Response to Reviewer 1

Key
Comments have numbered as Reviewer_number#comment_number (e.g. R1#12).

*Italics: original comments by the reviewer*
Normal font: response
**Bold: changes in the manuscript.**

Citations without reference correspond to papers cited in the manuscript. New references are specified here.

*R1#1. This paper compares the performance of different imputation methods for a trait dataset. Although this topic has already been studied before, the authors bring three novelties: (i) they use a spatially-explicit dataset (ii) which includes intra-specific information, and (iii) they use of a set of measures to assess imputation performance in terms of multivariate trait structure. This type of analysis is interesting, in a time where gap-filling methods are used more and more often to impute trait datasets.*

- We would like to thank the reviewer for acknowledging the novelty and relevance of our study.

*R1#2. However, the paper would need some clarifications and better justifications, in particular for the choice of the methods.*

- Following the reviewer's suggestion, we have made some changes to better justify the methods employed. We have modified the section '2.3. Imputation methods' so that the first clear paragraph now delineates the main reasons for the selection of imputation methods: mean and Spmean as baseline, widely used approaches, kriging methods, which account for spatial structure of the data and kNN/MICE, which are designed to impute multivariate datasets. The paragraph now reads (section 2.3):

- **We compared imputation methods with different degrees of complexity. We used two simple approaches to provide baseline imputations: Mean imputation ('Mean') filled missing data using the overall mean value for each trait and species mean imputation ('Spmean') replaced missing values with trait means computed for each species. Because of the spatial nature of the dataset, we also tested two geostatistical approaches, ordinary kriging ('OrdKrig') and regression kriging ('RegKrig'). Lastly, we also used two methods designed to handle multivariate datasets: *k*-nearest neighbour imputation ('kNN') and MICE (Multivariate Imputation using Chained Equations).**

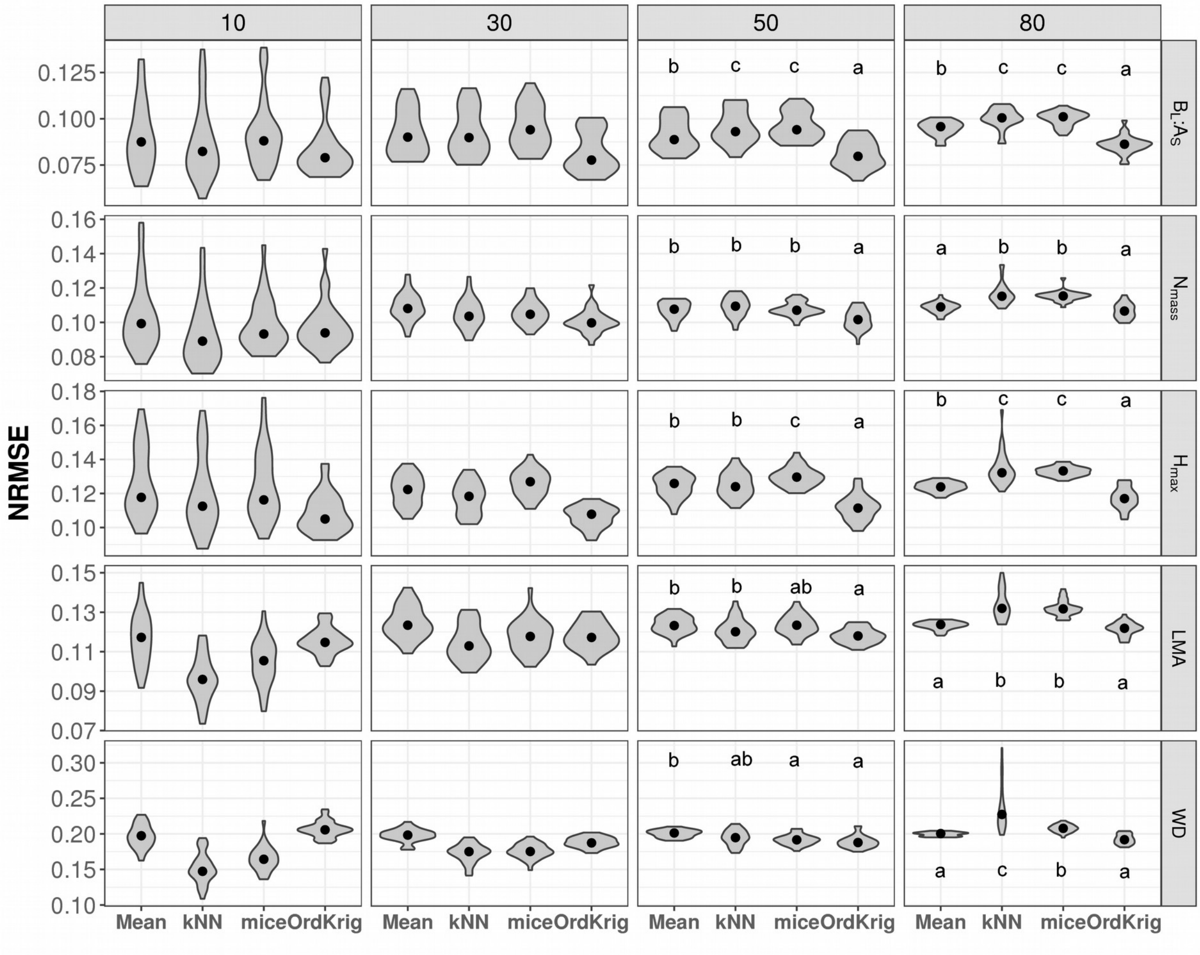
- We have also improved the justification for some more specific methodological issues, such as the use of PMM or the specific tuning of kNN and MICE (see replies to comments *R1#9* , *R1#29*).

