviewer for this valid point. We agree that this is a key element of our manuscript that should be clarified much earlier in the text, and have a such included lines to address this topic in the very beginning of the Introduction.**

RESULTS: Could you add a summary table with numbers of species in different groups in different bioregions? It would provide some nice background for further discussions of results. You have those numbers already!

**RESPONSE: We understand that this might make it much easier to follow some of the reasoning, plus it would benefit authors who would like to build on our analyses. We have therefore followed your advice and added a supplementary table (Table S1) summarizing these data.**

Lines 224-231: I do not understand how you can model the relationship between woodpeckers and the three other groups in Australasia, where, as you state below, there is no woodpeckers or even other strong excavators are largely lacking.

**RESPONSE: Thank you for pointing this out, this is indeed a mistake. We have removed the 'woodpecker part' for Australasia and have added text to make this clear in methods as well ('We repeated all of these analyses for woodpeckers as a**

**subset of the excavators, with the notable exception of Australasia where woodpeckers are absent.')**

DISCUSSION: a bit confusing use of words "excavators/woodpeckers" (Line 244) and "excavators" (Line 275). Please check if necessary to use both of them!

**RESPONSE: We agree that this is a bit confusing and have simplified this, by simply using excavator/woodpecker when an argument or explanation concerns both groups equally and 'excavator' or 'woodpecker' by itself if it is particular to only one of these groups (e.g., when evidence does not extend beyond woodpeckers or when discussing specific results (e.g., ratios)).**

Lines 239-243: Worthy to mention that forests in some bioregions supply decay-formed cavities in high numbers (particularly non-managed forests) and some other not (e.g. boreal forest in Europe – see Andersson et al. (2018): Andersson J., Domingo Gomez E., Michon S., Roberge J.-M. (2018) Tree cavity densities and characteristics in managed and unmanaged Swedish boreal forest. Scandinavian Journal of Forest Research, 33 (3), pp. 233-244. It would add the management angle in discussion about the role of woodpeckers/excavators for other species.

**RESPONSE: We have added more text on this (esp. lines 304-309) including the reference suggested. We absolutely agree that this is a key element of the story, yet we aimed not to add too much to an already rather lengthy manuscript.**

Lines 272-273: Please refer to studies on the global species richness of woodpeckers e.g. Mikusinski, G. 2006. Woodpeckers (Picidae) - distribution, conservation and research in a global perspective. Annales Zoologici Fennici 43: 86–95.

**RESPONSE: We have added this reference.**

Lines 289-294: Refer also to the "primeval" Bialowieza Forest case in temperate zone being in stark contrast to managed forests (i.e. higher predation risk and subsequently preference for decay-formed cavities among secondary users. See: Wesolowski and Martin (2018) and references therein.

**RESPONSE: We have added a section on this, including additional references.**

Lines 299-304: Please refer to papers by Wesolowski here: Wesolowski T. 2011."Lifespan" of woodpecker-made holes in a primeval temperate forest: A thirty year study. Forest Ecology and Management, 262 (9) , pp. 1846-1852.

RESPONSE: We added this reference.

Reviewer 2:

What is the difference between 'global' and 'universal'. There is nothing in the introduction, nor in the discussion, justifying the usage of these two words. I suggest to delete 'universal'

**RESPONSE: We thank the reviewer for this remark, it made it clear to us that we needed to clarify these terms. When we use the term 'global' we imply that these relationships can be found in nearly every region of the world, with 'universal' we mean that they are of similar nature (strong and positive).**

**We clarify these terms in both the Introduction and the Discussion (e.g., by adding that 'Around the world, we can find relationships of a universal nature (strong and positive) between excavator and forest bird richness.').**

I see this paragraph as mostly unnecessary, with some of this information that can be fusioned with the second paragraph

**RESPONSE: We understand that this start of the Introduction could be stronger, highlighting both the problem (need for indicators) and the opportunity (excavators/woodpeckers could make great indicators). We have reworked the introduction to accommodate these changes.**

**The reviewer mentions multiple inconsistencies in citations/references, we have now adopted the 'Open Biology/Royal Society Open Science' style and all issues should be resolved.**

I am not aware of this. I've seen some parrot species burrowing their own cavities in termitaria and cliffs, or 'arranging' cavities already done by woodpeckers or fungi. But I have not seen/heard about parrots excavating 'brand new' cavities in trees. Please, could you add a reference for that?

**RESPONSE: Although not common, parrots especially in Australasia may excavate in trunks that are in advanced stages of decay, without there having been a previous cavity, see e.g., Courtney, J. 2010. An Observation of Nesting Behaviour in Marshall's Fig-Parrot 'Cyclopsitta diophthalma marshalli'. Australian Field Ornithology, Vol. 27, No. 4, Dec 149-152.**

.....So, unless you have a better argumentation for this association at a global scale, I suggest to delete this part.

**RESPONSE: We have, in this new version, followed up on your suggestion and removed this statement that the response of woodpeckers can be indicative of that of forest birds in general.**

This is not what Cockle et al. (2011) found. According to the map in the Figure 2a, you can see that the pattern that you mention (excavated cavities as main source for non-excavator birds) is only strong in North America, very weak in Europe (only 1 out of 4 studies showed that pattern), and opposite in South America and Australia, this is, non-excavator birds mainly used decay formed cavities (there is no study in Africa). After Cockle et al. (2011), Ruggera et al. (2016) quoted "Therefore, in the PF woodpeckers do not seem to play a key role in provisioning cavities to the nest-web, a pattern also shown for other South American and some European forests, and contrary to the findings in North America (Cockle et al., 2011a,b; Pereira et al., 2009; Wesołowski, 2007)." Please, be careful when citing other authors, and put strictly what they have found.

**RESPONSE: We agree that we may have overstated the importance of excavators for the provision of cavities, and have altered our language accordingly (e.g., stating that 'cavity formation by excavation is an importance source of nest holes for species in many regions of the world'). However, Cockle et al. has shown that woodpeckers are an important provider of cavities in farmlands and altered forests in Argentina.  Thus, even in South America, woodpeckers may provide a larger role in the provisioning of tree cavities than currently recognized.**

- Please, see the previous comment on this pattern. Actually, it seems that woodpeckers play a considerably smaller role than that you stated, as cavity providers in many non-disturbed ecosystems. If my previous comment is correct, how is this prediction held?

**RESPONSE: We think this new version of our manuscript does a better job at highlighting the two mechanisms by which excavators are indicators: due to their associations with particular forest elements and their role in facilitating the presence of other species through the provision of nest cavities. We therefore think this prediction is still valid, but we did alter the text to recognize this point:**

**"Nevertheless, we might predict that these birds could be reliable indicators of avian diversity and richness not only at stand or landscape-levels (8, 17), but also across large regions at a global scale, not only for the cavities that excavators supply but also  due to  excavators' associations with forest elements that are indicative of heterogeneous forests with a high degree of naturalness."**

I see necessary to call to this group with something that recalls that are cavity users, because both forest specialist species and forest birds in general include also non-excavator bird species. An option can be 'secondary cavity-nesters'

**RESPONSE: We have followed this useful suggestion and have changed non-excavator to 'secondary cavity-nester' throughout the text.**

Here or in Methods: it's necessary to clarify if these categories are mutually exclusive. For example, some secondary cavity-nesters are forest specialists, and of course, are also forest birds in general. These species are considered in the three categories or only in the 'non-excavator' category? How this nested data set would eventually influence your results?

**RESPONSE: We added a sentence in the Methods to explain that some of these numbers are indeed nested, with for example a forest specialist also being counted as a forest bird. We can see how it could be interesting to know (for example) details on the relationship between excavators and forest specialists that do not nest in cavities, which we do not provide at this point. One reason for this is that sample size for many grid cells would become too low for our models to converge, particularly when we would count forest specialists that do not breed in cavities as a separate group (e.g., there are relatively few forest specialists in the Nearctic that are not also cavity-nesters).**

**Another reason is that we aimed to know whether excavators make useful indicators and management surrogates. For this we wanted to know how indicative excavators are of larger and more inclusive suites of forest-associated birds, not of very specific subgroups (e.g., forest-associated species that do not breed in cavities and that do not exclusively use forest habitat).**

What about the other two bird groups?

**RESPONSE: We have altered this text to make clear we predict that spatial variation in forest characteristics, management regimes, and bird communities will lead to differences in relationships between excavators and forest birds.**

- I suggest to deeply restructure the introduction: 1) a first paragraph that talks in general about the relationship of excavators with other birds (fusion of the first two paragraphs); 2) Exclusive paragraphs for each excavator relationship with each of the other 3 groups of birds. In each paragraph express what is known and what is the relationship predicted by the authors, and how they think that these relationships may vary in relation to the biogeographic regions considered. Another option is that the geographical variations of the relationships are expressed together in a separate paragraph. On the other hand, I think that it must necessarily be emphasized and made clear, what is the novelty provided by this study, in comparison with other studies cited in the same introduction and that address comparisons very similar to those of this study (eg Drever et al. 2008, Mikusinski et al 2001, Virkkala 2006).

**RESPONSE: We thank both Reviewer 1 and 2 for this suggestion for restructuring, and have adopted these suggestions. We have given more attention to the novelty of our study in the very first paragraph of our new version (Larger scale, testing for general patterns across all major biogeographic areas), and have further regrouped and organized the paragraphs in the introduction.**

- I find necessary to clearly define the categories of bird groups you use. I tried to do this by copy-and-paste some information you wrote below. However, I don't know if I did it correct, and the definition of 'excavator' group is missing. Please, check it and correct it. Yet, something is not clear to me, Can a given bird species be part of more than one group? If the answer is yes, how that influences on results?

**RESPONSE: We have added some text to clarify this in the methods and provided clear definitions of all bird groups used (see also our response to an earlier query above.**

- I find necessary to clarify some 'ecological' issues (i.e. not statistical) in methods. 1) Did you include the whole area of each biogeographic zone? or 2) only the forest areas in each one of them? If (1): How do you think the different amount of area/forest area of each biographic zone can influence your results? How non-forest excavators (as some woodpeckers) can incluence your results? or did you exclude them? Another question: given the cnsideration of Paleartic and Oriental regions, what does the AUSTRALASIA region includes? what part of Asia?

**RESPONSE: We thank the reviewer for this question. We have added text to explain this in the Methods: "We did not restrict our analyses to forested regions, wanting to avoid making subjective decisions on the classification of a grid cell to a specific vegetation/habitat type. Yet, to make sure we did look for possible relationships between these forest-associated species in regions they actually occur, we did remove cells with zero excavators/woodpeckers and cells where the numbers of secondary cavity-nesters, forest specialists, or all forest birds were lower than that of excavators/woodpeckers from further analyses. "**

**That said, we are not sure how the amount of area/forest area would influence our results, but we have aimed to circumvent that issue as much as possible by randomly selecting (1000 times) 1000 grid**

**cells per region, thereby comparing similar surface (though not necessarily forest, but see above) areas per region.**

**Australasia encompasses the following regions, following our adaptation of the classification of van der Hoek et al. 2017. Diversity and Distributions, which is in turn based on that of the Handbook of the Birds of the World (Del Hoyo et al.): American Samoa, Australia, Bismarck Archipelago, Admiralty Islands, Cook Islands, Easter Island, Federated States Micronesia, Fiji, French Polynesia, Guam and the Marianas, Johnston Island, Kiribati, Macquarie Island, Marshall Islands, Nauru, New Caledonia, New Guinea, New Zealand, Niue, Norfolk Island, Papua New Guinea, Pitcairn Islands, Samoa, Solomon Archipelago, Tokelau, Tonga, Tuvalu, Vanuatu, Wake Island, Wallis and Futuna. Practically, we can say that most excavators in this region are from (Papua) New Guinea and surrounding islands.**

- What did you specifically model? which were the variables?

**RESPONSE: The gls models are more clearly explained now: " This implied the use of gls models with excavator richness as a predictor variable, the richness of one of the categories of forest-associated birds as a response variable, and a variable exponential spatial covariance structure…"**

- I am not an especialist in this kind of analyses, and I could not fully understand it. Given that many readers of this kind of papers are not especialists either, I find very important to better explain this methodological part. What are the predicted and what the observed data? What does tell us the regression slopes and what the mean spearman rho? Nevertheless, at this point, I have the impression that you modeled the richness of non-excavators and forest birds, relative the presence of excavators (explanatory variable), i.e. in a causal manner (= gls models). However, in the introduction this relationship was mostly raised in a correlational manner, this is, that both excavators and the other forest bird groups show similar responses to forest structure and disturbances. Exceptions to this correlational relationship are, for example, the FEW cases (in terms of global areas) in which excavators are essential for nonexcavators by providing new cavities or food resources (sap and insects in excavator perforations). In short, you are analysing a relationship that you mostly posted as correlational, with regression models. Please, if my reasoning is incorrect, just ignore it, but explain better the methodology.

**RESPONSE: We have added some clarification (see e.g., the answer above) that may help understand these methods better.**

**That said, it is correct that a gls model is basically an ordinary linear regression model with some different assumptions (or some assumptions not met; in this case related to spatial autocorrelation). However, whereas the reasoning behind a correlation vs. a regression differ, the statistics are, in this particular case, the same. A correlation can indeed encompass any relationship between two variables, without assuming cause and effect, whereas a linear regression can only be that: a linear relationship where we assume that X predicts Y. When the correlation is linear though, this becomes one and the same in terms of output (though not interpretation, which we therefore have been careful with, see our Discussion). In other words, when in this particular case both tests address the 'null hypothesis that the two variables are not linearly related. If run on the same data, a correlation**

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**test and slope test provide the same test statistic and p-value.' (see e.g.,**
**http://sites.utexas.edu/sos/guided/inferential/numeric/bivariate/cor/).**

**So why then this regression and not a correlation, if they provide the same outcome but correlations are easier to interpret? Largely because we would be unable to incorporate a measure to address spatial autocorrelation into a correlation test.**

- given that in Fig. 1 you detailed ellipses for each of the six zoogeographic region. I'd say that you can leave only the figure 2 and nothing would be lost

**RESPONSE: We have followed this suggestion and removed the first of the two figures, leaving only the multi-paneled one. That said, we opted to add one map that shows global distributions of excavators relative to secondary cavity-nesters, a map which we deem to be illustrative of the spatial variation and clustering (e.g., between zoogeographic regions) that we discuss in our manuscript.**

- It seems like sometimes your reasoning is associative/correlative (e.g. both excavators and other groups of forest birds have similar responses to disturbances), other times it is explanatory (e.g. the excavator richness determines the richness of other non excavator cavity-users by providing new cavities), and here it is predictive: the addition of 1 excavator species implies the addition of X forest bird species, ignoring any other type of causes, such as phylogenetic, biogeographical, etc. You must decide which of these visions you are going to explore, or clearly establish that all of them will be analysed, with their respective methodologies and theoretical support.

**RESPONSE: Although regressions provide both explanatory and predictive outcomes we understand that our language here is confusing, and our statements may be misinterpreted as meaning one can simply predict from a given number of excavators how many other forest birds there are at that location (which is, of course, not that simple as you rightly point out). Yet, whether the tested relationships are associative (similar habitat needs etc.) or causative (birds use the cavities created by excavators), the fact of the matter is that they are linear. But, in some regions, this relationship is stronger than in others. We should have focused on this and not the steepness of the slopes; and we have therefore removed these parts from the Results and Discussion sections.**

**That said, we explore whether there are relationships between excavators and other forest birds (the gls models themselves), but also aimed to see if this could then be used to determine to what extent excavator richness is indicative of that of other species (the matching with the test data set and derivation of Spearman rho's). We hope that this approach is clearer from our revised manuscript.**

- Commented [MOU25]: What exactly does the Rho (=strength) mean in this context? low values of Rho mean that the relationships are not very reliable? for example in australasian region. And more important, what would be the joint interpretation of the slopes, the percentage of models with p greater than 0.5 and the rho?

**RESPONSE: Rho would here give us an idea how 'perfect' the linear relationships are (with rho = 1 being perfect with all grid cells falling on one line), whereas the slope (which we now removed from further discussion (see above) but present in the Results section to be complete in our presentation of model statistics) would tell us how many other forest birds (other than excavators) there are likely to be in a given location (grid cell) relative to the number of excavators (this does thus present an idea of**

**'what richness' a certain number of excavators would possibly indicate). The % of models with a p < 0.05 gives us an idea whether these relationships are significant or not, given we had to iterate over many (1000) models, this would be a measure of reliability of the relationships given the combination of both the correlation coefficient and the sample size (which here is always 1000).**

**Low values of rho do not necessarily mean that that the relationships are not very reliable, but rather that they would not be strong enough to be able to 'use richness of excavators' to predict how many other forest birds are in a given location (here grid cell). Thus low values of rho would, in this case, show that excavators are rather poor indicators of other forest birds, even though the relationships might be real and significant.**

- Commented [MOU27]: I would like to read what are those differences to take into account from a practical point of view and Commented [MOU28]: The comment on nest-webs here, in the first paragraph of Discussion, is out of context. Besides, variation among nestwebs… in relation to what? Are you trying to relate the association of excavators and other forest birds with variations in nestweb characteristics? it's far from clear, and you are leaving out a key aspect: the diversity, persistence and characteristics of trees with cavities

**RESPONSE: We have made some substantial changes to our text and hope to now provide a clearer line of argumentation.**

- However, in several other nestwebs (for example in South America [Cockle et al. 2012, Ruggera et al. 2016] and India [Manikandan & Balasubramanian 2018]), most non excavator birds mainly use decay-formed cavities in living trees. Only 10-25% of interactions (including excavator interactions) are made with snags. So, the evidence to date (even in the Neotropics, where your results showed the strongest association between excavators and non-excavators), would not be explained by the number of snags or the amount of woodpecker-excavated cavities. Also, you need to better explain why forest especialist birds would benefit from the presence of 'certain levels (how much?) of availability of decaying and dead wood'

**RESPONSE: We have made substantial changes to the text in the Discussion, incorporating suggestions by both reviewers, which means that we now provide a clearer insight in the differences in the importance of decay vs. excavated cavities in the different regions. With that, we anticipate to have resolved these issues as well.**

- differences in relation to what of the nestwebs? you need to be more specific. You need to better explain this: how speciation and other macro-scale processes across the globe influence on the results you found. Explanations generally are biased to nestwebs. However, you have other bird groups that not necessarily are cavity-nesters. Also, you don't necessarily have to invoke networks (of which there are relatively few reports worldwide) to talk about cavitynesters (of which there are comparatively many more reports around the world)

**RESPONSE: We thank the reviewer for this comment. We have made substantial changes to our text, reflecting better that both direct facilitation through nest-webs and indirect associations play a role in shaping the observed relationships. As a result of these changes, we have also paid more attention to the role of differences in community composition etc. in shaping these relationships.**

- Australasia region doesn't lack Piciformes. As you say a few words later, SE Asia has a high diversity of Piciformes. So, be careful when you explain Australasia results as a unique region (see comment also about AUSTRALASIA in methods). In fact, I would like to find a better explanation of the results of the Australasian region, since it had the most contrasting results with the rest of the regions.

