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Title:
Landscape context explains changes in the functional diversity of regenerating forests better than climate or species richness

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Author's Response to Decision Letter for (GEB-2016-0483)

Dear Professor Enquist,

Thank you for the opportunity to revise our manuscript for reconsideration at Global Ecology and Biogeography. We have now carefully revised our manuscript in response to all reviewer comments noting when we disagreed and thus did not make a requested change. That said, we have modified the manuscript in response to the vast majority of editor and reviewer comments. To make it easier to traverse our revision, we have colored major text changes in blue and provided line numbers in our responses below.

Thank you for your consideration,

Margie Mayfield

Response to reviewers

EDITOR'S COMMENTS TO AUTHORS

Editor: Enquist, Brian

Comments to the Author:

I thank the authors for submitting an intriguing manuscript. The study assesses of trait and diversity patterns across disturbance gradients follow regular patterns consistent with local community determinism. A key finding of this paper is that landscape patterning are much more strongly related to the recovery of functional diversity in forests than any regional climate factor. The authors conclude that land management practices determine recovery trajectories rather than local community assembly processes.

This study challenges our local scale perspective on forest recovery after disturbance by providing a large scale comparison of species and trait diversity in remnant and regrowth forests. I agree with the first reviewer in that the "work provides detailed analyses of both canopy and understory strata, adding depth to its many interesting findings that will motivate future work."

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version record. Please cite this article as doi:10.1111/geb.12627.

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The paper has now been reviewed by two separate experts in the field who have worked with similar data and questions. As you will see the reviewers are split on the importance and relevance of the paper. In reading through these comments I do not believe that the comments are such that the conclusions and approach of the paper will change. However, I do think these comments reflect likely questions that will come up and I encourage the authors to take these comments to heart in any revision of their paper.

Specifically, I encourage the authors to address the following points.

Comment (1) This paper is dense. There are numerous analyses and results. While the presentation is for the most part clear some roadmap and summary of the most salient findings is needed. For example, a brief summary at the end of the results section would improve readability and interpretation. Reviewer #1 has some recommendations for how the manuscript could be improved.

Response: Thank you for this suggestion. We have now added a summary of our main findings at the end of the results as requested. Lines 368-377.

Comment (2) Reviewer #2 was generally not convinced by the authors arguments. While there are some good points here I suspect that overall addressing them will not change the authors conclusions. I encourage the authors to address these comments if they think that doing so would improve the interpretation and understanding of their results and convince readers who may be on the fence.

Response: Thank you for giving us the freedom to address these comments thoughtfully. We have carefully considered all of reviewer #1's comments and made modifications throughout the manuscript to attempt to streamline the manuscript and to provide a more consistent order of information. We have also attempted to address all of Reviewer 2's comments, specifics of which are listed below.

Comment (3) Several recent studies - not cited by the authors seem to provide not only some context of the submitted work but also may provide a necessary discussion focused on caveats and limitations of the the current study. For example, recently Norten et al. 2015 Successional dynamics in Neotropical forests are as uncertain as they are predictable. Proceedings of the National Academy of Sciences, 112(26), pp.8013-8018. definitely overlaps with the conclusions and focus as in the current manuscript. I was surprised not to see this manuscript included or discussed.

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Second, recently, several papers have assessed functional traits shifts during succession. Again, these papers are not discussed.

Buzzard et al. (2016). Re-growing a tropical dry forest: functional plant trait composition and community assembly during succession. Functional Ecology, 6(30), 1006-1013;

Boukili, V. K., & Chazdon, R. L. (2017). Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. Perspectives in Plant Ecology, Evolution and Systematics, 24, 37-47.

These papers would seem to suggest that there are some degree of predictability and generality. These papers show directional changes in traits.

Lastly, the conclusions from studies looking at phylogenetic signature during succession, for example Letcher, S.G., e al. 2012. Phylogenetic community structure during succession: evidence from three Neotropical forest sites. Perspectives in Plant Ecology, Evolution and Systematics, 14(2), pp.79-87 - a paper not cited by the authors seems to suggest that phylogenetic patterning does show structure. Granted this paper looks at phylogenetic patterning but given niche conservatism phylogenetic patterns presumably reflect functional differences and similarities etc.

Response: We thank the editor for drawing our attention to these references. We have now incorporated these references into the manuscript. We have also rewritten parts of the introduction and discussion to place our study in a more robust theoretical and literature supported framework using these papers. We note that our manuscript is already very long so though we agree we could have included even more papers from the literature we are already over the reference limits and thus have tried to use these recommended references to the maximal effect along with our previously included references. We have now also cut a few of our other references to keep the reference number the same as in our original submission but now including these. See lines: 28-38, lines 380-388, 408-411, 493-496.

Comment (4) An obvious question is if the use of species mean traits - the basis for all the functional conclusions of these analyses rest on using interspecific differences. A developing conclusion in trait based ecology is just how large intraspecific variation is. Granted, this study does look over large geographic gradients but I can't help to wonder just how important intraspecific variation is on the patterns found here. I understand the authors will likely not be able to fully address this but it would be worth considering the role of intraspecific variation in this study. At minimum a caveat or discussion point is needed.

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Response: We completely agree that intraspecific trait variation is clearly becoming the new norm for trait analyses and for good reason. We did actually attempt to collect intraspecific trait data in this study but species turnover was so high that there were not enough species found in more than one site to actually analyze these data. We now point this out in the manuscript. Lines 166-168.

Brian J. Enquist

Dr. Brian Enquist, Editor

REVIEWER COMMENTS TO AUTHORS

Referee: 1

Comments to the Author

This study uses a 1500 km transect of remnant and regrowth rainforests in eastern Australia to determine fundamental drivers of forest recovery trajectories of species and functional diversity. The study concludes that land management practices (specifically, proximity to neighboring forest) determine recovery trajectories rather than assembly processes, even across the broad climate and productivity gradient sampled in the study.

Comment 5: The broad climatic gradient (2000 mm annual rainfall differences between wettest and driest sites) on similar soil type and the paired-plot approach between remnant and regrowth forests provides an interesting case study. That soil did not systematically vary between primary and secondary rainforests given the history of clear-cut felling was surprising.

Response: We are not sure why this would be surprising. First, we carefully selected our sites to control for soil type and within sample locations site pairs were close together so it seems logical that pairs of plots would have pretty similar soils. Second, given the broad climate and landscape gradients across which our sites were found, we don't see why there would be any expectation for differences in soils to vary systematically across the continent, sites are found in very different environments.

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Changes to soils following clearing will be affected by rainfall amount, temperature and landscape context. For example, many regrowth sites were situated within a matrix of old growth forest, often directly adjacent to primary forest stands of various sizes. In other cases, regrowth sites were relatively isolated from primary forests. These landscape factors were not systematically correlated between secondary and primary forest regrowth among locations. This unexplained variability in soils is also accounted for in our location random effects of the model. Given that our paper is already long and we would like to keep within the journal word count, we have not added a great deal of text explaining these points, though we have provided sufficient detail in our methods for the reader to understand why we might have the patterns of soil variance that we do. Lines 126-136.

5b. Also, the sampling (six locations each with three 20x20m plots in primary forest and three in secondary forest, with one location excluded from understory analyses) seems rather limited for diverse tropical rainforests.

Response: In this study, we aimed to control for significant sources of variation in forest structure, particularly regrowth stand age and soil type to better resolve variation by climate and landscape factors. Unlike many tropical regions of the world, there is actually very little rainforest regrowth in Australia as most cut forests stay cut here. Thus, to maintain a well-controlled study we were somewhat restricted in the number of sites we had available and could reliably date. Despite the small number of locations, patterns did emerge suggesting that it was not too small to observe prominent patterns, which is what we were looking for.

We selected our plot size of 20m x 20 m for three reasons. First, this is a fairly standard forest plot size in Australian studies, so by using this plot size we opening up access to several existing surveys that we were able to incorporate in our analyses. Second, patches of regrowth in Australia are often quite small, again Australian rainforests are quite different from rainforests in much of the rest of the world's tropics in that they are naturally restricted and patchy. Add in human land use modification and patches often just aren't very big. Given how diverse these forests are, we felt it was better to use several smaller plots to survey each site that would minimize edge effect issues while keeping as many available sites available as possible. Third, the goal of this study was not to comprehensively assess total diversity of Australian primary and secondary rainforest but to use a controlled study design to gain a robust understanding of the importance of regional climate, species pool size and landscape fragmentation on rainforest recovery. With our nested design of three 20m x 20m plots per site we believe that we have a dataset that effectively allows us to achieve this goal. We have added brief text in line 79-80 of the introduction and lines 127-128 and 136-140 to better outline the strengths of this approach.

5c It was difficult to gauge whether the reported species richness was underestimated. I expected to see rarefaction curves used as a way to compare the observed plot species richness to expected, not as a way to estimate a regional species pool as it was used in the study.

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Response: Please see our response to reviewer 2's comment # 21 below, which addresses this question in depth. In brief, we used rarefaction methods to estimate species pool because there were not reliable species lists for our study sites to reasonably assess each site's "expected" species pool. However, we did compare our rarefactions measure to expected species pool size in a fashion, by comparing rarefaction outcomes to other proxies for each species pool published qualitative expectations for diversity in each of our study regions. This is outlined in detail in Appendix D and lines 214-227 in the manuscript. Given our constraints on word limits we have not moved the detail from Appendix D into the manuscript, but have made associated edits to the language lines 214-227.

5d It was also unclear why the sampling included 1-59 individuals per species if there was no interest in intraspecific trait variation.

For all species we used a species mean value from many leaves. Ideally the higher the number of leaves and individuals measured to calculate that mean the better our estimate, so in all cases we tried to obtain as many leaves from as individuals as possible. It is also worth noting that there is high turn over of species between locations (see MDS plot) and interspecific variation is likely to be a very important driver of differences. We investigated the options of looking at intraspecific variation, and originally were interested in doing so, but found very few species that occurred across more than a few plots in sufficient abundances to make such an analysis worthwhile. Even though we ended up excluding any analyses of intraspecific trait variation, we see no issue with including all the data we had available on each species in our study to develop our mean trait values. We have added brief text to explain this. Lines 169-172.

Comment 6: Regardless of these minor issues, the study provides detailed and interesting insight on effects that are often difficult to disentangle. This study is dense with analyses and results, however, the presentation is sufficiently clear. A summary of the most salient findings at the end of the results section would improve readability and condense the rote listing of results. The first paragraph of the discussion section attempts to do this but the generalizations are so broad and sweeping that it makes it difficult to match the general outcome with a specific result (and there were many). Including a short paragraph linking 2 or 3 specific results to generalizations would be beneficial. The discussion does this exercise throughout and of course in more detail, however.

Response: We have added a new section at the end of the results summarizing our key results. Lines 368-377.

Comment 7: In sum, this study challenges our local scale perspective on forest recovery after disturbance by providing a large scale comparison of species and trait diversity in remnant and regrowth forests. The study provides detailed analyses of both canopy and understory strata, adding depth to its many interesting findings that will motivate future work.

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Response: Thank you!

Minor comments:

Comment 8: The abbreviations relevant for Table 1 and Table 2 (like Loc, cvMI, etc) should be included in main text as well as the supplementary Tables (where they are exclusively included currently).

Response: Done – we have added these abbreviations to main text as suggested.

Comment 9: L158: To add clarity to the sentence, clearing should be “cleared”

Response: Done

Comment 10: L237: specie should be species

Response: Done

Comment 11: L281: calculated

Response: Done

Comment 12: L474: permanent

Response: Done

Comment 13: L545: interested

Response: Done

Comment 14: The supplementary sections also contain spelling, grammatical, and punctuation errors throughout.

Response: We have carefully read through all our appendices and corrected spelling and grammatical errors throughout.

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Comment 15: Keywords: Forest recovery more appropriate than ‘recovery’. Perhaps consider 'regeneration' or 'succession' for broader searchability.

Response: Changed and added

Comment 16: Table 1 and 2: Is there a clearer way to represent these detailed results? For example, could the best model equation (including slope, intercept, etc) be supplementary while still retaining the influential variables in the model (e.g. cvMI, SpPool, etc.)? This may help improve the presentation.

Response: We have changed Tables 1 and 2 based on the reviewer’s suggestions to improve the presentation. We have moved the table containing co-efficient equations into the supplementary materials but left in the influential variables.

Referee: 2

Comments to the Author

Comment This study compared pairs of secondary and mature forest plots across six locations along Australia’s east coast (tropical rainforest) and evaluated the relation between either species or functional diversity with several predictors including climatic variables, size of the regional species pool and landscape metrics. Understanding which are the main drivers of forest recovery in secondary forests in a human-impacted landscape is a very relevant question nowadays.

Although the findings are interesting, I have some critical concerns that need to be addressed before this paper is ready for publication.

Comment 17: Conceptual framework.

Overall, the manuscript does not provide a strong conceptual framework in setting up the ecological questions the authors sough to examine. I think there is too much text dedicated to the description of Australian rainforests and their suitability to test the predictions, but too little to the actual theoretical rationale that supports the different predictions made at the end of the Introduction.

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Response: We added in the extensive details on our Australian system in response to previous reviews of our manuscript that made it clear to us that many northern hemisphere readers are not sufficiently familiar with Australian rainforests to understand some of the decisions that we made in regards to this study. We completely agree, however, that this detail was getting in the way. We have removed much of the Australian details from the introduction, moving key bits to the methods. Lines 67-84 and lines 125-140. We have also rewritten parts of the introduction to bulk up the theoretical rationale for the study. Lines 29-38 and 87-111.

For instance, in prediction 1, the first sentence is somewhat vague. Why are climate variables expected to influence rates of establishment, growth and productivity? Why do you mention the relative importance of competition and environmental filtering? The reader may think that you are going to address this too, and it's not the case. What's the background for predicting that climatic variables affect all these dependent variables?

Response: We clarified our rationale for linking climate variables to recovery following disturbance. Briefly, increasing key climate variables such as rainfall and irradiation should increase establishment, growth rates, and recovery rates in secondary forests. Thus, secondary forests should be more similar to primary forests in more productive locations. Lines 93-99.

Why is your expectation that species and trait diversity in secondary forests will be more similar to those in primary forest of high and low rainfall and available energy? The reason given (faster rates of colonization, higher productivity and resource supply) needs further development. What does the relative importance of competition and environmental filtering have to do with this specific prediction?

Response: In being mindful that our manuscript is already long we have not added a lot of text to explain this prediction but we have altered to text to try and be clearer without adding a lot of length. Lines 93-103.

What are the specific expectations for species diversity and functional diversity? Will these two variables respond in the same way?

Response: Species and functional diversity at a given site will be governed by many factors, and may not change predictably with resource supply or productivity. We make two specific predictions about how diversity patterns will change with climate. This has been clarified in the revised manuscript. Lines 93-103.

Author's Response to Decision Letter for (GEB-2016-0483)

Prediction 2 also deserves further explanation about the possible causes of the influence of the species pool in taxonomic and functional recovery. As in prediction 1, I would like to see more specific predictions for taxonomic and functional recovery. Maybe taxonomic composition would be more affected by the species pool than functional composition?

Response: Our prediction here is based on the species pool hypothesis in explaining species diversity within a site (a common and well understood mechanism in ecology). We clarified our prediction as requested, but we did not wish to add too much text to explain this hypothesis. We agree that taxonomic composition could influence functional diversity here (particularly if functional traits are phylogenetically conserved – see our response to the associate editor above, and our revised text in the discussion). However, we did not examine taxonomic or phylogenetic patterns within the regional species pools, and we don't think it would be appropriate to raise unexamined issues in the predictions. Lines 104-111.

Finally, prediction 4 is very vague. What are the expectation more precisely? Are you talking about saplings vs. trees, or about canopy vs. understory trees? Which one do you expect to be slower?

Response: This prediction is intentionally vague because the existing research on these differences give us little to go on for mechanisms or evidence that canopies and understory differ consistently. That said it is clear that canopies and understory recover differently. Since the state of knowledge about this prediction is not sufficiently developed to provide a more detailed we have removed prediction 4 and transferred it to the methods, simply using the literature on this as a reason for why we analyse the canopy and understory separately. This also addresses the reviewer's bigger concern that the predictions were not working well as a cohesive group of predictions. Moved to lines: 141-145.

Overall, all these four predictions need more connected.

Response: As the reviewers have already pointed out our paper is very long and complicated. We have done our best to clearly articulate key predictions when there are many many specific predictions that could be made but would just make the paper unreadably complex and long. We simply can't go into great detail about each prediction and have thus opted to use the common practice of referencing studies that do go into these details for each prediction. We have changed the text to clarifying our predictions as much as we can without added extensive length to the paper. We have reformatted and changed the writing of the predictions to make them flow in paragraph form and we think that this compromise works well to address the reviewers concerns. Lines 86-118.

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Comment 18: Methods.

I have a concern about sample sized. Although the total number of plots seems correct, the plots are very small and only trees > 10 cm DBH were censused. Overall, 1806 stems do not seem like a very big number… Moreover, it seems that you separated secondary from mature forests in the regressions, which makes that each regression has only 18 points…

Response: Our study has a modest sample size because we went to great lengths to control for key factors that cause variation in rainforest traits, including stand age and parent soil type (see response to reviewer 1 comment 5 for detail). In addition, we also were deliberate in selecting sites that would allow us to disentangle key climate factors such as PER and PET (see our Reviewer 2 comment 20 for relevant changes). This allowed for minimal correlations between our key climate effects (e.g. rainfall and PET, see Appendix B). By controlling for these factors we limited the number of sites we had to choose from in our study areas but have greatly increased the ability of our statistical models to detect change in traits by limiting major sources of variation.

The statistical methods we adopted compared models with only a modest number of parameters (no overfit models) to an intercept only model, and used Akaikes selection criteria for small sample sizes (AICc). The key concern for small sample sizes is not having the statistical power to detect effects, but we were able to detect a range of statistically significant effects because of the way we controlled external factors through our site selection (described above). Much of this rationale is described in detail in the supplementary materials (Appendix F), given the that the paper is long already we have left this description in the supplementary materials.

