How much of the world is woody? -- Response to reviewers' comments

We greatly appreciate the thorough comments from the reviewers. We have gone through them in detail and hopefully have addressed most of the reviewer's concerns, including performing several new analyses.

Editor's Comments

> This manuscript is ambitious, thought-provoking, and relatively well-written. I agree with the reviewers, however, that not enough detail regarding definitions, models, and data are provided. The scope of the changes needed to make the manuscript clearer are large enough to warrant rejection of this draft, in my opinion. As I really liked this manuscript, I would encourage the authors to attend to these issues (please note the consistency of the reviewers' comments). I recommend rejection of this draft, but would like to encourage re-submission.

In going through all of the comments, we agree with the editor's assessment that they revolve broadly around the same general theme that insufficient detail was supplied in our original submission. In this re-submission we have:

- *Expanded the methods section to be more explicit about how the approach was carried out, and where the data came from*
- *Included a supplement in which all source data and code are included so that readers can see precisely what is done or modify the analysis.*
- *Included a .csv file containing the specific results from every genus, family and order that researchers can examine in detail and hopefully re-purpose for other studies*
- *Included a number of supporting figures stemming from reviewers concerns that explore potential biases in the data.*

We think that the study is now much more comprehensive and are appreciative for the comments of the editor and the reviewers which pushed us to make it better. We address the specific comments of the reviewers in detail below.

Reviewer: 1

> FitzJohn et al. present a simple statistical model for estimating the fraction of species with one or the other of two character states from an incompletely sampled hierarchy, and then use that to provide an improved estimate of the fraction of woody vascular plants.

> Specifically, the authors provide estimates based on hypergeometric vs. binomial distributions of binary character-states, and use these to extrapolate the proportion of species in each vascular genus (apparently, statement is never made to this effect), including unsampled genera, which were assumed to have the same proportion of woody species as sampled genera within those orders. Numbers of species per genus

were apparently drawn from The Plant List, and the resulting superimposed on a phylogeny by Zanne et al. in review, a copy of which was not provided to the reviewer.

This is an interesting paper, and no doubt would draw substantial attention from the readers of JE.

Thanks for the kind words.

However, there are a number of points that need to be clarified:

1. The definition of woodiness used (lines 89-91) is too vague. I'm not complaining about the functional vs. morphological nature of the definition, but simply the English phrasing of "woody species have a prominent aboveground stem through time, and herbaceous species lack such a stem". Cute and short, but really vague. What about shrubs and other woody plants that have multiple stems? What exactly does "prominent" mean here? Is it being introduced to exclude species like Gaultheria procumbens or Epigaea repens from being woody? If so, why? What does "prominent" mean, explicitly, in terms of height and/or diameter? What is meant, exactly, by "through time"? Surely the authors could indicate whether that means that the stems are at least super-annual (which would still let bananas and bamboos into the woody legions).

We have thought carefully about the woodiness definition and it generated substantial debate among the co-authors. The first important point is that with any definition (of any trait, not just woodiness) there will be both grey-area species and species for which reasonable botanists might make different interpretations. That said, we sought a definition that matched the general intuition for woodiness and created the smallest number of problem species possible. This issue is discussed in detail in the Zanne et al. (ZEA) paper, which is now published (Nature, 2013 doi:10.1038/nature12872). But for clarity we copy the relevant point from the ZEA discussion here:

"Woody/herbaceous is a basic dichotomy that falls under the "you know it when you see it" but has no easily quantifiable definition. We chose a long-standing definition put forward by Asa Gray (1887) and followed by subsequent generations of biologists that accurately captures a relevant trait for our study. Woody species maintain a prominent stem through time and across changing environmental conditions that may or may not include freezing temperatures.

Since Asa Gray's definition, botanists have attempted to formalize this definition more precisely by suggesting the use of 1. lignin content or 2. bifacial vascular cambium. Both of these definitions fall short. For example, all stems, including some that are widely called herbaceous, have high concentrations of lignin in their stems, and many have bifacial vascular cambium. Because of these problems, we decided that the only workable definition was Gray's."