**RESPONSE: There is a difference between the Oriental and Australasian zoogeographic regions that may have gone unnoticed to the reviewer. Most of Indonesia and other SE Asian countries falls within the Oriental region, with the Wallace line separating this region from the Australasian region (e.g., Papua/New Guinea) where some excavators exist but Piciformes are notably absent (see also e.g., Mikusiński, G. (2006, January). Woodpeckers: distribution, conservation, and research in a global perspective. In Annales Zoologici Fennici (pp. 86-95). Finnish Zoological and Botanical Publishing Board.). That said, we do agree that the results we found for the Australasian region deserved more attention, and have thus extended on this in the text.**

- what differences? you have not established what are the differences along the neotropical region in terms of climatic variables, tree species composition, tree availability and their formation agents. Also, include in this comparison the work by Ruggera et al. 2016, how their results fit in the explanation your trying to develop?

**RESPONSE: In our revised version you will find references to Ruggera et al. as well as more comprehensive explanation of the differences found across and within regions.**

- then, if non-excavators do not 'need' excavators as cavity-forming agents, why did they show the greatest association in richness in the Neotropics?

**RESPONSE: We anticipate that we have now explained this better, focusing on the fact that indirect associations (shared forest elements etc.) are more important than direct facilitation (cavities) in explaining these relationships.**

- Commented [MOU40]: Altamirano et al. 2017 wrote: 'Among SCNs, ten species (40%) were obligate and 15 (60%) were non obligate cavity nesters. Non obligate cavity nesters included six (24%) facultative, five (20%) marginal, and four (16%) incidental SCN'. If we include also PCN, facultative cavity nesters are 20%. Commented [MOU41]: how are they influenced? Again, I lost the point. You began talking about 'spatial variation in the relationships between excavators and other forest birds within zoogeographic regions', but then you focused (again) only on excavators and non-excavators, especially in the Neotropics.

**RESPONSE: We have changed these parts of text substantially, hopefully addressing these issues and providing more clarity.**

- I believe that this is a central point, that it should be better developed in the introduction, and that the methodology should be chosen according to that. It is not the same to analyze something in a correlative way, that in an explanatory or predictive way

**RESPONSE: Yes, we agree. We have made an effort to provide more attention to these two different mechanisms (direct facilitation and indirect association) by which relationships between excavators and other forest birds may be formed.**

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# Appendix D

We thank the Editor and reviewers for the chance to submit a revised version of our manuscript, and for the many constructive comments we received. As per request from the editor and reviewers, we have redone some analyses (specifically we now present non-overlapping 'response groups' of forest birds), use ecological language rather than the statistical aspects of the correlations (slopes etc.), and discuss in more detail the results as they pertain to evidence for the two main drivers of possible relationships between excavators and forest birds.

We provide more detailed responses below, and hope you will find this renewed version sufficiently improved to merit publication.

Ps. We would like to point out that most changes we made can also be found in the track change version of our new manuscript, though the final version without track changes has a few more grammar, writing, and outline changes and should thus be considered as the final version.

Response to the reviewers are preceded by an *

1) work on the predictions, making them more precise, with more ecological language, and that revolve around the two main causes that the authors propose as the main drivers determining the relationships of excavators and forest birds: the sharing of habitat requirements, and the provision of excavated cavities. How these causes spatially vary based on geographic, climatic and historical characteristics in each region, will determine the predictions that will be tested.

   *We thank the reviewer for the comments and have made substantial changes to the Introduction (especially the prediction part). We have reduced our attention to secondary topics, such the analyses of the relationships that include woodpeckers (which are now in supplementary materials) and statistical elements (such as the steepness of slopes), and instead focus more on the two drivers mentioned in this comment. Where possible, we aimed to also strengthen our discussion of differences across regions, though we are admittedly limited in our knowledge of the more tropical regions (e.g., the Afrotropics), for which there is but little relevant literature available.

2) rethink the overlapping of the bird categories, assessing which is the best option to determine which of the aforementioned factors (i.e. sharing of habitat requirements and cavity provisions), are the most likely drivers of the proposed relationships. As I comment in the text, the definition of the categories is inconsistent with the methodology used. And, if I understood well the methodology, I also have the impression that the overlapping of categories used may be influencing the results, inflating the relationships between excavators and forest birds, since in this last category are also included many SCNs and forest specialists. I have seen your response to a related comment I made in the previous version. I guess that a good possibility is that the only categories that overlap are 2 (SCN) and 3 (forest specialists). That way, you can see relationships that supposedly may be due more exclusively to provision of cavities (relationships of excavator with 2 would be stronger than with 3), or more related to sharing habitat requirements (relationships of excavator with 3 would be stronger than with 2). Also, leaving category 4 without overlapping can lead to different results and interpretations I think could be more interesting.

*We agree that this decision, to use nested categories, might limit our ability to separate relationships that are more shaped by the provision of cavities from those relationships that rely solely on mutually shared preferences for certain habitat elements etc. We therefore opted to re-run all the analyses for groups that do not have any overlaps. For example, in this revised manuscript version, the group of forest specialists does not include any secondary cavity-nesters, etc.

The results of these new analyses are largely in line with those we obtained previously, but there are some changes that we have more extensively discussed in Results and Discussion. Notably though, the relationships between excavators and forest birds that do not nest in cavities are now particularly strong (in most cases, stronger than those between excavators and secondary cavity-nesters). In other words, we [still] see that excavators are mainly indicators of other birds probably due to their mutual association with habitat elements etc., rather than the provision of cavities.


3) The discussion needs a lot of work. I would suggest that you focus on the differences between the zoogeographic regions, which is the main objective of the paper and what has been evaluated. The differences that may exist within each region should be minimized to the maximum, and only mentioned when strictly necessary. The discussion still has a great bias to try to explain the relationships between excavators and SCN, and there is a considerably smaller space in trying to explain the relationships with forest birds that do not nest in cavities. Finally, relationships in the Australasia region, which showed a different pattern from the rest (even in sign), were not explained, and these results are practically ignored when proposed, from the title, and the first and last paragraph of the discussion, that relationships are common to all zoogeographic regions.

*We did a major rewrite of the discussion to reflect our revised strong and consistent results. We agree that the differences between the zoogeographic regions are important, though we personally think another topic is the main objective of this paper: that excavators can be indicators of other birds at global scales. Yet, we see that we need to minimize our attention to within regions variation, and have done so, and understand that we need to emphasize how the Australasian region differs from others (and attempt to explain why). To that end, and as per your request, we removed some of the analyses that concern Australasia, notably those on woodpeckers which are not found in the region (but which we erroneously, and inaccurately, included in some of the tables and text).

Overall, we re-worked the Discussion, also taking into account the comments below and in the PDF, to provide a simpler but clearer story.

Many other comments have been made in the attached file

Reviewer: 1

Comments to the Author(s)
Line 130: add a bracket at the end of the sentence

*done

Lines 164-187: I opt for a very short explanation what do you mean by "universal" used in the title of the paper already here.

*We have removed the word 'universal' from the title following other reviewer comments, but have nevertheless added some text in this paragraph to illustrate that we expect these relationships to be of similar nature across the world.

Lines 268-277: In contrast with added information about not analysing woodpeckers in Australasia (lines 236-238), you report it here and in Table 2. It is confusing to me.

*This text has been altered, and there is no reporting of results for Australia left in this part of the manuscript.

Line 293: I have a hard time finding the paper by Tikkanen et al. 2006 as supporting your claim here. Possibly cite several paper based on single-species woodpecker studies or use some of those:
JM Roberge, P Angelstam, MA Villard. 2008. Specialised woodpeckers and naturalness in hemiboreal forests–deriving quantitative targets for conservation planning. Biological conservation, 2008
or
Angelstam, P., & Mikusiński, G. 1994: Woodpecker assemblages in natural and managed boreal and hemiboreal forest - a review.  Annales Zoologici Fennici 31: 157-172.


*We think the suggestions are very valid references here, but we think Tikkanen et al. 2006's reference is a perfect fit here, and is actually very easy to find (Google 'Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. ' provides it right away). That said, we do see that especially Roberge and Angelstam would be a good it here as well, and have included that reference accordingly.


Lines 392-394:  I suggest adding further argument here i.e. that woodpeckers are highly responsive to playbacks (both calls and particularly drumming) that, if applied in right season are very effective survey tool and cover relatively large areas. See e.g. Kumar, R. and Singh, P. (2010), Determining woodpecker diversity in the sub-Himalayan forests of northern India using call playbacks. Journal of Field Ornithology, 81: 215-222. doi:10.1111/j.1557-9263.2009.00267.x  or Jeremy A. Baumgardt, Joel D. Sauder, and Kerry L. Nicholson (2014) Occupancy Modeling of Woodpeckers: Maximizing Detections for Multiple Species With Multiple Spatial Scales. Journal of Fish and Wildlife Management: December 2014, Vol. 5, No. 2, pp. 198-207.

*We again thank the reviewer for this valuable recommendation. We have added such text at this point as well as the Baumgardt et al. 2014 reference.

Table 2: remove data concerning the woodpeckers (see my comment above)

*We have changed Table 2 to be a new supplementary table (Table S2).

There is one important paper dealing with woodpeckers at the global scale that is relevant to your study but omitted namely: Vergara-Tabares, D. L., M.Lammertink, E. G.Verga, A.Schaaf, and J.Nori (2018). Gone with the forest: Assessing global woodpecker conservation from land use patterns. Diversity and Distributions 24:640–651.
Please consider mentioning the results of this paper in the Introduction or Discussion. It is particularly interesting from the management perspective and the human influence on forest qualities.

*We were aware of this paper but previously did not see a particular text location where this reference would fit well. But, in this revised version, we found that this reference fits very well in the Discussion and strengthens our story.

*A few specific responses to comments made to the PDF (other changes can be found in the document version with track changes):

- After reading your response to my comment on the title, I must kindly say that I still disagree with the use of the word 'universal'. First, because the meaning of the word itself is more a synonym for global, than what you want to express; and second, because what you found is not universal (in the sense that you want to give it), the Australasia region does not have the same relationships, either in strength or in sign, as the other regions.

*We have removed the word universal from the title following this recommendation.

- Even when I understand your point here, when you say 'natural', in my opinion this is a long-standing misuse of the word. Bird-excavated cavities are also 'natural'. I suggest changing those terms, maybe write directly 'fungal formation'?

*We agree with this observation and have altered the text to say 'fungal formation'.

- I don't see a clear and direct link between the first two sentences of the paragraph. Moreover, as I mentioned in the previous version, nest-webs involve only one of the subsets of birds that you are trying to associate with excavators. I suggest deleting the first sentence, and slightly modifying the second to be the beginning of the paragraph

*We have made considerable changes in the text in this section.

- Taking into account these arguments, how do you explain that in the Neotropical region, where the relationship between excavators and SCN found is the strongest association between excavators and SCN in the world, SCN do not rely heavily on excavated cavities?

*We refocused on the relatively more important role of indirect association, rather than direct facilitation, in shaping the relationships between excavators and other forest birds. As a result, we largely changed the text in the Discussion, including providing explanations related to the relative 'natural state' of forests in the Neotropics as compared to other regions, the larger number of niches available in the Neotropics, etc. We kindly refer to the altered Discussion for all details.

**Appendix E**

# ROYAL SOCIETY
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## Global relationships between tree-cavity excavators and forest bird richness

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## **Author-supplied statements**

Relevant information will appear here if provided.

### *Ethics*

*Does your article include research that required ethical approval or permits?:*
This article does not present research with ethical considerations

*Statement (if applicable):*
CUST_IF_YES_ETHICS :No data available.

### *Data*

*It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:*
Yes

*Statement (if applicable):*
Links to the data and R scripts to reproduce analyses presented in Global and universal relationships between tree-cavity excavators and forest bird richness can be found in Appendix S1.

### *Conflict of interest*

I/We declare we have no competing interests

*Statement (if applicable):*
CUST_STATE_CONFLICT :No data available.

### *Authors' contributions*

This paper has multiple authors and our individual contributions were as below

*Statement (if applicable):*
YH and GVG carried out the data analysis, and led the design of the study and writing of the manuscript; MC and KM critically revised the manuscript. All authors contribute to the writing of the final manuscript, gave final approval for publication and agree to be held accountable for the work performed therein.

We thank the Editor and reviewers for the chance to submit a revised version of our manuscript, and for the many constructive comments we received. As per request from the editor and reviewers, we have redone some analyses (specifically we now present non-overlapping 'response groups' of forest birds), use ecological language rather than the statistical aspects of the correlations (slopes etc.), and discuss in more detail the results as they pertain to evidence for the two main drivers of possible relationships between excavators and forest birds.

We provide more detailed responses below, and hope you will find this renewed version sufficiently improved to merit publication.

Ps. We would like to point out that most changes we made can also be found in the track change version of our new manuscript, though the final version without track changes has a few more grammar, writing, and outline changes and should thus be considered as the final version.

Response to the reviewers are preceded by an *

1) work on the predictions, making them more precise, with more ecological language, and that revolve around the two main causes that the authors propose as the main drivers determining the relationships of excavators and forest birds: the sharing of habitat requirements, and the provision of excavated cavities. How these causes spatially vary based on geographic, climatic and historical characteristics in each region, will determine the predictions that will be tested.

   *We thank the reviewer for the comments and have made substantial changes to the Introduction (especially the prediction part). We have reduced our attention to secondary topics, such the analyses of the relationships that include woodpeckers (which are now in supplementary materials) and statistical elements (such as the steepness of slopes), and instead focus more on the two drivers mentioned in this comment. Where possible, we aimed to also strengthen our discussion of differences across regions, though we are admittedly limited in our knowledge of the more tropical regions (e.g., the Afrotropics), for which there is but little relevant literature available.

2) rethink the overlapping of the bird categories, assessing which is the best option to determine which of the aforementioned factors (i.e. sharing of habitat requirements and cavity provisions), are the most likely drivers of the proposed relationships. As I comment in the text, the definition of the categories is inconsistent with the methodology used. And, if I understood well the methodology, I also have the impression that the overlapping of categories used may be influencing the results, inflating the relationships between excavators and forest birds, since in this last category are also included many SCNs and forest specialists. I have seen your response to a related comment I made in the previous version. I guess that a good possibility is that the only categories that overlap are 2 (SCN) and 3 (forest specialists). That way, you can see relationships that supposedly may be due more exclusively to provision of cavities (relationships of excavator with 2 would be stronger than with 3), or more related to sharing habitat requirements (relationships of excavator with 3 would be stronger than with 2). Also, leaving category 4 without overlapping can lead to different results and interpretations I think could be more interesting.

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*We agree that this decision, to use nested categories, might limit our ability to separate relationships that are more shaped by the provision of cavities from those relationships that rely solely on mutually shared preferences for certain habitat elements etc. We therefore opted to re-run all the analyses for groups that do not have any overlaps. For example, in this revised manuscript version, the group of forest specialists does not include any secondary cavity-nesters, etc.

The results of these new analyses are largely in line with those we obtained previously, but there are some changes that we have more extensively discussed in Results and Discussion. Notably though, the relationships between excavators and forest birds that do not nest in cavities are now particularly strong (in most cases, stronger than those between excavators and secondary cavity-nesters). In other words, we [still] see that excavators are mainly indicators of other birds probably due to their mutual association with habitat elements etc., rather than the provision of cavities.

3) The discussion needs a lot of work. I would suggest that you focus on the differences between the zoogeographic regions, which is the main objective of the paper and what has been evaluated. The differences that may exist within each region should be minimized to the maximum, and only mentioned when strictly necessary. The discussion still has a great bias to try to explain the relationships between excavators and SCN, and there is a considerably smaller space in trying to explain the relationships with forest birds that do not nest in cavities. Finally, relationships in the Australasia region, which showed a different pattern from the rest (even in sign), were not explained, and these results are practically ignored when proposed, from the title, and the first and last paragraph of the discussion, that relationships are common to all zoogeographic regions.

*We did a major rewrite of the discussion to reflect our revised strong and consistent results. We agree that the differences between the zoogeographic regions are important, though we personally think another topic is the main objective of this paper: that excavators can be indicators of other birds at global scales. Yet, we see that we need to minimize our attention to within regions variation, and have done so, and understand that we need to emphasize how the Australasian region differs from others (and attempt to explain why). To that end, and as per your request, we removed some of the analyses that concern Australasia, notably those on woodpeckers which are not found in the region (but which we erroneously, and inaccurately, included in some of the tables and text).

Overall, we re-worked the Discussion, also taking into account the comments below and in the PDF, to provide a simpler but clearer story.

Many other comments have been made in the attached file

Reviewer: 1

Comments to the Author(s)
Line 130: add a bracket at the end of the sentence

\*done

Lines 164-187: I opt for a very short explanation what do you mean by "universal" used in the title of the paper already here.

\*We have removed the word 'universal' from the title following other reviewer comments, but have nevertheless added some text in this paragraph to illustrate that we expect these relationships to be of similar nature across the world.

Lines 268-277: In contrast with added information about not analysing woodpeckers in Australasia (lines 236-238), you report it here and in Table 2. It is confusing to me.

\*This text has been altered, and there is no reporting of results for Australia left in this part of the manuscript.

Line 293: I have a hard time finding the paper by Tikkanen et al. 2006 as supporting your claim here. Possibly cite several paper based on single-species woodpecker studies or use some of those:
JM Roberge, P Angelstam, MA Villard. 2008. Specialised woodpeckers and naturalness in hemiboreal forests–deriving quantitative targets for conservation planning. Biological conservation, 2008
or
Angelstam, P., & Mikusiński, G. 1994: Woodpecker assemblages in natural and managed boreal and hemiboreal forest - a review.  Annales Zoologici Fennici 31: 157-172.