*R1#3. Some proper synthesis of the results is missing (shown by the total number of figures in main text and appendix) and no tests are performed, giving the general impression that none of the methods performs better than others.*

- We are aware that, although the main manuscript is not excessively long, the overall number of figures is very high. We deal with various different aspects related to the imputation of plant traits (imputation methods, auxiliary information used in the imputations, missingness, multiple traits) and these require extensive analyses. We also wanted to show the impact of different settings on MICE and kNN, because we often see that these methodological details are neglected in many studies, and one wonders whether they may cause differences in the final imputations.
- It is also true that, sometimes, we repeat (albeit expanded) some information in the Supplement that has already been shown in the main text (e.g. Fig. 4 and Fig. S10). Therefore, following the reviewer's comment, we propose to delete the following figures from the Supplement: Figs: S2, S4, S7, S10, S12, S13-S17. We will also merge sections S3 and S4 and put all references at the end of the supplement, following other comments by the reviewer (*R1#27, R1#28).*
- The reviewer comments that we do not perform statistical tests for all the results we show in the paper. Certainly, we do not use statistical tests for every single comparison, but we do use statistical inference in the last comparison (Supplement S8), which is, in our view, the most important. To make this more visible, we propose to move current Table S2 to the main text, as Table 1, showing how the different imputation methods perform with increasing missingness. This also implies a modification of the corresponding text in the results (section 3.3):
- **The LME model showed that the rate of increase in KGE with increasing missingness was lowest for 'Spmean' in four out of five traits (Table 1). Compared to 'Spmean' and 'RegKrig', performance of MICE and kNN declined more with increasing missingness (Table 1, Fig. S22, Table S1), but MICE generally outperformed kNN (Fig. 2, 3), as already observed in a recent imputation assessment of species-level, life-history traits (Penone et al. 2014).**

- In a revised version, we will propose to use mixed-effects models and pairwise comparisons to statistically test differences across methods. We will add the significance of the most important tests in the main text when describing the corresponding results (as would be described in a modified paragraph in the methods section 2.5):
- **Throughout the paper, we show violin plots representing the median and the distribution of each performance metric as a function of missingness levels, but we only graphically display the 10%, 30%, 50% and 80% levels, for ease of visualisation. We modelled imputation metrics in a linear mixed-effects model (LME) as a function of the interaction between imputation method and missingness, with dataset replicate as random effect. The LME model was fitted using the nlme package in R (Pinheiro et al., 2012) and pairwise comparisons of model coefficients were performed using the lsmeans and lstrends functions in the lsmeans package (Lenth, 2016).**