We think the reviewer's concern is legitimate and we believe it is important to present this discussion for biologists to see our logic in the ZEA Supplementary Information (also now

included with the manuscript for the reviewers to view), in which this issue is extensively discussed. We don't think there is a need to repeat this discussion in full in this paper.

We are constrained in our use of our definition of woodiness at this point in the process as we used the dataset assembled as part of the ZEA paper and because we used this definition in our survey, though we would be happy if this approach stirred others to attempt similar analyses with different definitions. We have updated the text to clarify that some of the decisions were made at the dataset assembly stage as part of a now published study - we simply outline the core definitions here for clarity.

That being said, we have tried to include a more thorough discussion of this point in the manuscript and hope that the reviewers (this point was also raised by reviewer 2) and the editors are satisfied with the result. Even if the reviewers/editors disagree that our definition is the best one -- and undoubtedly there is room for debate here -- we hope that at least they will judge ours to be reasonable and pragmatic.

In addition, it is easy to cull out the main location in the phylogeny where opinions may differ. The monocots (including taxa such as palms, bamboos, and screw pines), for example, lack a bifacial vascular cambium but maintain aboveground tissue for many years. We now provide all code and data so readers can easily rerun the analysis excluding groups they see as problematic.

> 2. The figure captions consistently refer to differences between models in terms of sampling with or without replacement, but the text explanation of those models (pp. 7-8) only attaches sampling w/o replacement to the hypergeometric model. The authors need to insert a brief statement indicating that the binomial model involves sampling with replacement, and cite an appropriate mathematical reference to justify the characterization of these two models as based on sampling with or without replacement.

We have made the connection between the binomial model and sampling with replacement explicit in the text, and have made the language more consistent to refer to "weak" and "strong" priors. Hopefully it is more clear. However, we have decided not to provide a citation the characterisation of these distributions as sampling with and without replacement as this can be found in any basic probability text.

> 3. I was put off by the authors' seeming to obscure a fundamental point underlying their estimates: namely, the actual numbers of species assumed in a specific, actual number of genera. The only place in the methods where the number of species comes up is on line 191, and the source of data is not given, nor is the number of genera given. So far as I can see, the only place the source of data on the number of species in each genus is given is in the captions to figures 2 and S3. No tabulation of the number of genera per APGIII-blessed order is provided, nor of the number of genera AND species in the orders not blessed by APGIII, despite the centrality of such data to the calculations made. The authors MUST provide these data!

We agree that the presentation here is unclear, though we did not intend to obscure the actual numbers involved in the analysis. We have clarified this in the second to last paragraph of the "Estimating" section in the methods, and the supplementary information now includes complete tabulation of all data at the genus level (see also the response to reviewer 2, point 1) as well as at the family and order level. We have also included further details on the actual number of species, genera and %woodiness throughout the main text of the manuscript

> 4. While it may be mathematically enjoyable for the authors to include both the hypergeometric and binomial models in their presentation, I would gently suggest that –for understanding by non-mathematical readers – it would be extremely useful to explain IMMEDIATELY in the text that the binomial model is, a priori, the better one to use.

We disagree with the reviewer's perspective here. We decided to use both statistical models in order to provide a lower and upper bound for our estimate. The fact that both of them give similar results is reassuring. As we state in the text, the two models represent two extreme scenarios; the "true" model of sampling is probably somewhere in between. We did not think that the binomial was a priori *the best model and do not want to make this claim up-front. (From first principles, we originally thought of the hypergeometric as the more reasonable sampling model). The only reason we suggest that the result from the binomial may be more accurate is that it corresponds more closely with the observed per-genus distribution of woodiness. That is, we suggest that the binomial distribution may be more accurate as a result of looking at the actual data (so,* a posteriori *rather than* a priori*). We think to imply otherwise would be misleading.*

> 5. Despite their exposition, the authors are – in my opinion – utterly opaque on how the actual numbers of woody species were calculated. Specifically, equations (1) and (2) give probability distributions. Were these used, for thousands of genera, to generate thousands of Monte Carlo simulations of the numbers of woody and herbaceous genera, and then the average or expected values of such numbers calculated? Or were the equations used to generate equations for the mean number of species expected to be woody or herbaceous, and those mean values simply summed? The authors MUST be explicit about what they actually did.