\*We think the suggestions are very valid references here, but we think Tikkanen et al. 2006's reference is a perfect fit here, and is actually very easy to find (Google 'Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. ' provides it right away). That said, we do see that especially Roberge and Angelstam would be a good it here as well, and have included that reference accordingly.


Lines 392-394:  I suggest adding further argument here i.e. that woodpeckers are highly responsive to playbacks (both calls and particularly drumming) that, if applied in right season are very effective survey tool and cover relatively large areas. See e.g. Kumar, R. and Singh, P. (2010), Determining woodpecker diversity in the sub-Himalayan forests of northern India using call playbacks. Journal of Field Ornithology, 81: 215-222. doi:10.1111/j.1557-9263.2009.00267.x  or Jeremy A. Baumgardt, Joel D. Sauder, and Kerry L. Nicholson (2014) Occupancy Modeling of Woodpeckers: Maximizing Detections for Multiple Species With Multiple Spatial Scales. Journal of Fish and Wildlife Management: December 2014, Vol. 5, No. 2, pp. 198-207.

\*We again thank the reviewer for this valuable recommendation. We have added such text at this point as well as the Baumgardt et al. 2014 reference.

Table 2: remove data concerning the woodpeckers (see my comment above)

*We have changed Table 2 to be a new supplementary table (Table S2).

There is one important paper dealing with woodpeckers at the global scale that is relevant to your study but omitted namely: Vergara-Tabares, D. L., M.Lammertink, E. G.Verga, A.Schaaf, and J.Nori (2018). Gone with the forest: Assessing global woodpecker conservation from land use patterns. Diversity and Distributions 24:640–651.
Please consider mentioning the results of this paper in the Introduction or Discussion. It is particularly interesting from the management perspective and the human influence on forest qualities.

*We were aware of this paper but previously did not see a particular text location where this reference would fit well. But, in this revised version, we found that this reference fits very well in the Discussion and strengthens our story.

*A few specific responses to comments made to the PDF (other changes can be found in the document version with track changes):

- After reading your response to my comment on the title, I must kindly say that I still disagree with the use of the word 'universal'. First, because the meaning of the word itself is more a synonym for global, than what you want to express; and second, because what you found is not universal (in the sense that you want to give it), the Australasia region does not have the same relationships, either in strength or in sign, as the other regions.

*We have removed the word universal from the title following this recommendation.

- Even when I understand your point here, when you say 'natural', in my opinion this is a long-standing misuse of the word. Bird-excavated cavities are also 'natural'. I suggest changing those terms, maybe write directly 'fungal formation'?

*We agree with this observation and have altered the text to say 'fungal formation'.

- I don't see a clear and direct link between the first two sentences of the paragraph. Moreover, as I mentioned in the previous version, nest-webs involve only one of the subsets of birds that you are trying to associate with excavators. I suggest deleting the first sentence, and slightly modifying the second to be the beginning of the paragraph

*We have made considerable changes in the text in this section.

- Taking into account these arguments, how do you explain that in the Neotropical region, where the relationship between excavators and SCN found is the strongest association between excavators and SCN in the world, SCN do not rely heavily on excavated cavities?

*We refocused on the relatively more important role of indirect association, rather than direct facilitation, in shaping the relationships between excavators and other forest birds. As a result, we largely changed the text in the Discussion, including providing explanations related to the relative 'natural state' of forests in the Neotropics as compared to other regions, the larger number of niches available in the Neotropics, etc. We kindly refer to the altered Discussion for all details.

Title: Global and universal relationships between tree-cavity excavators and forest bird richness

Running title: Excavator and forest bird relationships

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**Abstract**

Global monitoring of biodiversity and ecosystem change can be aided by the effective use of indicators. Tree-cavity excavators, the majority of which are woodpeckers (Picidae), are known to be useful indicators of the health or naturalness of forest ecosystems and by the diversity of forest birds. They are indicators of the latter due to their associations with particular forest elements and because of their role in facilitating other species through the provision of nest cavities. Here, we investigated whether these positive correlations between excavators and other forest birds are also found at global scales. We used global distribution maps to extract richness estimates of tree-cavity nesting and forest-associated birds, which we grouped by zoogeographic regions. We then created generalized least squares (gls) models to assess the relationships between these groups of birds. We show that richness of tree-cavity excavating birds correlates positively with that of cavity-nesters and forest birds at global scales, but with variation across zoogeographic regions. As many excavators are relatively easy to detect, play keystone roles at local scales, and are effective management targets, we propose that excavators are useful for biodiversity monitoring across multiple spatial scales and geographic regions, especially in the tropics.

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**Introduction**

93  Forests worldwide are facing increasing anthropogenic pressures, with both a rapid decline in the
94  surface area of natural forests and a decrease in the naturalness of forests as a result [1, 2]. In
95  turn, these reductions of high-quality forest habitats have led to a loss of forest-associated
96  biodiversity [3-5]. To monitor these changes in forest ecosystems and their denizens, we often
97  look at specialized animals that require the availability of specific habitat structures and
98  processes across long temporal and large spatial scales [6], such as birds that respond not only to
99  a loss in overall forest cover but also to a change in forest health, quality, and integrity [7-10].
100  Excavators such as woodpeckers, barbets, nuthatches, trogons and certain parrot species—among
101  which woodpeckers are the most numerous group [11]—may be especially effective indicators
102  due to their associations with particular forest elements and their role in facilitating the presence
103  of other species through the provision of nest cavities. Indeed, there is empirical evidence that
104  their presence can be indicative of the state of both the forest (e.g., the presence of large trees
105  [12], heterogeneous forest structure [13], or a high level of naturalness [14-18]) as well as the
106  richness and abundance of other forest-associated species [19-21]. However, we may question
107  whether excavators are universally effective indicators, at least of biodiversity, in all geographic
108  regions or forest types. For example, excavators are better predictors of richness and abundance
109  of other forest resident birds in deciduous versus coniferous forests of certain parts of hemiboreal
110  Europe [15].

111       If relationships between excavators and other forest-associated biota are universally
112  positive in nature, and common not only at stand- and landscape-scales but hold across large
113  geographic regions, then excavators could form a unique group of indicators that may be
114  effective across multiple locations and spatial scales [22]. To find species that are effective as
115  both indicator and management surrogates across multiple regions would be especially useful in
116  the largely understudied tropics where comprehensive biodiversity assessments are costly and
117  logistically challenging [23]. The first signs are promising as the overwhelming majority of tree-
118  cavity excavators are forest or woodland birds and general patterns of woodpecker richness
119  correlate positively with the amount of forest cover at the global scale [24]. Moreover, many
120  excavators are regarded as habitat specialists and tend to have highly specific habitat
121  requirements, requirements which are usually only met in forests with high degrees of
122  naturalness and low levels of disturbances (e.g., logging). In fact, restoration efforts have
123  effectively made use of woodpeckers to indicate that restoration has successfully reached a
124  certain level of naturalness [25, 26]. This group of birds often utilizes large, live or decaying
125  trees, or coarse woody debris, for nesting, roosting, and feeding, and the availability of dead
126  wood is in particular found to be important [27-29]. This role of excavators as indicators of the
127  naturalness of ecosystems, whereby their presence correlates strongly with other aspects of
128  biodiversity, is enhanced by the fact that the majority of species are forest residents, which
129  arguably makes them more responsive to local changes in habitat quality (see e.g., [30]).

130       Excavators are not only reliable indicators of other forest birds by means of their mutual
131  associations with forest characteristics, but correlations between both groups of birds are also
132  partially determined by species interactions. Taken together, these 'nest-webs' [31] of interacting
133  species are structured by the availability and acquisition of tree-cavities formed by two major
134  processes: 'fungalnatural formation', in which fungi decompose wood over an extended period,
135  or animal excavation [32, 33]. Since most excavators—at least the majority of woodpeckers—
136  excavate a new nest cavity each year, this mode of cavity creation steadily provides a large
137  number of potential sheltered roosting and nesting sites available tofor secondary-users: both for

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139 vertebrates [33] and invertebrates [34, 35]. As a result, cavity formation by excavation is an
140 important, and often more rapid, source of nest holes for species in many regions of the world,
141 especially North America [33]. However, decay-formed cavities have shown to be~~are likely to be~~
142 more important nest sites in other regions, especially the tropics, and it is very likely that the
143 relative importance of both processes of cavity formation—and thus the strength of the
144 relationship between excavator richness and secondary cavity-nester richness—varies globally
145 [33]. ~~Finally, it is worth noting that excavators play additional roles (beyond the direct provision~~
146 ~~of cavities) that may facilitate other species. For example, as excavators perforate the bark of~~
147 ~~trees they may expose insects or sap for other species to forage on [36, 37].~~ In addition,
148 excavators can aid in the dispersal of fungi, which in turn enhances processes of wood softening
149 and the formation of decay-formed cavities [3~~6~~8]. Finally, it is worth noting that excavators play
150 additional roles (beyond the direct provision of cavities) that may facilitate other species that are
151 not necessarily cavity-nesters. For example, as excavators perforate the bark of trees they may
152 expose insects or sap for other species to forage on [37, 38].
153     ~~Local studies of cavity-nesting birds and their interactions are largely biased towards~~
154 ~~temperate zones, and only a few authors have explored global variation in nest-web~~
155 ~~characteristics or addressed how such variation should be taken into account when considering~~
156 ~~cavity-nester communities in forest conservation or management (e.g., [33, 39]). Nevertheless,~~
157 ~~we might predict that these birds~~Excavators ~~could~~are arguably ~~be~~ reliable indicators of forest-
158 bird~~avian~~ diversity and richness ~~not only~~ at stand or landscape-levels [9, 19], but it is unclear if
159 this~~, but also across large regions at a global scale, if not for the cavities that excavators supply~~
160 ~~but for the associations of excavators with forest elements that are indicative of heterogeneous~~
161 ~~forests with a high degree of naturalness.~~ scales up across larger regions or holds across the
162 globe given, for example, indications that the interactions between cavity-nesting birds may vary
163 spatially (e.g., []) or the notion that certain dominant groups of excavators (woodpeckers in
164 particular) vary in richness across zoogeographic regions [11]. Therefore, the aim of the present
165 study is to investigate whether there are consistent patterns in the relationships between avian
166 tree-cavity excavators (hereafter: excavators) and species richness of non-excavating tree-cavity
167 nesters (hereafter: secondary cavity-nesters), forest specialist species, and forest birds in general,
168 across the globe. If previously observed relationships between cavity-excavators and other forest
169 birds scale up from local forest stands [17] or ecosystems [19] to zoogeographic or global levels,
170 then this strengthens the potential of tree cavity-excavators as both indicators and management
171 surrogates.
172     Given the important, and potential indicator, role of excavators in forest ecosystems
173 across the world, we predict~~ed~~ a global tendency for ~~that~~ secondary cavity-nester, forest
174 specialist, forest generalist and overall forest bird (specialists + generalists) richness ~~generally~~
175 ~~will~~to increase ~~with~~ in correlation the number of excavators present in the ecosystem, regardless
176 of the ecosystem or location. However, we also predict~~ed~~ that the nature (e.g., the strength and
177 slope of correlations) of the relationships between excavators and richness of other forest birds
178 will vary across zoogeographic regions, reflecting differences in forest characteristics (e.g.,
179 deciduous vs. coniferous forests), forest management practices (e.g., forests being more or less
180 intensively managed), and bird communities (e.g., the relative richness of different groups of
181 forest-associated birds), as previously discussed in e.g., [33]. In particular, we predict~~ed~~ that
182 correlations between excavators and ~~other birds~~secondary cavity-nesters would be particularly
183 strong~~, but with relatively shallow regression slopes,~~ in regions with relatively ~~high intensities of~~
184 ~~forest management (vs. unmanaged natural forests) and~~ low overall avian diversity and slow

185 processes of decay-related tree-cavity formation. In such regionsthese predominantly temperate
186 and boreal regions, particularlysuch as the Nearctic and Palearctic, relationships between
187 excavators and other forest birdsand secondary cavity-nesters would be that are driven by mutual
188 associations with particular forest elements butwould be enhanced by direct interactions through
189 the provision of nest cavities, as a lack of available decay-formed cavities may increase the
190 dependence of secondary-cavity nesters on excavated cavities. We predicted relatively shallow
191 regression slopes in these regions (Nearctic, Palearctic), as there is a relatively low ratio between
192 the numbers of excavators and secondary-cavity nesters [11]. In contrast, fFor regions that
193 largely span the tropics, such as the Neotropics, Afrotropics, and Oriental regions, we also
194 predictedpredict weaker, though still positive, correlations between excavators and secondary
195 cavity-nestersother forest birds, but asas these relationships would be driven mainly by mutual
196 associations with particular forest elements and less by direct interactions through the provision
197 of nest cavities—decay-formed cavities being more pr⬚ent here. As a result, we also predict
198 that relationships between excavators and secondary cavity-nesters ⬚ stronger than those
199 between excavators and non-cavity-nesting forest birds (specialists or generalists) in the Nearctic
200 and Palearctic, but that there is no such clear pattern in of differences in strength of correlations
201 for the tropical regions. For Australasia, where the largest group of excavators (woodpeckers) is
202 notably absent, we predict relationships between the present excavators, often weaker excavators
203 that require softer or rotting wood (see [11] for species), and other groups of birds to be
204 relatively weak and to be solely based on certain shared habitat preferences. Finally, for all
205 regions, we predict that relationships between excavators and secondary cavity-nesters and
206 between excavators and forest specialists ⬚ stronger than those between excavators and forest
207 generalists, as the latter group includes species that are unlikely to have either direct interactions
208 or mutually shared habitat preferences with excavators. In fact, many generalist forest birds may
209 have traits (e.g., ground-nesting behaviour and a preference for early-successional forests with
210 small trees ⬚]) that can lead to habitat requirements opposite from those required by
211 exc⬚tors.　— we predicted these correlations to be weaker. However, as these regions are
212 more diverse, we also predicted that there would be relatively higher numbers of forest birds per
213 excavator, resulting in steeper regression slopes.

214

215 **Material and Methods**
216 We used published global distribution maps of tree-cavity nesting birds [11] and forest birds
217 [410] to extract richness estimates per 10×10 km grid cell (Table 1). Maps for both tree-cavity
218 nesters and forest birds were based on the same species range maps provided by BirdLife
219 International and NatureServe [421]. We selected and classified focal bird species following [11,
220 410] as 1) excavators (species that are known to often or always excavate their own nesting
221 cavities), 2) secondary cavity-nesters: birds which are known to nest in tree cavity but which
222 never or rarely excavate their own cavity, 3) forest specialists: birds that exclusively use forest
223 habitat, and 4) for⬚birds: birds that use forest habitat but also at least one other type of habitat.
224 We note that some species were counted in more than one category (e.g., a species that is a
225 'forest specialist' is per definition also coun⬚as a 'forest bird'). However, excavators were
226 never counted in any other category.
227 　　　We used only range polygons where a species' presence was classified as 'Extant' or
228 'Probably extant', and assigned 'presence' to all grid cells that overlapped with range polygons.
229 Next, we created generalized least squares (gls) models to assess the linear relationships between
230 excavators and other categories of forest-associated birds. To take biogeographical differences

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231 into account, we proceeded to separate trends across the globe, and created gls models for the six
232 zoographic regions separately: Nearctic, Palearctic, Neotropical, Afrotropical, Oriental, and
233 Australasia. We did not restrict our analyses to forested regions, wanting to avoid making
234 subjective decisions on the classification of a grid cell to a specific vegetation/habitat type. Yet,
235 to make sure we did look for possible relationships between these forest-associated species in
236 regions they actually occur, we removed cells with zero excavators/woodpeckers and cells where
237 the numbers of secondary cavity-nesters, forest specialists, or all forest birds were lower than
238 that of excavators/woodpeckers from further analyses.
239      Our data were spatially structured (i.e., high and low richness of birds in different
240 categories (excavators etc.) was spatially clustered) across and within zoogeographic regions, as
241 demonstrated by the global distribution of the relative number of cavity excavators to non-
242 excavating cavity-nesting birds (expressed as the ratio of excavator / non-excavating cavity-
243 nester; Fig. 1). Thus, we followed similar protocols to adjust for spatial autocorrelation as per
244 Storch et al. [432]. This implied the use of gls models with excavator richness as a predictor
245 variable, the richness of one of the categories of forest-associated birds as a response variable,
246 and a variable exponential spatial covariance structure, as these models had the best fit in
247 preliminary tests, which reduced—rather than eliminated—the influence of spatial
248 autocorrelation on our models. In these tests, exponential gls models consistently had the lowest
249 Akaike's Information Criterion (AIC) value compared to a set of models, including an ordinary
250 least squares model with no spatial structure, and gls models with Gaussian, linear, rational
251 quadratics and spherical spatial covariance structures.
252      Even though gls models work well with large datasets, we found that gls models fitted on
253 all data failed to converge (using the R package "nlme" [443]). To circumvent this computational
254 problem, we first grouped grid cells by zoogeographic region. We thereafter ran 1000 models on
255 bootstrap permutations of 1000 randomly selected grid cells (see [24, 454]). Of these 1000 model
256 iterations, we subsequently calculated the mean (±SD), minimum and maximum coefficients of
257 the regression slope. As gls models do not provide a measure of the strength of relationships, we
258 proceeded with a different measure of the strength of each correlation: fitting each exponential
259 gls model to a different, non-overlapping, test data set of 1000 randomly selected grid cells. We
260 then proceeded to calculate the Spearman rho coefficient of the correlation between predicted
261 and observed data, for all 1000 models per zoogeographic region. Finally, we calculated the
262 mean Spearman rho of all significant models per zoogeographic region. We repeated all of these
263 analyses for woodpeckers as a subset of the excavators, with the notable exception of analyses
264 for Australasia where woodpeckers are absent. All data, R scripts, and initial results needed to
265 reproduce our analyses presented here are deposited online (Appendix S1).
266

**Results**
268 Using gls modelling to assess the global patterns for the relationships between excavator richness
269 and that of secondary cavity-nesters, forest specialists, and all forest birds, we found positive
270 relationships between all pairs of comparisons. However, these relationships differed in relative
271 strength and characteristics (e.g., steepness of regression slope) -depending on the group of birds
272 and zoogeographic region analysed (Fig. 2, Table 21; see Table S1 for an overview of the
273 number of species per group per region)).
274      In terms of variation across zoogeographic regions, the relationships between excavators
275 and all other groups of forest-associated birds were typified by particularly steep regression
276 slopes in the Neotropics, where the presence of one additional excavator species in a grid cell

277 ~~implied an increase of more than two additional secondary cavity-nesters, ten forest bird species,~~
278 ~~or four forest specialists. In contrast, regression slopes were less steep in predominantly~~
279 ~~temperate and boreal regions such as the Nearctic and Palearctic, where an increase of one~~
280 ~~excavator species signified an increase of approximately one secondary cavity-nester species,~~
281 ~~four to five forest birds, or one forest specialist. More importantly, and similar to variation in the~~
282 ~~slopes of the regressions, we found differences in the strength (as represented by Spearman's~~
283 ~~rho) of these relationships, with aga~~We found~~in~~ stronger relationships (higher Spearman rho) in
284 the predominantly tropical Afrotropical, Oriental, and Neotropical regions than in the
285 comparably more temperate/boreal Nearctic and Palearctic regions, and particularly weak
286 relationships in Australasia ~~(Table 1)~~.