That said, we have added information that highlights these strengths and rationale to the introduction lines 76-84 and the methods: lines 279-287.

Comment 19: Line 196: Why only 91% of the species have data on SLA if you took measures on the field?

Response: In Australia we are not permitted to use some of the standard approaches for obtaining leaves from very tall trees (like guns and cross bows) and thus we were not able to obtain leaves from a few species that were only represented by a small number of individuals in our study and/or for which leaf data were not available from existing datasets. We have now clarified this in the methods. Lines 169-172.

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Comment 20: lines 219-223. So, MER/PET is not correlated with PET? Please provide more details justifying that the variables chosen are not correlated among them. It's hard to believe that MER/PET is not correlated with PET. Or am I missing something? Are they included in the same model? They shouldn't.

Response: The correlations of each of our climate variables are shown in detail the supplementary materials appendix, which provides strong evidence as to their correlation or lack there of. MAP/PET (assuming MAP is what the reviewer means by MER) was not strongly correlated with PET (R2=0.26) or the coefficient of variation of MAP/PET (R2 = -0.12). PET and the coefficient of variation of MAP/PET were correlated (R2=0.76). We have added text to highlight this on lines 209-211.

We note that we deliberately selected sites that would allow us to disentangle the effects of rainfall from PET, which certainly reduced the level of correlation between these factors. For example, we chose sites at similar latitudes, where PET is similar but across a very broad rainfall gradient (common in eastern Australia). No models contained highly correlated variables. We have provided some detail on this in lines 202-211. Changes we have made in relations to comment 24 below should also help clarify some of the statistical questions raised in this comment.

Comment 21: Does the number of species randomly drawn from 100 individuals really represent species pool size? I think this is very rough... As the plots are very small, you can be missing a lot of rare species and your sampled number of species may not be representative of the species pool for each location. I understand you provide a good justification that this is a good proxy, but I'm not completely convinced.

Response: We agree that this method is not perfect, including for reasons raised by this reviewer. However, we have openly described its limitations as well as benefits compared to other methods available to us in the methods section and in Appendix D. Given that there just are not sufficient data on Australian rainforests to get great estimates of species pool size we consider is the best method available (and believe me we talked about it a lot!), we have provided multiple lines of evidence that our estimates are decent and most importantly there is no reason to suppose that the quality of our estimates vary among our sites. Since our primary purpose of creating these species pools is to compare recovery in systems with relatively large and small species pools, it is the comparability that is most important. We have provided strong support for these aspects of our estimates. The amount of information provided in the manuscript should be adequate for reader to critically evaluate our approach. See lines: 214 – 227 and relevant appendices

Comment 22: P13, lines 255-265: Forest cover seems like a good approximation to describe the landscape context, but is it enough? Although the authors claim that the landscape is less complex that in other tropical regions, there are other metrics related with fragmentation and patch size that may be insightful.

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Response: We agree that there are more complex finer scale metrics that can provide insights into rainforest recovery responses to landscape context. However, these types of metrics are beyond the scope of this particular paper and would be best placed in the context of a paper that explores recovery across a range of spatial scales. As both reviewers have pointed out this paper is already long, dense and complex we do not feel it appropriate to add more analyses at this point. This all said, we have refined some of the wording in the methods (lines 238-239 and 247-250) to make the rationale for the use of this measure clearer.

Comment 23: P13, line 269: Why Bray-Curtis? this metric shows several shortcomings, see Chao and Jost papers.

Response: We agree, this method does have short comings and probably wasn't the best choice – we have re-run the nMDS with Jaccard index, which is better, and updated the supplementary materials accordingly. (line 258)

Comment 24: The section where linear mixed models are described needs to be detailed. If I understand well, N=36. Non-independency among plots belonging to the same location is treated by including location as a random effect? Please provide some justification about this. Also, how do you deal with the fact that you have some independent variables at the plot level, and others at the location level (climatic variables)? If many of your independent variables are at the location level, you would have a regression with six points only...

How many independent variables had each model?

Response: Our most complex linear effects models consisted of the effect of land clearing (categorical fixed effect with two levels: primary or secondary rainforest) a single climate variable (continuous fixed effect spanning six locations) and an intercept only random effect at each location, with random intercepts and variance estimated from six plots within each location. In total, we had 36 plots in the canopy and 30 in the understory but with complex variance structures in our model. We have added these details to clarify our statistical approach. Lines 279-287.

All of our independent variables are at the location level – climate variables, species pool and forest cover. Land-use can effectively be thought of as a "treatment " or categorical fixed effect with two levels at each location that is crossed with continuous fixed effects. We have added these details to line 279-287 to clarify.

Results:

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Comment 25: This section is structured around each dependent variable; I suggest to structure this section based on specific ecological questions.

Response: We have attempted structuring the results a variety of ways in drafting this manuscript, including based on ecological responses. We have found that the results are simpler to navigate and relate to tables and figures by structuring them around the main response measures (species richness, diversity, multivariate functional indices and functional traits) and by understory and canopy. We also address our ecological questions and synthesize results in the discussion extensively.

However, based on this reviewers comments we have restructured the section on individual functional trait measures to be based around the ecological questions we have asked.

Comment 26: In figure 2, it seems like all the regressions are univariate, but from the Methods, I thought they were multiple regressions. Please clarify.

Response: Our regressions are univariate in the sense that they are estimating the response of a single dependent variable, and are not multivariate but are multiple regressions in the sense that they contain more than a single fixed independent variable. This has been clarified in line 279-287.

Discussion:

Comment 27: Again, the structure of this section does not follow clearly the structure of the predictions of the Introduction. This makes the text a bit confusing and does not help for showing the readers the novelty of the paper.

Response: We have reworked the discussion to follow a more consistent structure with the rest of the paper, though we do not follow all the exact sections as were found in the results because we felt this would have led to unnecessary redundancy. Also, this manuscript is very long, we have written our discussion to highlight our key findings, going through each finding in order would simply add so much length that it would make a long manuscript even long and in our opinion, this exercise would make the manuscript dry and harder to follow. We feel our revisions to the discussion have made our findings clearer and we hope they address this general concern. See blue text in discussions section.

Comment 28: Lines 434: 437: Confusing. If you're expecting the relationship between independent and dependent variables to be stronger in dry sites that in wet sites, I would expect to see two sets of regressions, one for wet locations and one for dry locations. However, this was not the case. Am I missing something?

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Response: Please see our responses to comments 22 and 24 – we believe that there was some confusion about our analyses that we have now clarified. In brief, we do have two sets of regression (primary and secondary) and we would expect to see a trend across the gradient from wet to dry if responses differ. This is now clearer given the changes made in response to comment 24 above.

Specific comments:

Comment 29: Line 57: I wouldn't call "species" and "trait diversity" factors.

Response: Changed to "types of diversity" line 53

Comment 30: Line 158: replace "clearing" by "cleared"

Response: Done

Comment 31: Line 162: are they really "primary"? maybe "mature" is a better term to use?

Response: There is no reason to believe that these forests have been modified by human activities. Even the indigenous peoples of this region were not known for clearing forests and thus we feel this term is appropriate. To us mature implies that it is old regrowth, which is not the case for our study sites. Certainly these forests may have been periodically damaged by storms but we don't believe that such disturbance makes our term inappropriate. In our experience there is no single term (mature, primary) that satisfies everyone and after many rounds of discussions and reviews we decided on "Primary" which we would prefer to keep. That said, if this is a sticking point we can change it.

Comment 32: Line 183: "selected based on their recognized importance to assembly processes" seems like a vague justification

Response: Yes, it is. We had to cut an indepth discussion of these links to keep the manuscript within the page limits. We have referenced classic papers in this field that explain why our specific traits are ecologically important. We generally agree that it is best not to expect the reader to go read another paper to find out such information but these traits are so commonly used in functional ecology that we feel most readers will not need this detailed at this point. To do this properly would add quite a bit of text to an already long paper.

Comment 33: Line 187: how many leaves per individual?

Response: Done

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Comment 34: line 237: species not specie

Response: Done

Title: Landscape context explains changes in the functional diversity of regenerating forests better than climate or species richness

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Keywords: Land-clearing; Species diversity; Functional trait; Climate; Australian rainforest; Forest recovery; Land-use change; Succession

Short running title: Landscape context best explains recovery of functional diversity

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Abstract

Aim: A rich literature on forest succession provides general expectations for the steps forests go through while reassembling following disturbance, yet we still have a surprisingly poor understanding of why the outcomes of forest recovery following logging (or other disturbances) vary so extensively. In this paper, we test the hypothesis that regional species pool, system productivity, climate and landscape structure are important drivers of forest reassembly outcomes.

Location: 1500 km transect along Australia's east coast

Time Period: Survey of 50-60 year old rainforest regrowth and primary forest in 2012 and 2013.

Major taxa studied: Rainforest plants

Methods: In this study, we compare species and functional diversity patterns in pairs of remnant and regrowth ("secondary") rainforests spread across a 1500 km climate and productivity gradient along Australia's east coast. Our controlled natural experiment was designed to test the importance of regional species pool, system productivity, climate and landscape structure as drivers of species and functional diversity in regenerating forests. Notably, our study design allowed us to hold soil type, general forest type and disturbance history relatively constant in order to effectively test our hypotheses.

Results: Counter to expectations, few tested factors were strongly related to the recovery of species or functional diversity in regenerating Australian rainforests. The extent of local forest fragmentation was the only factor strongly related to differences between regrowth forests and primary forest remnants, and then only for functional diversity. We found no evidence that species diversity is a reasonable proxy for, or potential driver of, functional diversity patterns.

Main Conclusions: Our findings suggest that forest functional recovery over decades is influenced more by regional landscape context than distinct assembly processes operating across climate and productivity gradients.

INTRODUCTION

Human impacts on ecosystems through resource extraction, agriculture and logging are driving changes in biodiversity and ecosystem functions worldwide (Chapin *et al.*, 2000). Despite a long history of studying human impacted systems, we still have a limited ability to predict if and how natural systems will recover following even the most common land use changes (Mayfield *et al.*, 2010; Buzzard *et al.*, 2016; Boukili & Chazdon, 2017). It is increasingly accepted that a range of factors (both deterministic and stochastic) are important drivers of the diversity patterns observed in successional or "regrowth" systems (Norden *et al.*, 2015). Yet how ecosystem-scale factors that are considered important to community assembly (such as size of the regional species pool, climate and productivity) impact succession outcomes remain unclear. Of the studies that have conducted such analyses, few have identified factors that are strongly related to specific forest recovery outcomes (Mayfield *et al.*, 2013; Norden *et al.*, 2015).

Studies of recovering plant communities have provided key insights into both secondary succession and community assembly processes (Pickett & White, 1985). In recent years, studies of successional forests have shifted from describing patterns of species diversity, to quantifying both species and functional responses (Letcher *et al.*, 2012; Buzzard *et al.*, 2016). The realization is growing that functional traits provide more specific information than species about how communities are structured, change and assemble, and that they may also provide useful proxies for more difficult to measure ecosystem functions (Vandewalle *et al.*, 2010). The ecological functioning of a community depends on the diversity of functional trait states found in the community as well as the number of species that express them (Díaz & Cabido, 2001). Thus, the relationship between species richness and functional trait diversity is also important for understanding the mechanisms driving ecosystem recovery following land-use change (Mayfield *et al.*, 2010).

The relationship between species and functional trait diversity (e.g. the range, relative abundance and variation in the characteristics of functional traits in a community; Garnier *et al.*, 2004) is complex and the interdependence of these types of diversity is still unclear (Mayfield *et al.*, 2010). Empirical studies of the relationship between species and functional diversity in response to land-use change remain rare (e.g. Ernst *et al.*, 2006; Girao *et al.*, 2007; Boukili & Chazdon, 2017) and illuminate little other than the fact that functional diversity responses to land-use change are hard to predict (Mayfield *et al.*, 2010; Mayfield *et al.*, 2013). This is at least in part due to a lack of appropriately controlled datasets available to explore this issue (Mayfield *et al.*, 2013). Studies testing how changes in the environment impact species and functional diversity at the community scale are largely limited to small spatial gradients (Lohbeck *et al.*, 2012), meta-analyses of data collected for other purposes (Laliberté *et al.*, 2010; Mayfield *et al.*, 2013) or small-scale experiments (Chase, 2010). Past studies of community assembly and forest succession point to several ecosystem features as potentially useful for understanding species and functional responses to land-use change, notably: i) regional climate (Ernst *et al.*, 2006), ii) the size of the regional species pool (Mayfield *et al.*, 2010) and iii) landscape context (i.e. connectivity and extent of fragmentation; Girao *et al.*, 2007).

Australian rainforests are highly appropriate for tests of broad scale factors controlling functional and species diversity responses to disturbance. They occur from tropical to temperate latitudes, spanning a large north-south gradient in climate seasonality and solar energy (Schneider *et al.*, 2014) and a large east/west rainfall gradient (Webb *et al.*, 1984), both of which are accompanied by extensive variation in species pool sizes (Kooyman *et al.*, 2013a). Australia's rainforest systems have also been heavily impacted by logging in the last 150 years. Though much cleared rainforest land has remained in agricultural production, relatively recent (~50-60 years old) waves of extraction logging have left a legacy of easily dated regrowth often close to remnants of primary rainforest.

In this study, we present results from a broad-scale, controlled study of woody species and functional diversity in tropical and subtropical Australian rainforests. To do this we compare pairs of primary and regenerating ('secondary') forests, all surveyed 50-60 years post clear felling, using sites selected to allow us to disentangle major sources of climate variation and landscape context. With this dataset, we were able to control factors typically uncontrolled for in global meta-analyses (Mayfield *et al.*, 2013). Specifically, we ask whether the differences in species and functional diversity observed between primary vs. regrowth forest are correlated with regional climate, the size of the regional species pool and/or the extent of surrounding landscape forest clearing.

Predictions:

A recent study of how a similar list of ecosystem factors related to the structural recovery (stem density, basal area and species density) of Neotropical rainforests found little evidence that any ecosystem factors could be clearly used to predict recovery outcomes (Norden *et al.*, 2015). That study did not, however, assess the recovery of species or functional diversity as we do here. Both species and functional diversity have been proposed to relate to the ecosystem factors we test in this study. Based on theoretical expectations detailed below we make the following predictions:

First, increases in key climate variables such as rainfall, temperature, and solar irradiation can increase rates of establishment, growth, and ecosystem productivity (Macdougall *et al.*, 2008; Chase, 2010; Maza-Villalobos *et al.*, 2013). As such, we expect recovery trajectories following disturbance to vary systematically along a productivity gradient (Buzzard *et al.*, 2016). Due to faster rates of colonization and resource supply rates (Macdougall *et al.*, 2008) we also expect that both species and functional diversity will recover faster following land-clearing in sites with higher rainfall, temperature, and irradiation. This should be reflected in species and trait diversity patterns in secondary forest that are more similar to those in primary forest in areas with higher

rainfall and more available energy (high productivity systems). Importantly, we do not predict a specific relationship between either species or functional diversity and site resource supply / productivity, which we expect to be quite system specific.

Second, at landscape-scales, variation in the size of the regional species pool is known to influence site scale species diversity, with high diversity sites more likely to emerge from large regional species pools. High functional trait diversity within a site may also be associated with large species pools through sampling effects (i.e. the increased probability that communities with larger species pools will contain more species with different traits; Srivastava & Vellend, 2005). We predict that forests with larger regional species pools will recover from logging faster due to sampling effects and thus, differences in species and functional diversity between primary and secondary forests will decrease as species pool size increases.

Finally, as landscape-scale fragmentation increases, connectivity among remnant patches decreases, potentially resulting in dispersal limitation exerting a strong influence on community assembly (Myers & Harms, 2009). Some within-region studies of diversity in fragmented landscapes have shown that species and functional diversity decline with increasing levels of isolation (e.g. Cook *et al.*, 2002). We expect a similar pattern in our study because the extent of forest clearing in a landscape is an important influence on dispersal and recovery of species and functional diversity.

METHODS

Study system and design

Between 2012 and 2014, we surveyed Australian tropical and subtropical rainforest in six locations, spanning 13° of latitude (17° -- 30° south, ~ 1500 km; Fig. 1). Australian subtropical and tropical rainforests have many plant taxa with shared evolutionary and biogeographic histories (Kooyman *et al.*, 2013b) and fire is not a typical disturbance in this ecosystem type even

following land clearing (Bowman, 2000). The six study locations differed extensively in annual rainfall, seasonality and daily to annual temperatures, and occurred in locations with limited co-variation among these climate variables (correspond to letters in Fig. 1, Appendix Table A4, see *climate variables* below). To ensure sites were as comparable as possible, however, we held the following characteristics constant: general forest type, disturbance levels, and parent soil type. One of the most common substrates to support Australia rainforests are tertiary basalt soils (Adam, 1994). We only included rainforests on basalt substrates because of the relatively consistent geological history of these soils and the rarity with which basalt-based Australian rainforests extend their boundaries to adjacent lower nutrient soil types. Though soils inevitably varied somewhat among sites, there was also no evidence of systematic variance in the soils in primary and secondary rainforest plots (data not shown). Australia's relatively recent and well documented land-use history makes it much easier to find patches of re-growing forest of similar ages and history in close proximity to remnants of unlogged forest than in most tropical regions of the world. We selected secondary rainforest sites that were all known to have been cleared 50-60 years prior to our surveys, minimizing variation in regrowth age.

Previous studies have shown that canopy and understory components of forest communities often exhibit different responses to land-use change (Chazdon *et al.*, 2003; Mayfield *et al.*, 2013); likely due to the distinct environments found in these forest strata (Van Den Berg *et al.*, 2012). We expected trait recovery trajectories of the canopy and understory to differ and thus we collected and analyzed data for the canopy and understory strata of our forests, separately.