We have clarified this in the text (final paragraph of the "Estimating" section of the methods). Additionally, In the provided code we give a completely precise, though perhaps less accessible, presentation of everything we have done.

> 6. To me, the number of species included in the data base, as cited in the abstract, is quite misleading – 45K in the abstract vs. the actual number used of 37.5K (line 131).

We agree that this was (unintentionally) misleading. We have updated the abstract to use the 37 K number in the abstract and described in the text that this was pruned down from 45 K after removing synonymies and ambiguous data. (Note that numbers have changed slightly in the course of re-cleaning the data in preparation of the revised manuscript.)

7. I found that supplementary conversion table of 103 growth forms to a binary woody/herbaceous split – fundamental to the papers analysis – to be unsatisfying. Quite a large number of growth forms were simply not assigned to woody or herbaceous character-states, even though they clearly should have. For example, "biennial or hemicryptophyte" clearly should be herbaceous, while most of the chamaephyte or ... categories (but not ... or neophyte) clearly should be woody, based on the definition of the component growth forms. Why aren't climbing or epiphytic chamaephytes clearly woody?? The fact is that, elsewhere in the look-up table, similar growth forms (e.g., scrambling hemicryptophytes, scrambling nanophanerophytes) WERE assigned by the authors to woody or herbaceous categories, so the process appears somewhat arbitrary. I'm not convinced that the authors made lots of capricious decisions, but they need to go back to the basic data and recalculate after they've maximized the justifiable dichotomization of the 103 growth forms. Obviously, some of the latter can't be pigeon-holed (e.g., lithophytes), but the present mapping is not justifiable.

This point does apply to many of the Kew growth form categories, but in fact it does not apply to many species; there are certainly species which fall into a grey area, but this number is very small compared to the database. We have updated this table to include the number of species scored in each category so it is easier to see which of these really matter. Also, note that this is one of several data sources used by ZAE to assemble the data set, so species that were not scored unambiguously here may have unambiguous scores elsewhere.

The Kew categories use "or" to represent intraspecific variation. That is, a "Biennial or hemicryptophyte" classification might have populations that are biennial and populations that are hemicryptophytes. As such, we think treating species in those categories as "variable" is justified.

That said, we are certain that reasonable botanists will disagree about the implementation of any woodiness definition for specific species. (Similarly, reasonable botanists may disagree on assigning species to Raunkiaer life-forms for certain species.) We think that there is value in many different functional categorical schemes.

To address the specific questions raised, we did some detective work and went through the original species records and tabulated how many species in the dataset were in the categories the reviewer brought up. The number of species in each category are here:

Biennial or hemicryptophyte -- 10 species
Scrambling chamaephyte -- 6 species
Rhizome chamaephyte -- 3 species
Scrambling hemicryptophytes -- 6 species
Lithophytes -- 3 species
Climbing chamaephyte -- 4 species
Epiphytic chamaephyte -- 11 species
Epiphytic hemicryptophyte or chamaephyte -- 3 species
Epiphytic scrambling chamaephyte -- 1 species

We certainly agree that the woody/herbaceous classification of these categories is certainly debatable. (In fact there was some debate amongst us regarding the optimal categorization). However, given that the actual numbers of species in each of these categories is extremely small relative to the size of our dataset, categorizing them one way or another would have virtually no effect on the research question.

In any case, since this paper was originally submitted the Zanne et al. paper is now published including what was previously Supplementary Table 1 in their supplementary material. That is available here: http://www.nature.com/nature/journal/vaop/ncurrent/extref/nature12872-s1.pdf In order to avoid repeating that already-published table and the extensive discussion that accompanies it, we are removing table s1 and instead referencing that paper.