287 ~~Although t~~The relationships between excavators and the other three groups of cavity-
288 nesting and forest-associated birds were generally similar in nature (positive), without clear
289 evidence for our prediction that the relationship between excavators and other cavity-nesters
290 would be stronger than that between excavators and ~~larger groups of forest-associated birds that~~
291 ~~include~~ non-cavity-nesters (forest specialists or all forest birds). Instead, we found that ~~there~~
292 ~~were some~~ differences in the relative strength of these relationships (between excavators and the
293 three groups of forest-associated birds) ~~differed~~ largely across zoogeographic regions. For
294 example, excavator richness was a particularly strong predictor of secondary cavity-nester
295 richness and of all forest birds in the Oriental region (rho = 0.8~~and 0.86, respectively~~), and
296 slightly less so for forest specialists (rho = 0.72~~7~~), whereas excavator richness in the Afrotropics
297 showed a strong relationship with forest specialists (rho = 0.83), forest generalists (rho = 0.91)
298 and all forest birds taken together (rho = 0.93~~4) and with forest specialists (rho = 0.88~~), but a
299 somewhat weaker association with secondary cavity-nesters (rho = 0.79). Finally, we note that
300 excavators in ~~Nevertheless, despite the complete absence of woodpeckers from~~ Australasia
301 (which include no woodpeckers) showed a moderately strong~~this region, we did find a weak~~ (rho
302 = 0.73~~69) but often~~and significant (p < 0.05 in 100~~97~~ percent of model iterations) positive
303 relationship ~~between richness of excavators and~~with forest specialists, and none with secondary
304 cavity-nesters or more generalist forest bird~~s~~.

305 We repeated all analyses for woodpeckers as a subset of excavators and found nearly
306 identical results, which is why we opted to list results of these analyses in supplementary Table
307 S2 and limit our further discussion of these analyses. ~~with again significant positive relationships~~
308 ~~between woodpeckers and other groups of cavity-nesting or forest-associated birds in all regions~~
309 ~~but Australasia, and with steeper regression slopes and stronger relationships in the~~
310 ~~predominantly tropical Neotropical, Oriental and Afrotropical regions as compared to more~~
311 ~~shallow slopes and weaker associations in the Nearctic and Palearctic (Table 2). The relative~~
312 ~~strength of the relationships between woodpeckers and the three other groups of cavity-nesting~~
313 ~~and forest-associated birds again depended on the zoogeographic region (in similar ways as for~~
314 ~~entire group of excavators) such that woodpeckers were strong predictors of the richness of other~~
315 ~~birds as excavators in general, with the notable exception of Australasia. Nevertheless, despite~~
316 ~~the complete absence of woodpeckers from this region, we did find a weak (rho = 0.69) but~~
317 ~~often significant (p < 0.05 in 97 percent of model iterations) positive relationship between~~
318 ~~richness of excavators and forest specialists.~~

319

320 **Discussion**
321 We found strong positive relationships between excavators~~/woodpeckers~~ and secondary cavity-
322 nesters, forest specialists, forest generalists and forest birds in general and ~~forest specialists~~ at

global and zoogeographic scales, although these relationships differed in both strength and characteristics (regression slopes) across zoogeographic regions. Moreover, we found that it depended on the region whether relationships between excavators and secondary cavity-nesters were stronger or weaker than those between excavators and non-cavity-nesting forest birds. This indicates that both direct facilitation of nest-cavities and indirect associations with forest elements and shared habitat preferences are likely to play a role in shaping these relationships, but that the relative importance of both depends on the region under consideration. Our results imply that excavators and woodpeckers (a predominant subset of excavators) hold potential as indicators and management surrogates across most of the world [465], with the possible exception of the Australasian region, but also that we need to take differences among zoogeographic regions (e.g., in the composition of local and regional nest-webs with regards to the relative numbers of excavators and secondary cavity-nesters as seen in Fig. 1) into account if we are to adopt these as surrogates for conservation or management.

Many excavators, woodpeckers included, have strong preferences for specific forest elements, such as dead and decaying trees or particularly large trees (see e.g., [28]). In turn, these elements, and the processes that drive their presence and abundance, are of great importance to habitat formation and create additional niche space to support many groups of organisms [46]. Therefore, we can expect that forests that meet the habitat requirements of excavators (e.g., certain levels of availability of decaying and dead wood) provide high-quality habitat for many other wildlife species. This may explain the higher richness of forest birds in areas occupied by high numbers of excavators/woodpeckers. For non-excavating species that utilize tree-cavities for their nests, this relationship may be enhanced by the fact that excavators/woodpeckers create or facilitate potential nest substrates [31]. In other words, the strong habitat preferences of many excavators/woodpeckers, as well as the facilitatory role excavators play in providing nest substrates, make these birds potentially effective indicators of many forest-associated species and, by extension, of high-quality forests (i.e., natural, old-growth; [17, 18].

We did not find support for the prediction that relationships between excavators and secondary-cavity nesters are relatively stronger than those between excavators and secondary cavity-nesters in temperate and boreal regions (Nearctic and Palearctic), which would reflect the additional importance of cavity facilitation in these regions, nor that the reverse was true in all predominantly tropical regions. In general, we would predict excavated cavities to be less important for secondary-cavity nesters in the tropics as high rates of precipitation and temperature lead to relatively rapid formation of cavities through fungal activity [54] and lower persistence (i.e., longevity) of excavated cavities [33,55]. This, in turn, should lead to relatively higher use of decay-formed cavities by secondary cavity-nesters in the tropics [33, 55], and less dependence on excavators for the supply of nest-cavities. For example, even woodpeckers, occasionally use decay-formed cavities in Neotropical temperate rainforests where tree decay is the key driver of nest-web structure [55]. Indeed, we see that the relationship between excavators and secondary cavity-nesters is not stronger (Neotropics) or even weaker (Afrotropics) than those between excavators and non-cavity-nesting forest birds (specialists or generalists), in two of the more tropical regions. But we also found that the relationship between excavators and secondary cavity-nester was relatively strong in the Oriental region, stronger in fact than those between excavators and any other group of forest birds. This may be the result of the specific characteristics of the forests or avifaunal communities in this region, but is also likely to be influenced by relatively high logging rates in the Oriental region. Logging reduces the availability of large dead trees, which in turn diminishes substrate availability for excavators as

369 well as the opportunity for cavities to form via decay [1], potentially making secondary cavity-
370 nesters more dependent on excavated cavities. In contrast to our predictions, relationships
371 between excavators and secondary cavity-nesters and between excavators and forest specialists
372 were not necessarily stronger (though this was the case in the Neotropical region) than those
373 between excavators and forest generalists. We do not have a clear explanation for this finding,
374 though we argue that forest specialists are not necessarily closer linked than forest generalists to
375 forest elements (e.g., snags) also preferred by excavators and that both forest generalists and
376 excavators might share landscapes where forest specialists are hard to find, for example open
377 landscapes with scattered trees [2]. Finally, we found that regardless of the relationship, all
378 relationships between excavators and other bird groups were stronger in the more tropical
379 (especially the Afrotropical and Neotropical) regions, with the exception of Australasia (see
380 below), than in the temperate and boreal regions. Arguably, excavators are particularly strong
381 indicators of other bird groups in these tropical regions as these regions still contain vast tracts of
382 unlogged and unmanaged forest, a topic for further research.

383 Relationships between excavators and groups of all groups of forest-associated birds
384 were less evident in Australasia, which is a region that differs largely from all others in both
385 avifauna (e.g., there are no woodpeckers here but there is a relatively high richness of cavity-
386 nesters [11]) and forest structure and dynamics (e.g., cavity densities in Australasian forests are
387 among the highest globally [54]). Specifically, we found a moderately strong relationship
388 between excavators and non-cavity-nesting forest specialists in Australasia, but no such
389 relationships between excavators and secondary-cavity nesters or forest birds with broader
390 habitat requirements (i.e., forest generalists). This, we reason, indicates that the excavators in this
391 region (which notably excludes woodpeckers) show a preference for forest conditions (e.g., the
392 provision of trees that are in advanced stages of decay, given that many of these excavators are
393 weaker excavators that require softer or rotting wood; see [11] for species) that are shared by
394 many forest specialists. In contrast, secondary cavity-nesters in Australasia may depend on
395 elements not formed, or particularly required, by excavators (e.g., large trees of a certain age [3]
396 that contain many dead branches and have accumulated multiple decay-formed cavities [4]).

397 [2]We detected relative differences in strengths among the relationships between
398 excavators/woodpeckers and secondary cavity-nesters, forest birds, and forest specialists across
399 zoogeographic regions. These differences were most likely to stem from the same variation
400 among species and ecosystem characteristics discussed above (e.g., the distribution and relative
401 importance of cavity-forming agents), and indicate that richness of excavators/woodpeckers may
402 be a better indicator of richness of other cavity and forest-associated species in one region than in
403 another. In addition, the relative strength of relationships between excavators and other forest
404 birds might reflect whether excavators are indicative of the richness of other species due to
405 shared associations with particular forest elements (indirect association), due to their direct
406 facilitation of nest cavities (direct facilitation), or whether both factors play a role. For example,
407 we found that relationships between excavator and forest bird or forest specialist richness in the
408 Afrotropics are relatively strong, whereas the relationship between excavators and secondary
409 cavity-nesters is comparatively weaker. This might indicate that, in the Afrotropics, excavators
410 are especially strong predictors of other groups of forest-associated birds through their mutual
411 habitat requirements, rather than through their direct facilitation of tree-cavities. In contrast,
412 excavators are relatively stronger predictors of secondary cavity-nesters in the Oriental region,
413 which might lead to hypotheses that excavators play a more direct, nest-web structuring role
414 through the provision of cavities in the Oriental region.

9

415     Beyond variation in the strength of relationships between regions we also found that
416 regressions differed in slopes, both across regions and across the different relationships tested.
417 For example, t~~T~~he steep slopes we found for correlations between excavators/~~woodpeckers~~ and
418 ~~other~~ non-cavity-nesting forest birds in the ~~predominantly tropical~~ Neotropical region~~s~~
419 ~~(Neotropics, Oriental, Afrotropical)~~ contrast with~~to~~ more shallow slopes in the temperate/boreal
420 Palearctic and Nearctic regions ~~(Palearctic, Nearctic)~~. And, within the Neotropical region, the
421 relationship between excavators and secondary cavity-nesters showed shallower slopes than that
422 between excavators and non-cavity-nesting forest birds. These differences mainly in slopes
423 mainly reflect differences in richness between regions and between group of forest birds, with
424 relatively steeper slopes representing a relatively larger increase in richness of a particular group
425 of birds per increase in the number of excavators. In turn, we may look at m ~~M~~acro-scale
426 processes (e.g., as outlined by Gaston [48~~7~~]), such as speciation events, ~~are likely to account for~~
427 ~~some of these differences among zoogeographic regions. First, the~~that drive these differences in
428 overall richness of birds [49~~8~~], including cavity-nesting birds [11], and other possible factors
429 (e.g., ~~also of~~ trees as potential substrates for cavities may also differ across regions [50,49]). ~~,~~
430 ~~differs both among and within zoogeographic regions, likely inducing differences in tree-cavity-~~
431 ~~nesting assemblages [33].~~
432
433     ~~However, variation in species composition and associated variation in functional richness~~
434 ~~(i.e., the variety of functional traits varies across spatial and environmental gradients, as has been~~
435 ~~shown, for example, for dietary guilds [44]), is likely to contribute most to spatial variation in~~
436 ~~nest-web assemblages across global scales. Specifically, with regards to nest-webs, species with~~
437 ~~the ability to excavate cavities are not randomly distributed across the world. For example, the~~
438 ~~Australasian region lacks the presence of Piciformes, the Order to which nearly 75% of~~
439 ~~excavators belong [11], whereas speciation processes have led to a relatively high diversity of~~
440 ~~Piciformes in Southeast Asia [50, 51].~~
441     ~~The observed spatial variation in the relationships between excavators and other forest~~
442 ~~birds within zoogeographic regions may stem mainly from local differences in habitat and~~
443 ~~vegetation characteristics (e.g., tree species composition and climatic variables [52]) as well as~~
444 ~~spatial variation in tree cavity availability and their formation agents [53], rather than from~~
445 ~~speciation processes. Such differences would, for example, explain how in the Neotropics,~~
446 ~~cavity-nesting assemblages studied in the temperate mountain forests of Chile [54] had a 1:6~~
447 ~~ratio of excavators (4 species) to secondary cavity-nesters (25 species) whereas a subtropical~~
448 ~~Atlantic moist forest [32] supported relatively higher numbers of excavators with a 1:3 ratio of~~
449 ~~excavators (9 species) to secondary cavity-nesters (25 species). An important factor to consider~~
450 ~~here is the potential for regional variation in cavity substrate availability (e.g., large trees) and~~
451 ~~the supply of decay-formed cavities due to differences in the onset and rate of decay processes as~~
452 ~~well as forest management (e.g., [55-57]. For example, retention of large trees can, in many~~
453 ~~forests, provide nesting and roosting opportunities for additional species as both opportunities for~~
454 ~~excavation and processes of decay become more prevalent.~~
455     ~~In addition, we can hypothesize that at least some variation at regional scales stems from~~
456 ~~differences in the propensities for re-use of excavated cavities by secondary cavity-nesters. For~~
457 ~~example, there are signs that non-excavating cavity-nesters may experience higher predation risk~~
458 ~~in excavated versus decay-formed cavities, which may induce a preference for decay-formed~~
459 ~~cavities among secondary users if decay-formed cavities are in sufficient supply (e.g., a pattern~~
460 ~~found in some of the few unmanaged temperate forests in the European parts of the Palearctic;~~

461 [58, 59]). In turn, the availability of decay-formed cavities may correspond to the
462 aforementioned historical or current forest management practices as well as spatial patterns in
463 climatic factors. For example, proportions of decay-formed cavities used are particularly high in
464 parts of the world with high amounts of precipitation and more active regimes of fungal growth
465 (e.g., most of the wet tropics), with both being lower in anthropogenically-disturbed landscapes
466 than in primary forests [53]. In turn, high availability of decay-formed cavities might allow for a
467 relatively high richness of secondary cavity-nesters, with fewer species dependent on excavators
468 for the supply of nest-cavities. For example, even woodpeckers, commonly considered primary
469 excavators, occasionally use decay-formed cavities in Neotropical temperate rainforests where
470 tree decay is the key driver of nest-web structure [54].
471         Finally, we find that relatively higher numbers of secondary cavity-nesters, or cavity-
472 nesters in general, may occur in regions where many species are habitat generalists that utilize
473 other nest substrates than tree-cavities (e.g., 40% of cavity nesters in Neotropical temperate
474 forests are facultative users of tree cavities for nesting [54]), as compared to regions where most
475 cavity nesters are obligate tree-cavity users (e.g., over 85% of cavity nesters in temperate
476 Nearctic forests [59]). Finally, it is worth noting that cavity availability and use are also likely to
477 be influenced by cavity persistence (longevity), a characteristic that can have considerable spatial
478 variation due to factors such as land-use patterns (e.g., logging), climatic factors (e.g., rainfall),
479 and cavity characteristics (e.g., whether they are located in live or dead trees [60-62]).
480         We detected relative differences in strengths among the relationships between
481 excavators/woodpeckers and secondary cavity-nesters, forest birds, and forest specialists across
482 zoogeographic regions. These differences were most likely to stem from the same variation
483 among species and ecosystem characteristics discussed above (e.g., the distribution and relative
484 importance of cavity-forming agents), and indicate that richness of excavators/woodpeckers may
485 be a better indicator of richness of other cavity and forest-associated species in one region than in
486 another. In addition, the relative strength of relationships between excavators and other forest
487 birds might reflect whether excavators are indicative of the richness of other species due to
488 shared associations with particular forest elements (indirect association), due to their direct
489 facilitation of nest cavities (direct facilitation), or whether both factors play a role. For example,
490 we found that relationships between excavator and forest bird or forest specialist richness in the
491 Afrotropics are relatively strong, whereas the relationship between excavators and secondary
492 cavity-nesters is comparatively weaker. This might indicate that, in the Afrotropics, excavators
493 are especially strong predictors of other groups of forest-associated birds through their mutual
494 habitat requirements, rather than through their direct facilitation of tree-cavities. In contrast,
495 excavators are relatively stronger predictors of secondary cavity-nesters in the Oriental region,
496 which might lead to hypotheses that excavators play a more direct, nest-web structuring role
497 through the provision of cavities in the Oriental region.
498         Some secondary cavity-nesters might use cavities created by multiple excavator species,
499 whereas others predominantly use cavities formed by processes of degradation, damage or insect
500 activity [31, 32, 39]. In addition, certain excavators might be especially abundant or provide
501 cavities that are very commonly reused by several species, whereas others are scarce and leave
502 only a few short-lived cavities that would not be generally available for use by secondary cavity-
503 nesters. Given such complexities among nest-web interactions, it is important to emphasize that
504 we present general global patterns in the composition of tree-cavity-using assemblages (i.e.,
505 communities of linked species that often interact within networks). We lack evidence for direct

11

506 ~~causal links between the presence of one species group with another, as well as direct evidence~~
507 ~~of species interactions at the zoogeographic regional scale.~~
508       Around <u>most of</u> the world, we found <u>strong and positive</u> relationships ~~of a universal~~
509 ~~nature (strong and positive)~~ between excavator and forest bird richness. As such, we deem
510 excavators~~, of which woodpeckers are an important subset,~~ to be useful indicator species for
511 forest bird diversity at ~~multiple~~ <u>broad</u> spatial scales<u>, as was previously proven at stand- and</u>
512 <u>landscape-scales</u>. They form a small and fairly easy to identify (even by citizen scientists) subset
513 of a larger group of species (forest birds) often studied to understand the effects of anthropogenic
514 disturbances. <u>Moreover, many woodpeckers respond to playbacks, which may therefore become</u>
515 <u>an effective survey tool that allows researchers to fairly easily cover relatively large areas (e.g.,</u>
516 <u>[64]).</u> Studies of excavators ~~(or woodpeckers specifically)~~, especially in high biodiversity
517 tropical regions, might provide quick measures of forest quality and biodiversity, which may in
518 turn guide forest management decisions (e.g., improving the retention of large trees). A
519 comprehensive study of all forest birds in some regions like the Amazon or Congo basin <u>(where,</u>
520 <u>notably, there are hotspots of woodpecker richness [65])</u> would require considerable local
521 expertise and training, which is often difficult to achieve due to social and monetary limitations.
522 Thus, we conclude, excavators have excellent potential as study subjects for conservation
523 monitoring and planning initiatives, in comparative research, and to guide the establishment of
524 region-wide forest conservation strategies, especially in the largely understudied tropical regions
525 of the world.
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**Table 1. Species richness for forest-associated bird groups found in each of six zoogeographic regions.** In parenthesis the maximum number of species of each group found in a single 10×10 km grid cell in each region.

| Zoographic region | Excavators | Secondary cavity-nesters | Forest specialists[1] | Forest generalists[1] | All forest birds (specialists + generalists)[1] |
|---|---|---|---|---|---|
| Nearctic | 42 (16) | 111 (41) | 93 (36) | 365 (111) | 458 (140) |
| Palearctic | 67 (23) | 181 (58) | 155 (65) | 725 (221) | 880 (276) |
| Oriental | 120 (35) | 241 (67) | 463 (79) | 958 (238) | 1421 (300) |
| Neotropical | 173(36) | 373 (114) | 1078 (200) | 1764 (277) | 2842 (436) |
| Afrotropical | 78 (33) | 218 (68) | 220 (60) | 911 (287) | 1131 (331) |
| Australasia | 14 (7) | 178 (70) | 442 (67) | 1014 (190) | 1456 (226) |

[1]Note: these numbers do not include secondary cavity-nesters.