In each location, we sampled six 20 m x 20 m plots, three in 'primary' rainforest with no history of human land-use and three 'secondary' regrowth plots (clear-felled 50 to 60 years prior to study) left to regenerate with little or no secondary disturbance (e.g. grazing, burning) before abandonment. Primary and secondary rainforest plots within locations were all within 2 km of

each other. Land-use history and age of secondary rainforests were identified using aerial photographs, expert knowledge, and historical data.

To determine species abundance and diversity in the canopy of each plot, we counted and identified all stems with DBH ≥ 10 cm. For understory, we counted and identified to species all stems with DBH between 1 and 10 cm in a single 10 x 10 m subplot nested within each 20 x 20 m plot. Data from the Border Ranges National Park (Location E in Figure 1) were originally collected for a different study (using the same methods detailed above) and did not include data on understory plants. This location was thus excluded from understory analyses. In total, 235 species and 1806 stems were counted and identified across all six locations (36 total plots).

Functional Traits

We recorded four continuous traits for all identified species: specific leaf area (SLA), wood density (stem specific density or SSD), seed dry mass (SM), and maximum height at maturity (height) (correlations reported in Appendix Table A1), and two categorical traits: fruit-type (15 categories, Appendix Table A2) and dispersal mode (4 categories, Appendix Table A2). Traits were selected based on their recognized importance to assembly processes and known responses to land-use change in other plant systems (Garnier *et al.*, 2004; Vandewalle *et al.*, 2010). We used species mean trait values in all analyses of continuous traits because there were very few species in common among plots for which to assess intraspecific trait variation. We measured species mean SLA from leaves collected within study plots from as many individuals as we were able to sample (range 1- 59 individuals per species - a minimum of 3 leaves per individual). Due to a combination of terrain, species height and rarity, there were a few species for which we were unable to obtain leaves, which were also not included in published trait databases. Wood density and seed mass values were obtained from existing databases of field measurements and published sources (Metcalfe unpublished data; Kooyman unpublished data, Kooyman et al 2013, Chave *et al.*, 2009; Zanne *et al.*, 2009, see Appendix B for further details). Maximum height at maturity

and categorical functional traits were compiled from published floras (Floyd, 1989; Stanley & Ross, 1989; Cooper & Cooper, 2004; Williams *et al.*, 2009). All traits were measured using standard protocols (Perez-Harguindeguy *et al.*, 2013), except for SLA, for which we used shade not sun leaves due to the difficulty in consistently obtaining sun leaves from canopy trees. Trait data were not obtainable for rare species; thus, analyses are based on the following percentages of species by trait: wood density (98%), seed mass (99%), SLA (91%), maximum height (100%), dispersal mode (100%), fruit type (100%).

Multivariate functional diversity indices

To examine changes in overall functional diversity in response to land-clearing history and climate variation, we calculated three complementary multivariate functional diversity indices: functional richness (FRic; Cornwell *et al.*, 2006), functional evenness (FEve) and functional divergence (FDiv) (Villéger et al. 2008; see Appendix C for details on how these indices are measured).

Climate and Landscape measures

Climate measures

Rainfall, temperature, potential evapotranspiration (PET) and length of the dry season are all climate measures that drive net primary productivity (NPP). These factors are also known to influence the distribution, structure and life history of Australian rainforest trees and their functional traits (Webb *et al.*, 1984; Kooyman *et al.*, 2013a). Using the Australian SILO database, we gathered data on 12 rainfall, temperature and productivity variables (Appendix Table A3) for each site (Appendix Table A4). SILO uses observational data spanning the 1950s to present, to construct spatially and temporally complete interpolated climate data at 0.05 degree resolution, ~ 5km; Jeffrey *et al.*, 2001). Because plots within each location were separated by less than 5 km, climate data were only available at the location scale.

We selected study locations to disentangle often correlated climate variables such as temperature energy and rainfall. Specifically, we selected sites within the same latitudinal band, and thus with similar mean annual PET, but with large variation in rainfall (e.g., sites A and B and C and D, Figure 1 see inset). Despite these efforts, some of our climate variables associated with water availability/rainfall and energy were highly correlated (Appendix Table A5). To account for this we selected a set of climate and energy variables that were not highly correlated: mean annual rainfall/PET, mean annual PET and the co-efficient of variation in mean annual moisture index and PET (see below). Mean annual rainfall/PET was not strongly correlated with PET (R^2= -0.26) or the coefficient of variation of mean annual rainfall/PET (R^2 = -0.12). PET and the cv MAP/PET (CV MAP/PET) were correlated (R^2 = 0.76).

Species Pool

Reliable species lists that might have served as estimates of regional species pools were not available for comparable areas or sampling efforts for all locations. Thus, to estimate the species pool size for each location we generated 1000 species rarefaction curves using the total number of individuals and species found in the six plots surveyed in each location (Colwell *et al.*, 2004). From these curves, we calculated the mean number of species present after randomly sampling 100 individuals from each location as an indicator of species pool size. We acknowledge that these estimates are unlikely to actually reflect the full diversity of study regions given our restricted sampling effort. There is no reason to suspect, however, that they are more or less accurate for one location than another. We were not trying to estimate the total species diversity in any of our sites, but these conservative estimates do allow for a robust comparison of the relative species pool sizes of our study regions. Additional support for our rarefied species pool estimates include comparisons with National Park species lists and rankings based on expected levels of diversity for each surveyed Australian rainforest type (Webb *et al.*, 1984, Harden *et al.*, 2006) is provided in Appendix D).

Rarefied species pool size data were moderately positively correlated with mean annual PET (R^2=0.56) and mean moisture availability (R^2=0.60), and negatively correlated with the seasonality of moisture availability (R^2=-0.78). These correlations are reflective of larger species pools in areas with high rainfall and warm, stable climates. Species rarefaction curves and diversity estimates were calculated with the Vegan package in R (Oksanen *et al.*, 2016).

Forest cover

The area of forest surrounding our study locations varied widely, with some samples occurring in mostly continuous rainforest and others in largely cleared landscapes. The majority of Australian rainforest now persists only in protected areas surrounded by cleared agricultural landscapes. These landscapes are largely binary combinations of forest and agriculture, making it quite straight forward and accurate to calculate rainforest cover from satellite images, unlike in other rainforest regions in the world where matrix habitats are often diverse and complex (Katovai *et al.*, 2012). Because different amounts of forest cover could influence rates of seed dispersal and colonization (e.g. Myers & Harms, 2011), we calculated percent forest cover around study locations as a proxy for isolation and fragmentation (a task made easier by the simple structure of these landscapes) over distances larger than those expected to limit seed dispersal and affect abiotic conditions around fragments (Laurance *et al.*, 1998). Specifically, we calculated percent forest cover in 5 km and 10 km radii circles around the midpoint of surveyed plots in each location using satellite images (Google Earth Pro) and ImageJ analysis software. We selected a radius of this size to measure landscape forest cover as a broad-scale measure of landscape context that is consistent with the scale of climate data (~ 5 km envelope) and species pool estimates. Forest cover was calculated as the ratio of dark green (forest) to light green (agriculture) pixels within each 5 km or 10 km radius circle by location. Again it was not our intent to capture a precise measure of forest area, rather to allow for a consistent measure to be

compared among study locations. Forest cover was correlated with various climate factors and weakly positively correlated with species pool size (see Appendix Table A5 for details).

Data analysis

To assess compositional differences between pairs of primary and secondary forest plots and locations, we conducted nMDS ordination analyses based on Jaccard's dissimilarity indices calculated between all pairs of plots (Appendix E).

To assess differences in species and functional diversity between locations, we calculated for each plot: species richness, species evenness (Shannon Index, *H*), functional richness (FRic), functional evenness (FEve), the functional divergence (FDiv) of community-weighted mean (CWM) trait values (Garnier *et al.*, 2004), the range of trait values for each continuous trait (here, the distance between the 10^{th} and 90^{th} percentiles) and the diversity of each categorical functional trait (Shannon's Index, *H*, using the number of individuals in each functional type). Trait range represents the spread of trait values within a plot, with narrower ranges reflecting more similar trait values. Height, SLA, and seed mass values were log transformed for all trait analyses to reduce skew. Multivariate functional diversity indices were calculated with the 'FD' package (Laliberté *et al.*, 2014).

To test the importance of broad-scale climate and landscape factors, we built linear mixed effects models (LMMs) for each trait and diversity measure to represent competing hypotheses about the effects of climate, species pool size, forest cover, and land-clearing on diversity response variables. Land-clearing (LC) was a categorical effect with two levels, primary or secondary rainforest, while all climate and landscape variables were treated as continuous fixed effects. "Location" (represented by letters in Figure 1) was included as a random intercept in all LMMs (Appendix F), given that we could not exclude the potential role of unmeasured spatially auto-correlated environmental factors in our analysis.

Our primary interest in developing LMMs was to examine the main effect of land-clearing and its interactive effect with climate and landscape measures on diversity. Our most complex linear effects models, thus, contained the effect of land clearing (categorical fixed effect with two levels: primary rainforest or secondary regrowth) a single climate or landscape variable (continuous fixed effect spanning six locations for the canopy and five for the understory) and an intercept only random effect at each location, with random intercepts estimated from six plots within each location. We tested 19 models per response variable (Appendix F), with the most complex models restricted to two-way interactions between land-clearing (LC), a single climate or landscape measure and main effects because of our modest sample size. Models were compared using information theoretic methods (AIC; Burnham & Anderson, 2002) with strict criteria for model selection (Appendix F). Inferences were based on effect sizes (Pseudo R^2 and overlap of 95% confidence intervals of estimates between land-clearing categories; Nakagawa & Schielzeth, 2013). We tested all subsets of the most complex models to aid in the interpretation of individual fixed effects, including intercept-only models. All analyses with LMMs and model selection were conducted in R v3.1.1 with the lme4 (Bates *et al.*, 2015) and MuMin (Barton, 2016) packages.

RESULTS

Species diversity

Species composition varied among the six study locations and between primary and secondary plots in most locations (Appendix E). Compositional differences between primary and secondary forest were least evident for mesic upland tropical rainforests from North Queensland (Location A in Fig. 1, Appendix Figure E1).

In both primary and secondary forest canopy and understory, species richness decreased as the seasonality of moisture availability increased (Figs 2a,c Table 1 and 2). Shannon's diversity

decreased similarly in the understory (Fig. 2b), but not in the canopy (Table 1). Species diversity was not significantly associated with any other factor.

Functional Diversity Indices

In both the canopy and understory, functional richness (FRic) increased with species pool size. The effect of land-clearing also appeared in well supported models for FRic but explained little variation (Figure 2d and e).

Canopy functional evenness was 12% lower in secondary than primary rainforest (Primary: Mean = 0.82 mg, 95% CI [0.77, 0.87]; Secondary: Mean = 0.73, 95 % CI [0.68, 0.79]; Table 1), with a model containing 'land-clearing' weakly supported over an intercept-only model (Table 1). In the understory, there was strong evidence (all models contained these effects) that functional evenness was related to an interaction between land-clearing and forest cover (Table 1). Functional evenness was lower in secondary than primary rainforest when surrounding forest cover was minimal, a pattern that largely disappeared as forest cover increased (Figure 1f).

There was little evidence that functional divergence was affected by any tested factor in the canopy (Table 1). In the understory, there was evidence of an interactive effect of land-clearing and variation in mean annual PET on functional divergence (Table 2). The best model for functional divergence showed little change in secondary regrowth but a decline in divergence for primary rainforest as mean annual PET increased (Figure 2g).

Functional trait distributions and diversity

Canopy

In the canopy, tree height and SLA were affected by land clearing, but the strength of these effects varied by forest cover. Trees were shorter in secondary than primary forest (based on height CWM), and differences in tree height increased as the extent of forest cover decreased

(Fig. 2d, Table 1). The best supported models for height and SLA ranges also included an effect of land-clearing that varied with surrounding forest cover, though the response patterns differed for these traits (Fig. 2h and 2i, Table 1). Height ranges were wider in secondary than primary rainforest but became more restricted in primary forest as forest cover increased (Figure 2h).

Seed mass and wood density ranges varied in relation to land clearing in the canopy but these effects did not vary strongly across climate, landscape or species pool gradients (see best models Table 1). Seed mass ranges were three times greater in primary than secondary rainforest (Primary: Mean = 176.25 mg, 95% CI [73.54, 422.36 mg]; Secondary: Mean = 48.32 mg, 95 % CI [20.17, 115.81 mg]; Table 1) and wood density ranges in primary rainforest were about twice that of secondary rainforest (Table 1, Fig. 2j). We found only weak support for the effect of land-clearing on wood density and seed mass ranges across climate gradients, species pool size or forest cover (Table 1 and Fig. 2j).

Land-clearing did not have a strong effect on the CWMs of other traits in the canopy. Small effects of land-clearing on fruit-type and dispersal diversity were evident. The effect on fruit type varied across the annual moisture availability gradient, but differences between secondary and primary rainforest were weak (Table 1; Figs 2f, g). Seed mass CWM decreased with increasing seasonality of moisture availability (Figure 2e, Table 1). There was little evidence that wood density or SLA CWMs were affected by land-clearing across broad-scale climate, species pool or forest cover gradients (Table 1).

No traits that were affected by land clearing varied strongly across climate or species pool gradients in the canopy.

Understory

In the understory, we found that land-clearing affected the CWM of seed mass and the CWM of wood density, but these effects did not vary strongly across climate, forest cover or species pool gradients. The CWM of seed mass was one-third lower (Fig. 2k) and ~10% lower for wood density in secondary than primary rainforest (Fig. 2l), with land-clearing history explaining a moderate amount of variation in CWM for both traits (Table 2). Some well-supported models supported interaction effects between land-clearing broad-scale climate, species pool size, or forest cover gradients on wood density CWM but these interactions explained very little extra variation over models with land-clearing as the only main effect ($R^2m < 0.05$, Table 2). There was an interactive effect of land-clearing and forest cover on wood density range. Wood density range changed little with forest cover (10 km radius) in primary forest, but increased substantially in secondary rainforest (Fig. 2n, Table 2). Land-clearing did not appear to affect the CWM or range of SLA and height, the range of seed mass, or the diversity of dispersal modes and fruit/seed type (Table 2).

Similar to results for the canopy, no traits that were affected by land clearing varied strongly across climate or species pool gradients in the understory.

Summary of results

Consistent with our predictions, we found that wetter and more tropical sites had higher richness of canopy species, but patterns of species richness did not differ between primary and secondary forests. Secondary forests had higher understory seed masses and wood densities in wetter and more tropical sites. Sites with larger regional species pools had higher functional richness in both canopy and understory communities. Regional species pool size was not associated with recovery of species or functional diversity in secondary forests. Habitat fragmentation was associated with recovery in secondary forests. Secondary forests in fragmented habitats had lower functional trait

evenness, species with more variable and shorter overall heights, a narrower range of leaf functional traits, and narrower range of wood densities than primary forests.

DISCUSSION

The recovery of species and functional diversity 50-60 years post logging were largely decoupled, with no species richness, but significant functional diversity, differences (primarily for individual traits) found between primary and secondary forests. The only ecosystem factor significantly associated with differences in the diversity of primary and secondary forests was landscape forest cover, and then only for some functional diversity indices and trait means and ranges. Results provide little support for predictions that the recovery of forest species and functional diversity should vary systematically along regional climate, productivity and species pool gradients, a finding consistent with studies assessing the recovery of rainforest structural attributes (Norden *et al.*, 2015).

Patterns of Species and Functional Diversity

Species richness in both primary and secondary forests decreased as the seasonality of moisture availability increased; a pattern reflecting that sub-tropical forests have fewer species than tropical forests. Variation in the composition of species in paired primary and secondary forests, mirror patterns observed for functional diversity, which are discussed in detail below.

Differences in the functional diversity and specific trait means and ranges found in primary verses secondary forests varied widely suggesting that multiple processes are important for the reassembly of forests. For example, the range of seed mass and wood density observed in secondary forest canopies were narrower than in primary forest, with no correlated reduction in species diversity. This pattern arises from the absence in secondary regrowth of species with the smallest and/or largest seeds and lowest and highest wood densities, and their replacement by species with trait values closer to the mean. An increase in trait similarity (or loss of extremes),

however, was not observed for all traits. For example, maximum height ranges were wider in secondary than primary forests, particularly in highly fragmented landscapes. It could be that reduced competition for light in recovering secondary forests could allow species with a broader range of maximum heights to persist in secondary forest (Schamp & Aarssen, 2009) or dispersal limitation might restrict arrival at regrowth sites, thus limiting the range of growth strategies. While these mechanisms require further testing, they are consistent with the divergent trait patterns we observed.

The observed changes in trait but not species diversity between primary and secondary forests suggest high levels of functional redundancy in regional species pools. Differences in the phylogenetic structure of primary and secondary forests may also contribute to this pattern (Letcher *et al.*, 2012). Nevertheless, our results suggest that many species are functionally suitable for recolonization of cleared rainforest patches, which can support similar numbers of species as primary rainforest.

The Regional Species Pool and Climate

Our results demonstrate that climate and species pool size are less important than the extent of surrounding forest cover for explaining differences in functional trait diversity following land-clearing. Theoretical expectations suggest that large regional species pools typically possess greater functional redundancy and response diversity than systems with smaller species pools (Díaz & Cabido, 2001), which are often found in low or variable rainfall environments with extreme temperature conditions (e.g., Gaston, 2000). Thus, we predicted that species and functional diversity would not be related across primary and secondary regrowth sites in our wet tropical sites, which had the largest regional species pools, highest rainfall and warm, climates with low seasonal variability. Correspondingly, we predicted stronger relationships in more seasonal and drier sites with smaller species pools. As expected, we found no relationship among the differences in species and functional trait diversity between primary and secondary regrowth

forests in our wet tropical sites. Contrary to our expectations, however, we also found no such relationship in drier sites with smaller regional species pools. Given our focus on subtropical and tropical rainforest communities, which have high species diversity and larger regional species pools relative to many other forest types (such as temperate or boreal forests), deviations from our predictions about less diverse forests may result from a lack of truly low diversity sites. Our sites occurred across quite broad climate and species pool gradients, differing by as much as 2000 mm mean annual rainfall, 7°C mean daily minimum and maximum temperatures and 63 species per 100 trees sampled. The lack of an association between species and trait diversity in response to land-clearing patterns across these gradients suggest that if there are stronger associations between species and functional trait diversity in lower diversity and/or lower productivity systems, they are not evident above even the lowest thresholds of diversity/productivity examined here.