- We could also add the results of these multiple comparisons derived from the models in the main figures of the paper, except for Figure 4, where it would result in a highly cluttered figure. We would also restrict these for missingness of 50% and 80%, also to avoid unnecessary clutter. Although we don't think this would be necessary, given the changes we propose in the text (see above and comments to *R1#32, R1#33*), here is an example for Figure 2:



- See also some specific examples in some of our replies to your comments below (*R1#32, R1#33*).

*R1#4. There is also a number of problems in the results and figure presentations that should be fixed. Please refer to the comments below for more detail, in particular my points 7 to 10 are quite major.*

- We propose several changes to improve the presentation of figures and results. See also our responses to points 7-10 below (*R1#13 to R1#16).*

*R1#5. Another major point is the use of "ecological information" in the imputation process. The authors show that adding this information to the imputation improves its quality, as one would expect. However, in most ecological papers, authors usually look at the relationships between traits and this "ecological information". This introduces a serious problem of* *circularity on any analysis using trait data imputed with "ecological information". The authors never mention this potential bias, do not suggest in which type of analyses such dataset could be used and more importantly, they do not test for this potential bias. A simple test would be to look at the relationship between traits and "ecological variables" in the complete dataset, in the datasets with missing data and in the imputed ones. This would give an idea about the importance of the bias and warn (or not, depending on the results) the users about it.*

- This is a reasonable concern, but the entire multiple imputation framework would tend to minimise the potential effects of circularity in an eventual analysis. The developers of MICE (van Buuren 2012, p.128; van Buuren & Groothuis-Oudshoorn, 2011, p. 22) in fact recommend to include in the imputation models those variables that will also be employed in the analysis of scientific interest (i.e. the trait or trait-environment relationship) and suggest that failure to do so would lead to biased results. This is because imputations are non-deterministic (i.e. they are drawn from a distribution) and the differences between multiply-imputed values represent the uncertainty in the imputation process. The multiple imputation framework provides tools to perform analyses on the multiply-imputed datasets, which include the uncertainty derived from the imputation process. Given the already complex and relatively long manuscript, we would prefer not to expand on this aspects, but we have modified a paragraph in the 'Implications' section 4 to deal explicitly with the circularity issue:
- **Compared to other imputation approaches, MICE is well-suited to deal with multivariate missing data (i.e. MICE produce imputations when some predictors are also missing) and provides information to quantify the uncertainty associated with the imputed data (Fig. 8). MICE uses multivariate relationships in the dataset to impute missing data, and this may raise concerns about potential circularity in analyzing trait-trait or trait-environment associations with the imputed dataset. Despite these concerns, multiple imputation practitioners argue that the full inference framework based on multiply-imputed datasets, would minimise the problem of circularity. Because our comparative assessment of imputation methods is already complex, here we have only dealt with *imputation*, the first step of the full process (e.g. Nakagawa & Freckleton 2008). MICE produces multiple datasets, with imputed values drawn from distributions, and these datasets can be combined in the *analysis* and *pooling* steps. The analysis step refers to the estimation of the parameters of scientific interest (e.g. a regression coefficient) for each dataset. In MICE, parameters can be pooled across datasets to produce unbiased estimates and standard errors, providing a natural way to take into account the additional uncertainty introduced in the analysis by the presence of missing data, and to minimize circularity issues (van Buuren 2012). However, ecological studies using multiple imputation approaches usually only apply the imputation step (Baraloto et al. 2010, Paine et al. 2011, Pyšek et al 2015, Díaz et al. 2016) and do not take advantage of the multiple imputation framework to quantify the uncertainty resulting from the presence of missing data (but see Fisher et al. 2003).**

***Abstract***

*R1#6 (1)- L.16: "functional biogeography" is not mentioned elsewhere in the paper*

- ‘Functional biogeography’ appears in the ‘implications’ section.