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**Table 21. Results of generalized least square models of possible correlations between (1) excavator and secondary cavity-nester richness, (2) excavator and forest specialist bird richness, (3) excavator and forest generalistspecialist richness, (4) excavator and forest bird (specialists and generalists) richness.** Each result reflects the mean outcome of 1000 models d with 1000 randomly selected grid cell data points that include an exponential spatial covariance structure. The mean Spearman rho was calculated over the fit of each of 1000 models to a test data set.

| Zoogeographic region | Correlation | Mean Slope (Min. – Max.; SD) | % of models with p < 0.05 | Mean Spearman rho |
|---|---|---|---|---|
| Nearctic | 1 | 0.8 (0.4 - 1.3; 0.1) | 60 | 0.73 |
| | 2 | 1.04.3 (0.73.3 - 5.91.3; 0.14) | 9763 | 0.7184 |
| | 3 | 3.11.4 (2.01.2 - 1.64.5; 0.41) | 8971 | 0.7671 |
| | 4 | 4.2 (2.7 – 5.7; 0.5) | 94 | 0.81 |

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|---|---|---|---|---|
| Palearctic | 1 | 1.1 (0.7 - 1.4; 0.1) | 84 | 0.78 |
| | 2 | 0.6~~4.9~~ (0.3~~4.0~~ – ~~1.1~~6.7; 0.3~~4~~) | 83~~73~~ | 0.68~~85~~ |
| | 3 | 2.9~~1.1~~ (2.1~~0.8~~ - ~~1.7~~4.1; 0.3~~1~~) | 82~~3~~ | 0.80~~79~~ |
| | 4 | 3.5 (2.6 - 5.4; 0.4) | 88 | 0.80 |
| Oriental | 1 | 0.7 (0.6 - 0.9; 0.0) | 100 | 0.88 |
| | 2 | 1.1~~5.7~~ (0.9~~4.9~~ – ~~1.3~~6.6; 0.1~~3~~) | 100 | 0.72~~86~~ |
| | 3 | 3.5~~1.6~~ (3.0~~1.3~~ – ~~4.0~~1.9; 0.2~~1~~) | 100 | 0.86~~77~~ |
| | 4 | 4.6 (3.9 - 5.5; 0.2) | 100 | 0.83 |
| Neotropical | 1 | 2.4 (1.9 – 3.0; 0.2) | 83 | 0.95 |
| | 2 | 3.5~~10.8~~ (9.1 - 14.0; 0.2~~7~~) | 73~~2~~ | 0.95~~7~~ |
| | 3 | 5.2~~4.2~~ (3.9~~3.4~~ – ~~6.7~~5.2; 0.5~~2~~) | 77~~2~~ | 0.91~~6~~ |
| | 4 | 8.8 (7.1 - 11.0; 0.6) | 84 | 0.96 |
| Afrotropical | 1 | 1.1 (0.7 - 1.9; 0.2) | 76 | 0.79 |
| | 2 | 0.6~~6.8~~ (0.3~~5.0~~ – ~~1.1~~9.8; 0.1~~9~~) | 78~~3~~ | 0.83~~94~~ |
| | 3 | 5.8~~0.9~~ (3.7~~0.6~~ – ~~8.1~~1.5; 0.9~~1~~) | 84~~79~~ | 0.93~~88~~ |
| | 4 | 6.4 (4.3 – 9.2; 0.9) | 87 | 0.93 |
| Australasian | 1 | 1.8 (1.4 - 2.2; 0.1) | 88 | -0.14 |
| | 2 | 1.7~~7.5~~ (0.9~~2.3~~ – ~~2.5~~11.2; 0.3~~1.3~~) | 100 | 0.73~~31~~ |
| | 3 | 9.2~~1.0~~ (7.2~~0.1~~ – ~~11.2~~2.0; 0.6~~3~~) | 96~~7~~ | 0.19~~69~~ |
| | 4 | 11.0 (8.3 – 13.5; 0.8) | 99 | 0.50 |

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**Table 2. Results of generalized least square models of possible correlations between (1) woodpecker and secondary cavity-nester richness, (2) woodpecker and forest bird richness, and (3) woodpecker and forest specialist richness.** Each result reflects the mean outcome of 1000 models build with 1000 randomly selected grid cell data points that include an exponential spatial covariance structure. The mean Spearman rho was calculated over the fit of each of 1000 models to a test data set.

| Zoogeographic region | Correlation | Mean Slope (Min. – Max.; SD) | % of models with $P <$ 0.05 | Mean Spearman rho |
|---|---|---|---|---|
| Nearctic | 1 | 1.0 (0.5 - 1.6; 0.2) | 61 | 0.70 |
| | 2 | 5.3 (3.7 - 8.0; 0.7) | 67 | 0.79 |
| | 3 | 1.7 (1.1 - 2.2; 0.1) | 70 | 0.63 |
| Palearctic | 1 | 1.2 (0.9 - 2.3; 0.1) | 81 | 0.79 |
| | 2 | 5.6 (4.3 - 8.1; 0.6) | 73 | 0.83 |
| | 3 | 1.3 (0.9 - 2.0; 0.2) | 82 | 0.73 |
| Oriental | 1 | 1.0 (0.8 - 1.3; 0.1) | 100 | 0.88 |
| | 2 | 7.9 (6.6 - 9.8; 0.5) | 100 | 0.88 |
| | 3 | 2.2 (1.7 - 2.6; 0.1) | 100 | 0.80 |
| Neotropical | 1 | 3.3 (2.4 - 4.9; 0.4) | 68 | 0.94 |
| | 2 | 14.3 (10.8 - 20.5; 1.6) | 67 | 0.93 |
| | 3 | 5.2 (3.9 - 6.6; 0.5) | 73 | 0.88 |
| Afrotropical | 1 | 1.6 (0.9 - 3.5; 0.4) | 72 | 0.74 |
| | 2 | 9.9 (6.4 - 19.6; 1.9) | 69 | 0.86 |
| | 3 | 1.3 (0.7 - 3.2; 0.3) | 80 | 0.81 |
| Australasian | 1 | 1.9 (-0.1 - 4.4; 0.6) | 81 | -0.33 |
| | 2 | 8.6 (1.2 - 21.8; 2.4) | 75 | -0.30 |
| | 3 | 3.9 (-0.2 – 9.0; 1.2) | 96 | -0.08 |

851

852 **Figure legends**

853

854 **Figure 1.  Global map of the relative richness of tree cavity excavators versus secondary**
855 **cavity-nesting birds (expressed as the ratio excavator / secondary cavity-nester) in 10x10**
856 **km grid cells**.  Low values (light colors) indicate relatively low numbers of excavators as
857 compared to secondary cavity-nesters ~~(or, inversely, relatively high numbers of secondary~~
858 ~~cavity-nesters)~~ while high values (dark colors) indicate a relatively higher proportion of
859 excavators to secondary cavity-nesters.

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861 **Figure 2. Scatter plots of the correlation<u>s</u> between the richness (number of species) of**
862 **excavators and <u>secondary cavity-nesters</u> ~~all forest birds~~ (upper row), ~~all~~ forest specialists**
863 **(<u>second</u>~~middle~~ row), <u>forest generalists (third row)</u> and all non-<u>cavity-nesting forest birds</u>**
864 **(<u>specialists and generalists;</u>~~excavating cavity-nesters~~ (bottom row) in six zoogeographic**
865 **regions.** Points represent species richness values in 10x10 km grid cells, and the solid line
866 represents the fit of a linear regression model, created using all grid cell values. <u>Note that nearly</u>
867 <u>all secondary cavity-nesters are also forest-associated species, but were not included as forest</u>
868 <u>specialists or generalists.</u>

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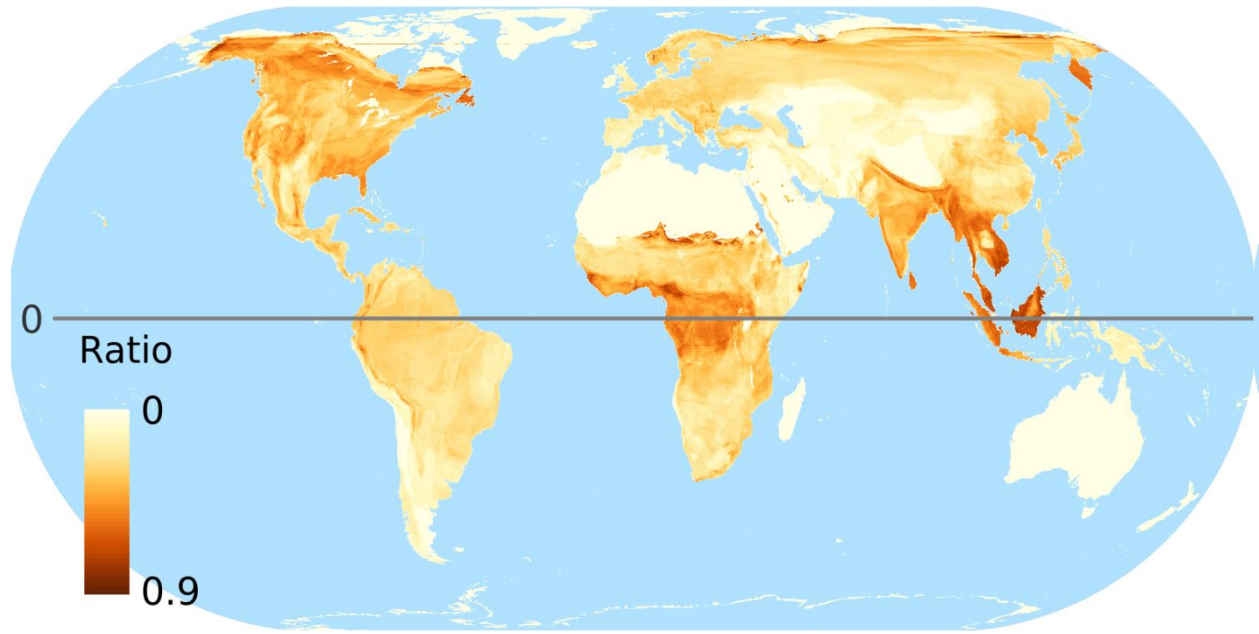
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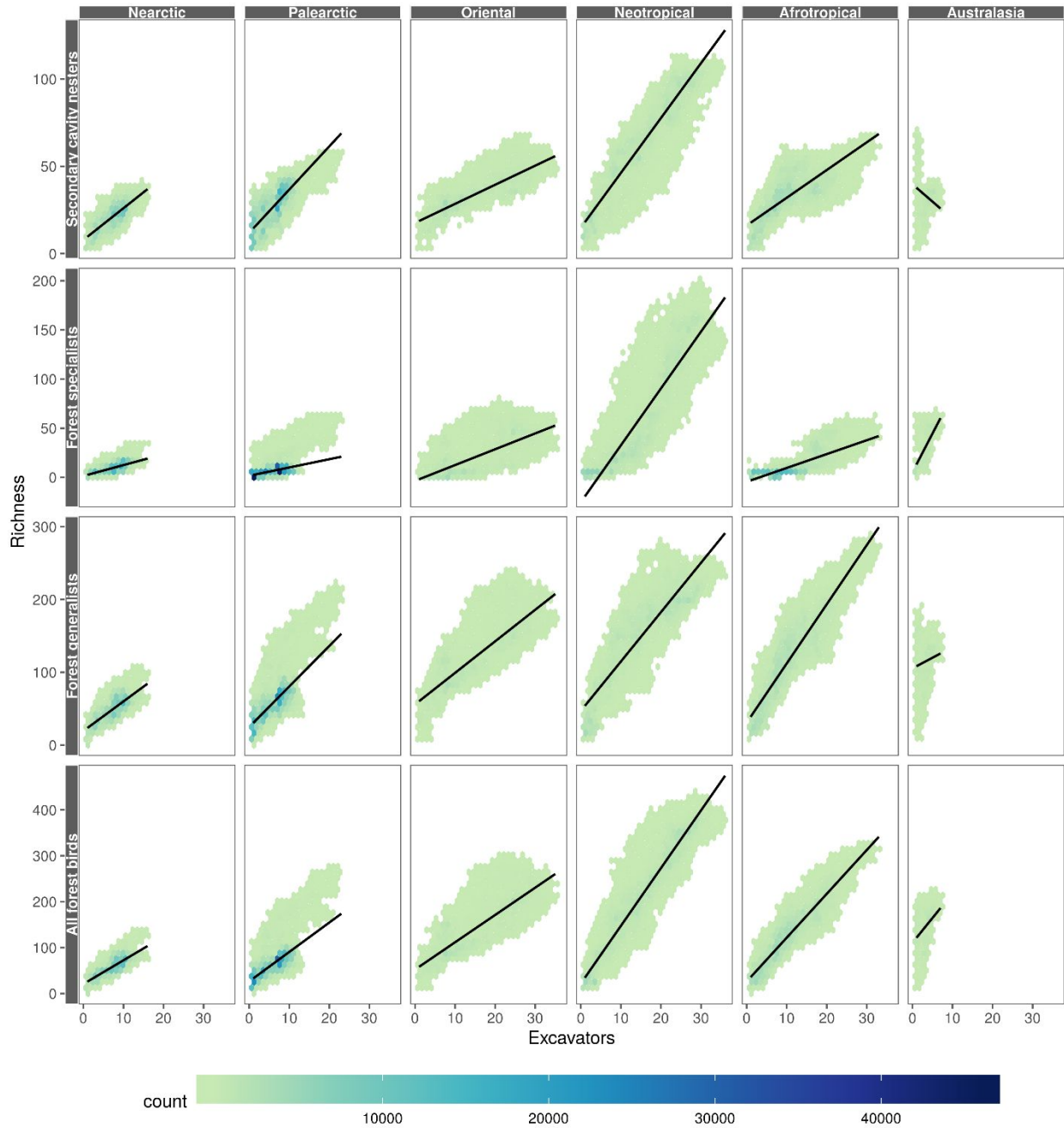890  **Figure 1.**
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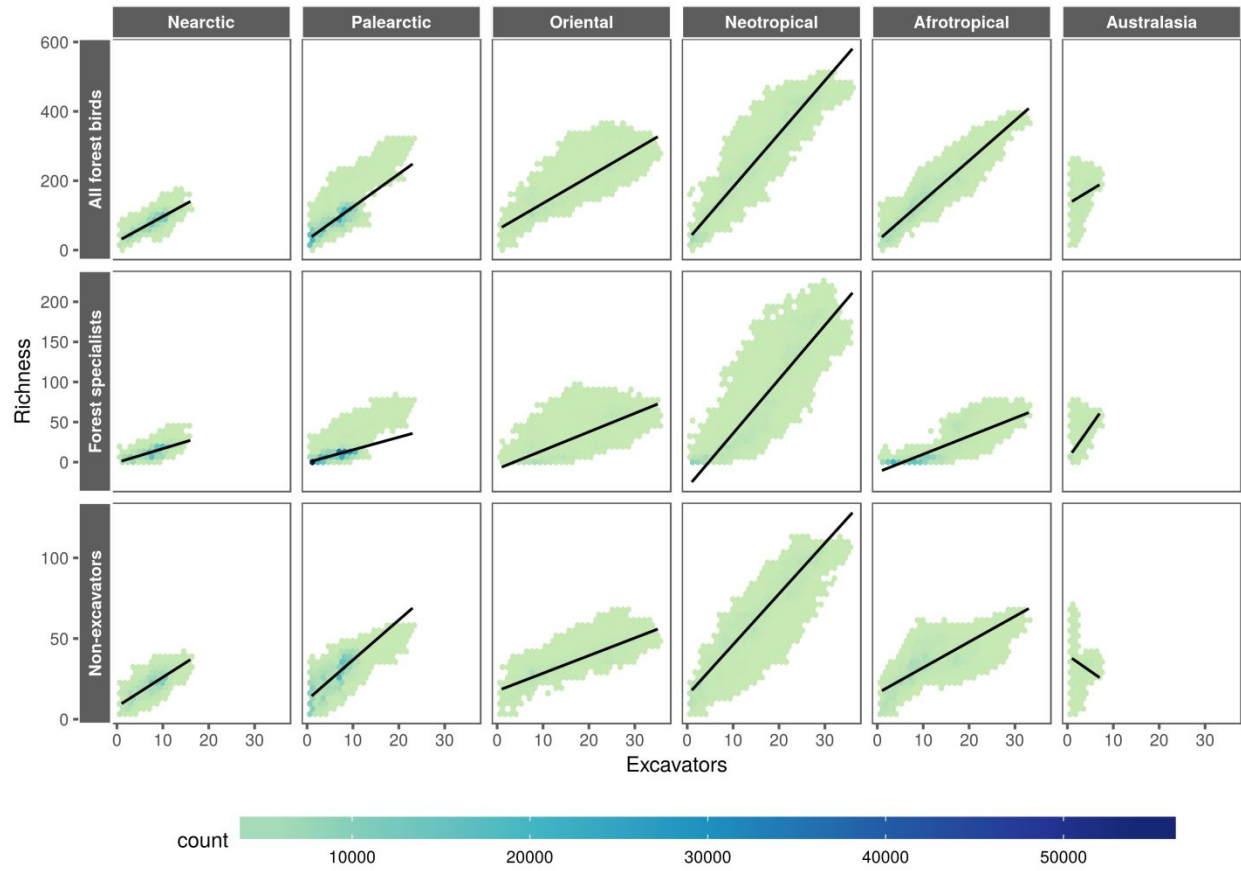
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**Figure 2.**