Forest Fragmentation

The strong relationship between percent forest cover at the landscape-scale (fragmentation extent), the range and CWM of multiple functional traits, as well as the multivariate measure of functional divergence, are probably due to strong effects of landscape configuration on the rate of propagule supply, species interactions, and microclimate conditions that affect forest recovery (Kooyman *et al.*, 2013b). Rainforests have soil seed banks dominated by a small number of early successional species (Hopkins *et al.*, 1990); thus, surrounding forests act as important sources of propagules for recolonization and community reassembly should be faster in regrowth forests surrounded by continuous forest than isolated remnants (Chazdon, 2003). In Amazonian rainforests, habitat fragmentation has also been linked to declines and loss of large, slow growing (i.e. high wood density) trees (Laurance *et al.*, 1998). The patterns observed in this study reflect similar responses to loss of forest cover. For example, trees in the canopy of secondary forest were, on average, taller with a narrower height range and were similar in height to primary forest

at sites in high forest cover landscapes but became, on average, shorter with a wider range of heights in areas with little surrounding forest cover. These changes in height distributions possibly reflect increased competition for light due to faster rates of recovery and canopy closure in landscapes with more forest cover (Chazdon, 2003). Tree species represented by saplings in the secondary forest understory also generally had lower wood density and narrower ranges when surrounded by less forest. These effects translated to secondary regrowth exhibiting greater functional unevenness than primary rainforest at low landscape forest cover, but becoming more similar in areas with high forest cover. Thus, the understory of more isolated patches of secondary forest appear to lack recruits of slow-growing and taller forest species compared to those surrounded by more continuous forest, at least 50-60 years post-clearing. This may result in permanent losses of larger and slow-growing species if land-use continues to create highly fragmented landscapes dominated by secondary regrowth.

Functional traits exhibited different responses in the canopy and understory to variation in percent forest cover in the landscape. This pattern likely reflects differences in the re-assembly processes that affect the diversity and distribution of traits between forest strata, which are environmentally distinct and composed of species in different age classes. For example, maximum tree height CWM and ranges differed between primary and secondary forest in the canopy, depending on the amount of surrounding forest cover, a pattern not evident in the understory. Differences in height responses in canopy and understory species assemblages can arise from differences in how species compete for light between these forest strata. Even in secondary rainforest, the understory was highly shaded by the canopy (average canopy cover was 90±3 % in primary and 79±2 % in secondary forest). Traits associated with shade tolerance (e.g., low SLA) will thus likely be more important for understory species and recruiting seedlings, while traits associated with light pre-emption will be more important in adult canopy trees (e.g. maximum height). Wood density and seed mass ranges were narrower, without a corresponding change in the community-weighted means (CWM), in the canopy of secondary forest. This was

not reflected in the understory, suggesting that there are stronger restrictions on growth and reproductive strategies of adult species in the canopy than recruiting seedlings in the understory. An observed shift to lower wood density and seed mass in the understory of secondary forest could reflect a directional shift towards faster growing species with less competition tolerant seedlings (i.e. gap species). Other studies have shown that these patterns can result from reduced competition in the secondary forest understories (Lasky *et al.*, 2014). The mixture of understory specialists and canopy species seedlings complicate the interpretation of understory patterns, as factors influencing these subgroups also likely differ as they do between seedlings and adults of canopy trees.

Conclusions

Our findings provide empirical evidence that broad-scale variation in climate and species pool size do not have generalizable, strong effects on species and trait diversity responses to land-clearing in a consistent forest type - Australian rainforest on nutrient-rich basalt soils. Other recent studies have also concluded that local scale factors are more important than broad ecological or environmental features in determining differences between primary and secondary forests (Norden *et al.*, 2015, Boukili & Chazdon, 2017). The often-independent responses of species and trait diversity to land-clearing, climate and landscape attributes highlight that species diversity should not be used as a proxy for functional diversity. There was, however, strong evidence that, in human-modified landscapes, the extent of forest fragmentation is useful for predicting functional differences between primary and secondary regrowth forests. Though previously shown for specific individual landscapes (Girao *et al.*, 2007; Mendes *et al.*, 2016), our study is the first to show that the extent of fragmentation in a landscape is more important than large-scale climate and productivity gradients for explaining forest recovery across landscapes.

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APPENDICES

Appendix A: Supplementary method tables.

Table A1: Correlation matrix of continuous traits

Table A2: Details of categorical traits

Table A3: Details of climate variables

Table A4: Climate and landscapes variables

Table A5: Correlation matrix of landscape and climate variables

Appendix B: Information on unpublished trait databases

Appendix C: Methods for calculating multivariate diversity indices

Appendix D: Supporting information for species pool estimate.

Figure D1: Rarefaction curves for species pool estimations

Table D1: Correlations between rarefied species pool estimates and alternative estimation approaches

Table D2: Correlations between the total number of individuals sampled, estimated species pools, and forest cover estimates.

Appendix E. Analysis of community composition

Fig E1. nMDS ordination of species composition

Appendix F: Model selection methods and results.

Tables F1-F30, model selection results for each trait's CWM and range in the canopy and understory strata

BIOSKETCH

MAS is a community ecologist with experience in marine and plant systems and is interesting in understanding the mechanisms underlying community diversity. The research team is composed of plant ecologists interested in the impacts of human activities on plant diversity, with diverse expertise in botany, phylogeography, Australian rainforests and ecological theory. This project idea was developed by MMM, SPB, PAV, DJM and JWM during an ARC-NZ Network for Vegetation Function workshop on functional diversity in human-altered landscape led by MMM. Data were collected by MAS and HRL with data contributions from RRK. MMM, MAS, SPB, and PAV designed the field study and MAS conducted all analyses and led manuscript production, with input from all authors.

DATA ACCESSIBILITY

All data are available through DRYAD DOI:// XXXXX (will be provided upon acceptance).

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Tables

Table 1. Best supported models for species and functional trait diversity measures in the canopy. Model coefficients are shown in Appendix F. All models contained study location as a random intercept, corresponding to locations in Fig. 1. Responses with asterisks and models in bold are those that had strong support for an effect on response variables (see methods). Shown next to best models are the ΔAICc of the most supported model to an intercept-only model, the

marginal co-efficient of determination (R^2m) for fixed effects and conditional co-efficient of determination R^2c for fixed and random effects that were used to determine the 'best' model. ΔAICc in bold are those with good to strong support (ΔAICc >5) over the null 'intercept only' model. LC = land-clearing; cvMI = coefficient of variation in the moisture index, MI = mean annual moisture index, PET = mean annual potential evapotranspiration; SpPool = size of the species pool at each location; Forest (5 km) = forest cover within a 5 km radius, Forest (10 km) = forest cover within a 10 km radius of plots. See Appendix F for model selection methods.

Response	Best model(s)	ΔAICc	R^2m	R^2c
	Diversity Metrics			
Species richness*	**cvMI**	**5.01**	0.57	0.74
Shannon's diversity	LC+cvMI	2.96	-	-
Functional* Rich	**LC + SpPool**	6.81	0.49	0.57
	SpPool	5.54	0.44	0.51
Functional Evenness	LC	4.71	-	-
Functional Diverg.	LC	3.42	-	-
	Trait CWM			
Wood density	LC	0.82	-	-
Height*	**LC + Forest(5km) + LC x Forest(5km)**	**17.78**	0.51	0.69
SLA	LC+MI + LC x MI	3.20	-	-
Seed Mass*	**LC + cvMI**	**14.53**	0.67	0.77
	LC + PET	**14.33**	0.66	0.77
	LC	**7.47**	0.08	0.77
	Trait Range			
Wood density*	**LC+Forest(5km) + LC x Forest(5km)**	**15.82**	0.49	0.49
	LC + SpPool	**15.77**	0.45	0.45
	LC	**15.42**	0.40	0.40
	LC + PET	**14.79**	0.43	0.43
	LC + cvMI	**14.30**	0.43	0.43
	LC + Forest(10km) + LC x Forest(10km)	**14.26**	0.47	0.47
	LC + Forest(5km)	**14.06**	0.42	0.42
	LC + cvMI + LC x cvMI	**14.03**	0.47	0.47
Height*	**LC + Forest(5km) + LC x Forest(5km)**	**31.80**	0.67	0.73
SLA*	**LC + Forest(10km) + LC x Forest(10km)**	**20.72**	0.45	0.70
	LC + Forest(5km) + LC x Forest(5km)	**18.17**	0.47	0.66
Seed Mass*	**LC**	**5.82**	0.17	0.38

	Categorical trait diversity			
Dispersal mode*	**LC + Forest(5km)** + **LC** x **Forest(5km)**	**13.73**	0.19	0.86
	LC + **MI**	**11.88**	0.39	0.83
	LC	**11.75**	0.09	0.83
	LC + **Forest(10km)** + **LC** x **Forest(10km)**	**11.71**	0.11	0.85
Fruit seed*	**LC** + **cvMI** + **LC** x **cvMI**	**5.47**	0.26	0.60

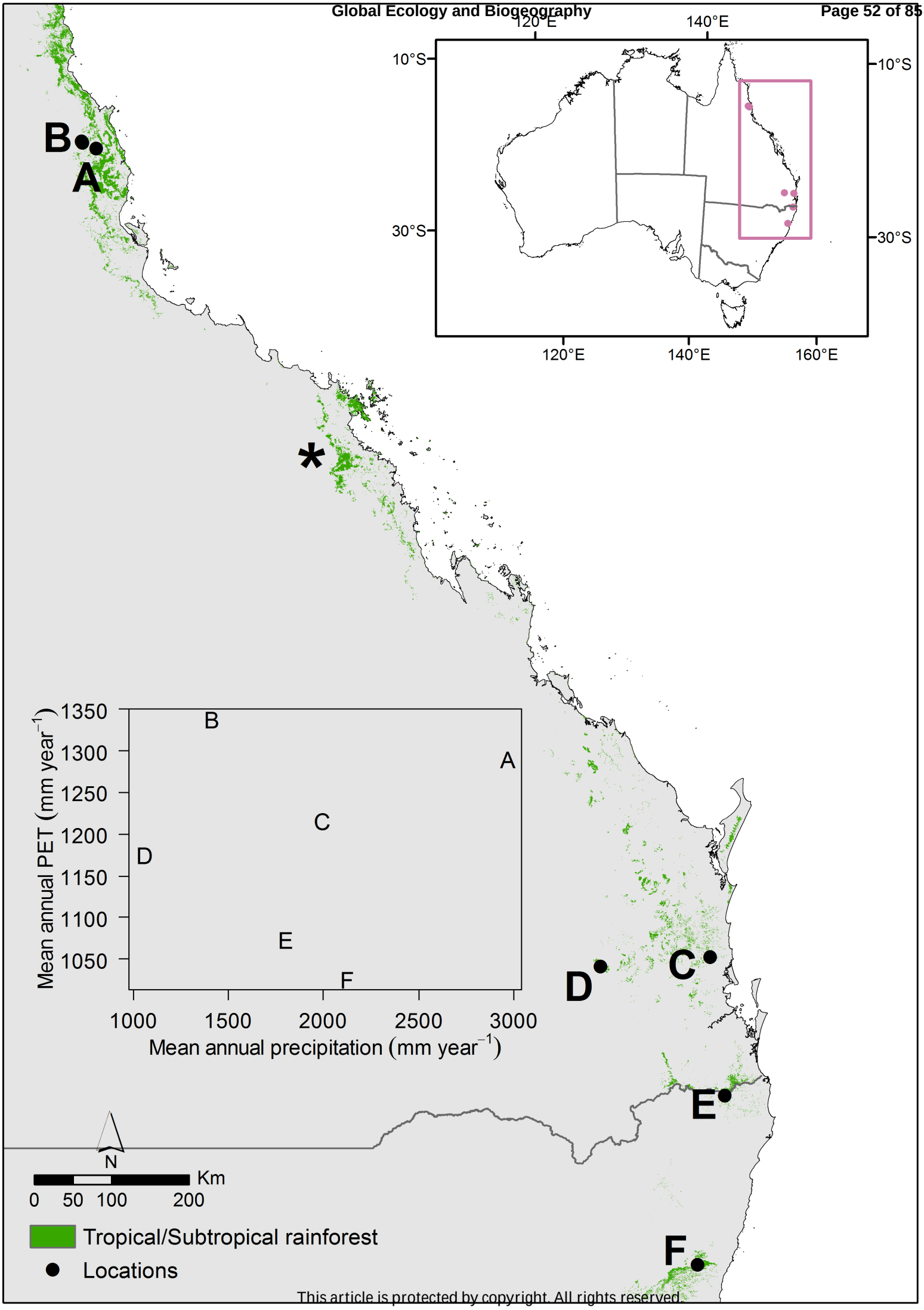
Table 2. Best supported models for species and functional trait diversity measures in the understory. All models contained study location as a random intercept, corresponding to locations in Fig. 1. Responses with asterisks and models in bold are those that had strong support for an effect on response variables (see methods). Shown next to best models are the ΔAICc of the most supported model to an intercept-only model, the marginal co-efficient of determination (R^2m) for fixed effects and conditional co-efficient of determination R^2c for fixed and random effects that were used to determine the 'best' model. ΔAICc in bold are those with good to strong support (ΔAICc >5) over the 'intercept only' model. See Table 1 for further details and Appendix F for model selection methods.

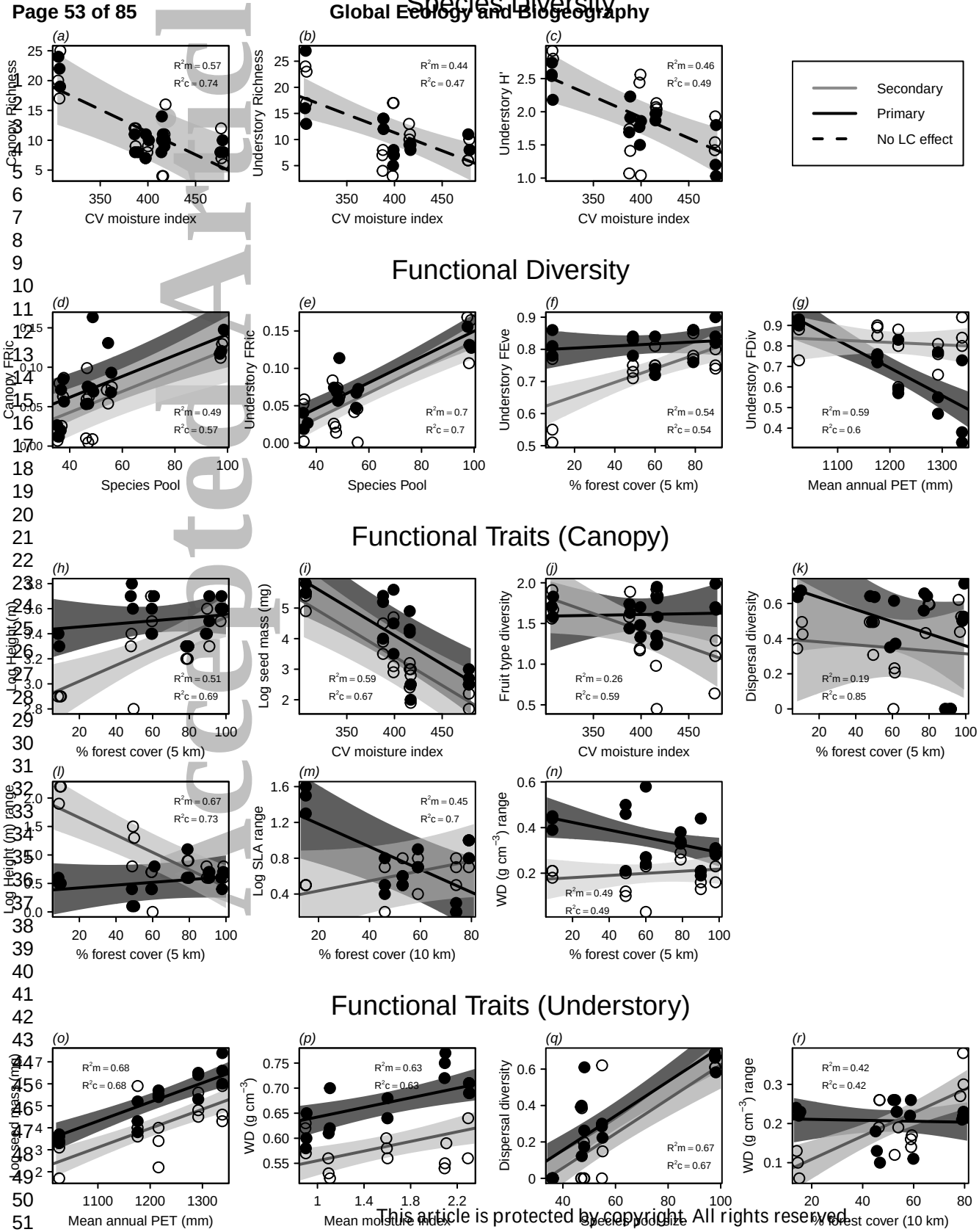
Response	Best model(s)	ΔAICc	R^2m	R^2c
	Diversity Metrics			
Species rich*	**cvMI**	**5.12**	0.44	0.47
Shannon's diversity*	**cvMI**	**5.13**	0.46	0.49
Functional Richness*	**SpPool**	**10.43**	0.67	0.67
	LC + SpPool	**9.72**	0.70	0.70
	LC + SpPool + LU x Spool	**7.2**	0.71	0.71
Functional *Even.	**LC + Forest(10km) + LC x Forest(10km)**	**14.14**	0.54	0.54
	LC + Forest(5km) + LC x Forest(5km)	**13.96**	0.54	54.00
	LC + Forest(10km)	**11.32**	0.44	0.44
	y = **LC + Forest(5km)**	**11.11**	0.44	0.44
Functional Diverg.*	**LC + PET + LC x PET**	**17.22**	**0.60**	**0.60**
	Trait CWM			
Wood density*	**LC + MI + LC x MI**	**20.33**	0.63	0.63
	LC + MI	**20.27**	0.58	0.58
	LC + Forest(10km)	**18.02**	0.55	0.55
	LC	**15.50**	0.43	0.53
Height	Intercept only	0.00	-	-
SLA	Forest(5km)	0.58	-	-
Seed Mass*	**LC + PET**	**21.11**	0.69	0.69
	LC + PET+ LC x PET	**19.45**	0.70	0.70
	Trait Range			
Wood density*	**LC + Forest(10km) + LC x Forest(10km)**	**5.90**	0.42	0.42

Height	LC + PET + LC x PET	1.76	-	-
SLA	PET	3.08	-	-
Seed Mass	LC + PET + LC x PET	3.18	-	-
	Categorical trait diversity			
Dispersal mode*	**LC** + **Spool**	**12.25**	0.68	0.68
	SpPool	**12.23**	0.64	0.64
	SpPool + **LC** x **SpPool**	**9.55**	0.68	0.68
Fruit seed*	**PET**	**8.05**	0.47	0.47

Figure 1. Map of study locations. Study locations are (A) mesic upland tropical rainforest; (B) dry upland tropical rainforest; (C) mesic warm subtropical rainforest; (D) dry subtropical rainforest; (E) mesic warm subtropical rainforest; and (F) cool subtropical rainforest. The asterisk indicates a major rainforest that was not sampled due to lack of rainforest subtypes on tertiary basalt soils. *Top right inset:* the broad geographic area spanning latitudes 17 to 30° S within which study sites were located. *Left inset:* Bi-plot showing variation in mean annual precipitation and potential evapotranspiration among study locations. Letters in biplot correspond to letters indicating study locations.