*R1#7. (2)- L.16: “they offer specific challenges in terms of data imputation”: these are not mentioned in the paper neither, it would actually be interesting to discuss these specific challenges*

- These aspects have been discussed in the paper, although the reviewer is correct that they could have been made more visible. For example, one important aspect is the fact that these are multivariate datasets and that they may also include missing data in the predictors. Another specific challenges are the spatial structure of the data (treated in our kriging approaches) and the fact that trait covariation and trait-environment relationships can be used to improve trait imputations (which we also address in the paper). We have added a paragraph in the ‘Implications’ section 4 discussing these issues:
- **This simulation study assesses different imputation methods in spatial, traits datasets with multivariate missing data. Amongst the methods assessed here, MICE and kNN are the most adequate to impute multivariate datasets, as they can be used when predictors also include missing data. Kriging methods may be more difficult to apply when predictors are also missing, but we have shown that, at high missingness levels and when environmental information is lacking, they can outperform MICE and kNN. This implies that methods including spatial variability may sometimes more provide more accurate imputations than those using trait covariation.**

**Introduction**

*Overall, the introduction is well written and clear, it just lacks some details on some aspects (see below).*

*R1#8. (3)- Please provide a reference and explanation for the following statement L.56: “they all alter, to different degrees, the univariate trait distributions and the covariance structure of the dataset”. Please also explain why multiple imputations do a better job in conserving trait distributions and covariances.*

- We acknowledge that our message here was a bit confusing. We now highlight that methods based on kNN and machine-learning are suitable to impute multivariate datasets and to preserve the covariance structure. We refer to Eskelson et al. 2009 and Penone et al. 2014 for examples on both types of methods. The modified sentences now read (section 1):

- **Single imputation methods replace a missing datum by one value and proceed with the analysis as if the imputed data had been observed (Nakagawa & Freckleton, 2008). Within these approaches, species mean or median imputation are probably the most widely used methods in ecology, but they ignore the variance of the imputed variables. Model-based imputation methods use other variables in the dataset to impute missing data, but they substantially alter the univariate trait distributions and the covariance structure of the dataset (Gelman & Hill, 2007). Approaches such as *k*-nearest neighbour (kNN) or machine-learning methods (Stekhoven & Bühlmann, 2012) may be**

**more appropriate to impute multivariate datasets, preserving their covariance structure (Eskelson et al. 2009; Penone et al. 2014).**

*R1#9. (4)- L60: Please cite which multiple imputation (MI) techniques are better to preserve structure and distribution of traits. MICE includes a high number of different algorithms, some accounting for variables distribution, others for interactions between variables, etc.. And actually some MICE techniques perform even worse than single imputations (e.g. see Stekhoven & Buhlmann 2012). MICE alone does not say much about the method and it would be important to specify quite early in the paper that it is MICEPMM which is tested.*

- We agree with the reviewer that MICE includes several variants, mainly defined by the specific univariate imputation model. In fact, our study is the first one to our knowledge  to make a comprehensive assessment of different variants within MICE within the biological/ecological literature. Other studies have either used PMM directly (Penone et al 2014) or have not even reported which univariate method was used within MICE (Stekhoven & Buhlmann 2012). We wondered whether the choice of method could have influenced the results of these papers, and it appears that it has not (see below).

- As for the information on the univariate imputation method in MICE early in the paper, we prefer not to include this in the introduction, and leave the description and justification of the use of PMM in the Methods section. The aim of our study is broader and includes multiple aspects (imputation methods, auxiliary information used in the imputations, missingness, multiple traits) and we prefer not to include such technical details in the introduction.  As we state in the Methods, we chose PMM because it is known to perform better when non-normal distributions and non-linear relationships between variables are present (see Morris et al. 2014, now cited in the main text).  But we also tested its performance compared to other algorithms (included a random-forest based one), and while it is true that in our tests PMM did not show a big improvement over the other algorithms, it did not perform worse either.