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3     1     Title: Global relationships between tree-cavity excavators and forest bird richness
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5     3     Running title: Excavator and forest bird relationships
6     4
7     5     Yntze van der Hoek[1,2*], Gabriel V. Gaona[1], Michał Ciach[3] and Kathy Martin[4,5]
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3      47   **Abstract**
4      48   Global monitoring of biodiversity and ecosystem change can be aided by the effective use of
5      49   indicators. Tree-cavity excavators, the majority of which are woodpeckers (Picidae), are known
6      50   to be useful indicators of the health or naturalness of forest ecosystems and the diversity of forest
7      51   birds. They are indicators of the latter due to their associations with particular forest elements
8      52   and because of their role in facilitating the occurrence of other species through the provision of
9      53   nest cavities. Here, we investigated whether these positive correlations between excavators and
10     54   other forest birds are also found at broad geographical scales. We used global distribution maps
11     55   to extract richness estimates of tree-cavity nesting and forest-associated birds, which we grouped
12     56   by zoogeographic regions. We then created generalized least squares models to assess the
13     57   relationships between these groups of birds. We show that richness of tree-cavity excavating
14     58   birds correlates positively with that of all forest birds and cavity-nesters at global scales, but with
15     59   variation across zoogeographic regions. As many excavators are relatively easy to detect, play
16     60   keystone roles at local scales, and are effective management targets, we propose that excavators
17     61   are useful for biodiversity monitoring across multiple spatial scales and geographic regions,
18     62   especially in the tropics.
19     63
20     64   **Keywords**
21     65   Facilitator species, Indicator species, Management surrogates, Secondary cavity-nesting birds,
22     66   Picidae, Species interactions
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**Introduction**

93 Forests worldwide are facing increasing anthropogenic pressures, with both a rapid decline in the
94 surface area of natural forests and a decrease in the naturalness of forests as a result [1, 2]. In
95 turn, these reductions of high-quality forest habitats have led to a loss of forest-associated
96 biodiversity [3-5]. To monitor these changes in forest ecosystems and their denizens, we often
97 look at specialized animals that require the availability of specific habitat structures and
98 processes across long temporal and large spatial scales [6], such as birds that respond not only to
99 a loss in overall forest cover but also to a change in forest health, quality, and integrity [7-10].
100 Excavators such as woodpeckers, barbets, nuthatches, trogons and certain parrot species—among
101 which woodpeckers are the most numerous group [11]—may be especially effective indicators
102 due to their associations with particular forest elements and their role in facilitating the presence
103 of other species through the provision of nest cavities. Indeed, there is empirical evidence that
104 their presence can be indicative of the state of both the forest (e.g., the presence of large trees
105 [12], heterogeneous forest structure [13], or a high level of naturalness [14-18]) as well as the
106 richness and abundance of other forest-associated species [19-21]. However, we may question
107 whether excavators are universally effective indicators, especially of biodiversity, in all
108 geographic regions of the globe or all forest types. For example, excavators are better predictors
109 of richness and abundance of other forest birds residing in deciduous versus coniferous forests of
110 certain parts of hemiboreal Europe [15].
111
112         If relationships between excavators and other forest-associated biota are universally
113 positive in nature, and common not only at stand- and landscape-scales but hold across large
114 geographic regions, then excavators could form a unique group of indicators that may be
115 effective across multiple locations and spatial scales [22]. To find species that are effective as
116 both indicator and management surrogates across multiple regions would be especially useful in
117 the largely understudied tropics where comprehensive biodiversity assessments are costly and
118 logistically challenging [23]. The first signs are promising as the overwhelming majority of tree-
119 cavity excavators are forest or woodland birds and general patterns of woodpecker richness
120 correlate positively with the amount of forest cover at the global scale [24]. Moreover, many
121 excavators are regarded as habitat specialists and tend to have highly specific habitat
122 requirements which are usually met only in forests with high degrees of naturalness and low
123 levels of human-related disturbances (e.g., logging). In fact, restoration efforts have effectively
124 made use of woodpeckers to indicate that restoration has successfully reached a certain level of
125 naturalness [25, 26]. Excavators often utilize large, live or decaying trees, or coarse woody
126 debris, for nesting, roosting, and foraging, and the availability of large amounts of dead wood is,
127 in particular, found to be important [27-30]. As a result, we find that excavators are highly
128 responsive to local changes in forest habitat quantity, quality and the loss of certain forest
129 elements, and may, therefore, be effective indicators of the naturalness of ecosystems (see e.g.,
130 [31]).
131         Excavators are not only reliable indicators of other forest birds occurrence by means of
132 their mutual associations with forest characteristics, but correlations between both groups of
133 birds are also partially determined by species interactions. Taken together, these 'nest-webs' [32]
134 of interacting species are structured by the availability and acquisition of tree-cavities formed by
135 two major processes: 'fungal formation', in which fungi decompose wood over an extended
136 period, or animal excavation [33, 34]. Since most excavators—at least the majority of
137 woodpeckers—excavate a new nest cavity each year, this mode of cavity creation steadily
138 provides a large number of potential sheltered roosting and nesting sites available to secondary-

139  users: both for vertebrates [34] and invertebrates [35, 36], as well as for maintenance of diverse
140  fungal assemblages [37]. As a result, cavity formation by excavation is an important source of
141  nest holes for species in many regions of the world, especially in North America [34]. However,
142  decay-formed cavities have been shown to be more important nest sites in other regions,
143  especially in the tropics [33]. Thus, it is very likely that the relative importance of both processes
144  of cavity formation—and thus the strength of the relationship between excavator richness and
145  secondary cavity-nester richness—varies globally [34]. In addition, excavators can aid in the
146  dispersal of fungi, which in turn enhances processes of wood softening and the formation of
147  decay-formed cavities [38]. It is worth noting that excavators play additional roles (beyond the
148  direct provision of cavities) that may facilitate other species that are not necessarily cavity-
149  nesters. For example, as excavators perforate the bark of trees they may expose insects or sap for
150  other species to forage on [39, 40].
151       Excavators have been shown to be reliable indicators of forest-bird diversity and richness
152  at the stand or landscape-levels [9, 19]. It is unclear if this relationship scales up across larger
153  regions or holds across the globe given indications that interactions between cavity-nesting birds
154  may vary spatially (e.g., [41]) as well as the notion that certain dominant groups of excavators
155  (woodpeckers, in particular) vary in richness across zoogeographic regions [11]. The aim of the
156  present study is to investigate whether there are consistent patterns in the relationships between
157  avian tree-cavity excavators (hereafter: excavators) and species richness of non-excavating tree-
158  cavity nesting birds (hereafter: secondary cavity-nesters), or non-cavity nesting forest birds
159  (forest specialist and generalists species), across the globe. If previously observed relationships
160  between cavity-excavators and other forest birds scale up from local forest stands [17] or
161  ecosystems [19] to zoogeographic or global levels, then this strengthens the potential value of
162  tree cavity-excavators as both indicators and management surrogates.
163       Given the important potential indicator role of excavators in forest ecosystems across the
164  world, we predict a global tendency for richness of secondary cavity-nesters, forest specialists,
165  forest generalists and overall forest birds (specialists + generalists) to increase in correlation with
166  the number of excavators present in the ecosystem, regardless of the ecosystem or location.
167  However, we also predict that the nature (e.g., the strength and slope of correlations) of the
168  relationships between excavators and richness of other forest birds will vary across
169  zoogeographic regions, reflecting differences in forest characteristics (e.g., deciduous vs.
170  coniferous forests), forest management practices (e.g., forests being more or less intensively
171  managed), and bird communities (e.g., the relative richness of different groups of forest-
172  associated birds), some aspects of which are previously discussed by e.g., Cockle et al. [34]. In
173  particular, we predict that correlations between excavators and secondary cavity-nesters would
174  be particularly strong in regions with relatively low overall avian diversity and slow processes of
175  decay-related tree-cavity formation. In such regions predominantly temperate and boreal regions,
176  particularly the Nearctic and Palearctic, relationships between excavators and secondary cavity-
177  nesters would be driven by mutual associations with particular forest elements but enhanced by
178  direct interactions through the provision of nest cavities, as a lack of available decay-formed
179  cavities may increase the dependence of secondary-cavity nesters on excavated cavities. In
180  contrast, for regions that largely span the tropics, such as the Neotropics, Afrotropics, and
181  Oriental regions, we predict weaker, though still positive, correlations between excavators and
182  secondary cavity-nesters as these relationships would be driven mainly by mutual associations
183  with particular forest elements and less by direct interactions through the provision of nest
184  cavities—decay-formed cavities being more prevalent here. Similarly, we also predict that

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185 relationships between excavators and secondary cavity-nesters are stronger than those between
186 excavators and non-cavity-nesting forest birds (specialists or generalists) in the Nearctic and
187 Palearctic, but that there is no such clear pattern of differences in strength of correlations for the
188 tropical regions. For Australasia, where the largest group of excavators (woodpeckers) is notably
189 absent, we predict relationships between the present excavators, often weaker excavators that
190 require softer or rotting wood (see [11] for species), and other groups of birds to be relatively
191 weak and to be based mainly on certain shared habitat preferences. Finally, for all regions, we
192 predict that relationships between excavators and secondary cavity-nesters and between
193 excavators and forest specialists are stronger than those between excavators and forest
194 generalists, as the latter group includes species that are unlikely to have either direct interactions
195 or mutually shared habitat preferences with excavators. In fact, many generalist forest birds may
196 have traits (e.g., ground-nesting behaviour and a preference for early-successional forests with
197 small trees [41]) that can lead to habitat requirements opposite from those required by
198 excavators.
199

**Material and Methods**
201 We used published global distribution maps of tree-cavity nesting birds [11] and forest birds [42]
202 to extract richness estimates per 10×10 km grid cell (Table 1). Maps for both tree-cavity nesters
203 and forest birds were based on the same species range maps provided by BirdLife International
204 and NatureServe [43]. We selected and classified focal bird species following [11, 42] as 1)
205 excavators (species that are known to often or always excavate their own nesting cavities), 2)
206 secondary cavity-nesters: birds which are known to nest in tree cavity but which never or rarely
207 excavate their own cavity, 3) forest specialists: birds that exclusively use forest habitat, and 4)
208 forest birds: birds that use forest habitat but also at least one other type of habitat. We note that
209 some species were counted in more than one category (e.g., a species that is a 'forest specialist'
210 is per definition also counted as a 'forest bird'). However, excavators were never counted in any
211 other category.
212     We used only range polygons where a species' presence was classified as 'Extant' or
213 'Probably extant', and assigned 'presence' to all grid cells that overlapped with range polygons.
214 Next, we created generalized least squares (gls) models to assess the linear relationships between
215 excavators and other categories of forest-associated birds. To take biogeographical differences
216 into account, we proceeded to separate trends across the globe and created gls models for the six
217 zoographic regions separately: Nearctic, Palearctic, Neotropical, Afrotropical, Oriental, and
218 Australasia. We did not restrict our analyses to forested regions, wanting to avoid making
219 subjective decisions on the classification of a grid cell to a specific vegetation/habitat type. Yet,
220 to ensure we looked for possible relationships between these forest-associated species in regions
221 they actually occur, we removed cells with zero excavators and cells where the numbers of
222 secondary cavity-nesters, forest specialists, or all forest birds were lower than that of excavators
223 from further analyses.
224     Our data were spatially structured (i.e., high and low richness of birds in different
225 categories (excavators etc.) was spatially clustered) across and within zoogeographic regions, as
226 demonstrated by the global distribution of the relative number of cavity excavators to non-
227 excavating cavity-nesting birds (expressed as the ratio of excavator / non-excavating cavity-
228 nester; Fig. 1). Thus, we followed similar protocols to adjust for spatial autocorrelation as per
229 Storch et al. [44]. This implied the use of gls models with excavator richness as a predictor
230 variable, the richness of one of the categories of forest-associated birds as a response variable,

231 and a variable exponential spatial covariance structure, as these models had the best fit in
232 preliminary tests, which reduced—rather than eliminated—the influence of spatial
233 autocorrelation on our models. In these tests, exponential gls models consistently had the lowest
234 Akaike's Information Criterion (AIC) value compared to a set of models, including an ordinary
235 least squares model with no spatial structure, and gls models with Gaussian, linear, rational
236 quadratics and spherical spatial covariance structures.
237       Even though gls models work well with large datasets, we found that gls models fitted on
238 all data failed to converge (using the R package "nlme" [45]). To circumvent this computational
239 problem, we first grouped grid cells by zoogeographic region. We thereafter ran 1000 models on
240 bootstrap permutations of 1000 randomly selected grid cells (see [24, 46]). Of these 1000 model
241 iterations, we subsequently calculated the mean (±SD), minimum and maximum coefficients of
242 the regression slope. As gls models do not provide a measure of the strength of relationships, we
243 proceeded with a different measure of the strength of each correlation: fitting each exponential
244 gls model to a different, non-overlapping, test data set of 1000 randomly selected grid cells. We
245 then proceeded to calculate the Spearman rho coefficient of the correlation between predicted
246 and observed data, for all 1000 models per zoogeographic region. Finally, we calculated the
247 mean Spearman rho of all significant models per zoogeographic region. We repeated all of these
248 analyses for woodpeckers as a subset of the excavators, with the notable exception of analyses
249 for Australasia where woodpeckers are absent. All data, R scripts, and initial results needed to
250 reproduce our analyses presented here are deposited online (Appendix S1).
251
252 **Results**
253 Using gls modelling to assess the global patterns for the relationships between excavator richness
254 and that of secondary cavity-nesters, forest specialists, and all forest birds, we found positive
255 relationships between all pairs of comparisons.  However, these relationships differed in relative
256 strength and characteristics (e.g., steepness of regression slope) depending on the group of birds
257 and zoogeographic region analysed (Fig. 2, Table 2). We found stronger relationships (higher
258 Spearman rho) in the predominantly tropical Afrotropical, Oriental, and Neotropical regions than
259 in the comparably more temperate/boreal Nearctic and Palearctic regions, and particularly weak
260 relationships in Australasia.
261       The relationships between excavators and the other three groups of cavity-nesting and
262 forest-associated birds were generally similar in nature (positive), without clear evidence for our
263 prediction that the relationship between excavators and other cavity-nesters would be stronger
264 than that between excavators and larger groups of forest-associated birds that include non-cavity-
265 nesters (forest specialists or all forest birds). Instead, we found that differences in the relative
266 strength of these relationships (between excavators and the three groups of forest-associated
267 birds) differed largely across zoogeographic regions. For example, excavator richness was a
268 particularly strong predictor of secondary cavity-nester richness and of all forest birds in the
269 Oriental region (rho = 0.88), and slightly less so for forest specialists (rho = 0.72), whereas
270 excavator richness in the Afrotropics showed a strong relationship with forest specialists (rho =
271 0.83), forest generalists (rho = 0.91) and all forest birds taken together (rho = 0.93), but a
272 somewhat weaker association with secondary cavity-nesters (rho = 0.79). Finally, we note that
273 excavators in Australasia (which include no woodpeckers) showed a moderately strong (rho =
274 0.73) and significant (p < 0.05 in 100 percent of model iterations) positive relationship with
275 forest specialists, and none with secondary cavity-nesters or more generalist forest birds.