Figure 2. Responses of species diversity and functional trait measures to land-clearing along broad scale climate and landscape gradients. Shown here are those responses based on the "best" linear mixed effects models with strong model support (Table 1 and 2, Appendix F). In cases where several models shared similar support we only show estimates of the most supported models. Not shown are functional traits that responded to land-use but not climate measures (reported in text). In species diversity plots dashed lines represent responses to climate gradients that did not differ between primary and secondary rainforest (i.e., no land-clearing effect). In functional trait plots, the solid black lines represent estimated responses in primary rainforest and solid grey lines represent estimated responses in secondary rainforest based on LMMs. Shaded areas are 95 % confidence intervals based on estimates from LMMs with study location as a random intercept. Circles are raw values of community weighted means (CWM's) or trait ranges, with open circles for secondary rainforest and solid for primary rainforest. R^2m values are the coefficients of determination for fixed effects while R^2c are the coefficients of determination for fixed and random effects.





Supplementary Information

Appendix A. Supplementary method tables.

Table A1. Correlation matrix of continuous traits. Correlations are based on species mean trait values for all species found across study sites. Correlations include untransformed and log transformed values.

	Ht	WD	SLA	SDM	logSLA	logWD	logSDM	logHT
Ht	1.00	-0.22	-0.21	0.11	-0.21	-0.22	0.12	0.93
WD		1.00	-0.10	0.06	-0.11	0.98	0.23	-0.20
SLA			1.00	-0.09	0.95	-0.13	-0.28	-0.20
SDM.mg				1.00	-0.10	0.07	0.51	0.11
logSLA					1.00	-0.13	-0.25	-0.20
logWD						1.00	0.26	-0.20
logSDM							1.00	0.19
logHT								1.00

Key: Ht= species maximum height (m); WD = wood density (g/cm^{-3}); SLA = specific leaf area ($mm\ mg^{-1}$); SDM= seed dry mass (mg)

Table A2. Details of trait categories used to calculate diversity for fruit type and dispersal mode. Species level information on fruit type and dispersal modes was obtained from published floras: Cooper & Cooper, 2004; Floyd, 1989; Stanley & Ross, 1989; Williams *et al.*, 2009.

Fruit category	**Description**
Achene (plumed)	Achene with plume for wind dispersal
Berry	Indehiscent fleshy fruit derived from single ovary with seeds embedded in fleshy tissue
Capsule(N)	Capsule containing seed without known reward, indicating passive dispersal
Capsule(R)	Capsule containing seed with food reward, indicating animal dispersal (e.g. aril, elaisome, fleshy funicle)
Capsule(W)	Capsule containing wind dispersed seed (e.g. samara, winged or plumed seed)
Cone	Reproductive organ of coniferous plants
Drupe	Indehiscent fruit with fleshy exocarp and woody endocarp
Fig	Involute, nearly closed fleshy receptacle with many small flowers arranged on the inner surface characteristic of *Ficus* spp. Dispersed by fruit-eating animals.
Follicle(N)	Follicle containing seed without known reward (indicating passive dispersal)
Follicle(R)	Follicle containing seed with food reward indicating animal dispersal (e.g. aril, elaisome, fleshy funicle)
Follicle(W)	Follicle containing wind dispersed seed (e.g. samara, winged or plumed seed)
Nut	Dry hard indehiscent one-seeded fruit
Pod(N)	Pod containing seed without known reward (indicating passive dispersal)
Pod(R)	Pod containing seed with food reward indicating animal dispersal (e.g. fleshy funicle)
Samara	Dry indehiscent fruit with a wing

Dispersal mode category	**Description**
Flying	Dispersal includes birds and bats
Non-flying	Dispersal restricted to non-flying vertebrates including mammals other than bats and cassowary (*Casuarius casuarius*)
Passive	Passively dispersed (i.e. seeds without specialised structures for wind dispersal or food rewards)
Wind	Wind dispersed

Table A3. Climate variables, with definitions and units, assessed in models. All data are interpolated from the Australian SILO database of historical climate data records provided by the Bureau of Meteorology (https://www.longpaddock.qld.gov.au/silo/about.html). PET is the expected amount of evaporation that would occur if water were unlimited. PET incorporates measures of temperature, solar irradiation, day length and wind speed into one metric as a proxy for the amount of energy available in an environment (Thornthwaite, 1948). The coefficient of variation in climate measures represents their variability or seasonality. All rainfall measures were strongly correlated with each other (mean annual rainfall, Coefficient of Variation (CV) of rainfall, wettest and driest month and quarter; Appendix Table A5), while PET and temperature measures (mean annual T_{min} and T_{max} and CV of temperature; Appendix Table A5) were strongly correlated with each other, and there were also moderate levels of correlation between mean rainfall and energy/temperature measures (Appendix Table A5).

Climate Variable Name	Definition
Mean Annual Rain	mean annual precipitation (mm y^{-1})
Driest month	mean precipitation driest month (mm $month^{-1}$)
Driest quarter	mean precipitation driest annual quarter (mm $quarter^{-1}$)
Wettest month	mean precipitation wettest month (mm $month^{-1}$)
Wettest quarter	mean precipitation wettest quarter (mm $quarter^{-1}$)
CV Rain	coefficient of variation of daily precipitation
PET	mean annual potential evapotranspiration (mm y^{-1})
Min temp	mean daily temperature minimum (°C day^{-1})
Max temp	mean daily temperature maximum (°C day^{-1})
PET CV	coefficient of variation in daily potential evapotranspiration
CV max temp	coefficient of variation of daily temperature maximum
CV temp min	coefficient of variation of the daily temperature minimum

Table A4 - Climate and landscape variables. Climate measures are calculated from daily values from 1950 until December 2013 interpolated at the scale of ~ 0.5 x 0.5 degrees (~5 x 5 km). Climate values were obtained from the SILO climate database (https://www.longpaddock.qld.gov.au/silo/about.html). Species pool size was estimated from species rarefaction curves (Colwell & Coddington, 1994; Colwell *et al.*, 2004) using the total number of individuals and species found in the six plots from each location and calculating the mean number of species (from 1000 iterations) present after sampling 100 individuals from each location as an indicator of species pool size. Forest cover was estimated within either a 5 km or 10 km radii around study locations from a central point among rainforest plots in each location, using satellite images (Google Earth Pro) and the image analysis software ImageJ. Highlighted in bold are the three climate variables (MI, cvMI and PET) that were selected as proxies for climatic differences between sites. See methods for rationale for selection of these variables and Table A5 for correlations between variables.

Loc	Loc name	MAP	DrMP	DrQP	WMP	WQP	cvP	MMI	DMI	**MI**	**cvMI**	**PET**	DaTmin	DaTmax	cvPET	cvTmax	cvTmin	SpPool	For5	For10
F	Dorrigo NP Border Ranges	2122.86	21.08	152.33	543.83	1021.77	311.54	2.07	3.83	2.10	478.11	1026.01	9.21	18.94	47.57	24.38	51.51	29	49.00	53.00
E	NP	1801.90	19.59	140.95	471.40	880.42	305.46	1.68	2.96	1.70	416.89	1074.01	11.01	19.98	45.48	22.33	40.47	35	98.00	74.00
D	Bunya Mnts NP	1055.46	11.03	96.54	239.70	476.71	322.06	0.90	1.55	0.91	398.93	1176.14	9.16	20.51	46.14	26.45	59.28	25	90.00	59.00
C	Maleny	1990.04	15.57	141.92	544.44	1032.66	327.73	1.64	2.81	1.66	415.67	1216.29	13.93	23.46	41.07	17.27	33.01	32	60.00	46.00
B	Curtain Fig NP	1408.57	6.93	62.00	430.43	866.94	289.98	1.05	1.52	1.06	387.58	1338.39	15.87	25.79	33.83	13.49	23.88	29	9.00	15.00
A	Topaz	2967.10	25.47	195.69	792.31	1637.23	240.30	2.30	3.61	2.32	307.47	1291.54	16.25	25.28	34.57	13.60	22.39	47	79.00	79.00

Key: **Loc** = Location corresponding to Figure 1; **Loc Name** = names of location; **MAP** = mean annual precipitation (mm y^{-1}); **DrMP** = mean precipitation driest month (mm $month^{-1}$); **DrQP** = mean precipitation driest quarter (mm $quarter^{-1}$); **WMP** = mean precipitation wettest month (mm $month^{-1}$); **WQP** = mean precipitation wettest quarter (mm $quarter^{-1}$); **cvP** = coefficient of variation of precipitation; **MMI** = mean moisture index (mean rainfall/mean PET); **DMI** = daily moisture index (mean daily rainfall/mean daily PET); **MI** = mean annual moisture index (mean annual rainfall/mean annual PET); **cvMI** = coefficient of variation of mean annual moisture index; **PET** = mean annual potential evapotranspiration (mm y^{-1}); **DaTmin** = mean daily temperature minimum (°C day^{-1}); **DaTmax** = mean daily temperature maximum (°C day^{-1}); **cvPET** = coefficient of variation in potential evapotranspiration; **cvTmax** = coefficient of variation Tmax; **cvTmin** = coefficient of variation Tmin; **SpPool** = species pool size (species per 100 individuals sampled); **For5** = % forest cover within 5 km radius; **For10** = % forest cover within 10 km radius.

Table A5. Correlation matrix of landscape and climate variables. See Table A3 for description of how values were estimated. Highlighted in bold are the three climate variables (MI, cvMI and PET) that were selected as proxies for climatic differences between locations. See methods for rationale for selection of these variables.

		Precipitation and Moisture Availability										Temperature and Energy								
		MAP	DrMP	DrQP	WMP	WQP	cvP	MMI	DMI	**MI**	**cvMI**	**PET**	DaTmin	DaTmax	cvPET	cvTmax	cvTmin	SpPool	For5	For10
Precipitation and Moisture Availability	MAP	1.00	0.87	0.90	0.98	0.97	-0.70	0.95	0.85	0.94	-0.41	0.06	0.45	0.27	-0.33	-0.47	-0.52	0.81	0.13	0.51
	DrMP		1.00	0.97	0.78	0.74	-0.47	0.94	0.94	0.94	-0.16	-0.38	-0.01	-0.21	0.13	0.00	-0.09	0.52	0.50	0.81
	DrQP			1.00	0.81	0.78	-0.45	0.93	0.90	0.93	-0.24	-0.27	0.07	-0.10	0.06	-0.08	-0.15	0.57	0.51	0.79
	WMP				1.00	0.99	-0.73	0.90	0.78	0.90	-0.45	0.19	0.58	0.41	-0.47	-0.61	-0.66	0.84	-0.01	0.37
	WQP					1.00	-0.79	0.86	0.72	0.85	-0.54	0.28	0.63	0.48	-0.54	-0.65	-0.69	0.90	-0.02	0.37
	cvP						1.00	-0.51	-0.32	-0.51	0.80	-0.50	-0.66	-0.59	0.70	0.65	0.66	-0.92	0.03	-0.30
	MMI							1.00	0.97	1.00	-0.12	-0.26	0.17	-0.04	-0.05	-0.21	-0.29	0.60	0.20	0.57
	DMI								1.00	0.97	0.09	-0.47	-0.04	-0.25	0.18	-0.01	-0.09	0.41	0.25	0.58
	MI									1.00	-0.12	-0.26	0.17	-0.04	-0.04	-0.21	-0.28	0.60	0.20	0.57
	cvMI										1.00	-0.76	-0.72	-0.75	0.76	0.65	0.63	-0.78	-0.15	-0.27
Temperature and Energy	**PET**											1.00	0.86	0.96	-0.92	-0.82	-0.73	0.56	-0.43	-0.41
	DaTmin												1.00	0.96	-0.97	-0.99	-0.97	0.73	-0.43	-0.25
	DaTmax													1.00	-0.98	-0.94	-0.88	0.67	-0.48	-0.37
	cvPET														1.00	0.96	0.91	-0.73	0.49	0.33
	cvTmax															1.00	0.98	-0.72	0.50	0.30
	cvTmin																1.00	-0.70	0.41	0.20
	SpPool																	1.00	-0.08	0.26
	For5																		1.00	0.90
	For10																			1.00

Key: **MAP** = mean annual precipitation (mm y^{-1}); **DrMP** = mean precipitation driest month (mm $month^{-1}$); **DrQP** = mean precipitation driest quarter (mm $quarter^{-1}$); **WMP** = mean precipitation wettest month (mm $month^{-1}$); **WQP** = mean precipitation wettest quarter (mm $quarter^{-1}$); **cvP** = coefficient of variation of precipitation; **MMI** = mean moisture index (mean rainfall/mean PET); **DMI** = daily moisture index (mean daily rainfall/mean daily PET); **MI** = mean annual moisture index (mean annual rainfall/mean annual PET); **cvMI** = coefficient of variation of mean annual moisture index; **PET** = mean annual potential evapotranspiration (mm y^{-1}); **DaTmin** = mean daily temperature minimum (°C day^{-1}); **DaTmax** = mean daily temperature maximum (°C day^{-1}); **cvPET** = coefficient of variation in potential evapotranspiration; **cvTmax** = coefficient of variation Tmax; **cvTmin** = coefficient of variation Tmin; **SpPool** = species pool size (species per 100 individuals sampled); **For5** = % forest cover within 5 km radius; **For10** = % forest cover within 10 km radius.

Appendix B. Information on unpublished trait databases

Species mean trait values for seed mass and wood density were obtained from published and unpublished trait databases. Descriptions of the methods for compiling published databases can be found in the associated published metadata (e.g. Chave *et al.*, 2009; Zanne *et al.*, 2009), while further details on unpublished databases are provided for traits below.

Seed mass

Species mean seed mass values for tropical rainforest species were taken from Grubb & Metcalfe (1996), unpublished datasets of directly measured seeds (Metcalfe, unpublished data), Metcalfe & Grubb (unpublished data) and the RBG Kew seed database (Liu *et al.*, 2008) (sites A and B, Figure 1). Species mean seed masses for subtropical rainforest species were obtained from a database curated by RM Kooyman (with the National Herbarium of NSW, Royal Botanic Gardens & Domain Trust, Sydney), which includes most Australian woody subtropical rain forest taxa. Seed volume (mm^3) was calculated using maximum dimensions (length, width, depth) of embryo plus endocarp, and converted to dry weight mass (SDM; mg) (following Moles *et al.*, 2005a; Moles *et al.*, 2005b). Further descriptions can be found in Kooyman *et al.* (2013).

Wood density

Species mean wood density values for tropical tree species were obtained from a database curated by DJ Metcalfe and consisted of measured densities for 168 species from CSIROs permanent rainforest plots (Bradford *et al.*, 2014) and estimated densities for nine species. Measured densities were compiled from field sampling (density determined after Heinrichs & Lassen, 1970), or conversion of air-dry data from Cause *et al.* (1989), Hyland (1983), or Hyland (1989). Estimated densities for nine further species were given as mean values of congeners or confamilials in existing CSIRO wood density databases. Wood density species mean estimates for adults of subtropical species were

obtained from RM Kooyman's database consisting of values extracted from published sources, and where necessary converted from dry weight (kg m^3) to basic density (Chave *et al.*, 2009). Further description can be found in Kooyman *et al.* (2013).

Appendix C. Methods for calculating multivariate diversity indices

Both continuous and categorical traits are included in multivariate diversity indices, which use principal co-ordinates analysis (PCoA) of a Gower dissimilarity matrix of abundance weighted traits to estimate the dispersion of traits in multivariate trait-space (Villéger et al. 2008). Gower dissimilarity matrices use distance based measures to deal with "mixed" data of continuous, binary, ordinal and nominal data. Functional richness (FRic) corresponds to the convex hull volume of traits in multivariate trait space, which is the trait space occupied by a community and represents extreme trait values without taking into account species relative abundances (Cornwell *et al.*, 2006). Functional evenness (FEve) is measured as the regularity of traits and their abundances across a minimum spanning tree through multivariate functional trait space. FEve is highest when trait abundances are evenly distributed and lowest when they are uneven (Villéger *et al.*, 2008). Functional divergence (FDiv) is measured as the deviation of abundance weighted trait distances for the mean abundance weighted trait distance from the center of multivariate functional trait space and provides a measure of the relative abundances of functionally distinct species. High levels of FDiv occur when the most abundant species are functionally very dissimilar (for detailed explanation of the calculation of these indices see Villéger *et al.*, 2008). Both FEve and FDiv range from 0-1.