*R1#10. (5)- L 62. I would not define kNN as a sophisticated method, it's in fact quite a simple One*

- We have replaced 'sophisticated' by 'statistical'. The text now reads (section 1):
- **While forest inventories have adopted statistical imputation methods for some time, as for example the kNN methods (Eskelson et al. 2009 and references therein), imputation methods have only recently been started to be used in trait-based ecology (Baraloto et al. 2010; Pyšek et al. 2015).**

*R1#11. (6)- L90: sampling date is not really "ecological information", also most of the predictors mentioned were not really introduced before.*

- We agree with the reviewer that the term 'ecological information' may not include all the different variables proposed here.  We will use 'environmental information throughout the paper instead of 'ecological information'. As for the predictors mentioned here, they were genericaly introduced previously in the introduction, but without mentioning them specifically (section 1):

- **However, intraspecific variability in plant traits may be substantial (Siefert et al. 2015; Vilà-Cabrera et al. 2015) and imputation methods that use environmental information may be more appropriate when assessing trait relationships and trait-environment covariance in a spatially explicit context. Biotic or abiotic variables other than the trait matrix of interest can be included in imputation algorithms as auxiliary variables to reduce imputation bias (Azur et al. 2011; Rezvan et al. 2015).**

**Methods*

*R1#12. In general, the methods are clearly explained but some things are understandable only when reading the supplementary information. The methods are quite dense, so it is OK to have some descriptions in the appendix. However, they should be selfunderstandable. Figure 1 is very helpful and important. I also think that the evaluation metrics are very interesting. However, I did not understand some of the choices, which I think should be better justified (see below).*

- We would like to thank the reviewer for the positive comments on our methodological description, including the praise for Fig. 1 and the choice of metrics. We expect to clarify some of the issues on clarity and justification below.

*R1#13. (7)- A quite major point is that the authors state that in the real dataset missing data is biased towards leaf traits deliberately. So data are not MCAR in the dataset (l.120). We also know that in trait datasets, values are often MAR (Nakagawa & Freckleton 2008). But the authors then remove data completely at random (L121). We also know that imputation methods are not designed for MCAR data (van Buuren & GroothuisOudshoorn, 2011). So why the authors chose to remove data MCAR? I would suggest to introduce data at random with the same structure as in the original dataset. This would be a fairer test than just removing data completely at random. It is important to*
*see how the methods behave when data is MAR.*

- As correctly pointed out by the reviewer, missing data in foliar traits were introduced deliberately and randomly, following the sampling design, because these traits were measured only in a random subset of the plots. Intentional (van Buuren 2012) or planned missing data design (Nakagawa 2015) are implemented when a certain variable, or set of variables, is costly to measure but another set of variables, the auxiliary variables, can be used in the imputations. And this is considered in our approach of including auxiliary information to improve imputation performance (for example, inclusion of topography would take into account any geographical pattern in missingness levels).

- Therefore, for foliar traits, a large proportion of the missing data were actually MCAR by design. However, we agree with the reviewer that, in general, missing data in our dataset is probably MAR. MAR implies that the probability of missingness depends on another variable in the dataset. As a simple test, we fitted the probability of missingness for all traits in the IEFC incomplete dataset using a logistic model including species as a factor. For all traits, except Hmax, species had a significant effect, but there was not a clear pattern of missingness associated to certain taxonomic groups (e.g. higher missingness in Pinaceae vs Fagaceae). This shows that there is no consistent pattern in the missing data mechanism within or across traits.

- Hence, we agree with the reviewer that simulations using MAR datasets may have been more realistic. However, because of the results mentioned above, but it would have been difficult to decide on how to apply this MAR assumption when introducing gaps in the datasets. In other studies missingness has been more consistently related to a variable in the dataset, allowing for an easier application of the MAR assumption. For example, Penone et al. 2014 simulated MAR gaps by assuming that missingness was higher in small carnivores, compared to large ones, according to missing data patterns observed in trait datasets. In that study, they did not find any difference compared to simulations using MCAR missing data.