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276    We repeated all analyses for woodpeckers as a subset of excavators and found nearly
277 identical results. We list results of these analyses in supplementary Table S1.
278

279 **Discussion**
280 We found strong positive relationships between excavators and secondary cavity-nesters, forest
281 specialists, forest generalists and overall forest birds at all zoogeographic scales, although these
282 relationships differed in both strength and characteristics (regression slopes) across
283 zoogeographic regions. Moreover, we found that it depended on the region whether relationships
284 between excavators and secondary cavity-nesters were stronger or weaker than those between
285 excavators and non-cavity-nesting forest birds, but that relationships between excavators and
286 non-cavity-nesting forest birds were particularly strong in most regions (e.g., the relationship
287 between excavators and all forest birds was the stronger than that between excavators and
288 secondary cavity-nesters in the Nearctic, Palearctic, Neotropical, and Afrotropical regions). This
289 indicates that the influence of direct facilitation of nest-cavities is likely less important than the
290 indirect associations with forest elements and shared habitat preferences in shaping these
291 relationships, but that the relative importance of both depends on the region under consideration.
292 Our results imply that excavators and woodpeckers (a predominant subset of excavators) hold
293 potential as indicator and management surrogates across most of the world [47], with the
294 possible exception of the Australasian region, but also that we need to take differences among
295 zoogeographic regions into account (e.g., in the composition of local and regional nest-webs with
296 regards to the relative numbers of excavators and secondary cavity-nesters as seen in Fig. 1) if
297 we are to adopt these as surrogates for conservation or management.
298    We did not find support for the prediction that relationships between excavators and
299 secondary-cavity nesters are relatively stronger in temperate and boreal regions (Nearctic and
300 Palearctic), which would reflect the additional importance of cavity facilitation in these regions
301 as compared to more tropical regions. In general, excavated tree cavities are less likely to be used
302 by secondary-cavity nesters in the tropics as high rates of precipitation and temperature lead to a
303 lower persistence (i.e., longevity) of excavated cavities [34] and to the relatively rapid formation
304 of cavities through fungal activity [48]. This, in turn, leads to relatively higher use of decay-
305 formed cavities by secondary cavity-nesters in the tropics [34, 49], and less dependence on
306 excavators for the supply of nest-cavities. For example, even woodpeckers will occasionally use
307 decay-formed cavities in Neotropical temperate rainforests where tree decay is the key driver of
308 nest-web structure [49]. Indeed, we see that the relationship between excavators and secondary
309 cavity-nesters is equally strong (Neotropics) or even weaker (Afrotropics) than those between
310 excavators and non-cavity-nesting forest birds (specialists or generalists), in two of these mainly
311 tropical regions. But we also found that the relationship between excavators and secondary
312 cavity-nester was relatively strong in the Oriental region, stronger in fact than those between
313 excavators and any other group of forest birds. This may be the result of the specific
314 characteristics of the forests or avifaunal communities in this region but may also be influenced
315 by relatively high logging rates in the Oriental region. Logging reduces the availability of large
316 dead trees, which in turn diminishes substrate availability for excavators as well as the
317 opportunity for cavities to form via decay [50], potentially making secondary cavity-nesters
318 more dependent on excavated cavities.
319    In contrast to our predictions, relationships between excavators and secondary cavity-
320 nesters and between excavators and forest specialists were not necessarily stronger (though this
321 was the case in the Neotropical region) than those between excavators and forest generalists. We

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322  do not have a clear explanation for this finding, though we argue that forest generalists and
323  excavators might share landscapes where forest specialists are hard to find, for example in open
324  landscapes with scattered trees [51]. Finally, we found that regardless of the relationship, all
325  relationships between excavators and other bird groups were stronger in the more tropical
326  (especially the Afrotropical and Neotropical) regions, with the exception of Australasia (see
327  below), than in the temperate and boreal regions. Arguably, excavators are particularly strong
328  indicators of other bird groups in these tropical regions as these regions still contain vast tracts of
329  unlogged and unmanaged forests, a topic for further research.
330       Relationships between excavators and all forest-associated bird groups were less evident
331  in Australasia, which is a region that differs largely from all others in both avifauna (e.g., there
332  are no woodpeckers here but there is a relatively high richness of cavity-nesters [11]) and forest
333  structure and dynamics (e.g., cavity densities in Australasian forests are among the highest
334  globally [47]). Specifically, we found a moderately strong relationship between excavators and
335  non-cavity-nesting forest specialists in Australasia, but no such relationships between excavators
336  and secondary-cavity nesters or forest birds with broader habitat requirements (i.e., forest
337  generalists). This could indicate that the excavators in this region (which notably excludes
338  woodpeckers) show a preference for forest conditions (e.g., the provision of trees that are in
339  advanced stages of decay, given that many of these excavators are weaker excavators that require
340  softer or rotting wood; see [11] for species) that are shared by many forest specialists. In
341  contrast, secondary cavity-nesters in Australasia may depend on elements not formed, or
342  particularly required, by excavators (e.g., large trees of a certain age [52] that contain many dead
343  branches and have accumulated multiple decay-formed cavities [53]).
344       Beyond variation in the strength of relationships between regions we also found that
345  regressions differed in slopes, both across regions and across the different relationships tested.
346  For example, the steep slopes we found for correlations between excavators and non-cavity-
347  nesting forest birds in the predominantly tropical Neotropical region contrast with more shallow
348  slopes in the temperate/boreal Palearctic and Nearctic regions. And, within the Neotropical
349  region, the relationship between excavators and secondary cavity-nesters showed shallower
350  slopes than that between excavators and non-cavity-nesting forest birds. These differences in
351  slopes mainly reflect differences in species richness across regions and groups of forest birds,
352  with relatively steeper slopes representing a relatively larger increase in richness of a particular
353  group of birds per increase in the number of excavators. In turn, we may look at macro-scale
354  processes (e.g., as outlined by Gaston [54]), such as speciation events, that drive these
355  differences across regions in overall richness of birds [55], including cavity-nesting birds [11],
356  and other possible factors (e.g., trees as potential substrates for cavities may also differ across
357  regions [56]).
358       In conclusion, we found strong and positive relationships between excavator and forest
359  bird richness around most of the world. As such, we deem excavators to be useful indicator
360  species for forest bird diversity at broad spatial scales, as was previously demonstrated at stand-
361  and landscape-scales. Excavators, especially woodpeckers, form a small and fairly easy to
362  identify (even by citizen scientists) subset of a larger group of species (forest birds) often studied
363  to understand the effects of anthropogenic disturbances. Moreover, many woodpeckers respond
364  to playbacks, which may, therefore, become an effective survey tool that allows researchers to
365  survey relatively large areas fairly readily (e.g., [57]). Studies of excavator presence and
366  abundance, especially in high biodiversity tropical regions, might provide quick measures of
367  forest quality and biodiversity, which may in turn guide forest management decisions (e.g.,

368 improving the retention of large trees). A comprehensive study of all forest birds in some regions
369 like the Amazon or Congo Basin (where, notably, there are hotspots of woodpecker richness
370 [58,59]) would require considerable local expertise and training, which is often difficult to
371 achieve due to social and monetary limitations. Thus, we conclude, excavators have excellent
372 potential as study subjects for conservation monitoring and planning initiatives (see also [59]
373 with regards to woodpecker conservation itself), in comparative research, and to guide the
374 establishment of region-wide forest conservation strategies, especially in the largely
375 understudied tropical regions of the world.

**Ethics statement**

No field data were obtained nor human or animal subjects used for this study.

**Data accessibility**

Supporting data as well as R scripts can be found on The GitLab repository
https://gitlab.com/gavg712/CB_cavity_nesters, the details of which are outlined in Appendix S1.

**Competing interests**

We have no competing interests.

**Authors' contributions**

YH and GVG carried out the data analysis, and led the design of the study and writing of the
manuscript; MC and KM critically revised the manuscript. All authors contribute to the writing
of the final manuscript, gave final approval for publication and agree to be held accountable for
the work performed therein.

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549 **Table 1. Species richness for forest-associated bird groups found in each of six**
550 **zoogeographic regions.** In parenthesis the maximum number of species of each group found in a
551 single $10\times10$ km grid cell in each region.

| Zoographic region | Excavators | Secondary cavity-nesters | Forest specialists[1] | Forest generalists[1] | All forest birds (specialists + generalists)[1] |
|---|---|---|---|---|---|
| Nearctic | 42 (16) | 111 (41) | 93 (36) | 365 (111) | 458 (140) |
| Palearctic | 67 (23) | 181 (58) | 155 (65) | 725 (221) | 880 (276) |
| Oriental | 120 (35) | 241 (67) | 463 (79) | 958 (238) | 1421 (300) |
| Neotropical | 173(36) | 373 (114) | 1078 (200) | 1764 (277) | 2842 (436) |
| Afrotropical | 78 (33) | 218 (68) | 220 (60) | 911 (287) | 1131 (331) |
| Australasia | 14 (7) | 178 (70) | 442 (67) | 1014 (190) | 1456 (226) |

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553 [1]Note: these numbers do not include secondary cavity-nesters.

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**Table 2. Results of generalized least square models of possible correlations between (1) excavator and secondary cavity-nester richness, (2) excavator and forest specialist richness, (3) excavator and forest generalist richness, (4) excavator and forest bird (specialists and generalists) richness.** Each result reflects the mean outcome of 1000 models build with 1000 randomly selected grid cell data points that include an exponential spatial covariance structure. The mean Spearman rho was calculated over the fit of each of 1000 models to a test data set.

| Zoogeographic region | Correlation | Mean Slope (Min. – Max.; SD) | % of models with $P < 0.05$ | Mean Spearman rho |
|---|---|---|---|---|
| Nearctic | 1 | 0.8 (0.4 - 1.3; 0.1) | 60 | 0.73 |
| | 2 | 1.0 (0.7 - 1.3; 0.1) | 97 | 0.71 |
| | 3 | 3.1 (2.0 - 4.5; 0.4) | 89 | 0.76 |
| | 4 | 4.2 (2.7 – 5.7; 0.5) | 94 | 0.81 |
| Palearctic | 1 | 1.1 (0.7 - 1.4; 0.1) | 84 | 0.78 |
| | 2 | 0.6 (0.3 – 1.1; 0.3) | 83 | 0.68 |
| | 3 | 2.9 (2.1 - 4.1; 0.3) | 82 | 0.80 |
| | 4 | 3.5 (2.6  - 5.4; 0.4) | 88 | 0.80 |
| Oriental | 1 | 0.7 (0.6 - 0.9; 0.0) | 100 | 0.88 |
| | 2 | 1.1 (0.9 – 1.3; 0.1) | 100 | 0.72 |
| | 3 | 3.5 (3.0 – 4.0; 0.2) | 100 | 0.86 |
| | 4 | 4.6 (3.9  - 5.5; 0.2) | 100 | 0.83 |
| Neotropical | 1 | 2.4 (1.9 – 3.0; 0.2) | 83 | 0.95 |
| | 2 | 3.5 (9.1 - 14.0; 0.2) | 73 | 0.95 |
| | 3 | 5.2 (3.9 – 6.7; 0.5) | 77 | 0.91 |
| | 4 | 8.8 (7.1  - 11.0; 0.6) | 84 | 0.96 |
| Afrotropical | 1 | 1.1 (0.7 - 1.9; 0.2) | 76 | 0.79 |
| | 2 | 0.6 (0.3 – 1.1; 0.1) | 78 | 0.83 |
| | 3 | 5.8 (3.7 – 8.1; 0.9) | 84 | 0.93 |
| | 4 | 6.4 (4.3 – 9.2; 0.9) | 87 | 0.93 |
| Australasian | 1 | 1.8 (1.4 - 2.2; 0.1) | 88 | -0.14 |
| | 2 | 1.7 (0.9 – 2.5; 0.3) | 100 | 0.73 |
| | 3 | 9.2 (7.2 – 11.2; 0.6) | 96 | 0.19 |
| | 4 | 11.0 (8.3 – 13.5; 0.8) | 99 | 0.50 |

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605    **Figure legends**

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607    **Figure 1.  Global map of the relative richness of tree cavity excavators versus secondary**
608    **cavity-nesting birds (expressed as the ratio excavator / secondary cavity-nester) in 10x10**
609    **km grid cells**.  Low values (light colors) indicate relatively low numbers of excavators as
610    compared to secondary cavity-nesters while high values (dark colors) indicate a relatively higher
611    proportion of excavators to secondary cavity-nesters.

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613    **Figure 2. Scatter plots of the correlations between the richness (number of species) of**
614    **excavators and secondary cavity-nesters all forest birds (upper row), all forest specialists**
615    **(second row), forest generalists (third row) and all non-cavity-nesting forest birds**
616    **(specialists and generalists; bottom row) in six zoogeographic regions.** Points represent
617    species richness values in 10×10 km grid cells, and the solid line represents the fit of a linear
618    regression model, created using all grid cell values. Note that nearly all secondary cavity-nesters
619    are also forest-associated species, but were not included as forest specialists or generalists.
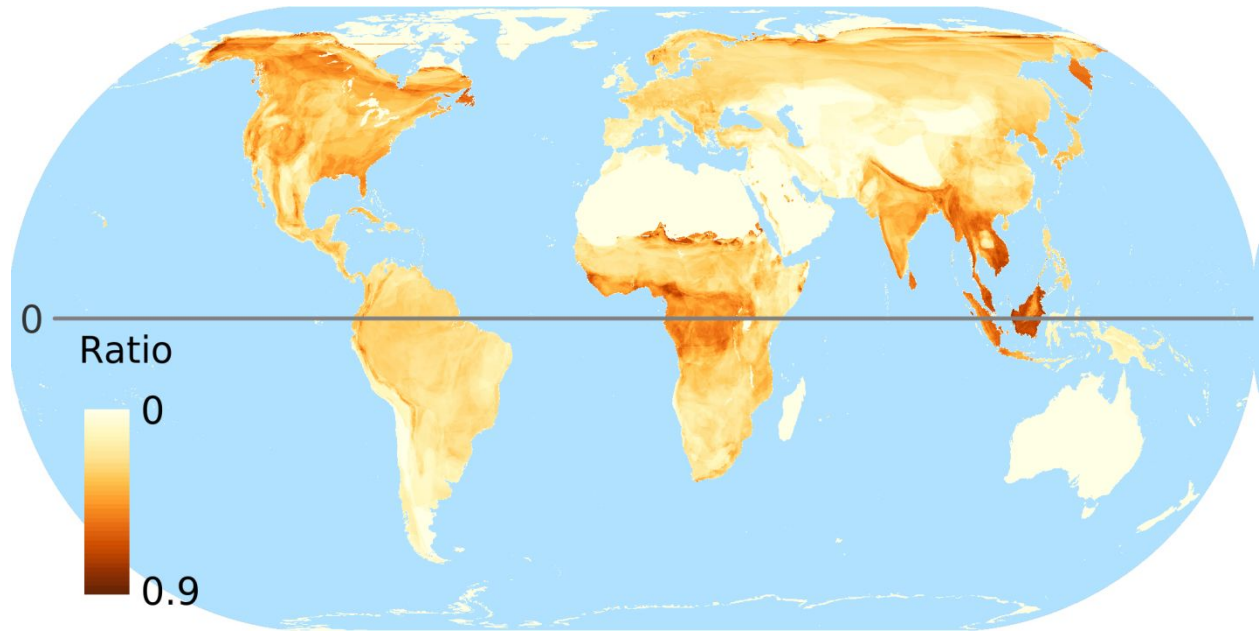
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**Figure 1.**

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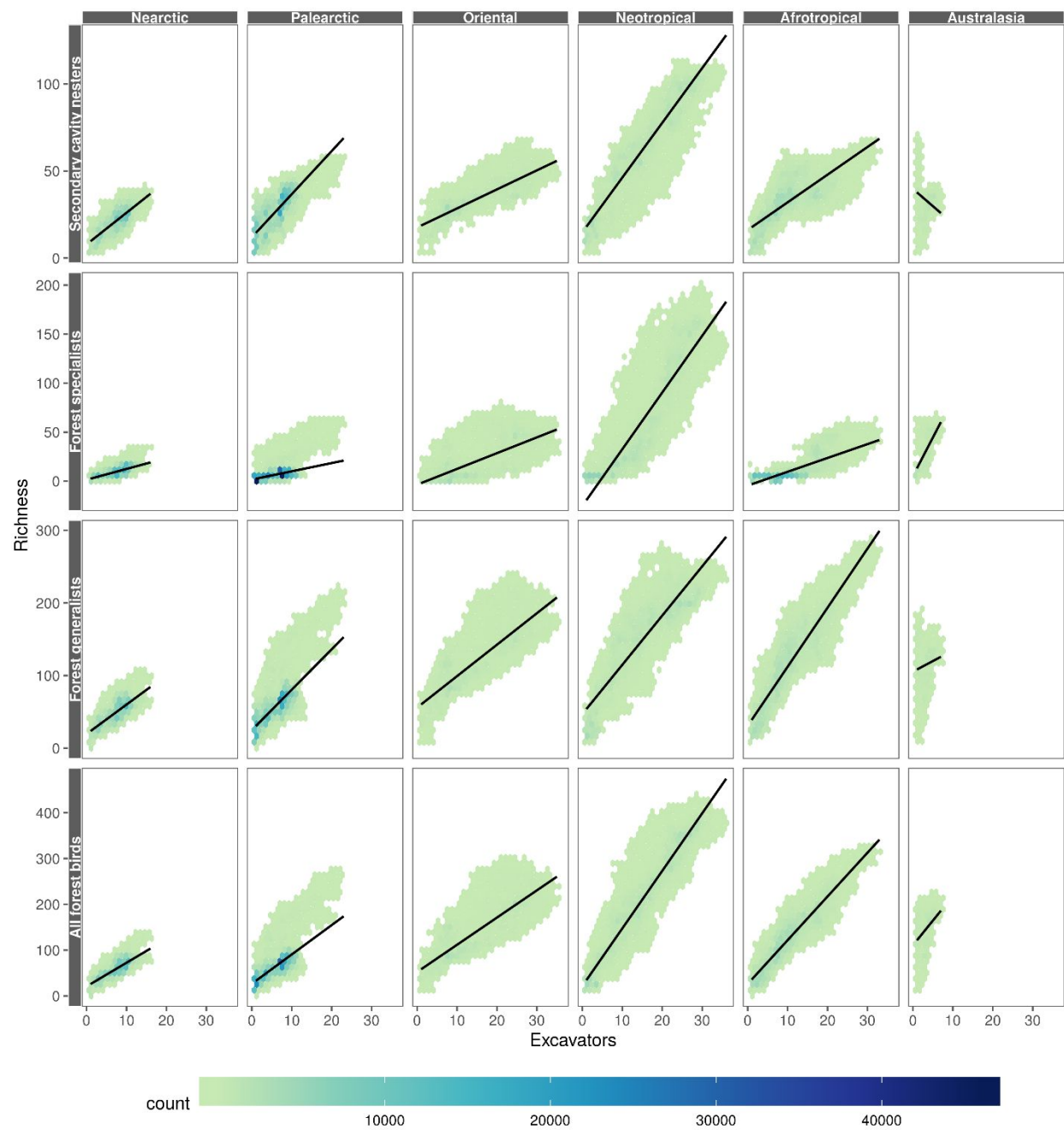646
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**Figure 2.**