Appendix D. Supporting information for species pool estimate.

Species pool estimation using rarefaction for the same number of individuals can be unrepresentative of real species pools if species accumulation curves cross (i.e. relative species pool estimates change as more individual are sampled). Some regions can support greater overall numbers of individuals due to variation in climate and surrounding forests, which can correspond to larger species pools due to sampling effects. Rarefied species also may not be a good representation of real species pools where this is the case. We consider our rarefied estimates of species pools to be robust representations of regional species pool size for several reasons. First, species pool estimates based on rarefied species richness matched our general expectations of species pool sizes for dry to wet, warm to cool and tropical to subtropical rainforest types based on published floras and literature (Williams *et al.* 2009). Second, while there was some uncertainty in the ranking of species pool size based on rarefaction curves for our locations with intermediate species pools (i.e., the curves cross as more individuals are sampled), the sites with the smallest and largest species pools were consistently the lowest and highest curves, indicating that there is reliability in our rarefied estimates of species richness of sites with the smallest and largest species pools (see Appendix Figure D1). Third, rarefied species richness, total species richness at each of our locations and species pool size generated from national parks tree species lists available for five of our six sites are all highly correlated. Last, forest cover did vary significantly across sites, but it was poorly correlated with total species richness and had low to moderate correlations with the number of individuals in our site. Our sites with lower species pools (e.g., 3 in rarefaction curves which correspond to location D, Bunya Mountains in Table A1) and highest species pool (2 and 6 in rarefaction curves which correspond to location E, Border ranges and A, Topaz, respectively, in Appendix Table A1) occurred in large areas of continuous forest in 5 and 10 km radii of similar sizes.

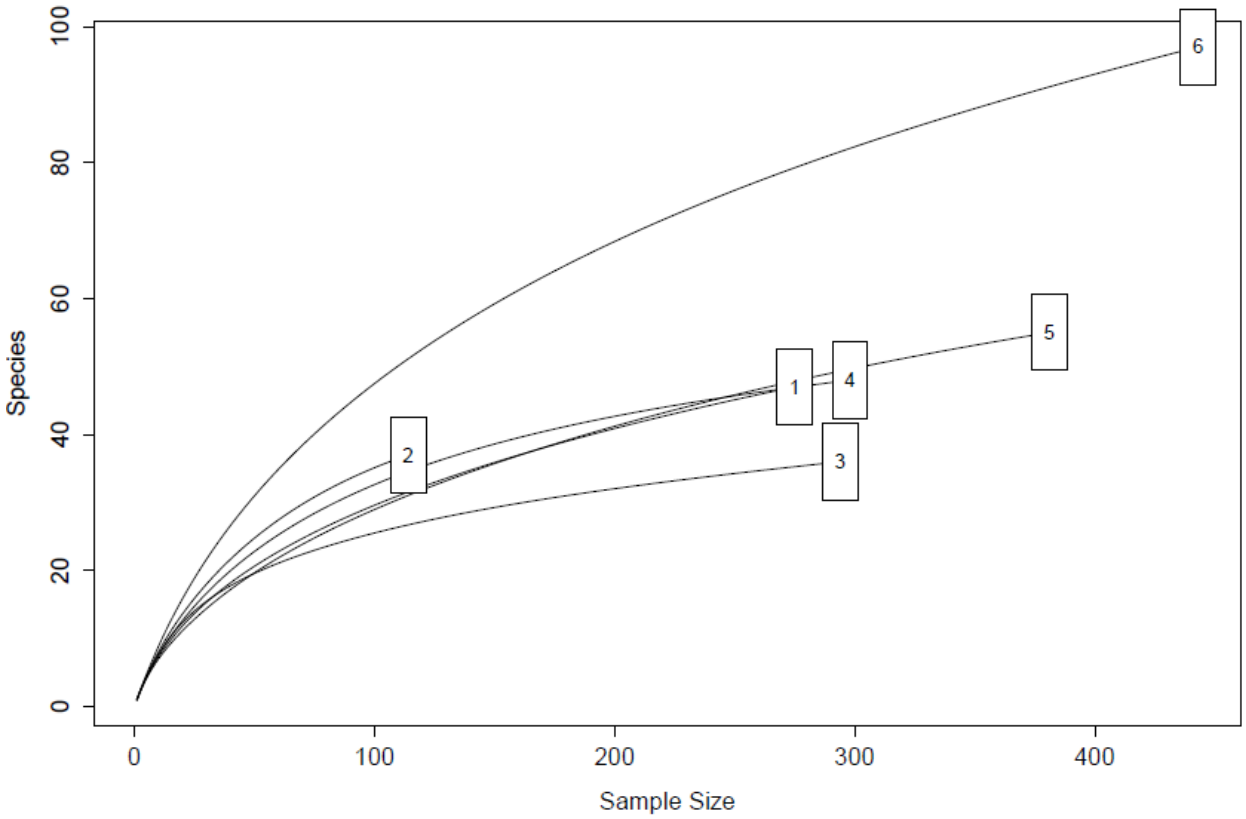


Figure D1. Rarefaction curves interpolated from all trees sampled in each location. Numbers correspond to rainforest types and locations (Figure 1, Table A4): 1- Cool Wet Subtropical Rainforest (Dorrigo, F), 2- Warm Wet Subtropical Rainforest (Border Ranges, E), 3- Dry Subtropical Rainforest (Bunya Mountains, D), 4- Warm Wet Subtropical Rainforest (Maleny, C), 5- Dry Tropical Rainforest (Curtain Fig B), 6- Wet Tropical Rainforest (Topaz, A).

Table D1. Correlations between rarefied estimates of species richness per 100 individuals sampled for each study location (rarefied species richness), total species richness at each location (total species richness) and species richness based on the number of rainforest tree species identified in national parks species lists for five of our six locations for which we could obtain species lists. Location B, Curtain Fig, a dry tropical rainforest was omitted as there were no complete species lists available.

	Rarefied species richness	Total species richness	National park species list richness
Rarefied species richness	1	0.89	0.97
Total species richness	0.89	1	0.9
National park species list richness	0.97	0.9	1

Table D2. Correlations between the total number of individuals sampled, total species richness, rarefied estimates of species richness per 100 individuals sampled in each location and the percent forested landscape cover surrounding study locations within a 5 km and 10 km radius.

	Stem density	Total species richness	Rarefied species richness	Forest cover 5km	Forest cover 10km
Stem density	1	0.74	0.34	-0.46	-0.26
Total species richness	0.74	1	0.83	-0.07	0.28
Rarefied species richness	0.34	0.83	1	0.28	0.59
Forest cover 5km	-0.46	-0.07	0.28	1	0.9
Forest cover 10km	-0.26	0.28	0.59	0.9	1

Appendix E. Analysis of community composition

We compared differences in the community composition of primary and secondary rainforest across our study locations using non-metric multidimensional scaling (nMDS) ordination of Jaccard's dissimilarity matrix based on species identity and abundance. Species composition was compared separately in the canopy and understory, consistent with analyses of trait and species diversity. Species composition differed considerably among locations in both the canopy and understory, with sites within each location generally sharing the greatest similarity. Primary and secondary forest within locations differed in both the canopy and understory strata, with the smallest differences between site pairs occurring in location A (Fig 1; both canopy and understory) and location E (Fig 1; canopy only).

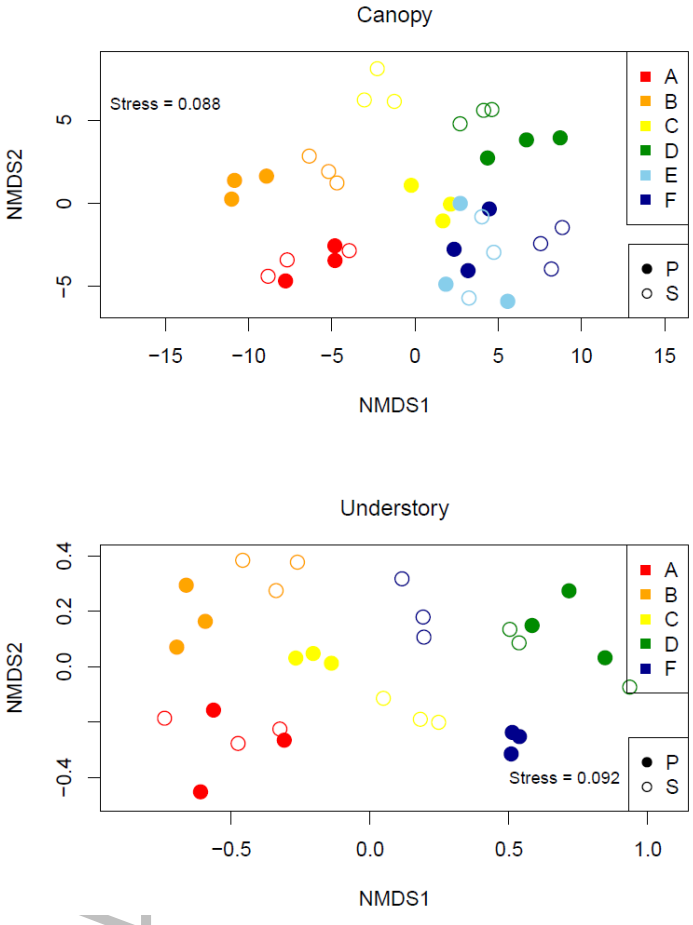


Figure E1. nMDS ordination of Jaccard's dissimilarity matrix of species composition in the canopy (top panel) and understory (bottom panel). Colours/letters in top legend refer to locations on Figure 1 of paper, closed circles are primary rainforest sites (P) and open circles are secondary forest sites (S).

Appendix F. Model selection supplementary methods and results

Supplementary methods for model selection

Model selection procedure

To identify important effects of our climate and landscape factors on species and trait diversity we built linear mixed effects models (LMMs) for each species or trait diversity measure (see primary methods for further details) and used information theoretic methods (Burnham & Anderson, 2002) with strict criteria for model selection, followed by inferences based on well-supported models. Our aim was to identify the direction, magnitude and uncertainty of important effects (Cumming & Finch, 2005; Nakagawa & Schielzeth, 2013). To do this we first needed to identify good candidate models and then from those models make quantitative inferences about model terms (effects). We selected the best model(s) and made inferences about effects based on the following:

(1) Does at least one model have strong support over an intercept-only (null) model (ΔAICc > 5). If YES, then (2), if NO, then no good model.
(2) Does a model have strong support over all other models (ΔAICc > 5). If YES, then choose that model (4). If NO, then (3).
(3) When several models had strong support over intercept-only models but shared similar support (ΔAICc <3, Burnham and Anderson 2002) we looked for common terms in those models, which might be driving high support. If YES, we found terms in common and concluded that there was good support for an effect of these common terms (4). If NO, i.e., models sharing strong support shared no terms, we concluded that either of these effects could plausibly explain patterns in species of functional diversity, and proceed to interpret these effects as separate, equally-plausible explanations of patterns according to (4). However, if more complex models only differed by one parameter and were within 2 ΔAICc with a similar maximised log-likelihood of the best model, we concluded there was no real

support for the larger model (Burnham and Anderson 2002) and interpreted effects of the simpler model (4).

(4) Does the term in supported models have a meaningful effect on the response variables directly or in combination with land-use categories? If YES, then interpret the effect. If NO, then do not interpret effect. We used Pseudo R^2 for LMMs (Nakagawa and Shielzeth, 2013). The methods for calculating Pseudo R^2 produce two measures of goodness of fit: R^2m, which represents the amount of variance explained by fixed effects, and R^2c, which represents the amount of variance explained by the combined fixed and random effects. As we were primarily interested in fixed effects, we focus on R^2m here. We considered $R^2m < 0.01$ as explaining no meaningful variation and $0.01 < R^2m < 0.1$ as explaining only a very small amount. If the change in R^2m from simpler to more complex model containing the same terms (including interactions) was <0.01, we concluded that terms in simpler models were driving strong model support. When there was an effect of land-clearing, we used means and 95% confidence intervals to assess magnitude and uncertainty of differences between land-clearing categories (secondary regrowth and primary rainforest) (Cumming and Finch, 2005). If there were clear effects of terms (i.e. $R^2m > 0.1$, confidence intervals less than one-third of their length overlapping) we then considered whether the size of differences was likely to be biologically important.

Supplementary Results.

Model selection tables

These tables present results of LMMs used in model selection for each response variable (a mean or diversity for a trait) in each forest stratum (canopy or understory). All models included "location" as a random intercept, corresponding to locations in Figure 1. Best models were selected based on our

model selection criteria outlined above. Bold font models are those that had strong support over both an intercept-only model and other models (ΔAICc > 5). Several models may be in bold where they shared similar support. Bold font models were used for analyses in the main text and are presented in detail in Table 2. Intercept only models are also in bold for ease of comparison. All models, including the intercept-only model, included "location" as a random effect, which is not shown in tables because inclusion of this term does not vary among models. The logLik refers to model generated log Likelihood values, AICc refers to Akaike information criterion values for small sample sizes, ΔAICc is the difference between each model's AICc value and the best model (indicated with a ΔAICc of 0.0) and "weight" refers to Akaike weights. Akaike weights reflect the probability of each tested model being the correct model given the set of tested models. Thus, weight values add to 1 for each trait. Fixed effects are abbreviated in tables and represent the following: **LC** = land-clearing (two categories: secondary regrowth and primary rainforest); **cvMI** = coefficient of variation in the moisture index (representing seasonality of moisture availability), **MI** = mean annual moisture index, **PET** = mean annual potential evapotranspiration; **SpPool** = size of the species pool at each location; **For5** = forest cover within a 5 km radius of plots, **For10** = forest cover within a 10 km radius of plots. Models for species richness and Shannon's diversity did not include the effect of SpPool, as species pool size was derived via rarefaction of richness in plots and examining the effects of species pool size on species richness and diversity would have been circular.

Table F1. Species Richness, canopy (20 x20) as the response variable.

Fixed effects	logLik	AICc	ΔAICc	weight
cvMI	**-90.75**	**190.80**	**0**	**0.56**
LC + cvMI	-90.59	193.18	2.38	0.17
MI	-93.26	195.81	5.01	0.04
Intercept only	**-94.54**	**195.83**	**5.02**	**0.04**
LC + cvMI+ LC x cvMI	-90.59	196.08	5.27	0.04
For10	-93.49	196.28	5.48	0.03
PET	-93.97	197.24	6.44	0.02
For5	-94.35	197.99	7.18	0.01
LC	-94.37	198.04	7.24	0.01
LC + MI	-93.09	198.19	7.39	0.01
LC+For10	-93.33	198.67	7.86	0.01
LC + PET	-93.81	199.63	8.82	0.00
LC+For5	-94.18	200.37	9.57	0.00
LC + MI + LC x MI	-93.02	200.95	10.14	0.00
LC+For10+LC x For10	-93.31	201.52	10.71	0.00
LC + PET + LC x PET	-93.78	202.47	11.66	0.00
LC+For5+LC x For5	-94.12	203.14	12.33	0.00

Table F2. Species Richness, understory (10 x 10 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
cvMI	**-86.65**	**182.90**	**0**	**0.54**
LC + cvMI	-86.60	185.71	2.80	0.13
LC+For5+LC x For5	-85.59	186.84	3.93	0.07
Intercept only	**-90.55**	**188.03**	**5.12**	**0.04**
For10	-89.28	188.16	5.25	0.03
LC + cvMI+ LC x cvMI	-86.43	188.52	5.61	0.03
LC+For10+LC x For10	-86.53	188.71	5.80	0.02
MI	-89.60	188.80	5.89	0.02
PET	-89.84	189.29	6.38	0.02
For5	-90.18	189.97	7.06	0.01
LC	-90.51	190.62	7.71	0.01
LC+For10	-89.23	190.97	8.06	0.00
LC + MI	-89.55	191.61	8.70	0.00
LC + PET	-89.80	192.10	9.19	0.00
LC+For5	-90.14	192.78	9.87	0.00
LC + MI + LC x MI	-89.52	194.70	11.79	0.00
LC + PET + LC x PET	-89.58	194.82	11.91	0.00

Table F3. Species Diversity, canopy (20 x20 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC + cvMI	-11.71	35.43	0	0.24
cvMI	-13.50	36.29	0.86	0.15
LC	-14.03	37.36	1.92	0.09
LC+For10	-12.97	37.94	2.51	0.07
LC + MI	-13.02	38.05	2.61	0.06
LC + cvMI+ LC x cvMI	-11.60	38.10	2.66	0.06
Intercept only	-15.82	**38.39**	**2.96**	**0.05**
For10	-14.75	38.80	3.37	0.04
MI	-14.81	38.91	3.48	0.04
LC + PET	-13.81	39.63	4.20	0.03
LC+For5	-13.83	39.66	4.23	0.02
LC+For10+LC x For10	-12.63	40.15	4.72	0.02
PET	-15.60	40.50	5.06	0.01
For5	-15.62	40.53	5.09	0.01
LC + MI + LC x MI	-13.00	40.91	5.47	0.01
LC+For5+LC x For5	-13.67	42.24	6.81	0.00
LC + PET + LC x PET	-13.71	42.31	6.88	0.00