> 8. As a reviewer, I find it uncomfortable to pass on a paper that uses a higher-level phylogeny for the vascular plants drawn from an unpunished manuscript (Zanne et al.) that was not provided to me. In some sense, this is not that important, because where the phylogeny is used (figures 2 and S3), it is essentially as eye-candy – the phylogenetic relationships among orders is not used in the analysis in any way except for graphical presentation. On the other hand, those figures have a fair chance of being reprinted, and I worry about the some of the details. For example, as I understand it, the Gymnosperm AToL group still has not settled on the relationships among all the gymnosperm orders (though the familial placements within orders are beyond doubt), yet a fully resolved tree for gymnosperms is presented in figure 2. The lack of labeling for the small orders makes it impossible to see what is being assumed about relationships of Gingko, Taxales, and Gnetales. In monocots, Arecales is placed sister to Commelinales-Zingiberales, yet the most extensive data set (in terms of characters per taxon) places Poales sister to Commelinales-Zingiberales. That same data set, and a number of other analyses, also places Asparagales sister to the commelinid monocots just mentioned, with Liliales, then Dioscoreales-Pandanales sister to those nested groups. I'm not seeing that in the figure presented. Also, the meaning of radial distance if figures 2 and S3 is never defined. The authors need to define that, provide access to Zanne et al., and defend the phylogenies shown for gymnosperms and monocots.

In retrospect we should have included the Zanne et al. (ZEA) paper to the reviewers along with our own manuscript (we provided it to the editors in the original submission). We were in a bit of awkward situation with this as we didn't know when or where ZEA would be published and didn't want to steal our colleagues' thunder. However, ZEA is now in press (at Nature) and is included with this resubmission. The phylogeny is available on the Dryad data repository (now referenced in the paper). The reviewer is correct in saying that the phylogeny is simply used as "eye candy" and that we do not use any of the relationships between orders in our analysis (and we too feel confident in assigning the families into the correct orders); we just wanted a nice graphical representation of the distribution of woodiness along the phylogeny. We think that for this purpose, it is rather effective. We certainly agree with the reviewer that the gymnosperm and monocot phylogenies are not entirely settled upon and the relationships presented in the large-scale hypothesis used by ZEA for their comparative analyses across angiosperms may not be entirely correct. However, we feel that this tree does provide a general overview of the state of vascular plant relationships and as a product of the NESCent working group from which

this study grew, we felt it was the best option for visualizing the data. Given that we don't actually use the relationships between the orders in our analysis and that we did not build this phylogeny in this paper, we don't think that a defense of the specific relationships is warranted here.

The radial distance is proportional to units of time and represents the maximum likelihood dates from ZEA. However, as we do not actually use the dates in the analysis, it is really just a graphical convention, fairly common for large trees that are challenging to display in any form.

> 9. The convention used in figures 2 and S3 to represent the fraction of woody vs. non-woody species is fine – EXCEPT that is almost illegible!! Do NOT use colors on the bar graphs (they're effectively used and exhausted portraying major plant clades); use black and white bar graphs (that is, black vs. hollow white portions of bars) instead.

We have adopted the reviewer's suggestion to make the bar graphs in black and white.

> 10. Given the otherwise brief but eloquent statement of the evolutionary significance of woodiness on lines 60-70, and the explicit statement that wood has been lost many times in diverse groups, it is bizarre that a comparable statement re the repeated evolution of the woody habit and the arborescent habit in island plants is missing. Cite Carlquist 1974 (Island Biology) and Givnish 1998 (in P. Grant (ed.), Evolution on Islands) to summarize the contrasting views as to why that happens.

We have added a statement regarding this and have cited the two key papers you mentioned. However, we didn't provide much detail regarding the evolutionary processes that are thought to have generated this pattern as we do not provide any background on the other statements. These statements are just intended to give a brief overview on why we find woodiness evolutionarily interesting.