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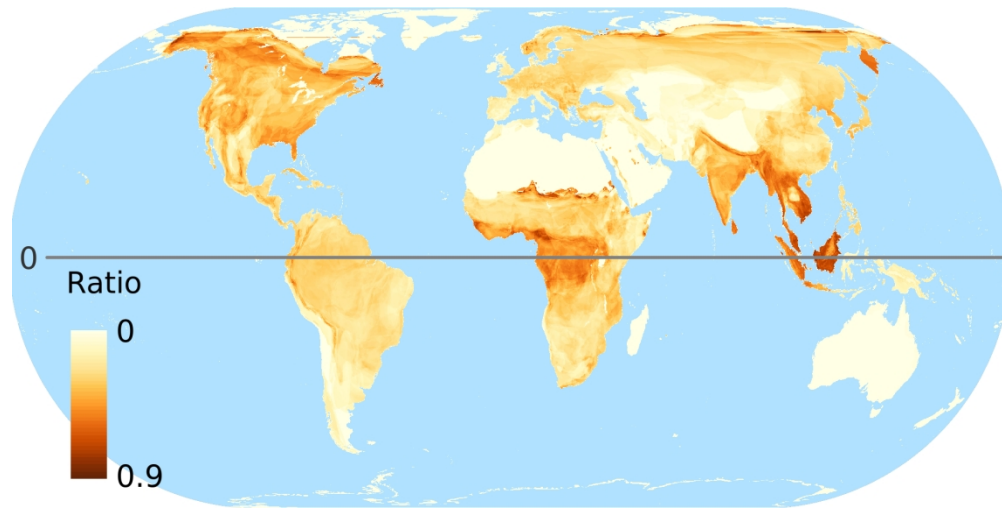51
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Figure 1. Global map of the relative richness of tree cavity excavators versus secondary cavity-nesting birds (expressed as the ratio excavator / secondary cavity-nester) in 10x10 km grid cells. Low values (light colors) indicate relatively low numbers of excavators as compared to secondary cavity-nesters while high values (dark colors) indicate a relatively higher proportion of excavators to secondary cavity-nesters.
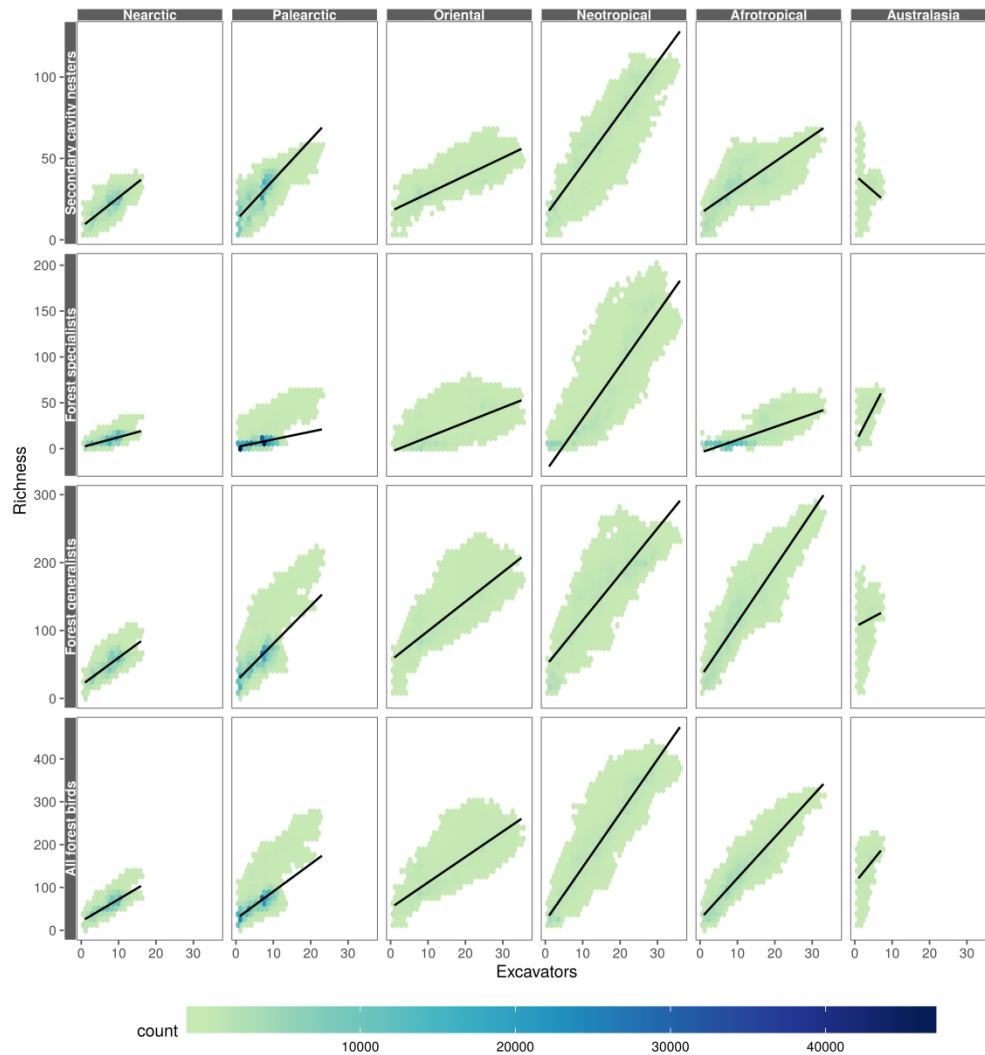
Figure 2. Scatter plots of the correlations between the richness (number of species) of excavators and secondary cavity-nesters all forest birds (upper row), all forest specialists (second row), forest generalists (third row) and all non-cavity-nesting forest birds (specialists and generalists; bottom row) in six zoogeographic regions. Points represent species richness values in 10x10 km grid cells, and the solid line represents the fit of a linear regression model, created using all grid cell values. Note that nearly all secondary cavity-nesters are also forest-associated species, but were not included as forest specialists or generalists.

# Appendix F

We thank both Editor and Reviewers for their suggestions and for giving us the chance to submit another version. We would like to point out that unfortunately the previous 'track-changed version' had some editing issues. The 'clean copy' (i.e. without track changes) was much clearer (some small writing issues only appeared after we had removed the track changes, which made it difficult to keep overview). In the clean copy version, which was, unfortunately, not used as a base for the new reviews, there were also some changes on the references (numbering) and a few different sentences.

We apologize to the Reviewers for not having submitted that comprehensive track-changed document. That said, we see that this time around we could still make some valuable improvements. For that, we thank the reviewers for their comprehensive and insightful comments.

You will find a new version with edits attached. A few larger changes are discussed below.

We identify our responses to reviewer comments with an * preceding our response.

Reviewer 1:

Lines 185-190: poor English – check and re-write

*We made changes to this part of the text that will hopefully improve the clarity of our message.

Lines 219-220: provide names of the authors in the text

*We added these references in parentheses rather: "We selected and classified focal bird species (following [11, 42]) as…"

Line 295: was rho really 0.88 in both cases?

*This was a mistake, we only wanted to highlight one relationship (between excavators and secondary cavity-nesters, rho=0.88). We have removed the mention of the other relationship.

Line 367: provide valid reference for this claim i.e. on high logging rates in Oriental Region

*We received the same comment from the other reviewer. We have altered this a bit to focus on the availability of mature forests instead, and have added a reference for that.

Line 373-377: it seems to be against your prediction. Whole sentence is a bit confusing.

*We have rephrased this, and reordered the paragraphs. We hope that this new version provides more clarity.

Line 386: what dynamics do you mean? Fire dynamics?

*We understand that this wording is a bit confusing. Rather, we are interested in discussing the 'processes' of cavity formation, tree decay and persistence, etc., for which reason we highlight the example of the 'process' of decay-formation of tree cavities.

Line 514-516: I would explicitly mention high detectability here

*We have added the words high detectability to this phrase.

Reviewer 2:

-38 and 39?? Please check again cite numbers throughout the manuscript

*These citations were not updated in the track-change version of the manuscript as Endnote did not update numbering until track-changes were accepted. The citations were correctly numbered in the actual, clean, version that was also submitted and that could be found later on in the PDF. In this new submission, both the track-change and clean versions of the manuscript are updated.

I'd suggest to change the name, because secondary-cavity nesters are also 'forest birds', and are not included in this group… can be confusing

*We have retained the name secondary-cavity nesters, but now explain in the methods that forest generalists are 'habitat generalist birds that use forest habitat but also at least one other type of habitat, but that this group in our study excludes all tree cavity-nesters.', following the reviewer's suggestion.

-incorrect. In Australasia, excavators and secondary cavity-nesters had a negative relationship (Fig. 2)

*We understand that this part was confusing. The gls slopes were positive for this relationship, but Spearman rho is negative. However, in general Spearman rho was so low for the relationships between excavators vs. secondary-cavity nesters and excavators vs. forest generalists (≤|0.19|for both) that we may question whether there are any relationships at all. We added a statement to explain this in the text. Finally, we also point out that due to computational constraints, the figure depicting the relationships (Figure 2) shows lines representing linear regressions rather than gls models, and that these models might have slightly different outcomes.  That said, to avoid further confusion, we removed the regression lines for the two relationships in Australasia that had the negligible relationships.

-Again, the use of 'all forest' is confusing. Besides, apparently you have made a correlation between excavators and specialists + generalists. In the responses to comments on the previous version, you have answered "We therefore opted to re-run all the analyzes for groups that do not have any overlaps", which somewhat contradicts this. In any case, although you in the introduction you mention that this relationship will be assessed, it is not explained in methods, and honestly I don't see the sense of evaluating these two groups together, at least with the information provided in the introduction.

*We thank the reviewer for his/her patience in pointing out these inconsistencies. We have altered the text to make clear that we have used non-overlapping groups for three of the relationships (and explained in the methods what these groups are, e.g., "forest generalist birds: habitat generalist birds that use forest habitat but also at least one other habitat type for nesting of habitat, again excluding cavity-nesters.". But we have also explained in more detail why we added tests of a fourth relationship, that between excavators and forest specialists + generalists (grouped). We opted to include this because it strengthens the notion that excavators may be effective indicators of not just the narrow group of specialist species, but of the larger forest bird community in general.

-well… you're saying that .96 is stronger than .95. I'd say that is a minimal difference in which the focus of a discussion doesn't have to be focused.

*In this version we have completely reworked this part of the Discussion, and we no longer make this point. We have followed the reviewer's advice elsewhere, and focus on other discussion points.

-I'd like to see more explanations/discussions on other patterns:

-why relationships between excavators and SCN are mostly weaker than the others relationships across regions? This was one of the relationship more strong that one expect by cavity facilitation

*We explain this is in more detail now.  For example, a part of the new text includes:

"This indicates that the influence of direct facilitation of nest-cavities is potentially less important than the indirect associations with forest elements and shared habitat preferences in shaping these relationships, but that the relative importance of both depends on the region under consideration." We add to that in other paragraphs, explanations such as "we found weaker relationships between excavators and secondary cavity-nesters than between excavators and forest specialists in both the Neotropical and Afrotropical regions, possibly because at least some secondary-cavity nesters do not share a preference for habitats and forest elements with excavators in this region and because a high reliance on decay-formed cavities releases secondary-cavity nesters from dependency on excavators to provide their cavities [34]. "

2) given the known pattern of the greater dependence of SCN in woodpecker-excavated cavities in Nearctic and Palearctic than in tropical regions, why these relationships showed the opposite pattern? (greater rho in tropics than in north temperate and boreal regions)

*We address these patterns in more detail now. For example, a part of the new text includes:

"Thus, the fact that the relationships between excavators and secondary-cavity nesters are stronger in all three largely tropical regions (Oriental, Neotropical, and Afrotropical) as compared to the predominantly temperate/boreal Nearctic and Palearctic may not reflect a larger dependency of secondary cavity-nesters on excavators for cavities in the tropics, but is more likely to stem from overall high species richness as well as from strong indirect associations that both groups of birds have with forest elements and shared habitat preferences."

-Logging is a highly heterogeneous activity in intensity and extension throughout the world, and of relatively recent impact. Therefore, resorting to this explanation to explain a biogeographic scale pattern, where evolutionary time scales and speciation rates are involved, seems inappropriate. Moreover, it is not clear to me how the changes produced by logging could be influencing the data set used in the analyzes. For example, do the maps you used include information on local extinctions across all world's forests due exclusively to logging?

*We understand that this might have come across a bit speculative. As we do think that historical deforestation patterns are very different in the Oriental than the Neotropical and Afrotropical regions, due to higher human densities etc., and that this could shape richness patterns, even at larger spatial scales. Therefore, we have altered our discussion to state that there is less mature forest left in this region, a more general statement that, we think, could have influenced the observed patterns.

# Appendix G

*We thank the Editor(s) and reviewers for their time and intellectual investment, this has surely led to a much-improved manuscript. We understood the need for further editing of the language, and both the first author as well one of the co-authors (a native English speaker with a long and substantial publication record) have made edits that ensure the manuscript is easier to read and avoid of grammatical or other language mistakes.

We do not have a point-by-point rebuttal at this point, but hope that the text is overall improved, and that there are no more errors such as those previously highlighted by the reviewer in lines 312-319 and 363-368.

*In addition, to the best of our knowledge, we have included all required statements (e.g., on funding etc.). Of course, should we have missed anything, we would be happy to provide further details.


On behalf of the Editors, I am pleased to inform you that your Manuscript RSOS-192177.R2 entitled "Global relationships between tree-cavity excavators and forest bird richness" has been accepted for publication in Royal Society Open Science subject to minor revision in accordance with the referee suggestions.  Please find the referees' comments at the end of this email.

The reviewers and Subject Editor have recommended publication, but also suggest some minor revisions to your manuscript.  Therefore, I invite you to respond to the comments and revise your manuscript.

• Ethics statement
If your study uses humans or animals please include details of the ethical approval received, including the name of the committee that granted approval. For human studies please also detail whether informed consent was obtained. For field studies on animals please include details of all permissions, licences and/or approvals granted to carry out the fieldwork.

• Data accessibility
It is a condition of publication that all supporting data are made available either as supplementary information or preferably in a suitable permanent repository. The data accessibility section should state where the article's supporting data can be accessed. This section should also include details, where possible of where to access other relevant research materials such as statistical tools, protocols, software etc can be accessed. If the data has been deposited in an external repository this section should list the database, accession number and link to the DOI for all data from the article that has been made publicly available. Data sets that have been deposited in an external repository and have a DOI should also be appropriately cited in the manuscript and included in the reference list.

If you wish to submit your supporting data or code to Dryad (http://datadryad.org/), or modify your current submission to dryad, please use the following link:
http://datadryad.org/submit?journalID=RSOS&manu=RSOS-192177.R2

• Competing interests
Please declare any financial or non-financial competing interests, or state that you have no competing interests.
• Authors' contributions
All submissions, other than those with a single author, must include an Authors' Contributions section which individually lists the specific contribution of each author. The list of Authors should

meet all of the following criteria; 1) substantial contributions to conception and design, or acquisition of data, or analysis and interpretation of data; 2) drafting the article or revising it critically for important intellectual content; and 3) final approval of the version to be published.

All contributors who do not meet all of these criteria should be included in the acknowledgements.

We suggest the following format:
AB carried out the molecular lab work, participated in data analysis, carried out sequence alignments, participated in the design of the study and drafted the manuscript; CD carried out the statistical analyses; EF collected field data; GH conceived of the study, designed the study, coordinated the study and helped draft the manuscript. All authors gave final approval for publication.

• Acknowledgements
Please acknowledge anyone who contributed to the study but did not meet the authorship criteria.

• Funding statement
Please list the source of funding for each author.

Please note that we cannot publish your manuscript without these end statements included. We have included a screenshot example of the end statements for reference. If you feel that a given heading is not relevant to your paper, please nevertheless include the heading and explicitly state that it is not relevant to your work.

Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript before  19-Jun-2020. Please note that the revision deadline will expire at 00.00am on this date. If you do not think you will be able to meet this date please let me know immediately.

To revise your manuscript, log into https://mc.manuscriptcentral.com/rsos and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions". Under "Actions," click on "Create a Revision."  You will be unable to make your revisions on the originally submitted version of the manuscript.  Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referees and upload a file "Response to Referees" in "Section 6 - File Upload".  You can use this to document any changes you make to the original manuscript.  In order to expedite the processing of the revised manuscript, please be as specific as possible in your response to the referees.

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1) A text file of the manuscript (tex, txt, rtf, docx or doc), references, tables (including captions) and figure captions. Do not upload a PDF as your "Main Document".
2) A separate electronic file of each figure (EPS or print-quality PDF preferred (either format should be produced directly from original creation package), or original software format)
3) Included a 100 word media summary of your paper when requested at submission.  Please ensure you have entered correct contact details (email, institution and telephone) in your user account

4) Included the raw data to support the claims made in your paper. You can either include your data as electronic supplementary material or upload to a repository and include the relevant doi within your manuscript

5) All supplementary materials accompanying an accepted article will be treated as in their final form. Note that the Royal Society will neither edit nor typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details where possible (authors, article title, journal name).

Supplementary files will be published alongside the paper on the journal website and posted on the online figshare repository (https://figshare.com). The heading and legend provided for each supplementary file during the submission process will be used to create the figshare page, so please ensure these are accurate and informative so that your files can be found in searches. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Once again, thank you for submitting your manuscript to Royal Society Open Science and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Kind regards,
Andrew Dunn
Royal Society Open Science Editorial Office
Royal Society Open Science
openscience@royalsociety.org

on behalf of Prof Kevin Padian (Subject Editor)
openscience@royalsociety.org

Associate Editor Comments to Author :
The reviewer is broadly satisfied with the scientific content of the paper, though they would prefer that you seek further English language support. Examples of professional services providing such advice may be found at https://royalsociety.org/journals/authors/benefits/language-editing/.

Reviewer comments to Author:
Reviewer: 1

Comments to the Author(s)
I am generally pleased with changes included in this version of the manuscript. However, it would be great to carefully read some of the new sentences and improve them linguistically. For example check lines 312-319 and 363-368 (clean version) for missing words.

***********************************************
Journal Name: Royal Society Open Science
Journal Code: RSOS

MS Title: Global relationships between tree-cavity excavators and forest bird richness

MS Authors: van der Hoek, Yntze; Gaona, Gabriel; Ciach, Michal; Martin, Kathy
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Contact Author State: NA
Contact Author Country: Rwanda
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Abstract: Global monitoring of biodiversity and ecosystem change can be aided by the effective use of indicators. Tree-cavity excavators, the majority of which are woodpeckers (Picidae), are known to be useful indicators of the health or naturalness of forest ecosystems and the diversity of forest birds. They are indicators of the latter due to their associations with particular forest elements and because of their role in facilitating the occurrence of other species through the provision of nest cavities. Here, we investigated whether these positive correlations between excavators and other forest birds are also found at broad geographical scales. We used global distribution maps to extract richness estimates of tree-cavity nesting and forest-associated birds, which we grouped by zoogeographic regions. We then created generalized least squares models to assess the relationships between these groups of birds. We show that richness of tree-cavity excavating birds correlates positively with that of secondary cavity nesters, and with other forest birds (generalists and specialists), at global scales, but with variation across zoogeographic regions. As many excavators are relatively easy to detect, play keystone roles at local scales, and are effective management targets, we propose that excavators are useful for biodiversity monitoring across multiple spatial scales and geographic regions, especially in the tropics.
EndDryadContent