Table F4. Species Diversity, understory (10x10 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
cvMI	**-13.59**	**36.79**	**0**	**0.53**
LC + cvMI	-13.36	39.23	2.44	0.15
For10	-15.99	41.58	4.79	0.04
Intercept only	**-17.43**	**41.78**	**4.99**	**0.04**
LC + cvMI+ LC x cvMI	-13.34	42.33	5.54	0.03
LC+For10+LC x For10	-13.37	42.39	5.60	0.03
For5	-16.59	42.79	6.00	0.02
PET	-16.65	42.90	6.11	0.02
MI	-16.89	43.39	6.60	0.01
LC+For5+LC x For5	-13.97	43.59	6.80	0.01
LC	-17.20	44.00	7.21	0.01
LC+For10	-15.76	44.02	7.23	0.01
LC+For5	-16.36	45.23	8.44	0.00
LC + PET	-16.42	45.34	8.55	0.00
LC + MI	-16.66	45.83	9.04	0.00
LC + PET + LC x PET	-15.21	46.08	9.29	0.00
LC + MI + LC x MI	-16.03	47.72	10.93	0.00

Table F5 Functional Richness, canopy (20 x20 m) as the response variable

Fixed effects	logLik	AICc	delta	weight
LU + Spool	**75.63**	**-139.27**	**0.00**	**0.42**
Spool	**73.64**	**-138.00**	**1.27**	**0.22**
LU +Spool+ LU*Spool	**75.66**	**-136.41**	**2.86**	**0.10**
LU + MI	**73.39**	**-134.78**	**4.49**	**0.04**
LU + CV.MI	73.16	-134.32	4.95	0.04
LU	71.59	-133.90	5.37	0.03
MI	71.40	-133.51	5.76	0.02
CV.MI	71.17	-133.05	6.22	0.02
LU + PET	72.26	-132.52	6.75	0.01
Intercept only	**69.60**	**-132.46**	**6.81**	**0.01**
LU + MI + LU*MI	73.56	-132.22	7.05	0.01
LU + CV.MI+ LU*CV.MI	73.19	-131.49	7.78	0.01
LU+F10.km	71.72	-131.43	7.84	0.01
LU+F5.km	71.66	-131.32	7.95	0.01
PET	70.27	-131.25	8.02	0.01
LU+F10.km+LU*F10.km	73.03	-131.16	8.11	0.01
LU + PET + LU*PET	72.93	-130.96	8.31	0.01
F10.km	69.73	-130.16	9.11	0.00
LU+F5.km+LU*F5.km	72.48	-130.07	9.20	0.00
F5.km	69.67	-130.05	9.22	0.00

Table F6 Functional Richness, understory (10x10 m) as the response variable

Fixed effects	logLik	AICc	delta	weight
Spool	**66.95**	**-124.31**	**0.00**	**0.51**
LU + Spool	**68.05**	**-123.60**	**0.71**	**0.36**
LU +Spool+ LU*Spool	**68.33**	**-121.00**	**3.31**	**0.10**
MI	62.76	-115.91	8.40	0.01
LU + MI	63.85	-115.20	9.11	0.01
CV.MI	62.21	-114.82	9.49	0.00
LU + CV.MI	63.30	-114.10	10.21	0.00
F10.km	61.76	-113.93	10.38	0.00
Intercept only	**60.40**	**-113.88**	**10.43**	**0.00**
LU	61.49	-113.39	10.92	0.00
LU+F10.km	62.86	-113.21	11.10	0.00
LU + CV.MI+ LU*CV.MI	64.19	-112.73	11.58	0.00
LU+F10.km+LU*F10.km	64.19	-112.72	11.59	0.00
LU + MI + LU*MI	63.85	-112.05	12.26	0.00
PET	60.66	-111.73	12.58	0.00
F5.km	60.64	-111.68	12.63	0.00
LU+F5.km+LU*F5.km	63.40	-111.14	13.17	0.00
LU + PET	61.76	-111.02	13.29	0.00
LU+F5.km	61.73	-110.96	13.35	0.00
LU + PET + LU*PET	61.81	-107.96	16.35	0.00

Table F7 Functional Evenness, canopy (20 x20 m) as the response variable

Fixed effects	logLik	AICc	delta	weight
LU	**32.25**	**-55.21**	**0.00**	**0.25**
LU + MI	32.84	-53.67	1.54	0.11
LU + Spool	32.67	-53.33	1.88	0.10
LU+F10.km	32.47	-52.95	2.26	0.08
LU + CV.MI	32.41	-52.83	2.38	0.07
LU + PET	32.27	-52.53	2.67	0.06
LU+F5.km	32.25	-52.50	2.71	0.06
LU + MI + LU*MI	33.25	-51.60	3.61	0.04
LU+F10.km+LU*F10.km	33.22	-51.54	3.67	0.04
LU +Spool+ LU*Spool	33.17	-51.45	3.75	0.04
LU + CV.MI+ LU*CV.MI	33.08	-51.26	3.95	0.03
Intercept only	**28.62**	**-50.50**	**4.71**	**0.02**
LU+F5.km+LU*F5.km	32.47	-50.05	5.16	0.02
LU + PET + LU*PET	32.27	-49.64	5.57	0.02
MI	29.21	-49.13	6.08	0.01
Spool	29.04	-48.79	6.42	0.01
F10.km	28.85	-48.41	6.80	0.01
CV.MI	28.79	-48.29	6.92	0.01
PET	28.64	-47.99	7.22	0.01
F5.km	28.62	-47.96	7.25	0.01

Table F8 Functional Evenness, understory (10x10 m) as the response variable

Fixed effects	logLik	AICc	delta	weight
LU+F10.km+LU*F10.km	**44.13**	**-72.60**	**0.00**	**0.41**
LU+F5.km+LU*F5.km	**44.03**	**-72.42**	**0.18**	**0.37**
LU+F5.km	**41.14**	**-69.78**	**2.82**	**0.10**
LU+F10.km	**41.04**	**-69.57**	**3.03**	**0.09**
LU	37.31	-65.02	7.58	0.01
LU + MI	37.63	-62.75	9.85	0.00
LU + CV.MI	37.57	-62.64	9.96	0.00
LU + PET	37.53	-62.56	10.03	0.00
LU + Spool	37.51	-62.53	10.07	0.00
LU + MI + LU*MI	38.93	-62.22	10.38	0.00
F5.km	35.68	-61.77	10.83	0.00
F10.km	35.61	-61.63	10.97	0.00
LU + PET + LU*PET	37.81	-59.97	12.63	0.00
LU +Spool+ LU*Spool	37.80	-59.95	12.65	0.00
LU + CV.MI+ LU*CV.MI	37.65	-59.65	12.95	0.00
Intercept only	**32.69**	**-58.46**	**14.14**	**0.00**
MI	33.01	-56.41	16.19	0.00
CV.MI	32.95	-56.30	16.30	0.00
PET	32.91	-56.22	16.37	0.00
Spool	32.89	-56.19	16.41	0.00

Table F9 Functional Divergence, canopy (20 x20 m) as the response variable

Fixed effects	**logLik**	**AICc**	**delta**	**weight**
LU	31.28	-53.27	0.00	0.25
LU + MI	31.72	-51.44	1.83	0.10
LU+F5.km	31.66	-51.31	1.96	0.09
LU + PET	31.51	-51.02	2.25	0.08
LU + CV.MI	31.46	-50.93	2.34	0.08
LU+F10.km	31.31	-50.62	2.65	0.07
LU + Spool	31.30	-50.59	2.68	0.07
Intercept only	**28.30**	**-49.85**	**3.42**	**0.05**
LU + MI + LU*MI	31.89	-48.88	4.39	0.03
LU+F5.km+LU*F5.km	31.81	-48.72	4.55	0.03
MI	28.73	-48.17	5.10	0.02
LU + PET + LU*PET	31.51	-48.13	5.14	0.02
LU + CV.MI+ LU*CV.MI	31.48	-48.06	5.21	0.02
F5.km	28.67	-48.05	5.22	0.02
LU+F10.km+LU*F10.km	31.35	-47.79	5.48	0.02
PET	28.53	-47.77	5.50	0.02
LU +Spool+ LU*Spool	31.30	-47.71	5.56	0.02
CV.MI	28.48	-47.68	5.59	0.02
F10.km	28.33	-47.37	5.90	0.01
Spool	28.32	-47.34	5.93	0.01

Table F10 Functional Divergence, understory (10 x 10 m) as the response variable

Fixed Effects	logLik	AICc	ΔAICc	weight
LU + PET + LU*PET	**25.68**	**-35.70**	**0.00**	**0.96**
LU + PET	20.45	-28.40	7.30	0.02
LU + CV.MI	18.48	-24.46	11.24	0.00
LU + CV.MI+ LU*CV.MI	19.88	-24.10	11.60	0.00
PET	16.41	-23.23	12.47	0.00
LU	16.19	-22.78	12.92	0.00
LU + Spool	17.32	-22.13	13.57	0.00
LU+F5.km	16.36	-20.23	15.47	0.00
CV.MI	14.89	-20.17	15.53	0.00
LU+F10.km+LU*F10.km	17.90	-20.15	15.55	0.00
LU+F10.km	16.28	-20.05	15.65	0.00
LU + MI	16.19	-19.88	15.81	0.00
LU + MI + LU*MI	17.75	-19.84	15.85	0.00
LU+F5.km+LU*F5.km	17.48	-19.31	16.39	0.00
LU +Spool+ LU*Spool	17.43	-19.21	16.49	0.00
Intercept only	**12.70**	**-18.48**	**17.22**	**0.00**
Spool	13.83	-18.05	17.65	0.00
F5.km	12.87	-16.14	19.55	0.00
F10.km	12.79	-15.97	19.73	0.00
MI	12.70	-15.80	19.90	0.00

Table F11. Mean wood density, canopy (20 x20 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC	67.55	-125.82	0	0.20
Intercept only	**65.87**	**-125.00**	**0.81**	**0.13**
LC + MI	67.67	-123.35	2.47	0.05
LC+For5	67.66	-123.33	2.48	0.05
LC+For10	67.59	-123.19	2.62	0.05
LC + PET	67.57	-123.15	2.66	0.05
LC + cvMI	67.56	-123.12	2.70	0.05
LC + Spool	67.55	-123.12	2.70	0.05
MI	65.99	-122.70	3.11	0.04
For5	65.99	-122.69	3.13	0.04
For10	65.91	-122.54	3.27	0.03
PET	65.89	-122.50	3.31	0.03
cvMI	65.88	-122.47	3.34	0.03
Spool	65.88	-122.47	3.34	0.03
LC+For5+LC x For5	68.19	-121.48	4.33	0.02
LC+For10+LC x For10	68.13	-121.37	4.45	0.02
LC + PET + LC xPET	68.00	-121.10	4.71	0.01
LC + MI + LC x MI	67.68	-120.47	5.35	0.01
LC + cvMI+ LC x cvMI	67.59	-120.28	5.53	0.01
LC +Spool+ LC x Spool	67.56	-120.22	5.59	0.01

Table F12. Range wood density, canopy (20 x20 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC+For5+LC x For5	**37.63**	**-60.37**	**0.00**	**0.16**
LC + Spool	**36.16**	**-60.32**	**0.04**	**0.15**
LC	**34.63**	**-59.97**	**0.39**	**0.13**
LC + PET	**35.67**	**-59.34**	**1.02**	**0.09**
LC + cvMI	**35.42**	**-58.85**	**1.51**	**0.07**
LC+For10+LC x For10	**36.85**	**-58.81**	**1.56**	**0.07**
LC+For5	**35.30**	**-58.60**	**1.77**	**0.06**
LC + cvMI+ LC x cvMI	**36.74**	**-58.58**	**1.79**	**0.06**
LC + MI	**34.99**	**-57.99**	**2.37**	**0.04**
LC +Spool+ LC x Spool	**36.44**	**-57.98**	**2.38**	**0.04**
LC+For10	**34.74**	**-57.48**	**2.88**	**0.03**
LC + PET + LC x PET	**35.68**	**-56.46**	**3.91**	**0.02**
LC + MI + LC x MI	35.09	-55.28	5.08	0.01
Intercept only	25.65	**-44.55**	**15.81**	**0.00**
Spool	26.56	-43.84	16.52	0.00
PET	26.27	-43.26	17.10	0.00
cvMI	26.13	-42.97	17.34	0.00
For5	26.05	-42.82	17.55	0.00
MI	25.87	-42.46	17.91	0.00
For10	25.72	-42.15	18.22	0.00

Table F13. Mean wood density, understory (10 x 10 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC + MI + LC x MI	**53.09**	**-90.53**	**0**	**0.35**
LC + MI	**51.48**	**-90.46**	**0.06**	**0.33**
LC+For10	**50.36**	**-88.22**	**2.31**	**0.11**
LC+For10+LC x For10	**50.94**	**-86.22**	**4.30**	**0.04**
LC+For5+LC x For5	**50.77**	**-85.90**	**4.62**	**0.03**
LC	**47.62**	**-85.65**	**4.87**	**0.03**
LC + Spool	48.89	-85.29	5.23	0.02
LC + cvMI+ LC x cvMI	50.34	-85.03	5.49	0.02
LC+For5	48.26	-84.02	6.50	0.01
LC + PET + LC x PET	49.56	-83.47	7.05	0.01
LC + PET	47.98	-83.46	7.06	0.01
LC + cvMI	47.71	-82.92	7.60	0.00
LC +Spool+ LC x Spool	48.91	-82.17	8.35	0.00
MI	41.06	-72.53	17.99	4.32E-05
For10	40.49	-71.39	19.14	2.44E-05
Intercept only	38.56	**-70.20**	**20.33**	**1.35E-05**
Spool	39.66	-69.72	20.80	1.06E-05
For5	39.16	-68.73	21.79	6.48E-06
PET	38.91	-68.22	22.30	5.03E-06
cvMI	38.64	-67.69	22.83	3.86E-06

Table F14. Range wood density, understory (10 x 10 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC+For10+LC x For10	**45.62**	**-75.58**	**0**	**0.39**
MI	41.47	-73.35	2.23	0.12
LC + MI + LC x MI	44.43	-73.20	2.38	0.12
Spool	41.11	-72.63	2.95	0.09
For10	40.83	-72.07	3.51	0.06
LC +Spool+ LC x Spool	43.27	-70.90	4.68	0.03
LC + MI	41.54	-70.59	4.99	0.03
LC+For5+LC x For5	42.78	-69.90	5.68	0.02
LC + Spool	41.18	-69.86	5.72	0.02
Intercept only	**38.31**	**-69.69**	**5.89**	**0.02**
LC+For10	40.90	-69.30	6.28	0.01
cvMI	39.00	-68.40	7.18	0.01
For5	38.86	-68.12	7.46	0.00
LC	38.37	-67.14	8.44	0.00
PET	38.31	-67.02	8.56	0.00
LC + cvMI+ LC x cvMI	40.67	-65.69	9.89	0.00
LC + cvMI	39.06	-65.62	9.96	0.00
LC+For5	38.92	-65.34	10.24	0.00
LC + PET	38.37	-64.25	11.33	0.00
LC + PET + LC x PET	38.44	-61.23	14.35	0.00

Table F15. Mean height, canopy (20 x 20 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC+For5+LC x For5	16.41	**-17.92**	**0**	**0.82**
LC+For10+LC x For10	13.34	-11.79	6.13	0.03
LC + PET	11.82	-11.65	6.26	0.03
LC+For5	11.47	-10.95	6.96	0.02
LC + cvMI+ LC x cvMI	12.33	-9.76	8.16	0.01
LC	9.50	-9.72	8.19	0.01
LC + Spool	10.71	-9.42	8.49	0.01
LC + PET + LC x PET	11.99	-9.09	8.83	0.00
LC+For10	10.37	-8.75	9.16	0.00
LC + cvMI	10.32	-8.64	9.27	0.00
LC + MI	9.53	-7.07	10.84	0.00
LC +Spool+ LC x Spool	10.83	-6.76	11.15	0.00
LC + MI + LC x MI	9.55	-4.21	13.70	0.00
PET	5.76	-2.23	15.68	0.00
For5	5.41	-1.53	16.38	0.00
Intercept only	3.44	**-0.13**	**17.78**	**0.00**
Spool	4.65	-0.01	17.91	0.00
For10	4.31	0.65	18.58	7.61E-05
cvMI	4.26	0.76	18.69	7.20E-05
MI	3.47	2.34	20.26	3.28E-05

Table F16. Range height, canopy (20 x 20 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC+For5+LC x For5	**16.41**	**24.44**	**0**	**0.98**
LC+For10+LC x For10	13.34	33.58	9.14	0.01
LC+For5	11.82	45.87	21.43	2.19E-05
LC+For10	11.47	47.11	22.67	1.18E-05
LC	12.33	48.43	23.99	6.09E-06
LC + PET	9.50	48.83	24.39	4.99E-06
LC + MI	10.71	50.21	25.77	2.50E-06
LC + cvMI	11.99	50.91	26.47	1.76E-06
LC + Spool	10.37	50.98	26.54	1.71E-06
LC + PET + LC x PET	10.32	51.24	26.80	1.49E-06
LC + cvMI+ LC x cvMI	9.53	51.85	27.41	1.10E-06
LC + MI + LC x MI	10.83	52.13	27.69	9.61E-07
For5	9.55	53.73	29.29	4.31E-07
LC +Spool+ LC x Spool	5.76	53.79	29.35	4.19E-07
For10	5.41	54.77	30.33	2.56E-07
Intercept only	**3.44**	**56.24**	**31.80**	**1.23E-07**
PET	4.65	56.47	32.03	1.10E-07
MI	4.31	57.85	33.41	5.49E-08
cvMI	4.26	58.55	34.10	3.88E-08
Spool	3.47	58.61	34.17	3.75E-08