> 11. Finally, the authors should explicitly state how uncertainty regarding the number of species per genus and family across the vascular plants would affect the uncertainty in their estimates of the proportion of woody vs. herbaceous species. Perhaps a worked example using plausible alternative numbers of orchids and grasses might drive the point home.

When we originally started working on this project we worked on a rarefaction-based procedure in order to attempt to account for the possible uncertainty in diversity numbers, which we need at the genus level. However, this turned out to be extremely challenging. For many of the groups we looked into, "collecting curves" (based on the year of species descriptions) showed no sign of saturation at this level. We do discuss the possibility of this approach in the main text of the manuscript, but note that Costello et al. (2011) found that collecting curves may not saturate the family level. Collecting the required information is hampered by the lack of comprehensive and open databases; we would not be able to distribute the data underlying the results we could generate that demonstrate the difficulty of the approach due to licencing requirements. We do not believe it is straightforward to generate even a reasonable estimate of the upper bounds of diversity for many groups.

We hypothesize that there are likely more undiscovered herbaceous plants than woody ones but we do not have any strong evidence from the available data to support this claim. We have added a brief note about this in the manuscript.

Reviewer: 2

Overview:

This paper addresses the global taxonomic distribution of an important plant trait, woodiness, using intriguing novel methods. Both the methods and data would be of great use to other researchers, and it is for this reason that the biggest flaw in this paper is the almost complete lack of presentation of useful/interesting taxonomic data summaries or the inclusion of raw data.

The paper heavily focuses on the overall "global" proportion of species that are woody, but this alone is more of a botanical curiosity – the really interesting and useful data resulting from this analysis is the proportion of woodiness across global orders, families, and genera, data that would undoubtedly be highly cited and used in future analyses if it were included. Aside from this, the paper would maximize its potential by including clarification of the definition of the central trait of "woodiness", expanding discussion of the potential biases in the methods used, and removing references to the opinions of untrained persons unfamiliar with plants as "expert knowledge".

Main points:

(1) The definition of woody given in the introduction is very broad. This doesn't necessarily harm the analysis, but the distinction between this definition and other widely-used definitions of "woody" should be emphasized much more, both in the introduction and discussion.

First, the difference in language between the survey ("perennial aboveground stem") and the text (line 90 – "prominent aboveground stem through time") should be fixed, probably with the introduction version modified as the survey can't be changed at this point. However, this may not be possible, as the survey definition of "perennial aboveground stem" does not seem to actually line up with the definition used to assign growth forms to the binary woody/herbaceous paradigm in the actual analysis. For instance, banana is an evergreen with a perennial aboveground stem, and many perennial basal rosette forbs have perennial aboveground stems, though neither of these would have been called "woody" in the analysis. The definition that is stated to have been used ("prominent aboveground stem through time") is ambiguous in two ways – first, "through time" should be changed to "perennial" if that is the actual meaning, and second, "prominent" is highly subjective – is this based on height? Relative biomass investment? This definition should be modified to be unambiguous and best reflect the distinction used to assign species to the binary paradigm. As currently stated in the introduction, the definition appears to be more of a "persistent perennial" than actual anything to do with woodiness.

Second, the discussion of alternative definitions of woodiness and their strengths and shortcomings should be expanded in the introduction (or perhaps could be placed in the discussion). The definition used in the introduction does not actually include all species producing secondary xylem, as stated, as even Arabidopsis has secondary xylem. I understand that the traditional definition of "true wood" as extensive secondary growth via the vascular cambium isn't feasible to use in this type of analysis, but it should at least be mentioned formally in the introduction.

A similar point was brought up by reviewer 1 and we understand that this is an important and difficult point to address. We refer the editors and reviewers to our response above and the Zanne et al manuscript (also submitted) where we discuss the same issue in depth. We hope that our additions to the manuscript are satisfactory on this point.