- Given these prior results and the approaches we follow towards the inclusion of auxiliary variables in the imputations, we did not expect a major impact of different missing data mechanisms in our simulations. In addition, our study already deals with many aspects (imputation methods, auxiliary information used in the imputations, missingness, multiple traits) and adding yet another source of variability would likely make the paper overly complex. However, we have added a sentence in the 'Implications' section recognising that there is some uncertainty in the results that arises from the assumption of missing data being MCAR (section 4):
- **One limitation of this study is that we simulate MCAR missing data when a MAR assumption would have probably been more realistic (Nakagawa 2015), although a recent study did not show differences in trait imputation performance between these two missing data mechanisms (Penone et al. 2014).**

*R1#14 (8)- Another point is that there is no comparison with the dataset including missing data. The question: "should I impute or not" is an important one so it would be good to know how well the imputation methods perform (in terms of KGE and structure) when compared to just using the dataset with gaps.*

- We indeed compared results (for the differences in trait relationships) when using complete, incomplete or imputed datasets (Figs. S20, S21). We have now expanded this part of the results (section 3.3):
- **Using incomplete (i.e. not imputed) datasets to retrieve trait correlations had an impact on the Nmass–LMA relationship at high missingness rates, compared to 'mice_ctsp' imputations (i.e. larger departure from the 'complete' line for 'incomplete' compared to 'imputed', Fig. S20), but this trend was not clear for Hmax –WD (Fig. S21). Many imputation methods did not seem to improve analyses performed with the incomplete dataset (Fig. S21). For example, kriging and 'Spmean' methods showed the largest departures in trait**

**relationships, when compared against analyses performed with 'complete' or 'incomplete' datasets (Fig. S21, S22).**

- We would also like to stress the fact that in some cases, imputation is really necessary, because some representation of geographic variability is needed for applications such as trait mapping or trait-driven modelling approaches. We now highlight this in the closing statement of the manuscript (section 4):
- **We also show that spatially-distributed layers of environmental information may improve trait mapping, increasing spatial resolution and/or sample size in trait-driven ecosystem process models (Christoffersen et al. 2016).**

*R1#15 (9)- Related to the previous, at the end, users would like to know which method is the best, considering together NRME, distributions, correlations, structure and regardless of the trait considered or the % of missing data. This could be analysed using a mixed model with the identity of the metric (NRMSE, KGE..etc) and the missing dataset identity as random factors.*

- We have shown that it is difficult to provide an unequivocal response to the question of what methods performs best in all situations. We show that, when no auxiliary variables are present, using a geostatistical method such as ordinary kriging can significantly improve imputations, compared to simple averaging approaches, but also compared to approaches using trait covariation (MICE, kNN). We show that, at intermediate missingness rates, MICE with some auxiliary variables tends to be the best performing method (especially if we consider distributions and the metrics related to covariance structure) but this advantage vanishes at higher missingness rates, and the best-performing method depends a lot on which trait we consider.
- Given these results, we emphasise the usefulness of MICE because it is naturally designed to handle multivariate missing data (mixed data types, missing data in the predictors) and it provides uncertainty estimations around the imputations. For example see our text in the 'Implications' section 4:
- **Compared to other imputation approaches, MICE is well-suited to deal with multivariate missing data (i.e. MICE produce imputations when some predictors are also missing) and provides information to quantify the uncertainty associated with the imputed data (Fig. 8).**

*R1#16 (10)- Given that the dataset has intraspecific variation and this is presented as a novelty both in the introduction and the "implication" section, I would have expected an analysis of the error at the species level. Also, it should be noted that adding species identity assumes that interspecific variation is higher than intraspecific variation, which is OK, but should maybe be stated somewhere.*

- Our study focused on questions that are of more general interest to ecologists (imputation methods, use of auxiliary variables) rather emphasising results that would be more specific to the study system in question (species-specific patterns). Moreover, a recent study (Vilà-Cabrera et al., 2015) has already looked at trait variability at different taxonomic levels, including the influence of environmental gradients on the same dataset.
- In our factorial experimental design we have seen that species identity always improved imputations, but for some cases (Hmax, for example) it is not the single

predictor that contributes most to improve the imputations (in this case it's forest structure). This factorial design, therefore, does not assume a priori higher interspecific variation and shows that other auxiliary variables may be better predictors than species identity.