Table F17. Mean height, understory (10 x 10 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
Intercept only	**-10.18**	**27.28**	**0**	**0.19**
PET	-9.13	27.86	0.57	0.14
cvMI	-9.32	28.25	0.96	0.11
For5	-9.77	29.14	1.86	0.07
MI	-9.82	29.24	1.95	0.07
LC	-10.08	29.76	2.47	0.05
For10	-10.15	29.91	2.62	0.05
LC+For5+LC x For5	-7.13	29.92	2.64	0.05
Spool	-10.17	29.95	2.66	0.05
LC + PET	-9.03	30.56	3.28	0.03
LC + cvMI	-9.22	30.95	3.66	0.03
LC + PET + LC x PET	-7.80	31.25	3.96	0.02
LC+For5	-9.67	31.84	4.56	0.01
LC+For10+LC x For10	-8.12	31.90	4.62	0.01
LC + MI	-9.72	31.94	4.65	0.01
LC+For10	-10.05	32.61	5.32	0.01
LC + Spool	-10.07	32.65	5.36	0.01
LC + cvMI+ LC x cvMI	-9.12	33.90	6.61	0.00
LC + MI + LC x MI	-9.35	34.36	7.07	0.00
LC +Spool+ LC x Spool	-10.02	35.70	8.41	0.00

Table F18. Range height, understory (10 x 10 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC + PET + LC x PET	-12.60	40.86	0	0.27
LC + cvMI+ LC x cvMI	-12.97	41.61	0.74	0.18
Intercept only	**-17.85**	**42.63**	**1.76**	**0.11**
PET	-16.84	43.29	2.42	0.08
cvMI	-17.17	43.94	3.08	0.05
Spool	-17.37	44.34	3.47	0.04
LC	-17.64	44.88	4.02	0.03
MI	-17.82	45.24	4.37	0.03
For5	-17.82	45.25	4.38	0.03
For10	-17.84	45.29	4.42	0.03
LC + PET	-16.62	45.74	4.87	0.02
LC + cvMI	-16.95	46.41	5.54	0.01
LC +Spool+ LC x Spool	-15.42	46.50	5.63	0.01
LC + Spool	-17.15	46.80	5.94	0.01
LC + MI	-17.61	47.72	6.85	0.00
LC+For5	-17.61	47.73	6.86	0.00
LC+For10	-17.63	47.77	6.90	0.00
LC + MI + LC x MI	-17.51	50.67	9.81	0.00
LC+For5+LC x or(5)	-17.60	50.86	9.99	0.00
LC+For10+LC x For10	-17.63	50.92	10.05	0.00

Table F19. Mean SLA, canopy (20 x 20 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC + MI + LC x MI	42.24	-69.59	0	0.25
For5	39.06	-68.84	0.75	0.17
LC+For5	39.79	-67.59	2.00	0.09
PET	38.16	-67.04	2.55	0.07
LC + PET + LC x PET	40.96	-67.02	2.56	0.07
Intercept only	36.56	**-66.38**	**3.20**	**0.05**
For10	37.54	-65.80	3.78	0.03
Spool	37.54	-65.79	3.79	0.03
LC + PET	38.89	-65.78	3.80	0.03
LC	37.29	-65.30	4.28	0.02
LC+For5+LC x For5	40.02	-65.15	4.44	0.02
LC+For10	38.27	-64.55	5.04	0.02
LC + Spool	38.27	-64.54	5.04	0.02
cvMI	36.91	-64.54	5.05	0.02
MI	36.66	-64.04	5.54	0.01
LC + cvMI	37.64	-63.29	6.30	0.01
LC + cvMI+ LC x cvMI	38.90	-62.90	6.69	0.00
LC + MI	37.39	-62.79	6.80	0.00
LC +Spool+ LC x Spool	38.55	-62.20	7.38	0.00
LC+For10+LC x For10	38.45	-62.01	7.58	0.00

Table F20. Range SLA, canopy (20 x20 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC+For10+LC x For10	**5.75**	**3.37**	**0**	**0.74**
LC+For5+LC x For5	**4.48**	**5.92**	**2.54**	**0.20**
LC + PET + LC x PET	2.86	9.17	5.79	0.04
PET	-5.61	20.52	17.14	0.00
LC + PET	-4.78	21.57	18.19	8.37E-05
LC + MI + LC x MI	-3.60	22.11	18.73	6.40E-05
cvMI	-7.14	23.58	20.20	3.07E-05
Spool	-7.25	23.79	20.42	2.75E-05
Intercept only	**-8.67**	**24.09**	**20.72**	**2.37E-05**
For5	-7.62	24.54	21.16	1.90E-05
LC + cvMI	-6.31	24.63	21.25	1.81E-05
LC + Spool	-6.42	24.85	21.47	1.63E-05
LC	-7.84	24.98	21.60	1.52E-05
LC+For5	-6.79	25.59	22.21	1.12E-05
For10	-8.18	25.65	22.27	1.09E-05
MI	-8.60	26.49	23.11	7.17E-06
LC+For10	-7.35	26.71	23.33	6.42E-06
LC + cvMI+ LC x cvMI	-5.96	26.83	23.45	6.04E-06
LC + MI	-7.77	27.54	24.16	4.23E-06
LC +Spool+ LC x Spool	-6.33	27.56	24.18	4.20E-06

Table F21. Mean SLA, understory (10 x 10 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
For5	22.47	-35.34	0	0.20
Intercept only	20.84	**-34.76**	**0.57**	**0.15**
cvMI	21.58	-33.56	1.77	0.08
LC + cvMI+ LC x cvMI	24.57	-33.50	1.84	0.08
LC + PET + LC x PET	24.50	-33.35	1.99	0.07
MI	21.43	-33.26	2.07	0.07
For10	21.26	-32.93	2.40	0.06
LC+For5	22.49	-32.49	2.84	0.04
PET	21.04	-32.48	2.85	0.04
LC	20.87	-32.14	3.19	0.04
Spool	20.84	-32.09	3.25	0.03
LC + cvMI	21.61	-30.72	4.61	0.02
LC + MI	21.46	-30.42	4.92	0.01
LC+For5+LC x For5	22.90	-30.14	5.19	0.01
LC+For10	21.29	-30.09	5.24	0.01
LC + PET	21.07	-29.64	5.69	0.01
LC + Spool	20.87	-29.24	6.09	0.00
LC + MI + LC x MI	21.77	-27.89	7.44	0.00
LC+For10 x LC x For10	21.33	-27.02	8.31	0.00
LC +Spool+ LC x Spool	21.30	-26.94	8.39	0.00

Table F22. Range SLA, understory (10 x 10 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
PET	5.03	-0.46	0	0.38
For5	3.94	1.70	2.16	0.12
LC + PET	5.03	2.43	2.89	0.08
Intercept only	**2.15**	**2.62**	**3.08**	**0.08**
For10	3.16	3.26	3.72	0.05
cvMI	2.75	4.09	4.55	0.03
Spool	2.62	4.35	4.82	0.03
LC + PET + LC x PET	5.58	4.47	4.93	0.03
LC+For5	3.94	4.60	5.06	0.03
LC+For5+LC x For5	5.34	4.96	5.43	0.02
MI	2.18	5.23	5.69	0.02
LC	2.15	5.29	5.75	0.02
LC+For10	3.16	6.16	6.62	0.01
LC+For10+LC x For10	4.46	6.71	7.17	0.01
LC + cvMI	2.75	6.99	7.45	0.00
LC + Spool	2.62	7.25	7.71	0.00
LC + MI	2.18	8.12	8.58	0.00
LC + cvMI+ LC x cvMI	2.75	10.13	10.59	0.00
LC +Spool+ LC x Spool	2.62	10.39	10.85	0.00
LC + MI + LC x MI	2.54	10.56	11.02	0.00

Table F23. Mean Seed dry mass, canopy (20 x20 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC + cvMI	**-36.70**	**85.40**	**0**	**0.36**
LC + PET	**-36.81**	**85.62**	**0.21**	**0.32**
LC + PET + LC x PET	**-36.20**	**87.31**	**1.90**	**0.13**
LC + cvMI+ LC x cvMI	**-36.66**	**88.23**	**2.82**	**0.08**
LC + Spool	**-39.05**	**90.11**	**4.71**	**0.03**
LC	-41.58	92.46	7.06	0.01
cvMI	-41.71	92.71	7.30	0.00
LC +Spool+ LC x Spool	-39.00	92.91	7.50	0.00
PET	-41.81	92.92	7.52	0.00
LC+For5	-41.52	95.04	9.63	0.00
LC+For10	-41.58	95.16	9.75	0.00
LC + MI	-41.58	95.16	9.76	0.00
LC+For10+LC x For10	-40.22	95.35	9.94	0.00
LC+For5+LC x For5	-40.80	96.49	11.09	0.00
LC + MI + LC x MI	-41.03	96.96	11.55	0.00
Spool	-44.06	97.42	12.01	0.00
Intercept only	**-46.59**	**99.94**	**14.53**	**0.00**
For5	-46.52	102.34	16.93	7.61E-05
For10	-46.58	102.46	17.05	7.16E-05
MI	-46.59	102.47	17.06	7.14E-05

Table F24. Range seed dry mass, canopy (20 x20 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC	**-62.37**	**134.03**	**0**	**0.29**
LC + Spool	-62.14	136.29	2.25	0.09
LC + MI	-62.24	136.48	2.44	0.08
LC+For5	-62.28	136.57	2.53	0.08
LC + cvMI	-62.29	136.59	2.55	0.08
LC+For10	-62.36	136.72	2.69	0.07
LC + PET	-62.37	136.74	2.70	0.07
LC +Spool+ LC x Spool	-61.46	137.81	3.78	0.04
LC + MI + LC x MI	-61.52	137.94	3.90	0.04
LC + cvMI+ LC x vMI	-62.02	138.94	4.90	0.02
LC+For10+LC x For10	-62.26	139.42	5.39	0.01
LC+For5+LC x For5	-62.27	139.44	5.40	0.01
LC + PET + LC x PET	-62.32	139.55	5.51	0.01
Intercept only	**-66.55**	**139.85**	**5.81**	**0.01**
Spool	-66.32	141.94	7.90	0.00
MI	-66.42	142.13	8.09	0.00
For5	-66.46	142.21	8.18	0.00
cvMI	-66.47	142.24	8.20	0.00
For10	-66.54	142.37	8.34	0.00
PET	-66.55	142.39	8.35	0.00

Table F25. Mean seed dry mass, understory (10 x 10 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC + PET	**-34.63**	**81.77**	**0**	**0.68**
LC + PET + LC x PET	**-33.88**	**83.42**	**1.65**	**0.29**
LC + cvMI	-38.80	90.11	8.34	0.01
PET	-41.75	93.11	11.34	0.00
LC	-41.76	93.13	11.36	0.00
LC + cvMI+ LC x cvMI	-38.79	93.24	11.47	0.00
LC + Spool	-40.92	94.34	12.57	0.00
LC + MI	-41.61	95.72	13.95	0.00
LC+For5	-41.62	95.74	13.97	0.00
LC+For10	-41.65	95.80	14.03	0.00
LC+For5+LC x For5	-40.48	96.62	14.85	0.00
LC +Spool+ LC x Spool	-40.79	97.24	15.47	0.00
LC+For10+LC x For10	-40.90	97.46	15.69	0.00
LC + MI + LC x MI	-41.48	98.62	16.85	0.00
cvMI	-45.01	99.63	17.86	8.99E-05
Intercept only	**-47.97**	**102.87**	**21.10**	**1.78E-05**
Spool	-47.13	103.86	22.09	1.08E-05
MI	-47.82	105.25	23.48	5.42E-06
For5	-47.83	105.26	23.49	5.38E-06
For10	-47.86	105.33	23.56	5.21E-06

Table F26. Range seed dry mass, understory (10 x 10 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC + PET + LC x PET	-51.07	117.79	0	0.28
PET	-54.28	118.16	0.36	0.24
Spool	-55.03	119.67	1.87	0.11
cvMI	-55.42	120.45	2.65	0.07
Intercept only	**-57.02**	**120.97**	**3.17**	**0.05**
LC + PET	-54.28	121.06	3.26	0.05
For5	-56.35	122.30	4.50	0.03
LC + Spool	-55.03	122.57	4.77	0.02
LC + cvMI	-55.42	123.35	5.55	0.01
For10	-56.90	123.41	5.61	0.01
MI	-56.93	123.47	5.67	0.01
LC	-57.02	123.65	5.85	0.01
LC + cvMI+ LC x cvMI	-54.33	124.33	6.53	0.01
LC+For5	-56.35	125.20	7.40	0.00
LC +Spool+ LC x Spool	-55.03	125.72	7.92	0.00
LC+For10	-56.90	126.31	8.51	0.00
LC + MI	-56.93	126.37	8.57	0.00
LC + MI + LC x MI	-55.54	126.75	8.95	0.00
LC+For5+LC x For5	-56.27	128.20	10.41	0.00
LC+For10+LC x For10	-56.29	128.24	10.45	0.00

Table F27. Fruit seed diversity, canopy (20 x 20 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC + cvMI+ LC x cvMI	**-2.64**	**20.19**	**0**	**0.46**
LC + PET + LC x PET	-4.09	23.07	2.88	0.10
LC	-6.95	23.20	3.00	0.10
LC + cvMI	-6.41	24.83	4.64	0.04
LC + Spool	-6.66	25.32	5.12	0.03
LC+For10	-6.74	25.49	5.30	0.03
Intercept only	-9.45	**25.66**	**5.46**	**0.02**
LC + MI	-6.88	25.77	5.57	0.02
LC+For5	-6.91	25.83	5.64	0.02
LC + PET	-6.92	25.85	5.65	0.02
cvMI	-8.92	27.13	6.93	0.01
LC +Spool+ LC x Spool	-6.11	27.13	6.93	0.01
Spool	-9.16	27.61	7.42	0.01
For10	-9.25	27.79	7.59	0.01
LC + MI + LC x MI	-6.45	27.81	7.61	0.01
MI	-9.38	28.06	7.87	0.00
For5	-9.42	28.13	7.93	0.00
PET	-9.42	28.14	7.94	0.00
LC+For10+LC x For10	-6.74	28.39	8.19	0.00
LC+For5+LC x For5	-6.90	28.70	8.50	0.00

Table F28. Fruit seed diversity, understory (10 x 10 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
PET	5.56	**-1.53**	**0**	**0.55**
cvMI	**4.35**	**0.88**	**2.42**	**0.16**
LC + PET	**5.72**	**1.04**	**2.58**	**0.15**
LC + cvMI	4.50	3.49	5.03	0.04
LC + PET + LC x PET	5.75	4.14	5.68	0.03
LC + cvMI+ LC x cvMI	4.90	5.84	7.38	0.01
Spool	1.57	6.44	7.98	0.01
Intercept only	0.20	**6.50**	**8.04**	**0.00**
LC	0.35	8.89	10.43	0.00
LC + Spool	1.72	9.05	10.59	0.00
For5	0.20	9.18	10.72	0.00
MI	0.20	9.18	10.72	0.00
For10	0.20	9.18	10.72	0.00
LC +Spool+ LC x Spool	2.95	9.74	11.28	0.00
LC+For5	0.35	11.79	13.33	0.00
LC + MI	0.35	11.79	13.33	0.00
LC+For10	0.35	11.79	13.33	0.00
LC + MI + LC x MI	1.70	12.23	13.77	0.00
LC+For10+LC x For10	1.00	13.64	15.18	0.00
LC+For5+LC x For5	0.47	14.71	16.25	0.00

Table F29. Dispersal mode diversity, canopy (20 x 20m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC+For5+LC x For5	**11.12**	**-7.34**	**0**	**0.33**
LC + MI	**8.74**	**-5.48**	**1.85**	**0.13**
LC	**7.32**	**-5.36**	**1.97**	**0.12**
LC+For10+LC x For10	**10.10**	**-5.32**	**2.02**	**0.12**
LC + Spool	**8.15**	**-4.30**	**3.03**	**0.07**
LC+For5	**7.60**	**-3.21**	**4.13**	**0.04**
LC + cvMI	**7.40**	**-2.80**	**4.53**	**0.03**
LC + PET	**7.33**	**-2.67**	**4.66**	**0.03**
LC+For10	**7.33**	**-2.66**	**4.67**	**0.03**
LC + MI + LC x MI	**8.74**	**-2.59**	**4.74**	**0.03**
LC +Spool+ LC x Spool	8.17	-1.44	5.89	0.01
LC + PET + LC x PET	7.86	-0.83	6.50	0.01
LC + cvMI+ LC x cvMI	7.60	-0.30	7.03	0.00
MI	1.59	6.09	13.44	0.00
Intercept only	**0.17**	**6.39**	**13.73**	**0.00**
Spool	1.00	7.27	14.62	0.00
For5	0.45	8.37	15.71	0.00
cvMI	0.25	8.78	16.12	0.00
PET	0.18	8.91	16.25	9.86E-05
For10	0.18	8.92	16.26	9.82E-05

Table F30. Dispersal mode diversity, understory (10 x 10 m) as the response variable

Fixed effects	logLik	AICc	ΔAICc	weight
LC + Spool	13.96	-15.43	0.00	0.44
Spool	12.51	-15.41	0.02	0.44
LC +Spool+ LC x Spool	13.99	-12.33	3.10	0.09
MI	8.09	-6.57	8.86	0.01
LC + MI	9.48	-6.46	8.97	0.00
cvMI	7.64	-5.69	9.74	0.00
LC + cvMI	9.04	-5.57	9.85	0.00
LC	7.46	-5.33	10.10	0.00
Intercept only	6.07	-5.22	10.21	0.00
LC + cvMI+ LC x cvMI	9.70	-3.74	11.69	0.00
LC + MI + LC x MI	9.69	-3.73	11.70	0.00
PET	6.57	-3.54	11.88	0.00
LC + PET	7.97	-3.43	12.00	0.00
For10	6.50	-3.39	12.04	0.00
LC+For10	7.89	-3.28	12.15	0.00
For5	6.07	-2.54	12.89	0.00
LC+For5	7.46	-2.43	13.00	0.00
LC + PET + LC x PET	8.37	-1.08	14.35	0.00
LC+For10+LC x For10	7.90	-0.15	15.28	0.00
LC+For5+LC x For5	7.47	0.71	16.14	0.00

APPENDIX REFERENCES

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