We agree with the reviewer that the "textbook" definition that uses secondary xylem as a criterion is not workable. As we state in response to reviewer 1s comment on this point, we were somewhat constrained in our definition owing to the fact that we used the database assembled by Zanne et al. and that we had conducted our survey prior to writing the paper. Looking back we acknowledge that we should have been more consistent in our language in the survey but tried to find a definition that could be clearly articulated to both botanists and non-botanists. We should note that the definition of perennial (despite its etymology) is vague: "lasting or existing for a long or apparently infinite time; enduring or continually recurring." (first definition from Google). There are of course other definitions of perennial including lasting through the winter, but as noted elsewhere in this response, any implementation of a definition that includes winter cannot be easily applied to the aseasonal tropics, which is where most of the "grey-area" species are.

Another specific responses to the reviewer's comments is that in the phrase "perennial aboveground stem", the key is the "aboveground" qualifier, which excludes perennial grasses from being characterized as woody.

So in summary, we are doubtful that a slightly alternative wording in the survey would have dramatically changed the responses we received, given the extremely subtle distintion between the wordings and how far off the survey results were from our estimates.

(2) The primary scale of "imputation" for this analysis is the genus level. One potential issue (alluded to in the discussion) is that woodiness is a major character used to delineate taxonomic groups, both genera and higher groupings like families and orders. I'm uncertain as to what effect this may have on the analyses (for instance, the strong bimodal pattern seen, and conclusions drawn from this), but this should be addressed more up front in the methods section, and more directly in the discussion. Perhaps the bimodality graphs should be repeated for higher taxonomic groupings as well (families and orders) to best gauge this effect (Figure 1 repeated for families and orders) .

Working with named groups in any context is a bit odd. They are clearly a non-random subdivision of biodiversity. Taxonomists have long grouped things together as a result of shared characters, convenience and the preferences of the individual worker. Genera were a natural

level for us to work at as the (estimated) diversity in each genus can be fairly easily tabulated. However the fact that genera may often be delineated on the basis of woodiness is a "feature not a bug" of the analysis. That is to say that if genera were defined solely on the basis of woodiness (distribution was completely bimodal), we would have even greater confidence in a global estimate of the woodiness fraction; we could simply tabulate the number of species per genera and calculate the total number of species that fell into the woody category and the only source of error would be in the diversity estimates. At the other extreme if woodiness was so labile that it was randomly distributed within genera, our approach would estimate the proportion of woodiness with considerably less confidence. The fact that both "extreme" sampling scenarios (binomial and hypergeometric) give strikingly concordant estimates with fairly high confidence, we feel that we are not being misled by the use of taxonomy. However, given that the data are what they are, and the distribution of woodiness does seem to be bimodal, we are not entirely clear what the reviewer intended by this comment.

We like the reviewers suggestion of including the distribution figures for both families and orders and these are now in the supplementary material. The distribution is largely bimodal at all levels. But as one would expect moving up taxonomic levels (from genera to families to orders), the distribution of woodiness becomes more evenly distributed. We now bring this point up in the manuscript as well.

> A related (but likely more important) issue surrounds understanding the effect of variation in the size of genera on imputation. A graph demonstrating this effect would help readers (and this reviewer) better assess the appropriateness of the genera-level imputation. The methods used seems to result in the assumption that genera are basically all-woody or all-herbaceous regardless of prior used, and it would be particularly interesting to see if the size of a genus corresponds to the probability that it is mixed versus all-woody or all-herbaceous. This sort of plot would allow the authors to potentially make further statements about how their overall estimate may be biased by the distribution of species with missing data across large versus small genera. (For instance, if we assume woodiness data are missing at random from the overall dataset, in a small genus one is more likely to have all-woody or all-herbaceous data than in a large genus if the true proportion is mixed, something like 0.2). Take for instance the genus Sonchus (Asteraceae) – the genus is mostly annual herbs, but there are a dozen exotic woody species in Macaronesia. If this were not a well-studied genus, the woody species would likely be missed if data on species growth form were missing at random, and Sonchus would be imputed as all-herbaceous. The likelihood of this happening would likely increase as genus size decreases. A simple plot of woodiness proportion versus genus size and a bit of discussion of this effect would make this paper much stronger.