*R1#17. (11)- L. 126: twhy m=5? MICE authors recommend to use at least 10 iterations (van Buuren& Groothuis-Oudshoorn, 2011). I saw later that this was explained in the appendix, I think that it should be at least mentioned in the main text.*

- The number of iterations (t) refers to the number of cycles through all missing variables in the dataset, and we set that to 20, more than the default number of iterations in the MICE algorithm (t = 5). We do this to improve the stabilisation of parameters in the imputation model and to minimise the effect of imputation order. We explain this in the supplementary material S4.
- The number of multiply imputed datasets (m) was set to 5, the default in the MICE algorithm, because this is a recommended setting during the test stage (van Buuren 2012) and because it makes simulations more efficient computationally (in terms of both computing time and data generation). This is also explained in detail in the supplementary material S4.

*R1#18 (12)- L.138: similar to the previous point, it would be good to state that k=7 comes from*
*an additional analysis (described in the appendix), otherwise the "7" is quite obscure.*
*All these omissions make the reading/methods understanding quite challenging.*

- We have rewritten this part of the Methods and now we explicitly say that these methodological decisions are a result of the preliminary tests performed:
- **We selected *k* = 7 and median aggregation after some preliminary tests (Supplement S2).**

*R1#19. (13)- The MICE paragraph (l.151) should give more details on what is described in appendix S4.*

- We decided to include the detailed explanation of the MICE algorithm in the Supplement because otherwise the Methods section would be even longer than it is now. We think that this makes the paper shorter and easier to read. What we have done is to merge sections S3 and S4 in the Supplement, so now the MICE explanation is more compact (see *R1#27*).

*R1#20. (14)- Why some variables are added sequentially whether others are included in a factorial design? (L175-180). Please clarify*

- We were interested in identifying which combinations of the variables with a major role in explaining trait variability (species identity, climate and forest structure; see Vilà-Cabrera et al 2015), led to improved imputations. Other variables which we expected to play a secondary role (topography, lithology, sampling month) were added sequentially. We have rewritten the corresponding explanation in the methods section, to make this clear (section 2.4):

- **Species identity ('s'), climate ('c') and forest structure ('t') were introduced in a factorial design to identify those combinations of variables leading to improved imputations. Because we expected them to play a secondary role in explaining trait variability, topography ('p'), lithology ('l') and sampling month '(m') were sequentially added to MICE and kNN imputations using species, climate and forest structure.**

*R1#21. (15)- Why lithology is not included into the RegKrig? And why is topography included in ordKrig? Isn't ordKrig only based on spatial coordinates? Please clarify.*

- As noted by the reviewer, ordinary kriging is only based on the geographic coordinates, as explained in the beginning of section 2.4. Lithology (as topography, or sampling month) was considered a predictor of secondary importance, compared to species identity, climate and forest structure. For this reason, and to avoid increasing the complexity of the analysis, these variables were only investigated within the mice imputations and not used in the other methods (kNN, kriging).

*R1#22. (16)- KGE is a very interesting metric. However, since high values represent better performance (contrary to NRMSE and deltaCORMAT) I would either use –KGE for the figures or remind in figure captions that high values=better performance (e.g. fig4).*

- Following the reviewer's suggestion, we will add a note in the caption explaining that high values of KGE mean better performance.

*R1#23. (17)- l233: for the imputation of the whole dataset the authors use m=50 imputations because it is recommend to choose a value closed to the missingness rate. Why this same rule was not applied for the simulations as well?*

- As also mentioned in comment #11 above, we followed the recommendations by the developers of MICE and we used 5 imputations during the test stage and a larger number for the application stage (van Buuren 2012). This avoided a large computational burden, in terms of processing time and data handling/storage.