We believe the reviewer may have somewhat misinterpreted what we did in the analysis and have attempted to clarify this throughout the manuscript. Using the "strong prior" (binomial) approach, the reviewer is correct that when all of the observed species in a genus are classified as woody, the estimate will be that the rest of the genus is also woody. The uncertainty in the estimate will not be affected by the number of species that have been unclassified.

In contrast, when using the "weak prior" (hypergeometric) approach, poorly studied genera (that is with many species in unknown state) will be likely to be scored as polymorphic (see the worked example for Microcoelia *in the text). This creates distributions that are markedly less bimodal.*

In the case of Sonchus, if we only had observations on the herbaceous species, with the binomial (strong prior) approach we would indeed infer the rest to be herbaceous. But with the hypergeometric (weak prior) approach we would infer that at least some of the missing species are woody.

For both approaches, in genera in which there is a mixture of woody and herbaceous species, the uncertainty of the estimate will increase as the number of unclassified species within a genus increases. It is not necessarily the size of the genus that makes the difference but the relative number of species for which growth form is known compared to those for which it is unknown.

However, the reviewer raises a very interesting question that we had not previously considered: are clades with many unknown *species more likely to be primarily herbaceous, woody or of mixed genera. We examined this relationship in a number of ways and have included this in the supplementary material. We find that, unsurprisingly, the more species in a genus, the more likely it is to be variable (this is partly a combinatorial necessity; there are fewer ways that smaller genera can be variable). Primarily herbaceous genera also tend to be larger, though this relationship is fairly weak and as we stress throughout the paper, the dataset is biased towards woody species.*

> (3) This data would be potentially useful to lots of researchers if it were presented at a finer scale. The overall estimation of the "global" proportion of species that are woody is more of a botanical curiosity, while the presentation of proportions of woody species for all analyzed orders and families would lend itself to being used for future analyses. Figure 2, in its current form, is not particularly interpretable due to size, circularity, and color (see minor comments below). I wonder what specific goal is being achieved by this figure, other than that such a broad analysis has phylogenetic implications, though this analysis is not directly phylogenetic. Replacing Figure 2 with some sort of figure or table with actual numerical species proportion estimates would be more useful to readers, as the current figure's green-brown bars are impossible to extract data from. If the authors want to present a tree figure, a noncircular one would be best, with orders presented as tips (replace wedges with actual species counts) and with actual woodiness proportion estimates listed.

This is a great idea which we had not considered. We have included a table in the supplemental material with the estimate woodiness proportion with confidence intervals for all orders, families and genera. We have included this information in a csv file rather a table in the pdf because it is rather large and difficult to typeset (it is also much easier for people to re-use in this format). We have also included our code such that these estimates can be reproduced fairly easily perhaps with alternative coding schemes for woody/herbaceous.

Regarding the figure, we would like to keep it in the main text. We are visual thinkers and think displaying the information in a phylogenetic context is helpful --- we think it helps captures the distribution of the woody character across vascular plants. We are also phylogenetic biologists and tend to have a very tree-centric perspective on things even if we are not using the tree directly. We have tried many different ways of representing the tree and settled on the one we did because it was the clearest to read and understand of all possible iterations we attempted. Displaying trees at this scale is a non-trivial task We would like to keep the figure as is though we have altered the green/brown representation of the tips to make it more legible.

(4) In relation to the above suggestion, I would like to see a supplemental file with strong and weak prior woodiness estimates for all genera, families, and orders included in the analysis (along with species count data, and raw number of woody/herbaceous members observed). Having published data like this available to other researchers not only is becoming standard practice with such huge datasets, but would highly increase the impact of this publication, elevating it from botanical curiosity to useful resource (with far more citations).

Agreed, as stated above, this is included as both a supplementary figure (families and orders) as well as a csv file (which includes all genera, families and orders) along with the raw data and code to generate the results. We would be very interested to see what other biologists could do with these results.

(5) Why were intermediate/variable species (1.3% of the dataset) just removed instead of being used in some form of analysis? In reality many species are facultatively woody depending on climate, including many that were likely coded as definitively woody or herbaceous in this analysis. The question "how much of the world is woody" isn't well-answered if facultative or intermediate woodiness is completely excluded. Also, the exclusion of these species likely increases the "bimodality" seen among genera.

We removed the species that were intermediate/variable because we could not come up with a clever and coherent way of including them in a sampling procedure -- the probabilistic model would have to be substantially different. Additionally it is oftentimes difficult to evaluate whether variable species in the original dataset are variable because the species is truly variable according to a single definition or because the data was contributed by different researchers with slightly different coding schemes.

To evaluate the sensitivity of the analysis to the coding of variable species, we coded all of the variable species as alternatively all woody or all herbaceous and re-ran the analysis. The results are presented in the supplemental material and referred to in the main text. Somewhat to our surprise, alternative coding schemes had a non-trivial difference to the final estimates. While neither of the extreme scenarios (all variable species coded as woody vs. all variable species coded as herbaceous) are biologically reasonable, doing these additional analyses gave us a better sense of how miscoding species may impact our results. We discuss the implications of alternate coding schemes to our inferences in the discussion section of the manuscript. We are glad that the reviewer brought this point up as we feel that addressing this has strengthened the paper.

(6) The survey is referred to several times in the main text as assessing "expert knowledge", but the average given in the results (31.7%) includes respondents with both no formal training and no familiarity with plants. This is misleading. A recalculation using only plant-familiar and trained researchers would be more appropriate, or at a bare minimum excluding the "What's a plant?" group of respondents. Also, why was only Portuguese chosen if the goal was to include more respondents from Latin America? Spanish and French translations would not have been hard to produce. As is, what is the overlap between "tropical" and Portuguese responses in the survey? Language of response would be a relevant demographic to include in the S2 analysis, or at least a statement that there was no effect or association if this is the case. Also, the Portuguese language translation of the survey should be included as a supplement.

We have rephrased this to be less strongly worded.

If we drop the "What's a plant?" category, we get a mean response of 32.4% (compared to 31.7% with those respondents included). The range is unchanged as 1-90%. If we repeat the analysis "using only plant-familiar and trained researchers" [so Familiarity of "Familar" or "Very Familiar" and Training of at least "Undergraduate degree in botany or a related field", we get a mean of 32.8% and a range of 1-90%. So including "non-experts" in the survey does not really substantially affect the overall conclusion that workers have a biased perspective of biodiversity.

Regarding the Portuguese language component, we didn't intend to be comprehensive in our survey and certainly did not have a statistically random sample given the volunteer nature of the respondents. We simply decided to include a Portuguese translation to get some additional respondents primarily from Brazil and our friend was on several Brazilian biology mailing lists. The Portuguese version of the survey is now included as a supplement as suggested.

Overall, the survey component was meant to be just a fun and hopefully interesting minor addition to the project and to demonstrate our point that this was indeed something that was not widely known. We feel that it served this purpose.

Smaller points:

Abstract, line 42 – "mean", not means

Good catch. This is fixed.

line 144 – "nh herbaceous species"

Also fixed

line 275 – are you suggesting that undiscovered species are more likely to be woody or non-woody? (I would guess the latter, but please clarify)

We don't really have strong evidence but we would predict that there are more undiscovered herbs in the world than there are woody plants. We have added this to the text, even if it is somewhat unsubstantiated.

Figure 2's color scheme is unreadable, even when printed in color on a high-quality laser printer. Gymnosperms, Monocots, and Eudicots are all nearly the same color. The tree branches are also so compacted as to prevent interpretation of relationships among tips. Furthermore, the bar graphs with proportions are so small as to be almost completely worthless. All of these, though, would be handled by the reformatting requested above. If that reformatting is not done, though, at a minimum these problems should be addressed.

As stated above we wish to keep the figure in the main text. However, we have tried to use a better scheme of representing the data and think it is more clear now.