*R1#24. (18)- It would also be important to test the correlations between environmental variables, to see at which point it is interesting or not to use highly correlated variables in the Imputation.*

- This is a good point, because it is known that MICE may have problems when input variables are highly correlated. We minimised this by only selecting variables which already showed low correlation (r<0.3) in a previous study using the same dataset (Vilà-Cabrera et al. 2015). In addition, we performed some preliminary tests using the 'quickpred' function included in the 'mice' package, which allows to select only those predictors below a given correlation value. These tests showed no improved performance compared to our 'mice' settings.

*R1#25. Supplementary information (SI) I would recommend to reduce this part, 32 pages of material is a lot. I would suggest to try to reduce it to the most important results.*

- We agree with the reviewer that the supplementary materials are very long. We have substantially reduced the supplementary materials (see commenr R1#3 for more details) and now, instead of 32 pages, they are 19 pages long.

*R1#26 (19)- Sentence L.106 of the appendix is misleading, its seems that the authors use MICE-RF in the paper.*

- We have rewritten the sentence to make it clear that we refer to the comparison of univariate imputation models within mice:
- **Here, in this comparison of univariate imputation models, we used the implementation of the random forest algorithm in MICE, a described in Doove *et al.*, (2014).**

*R1#27 (20)- Maybe it would be clearer to merge s3 and s4*

- Following the reviewer's suggestion, we have merged S3 and S4.

*R1#28 (21)- Please also place all references at the end of the appendix and not just after each paragraph, this makes it difficult to read the (already long) document.*

- Done.

*R1#29 (22)- S4: I do not see how PMM performs better than the other methods. Fig s4 shows that there is almost no difference between methods and some are better than others for some traits. Fig s5 and s6 only seem to show that mice_PAS is worse than the others. And nothing is supported by statistical tests. I would suggest to revise these analyses or provide a more complete explanation of why PMM was used. Please also add in the caption what the traits are or provide the complete trait names in the figure Itself.*

- We have already discussed the choice of PMM in an earlier comment (R1#9), as a method which can handle non-linear relationships and non-normality in the data. We think that a thorough analysis of the justification of PMM is too technical for the scope of this manuscript, and our preliminary tests may be viewed as a corroboration that PMM did not perform worse than other more computationally-intensive methods such as RF (mice_rf).
- We have added a full description of the traits in the corresponding figures. An example:
- **Figure S3. Trait-specific imputation performance (NRMSE) at increasing missingness levels (10% to 80%) using different MICE settings (see text for details). The following approaches used the predictive mean matching method (PMM) as the univariate imputation model: passive imputation of derived variables (mice_PAS), derived variables imputed as 'just another variable' (mice_JAV), imputation using log-transformed variables (mice_TRN). mice_PRD differed from PMM in that mice_PRD used the predicted trait from the sequential, multiple regression models in the MICE framework, without the**

**stochasticity in regression coefficients that is introduced in PMM. mice_RF uses a random-forest algorithm for univariate imputation instead of PMM (see text). The original trait distributions in the IEFC complete data set (Observed) are also shown. Traits: leaf biomass to sapwood area ratio, BL:AS (t m-2); nitrogen per unit mass, Nmass (%mass);  maximum tree height, Hmax  (m); leaf mass per area LMA (mg cm-2); wood density, WD, (gm cm-3).**

**Results and discussion**
*R1#30. This section is not very clear and sometimes the results are simply a description of the figures without any effort to synthesise what happens. The choice for the figures is also not consistent (see point 23). It is titled "results and discussion" but the discussion is almost absent. For instance, I missed some information on why some methods perform better than others or why some traits show better results. Please see some more detailed comments below.*

- We have changed the 'Results and discussion' section extensively, adding more statistical tests and rearranging parts of the text. See below for more detailed explanations.

*R1#31 (23)- Figures in the main text are a bit confusing. Fig2 is NRMSE and 4 methods, fig3 is deltaCoeff and 4 methods, fig4 is KGE, but this time with 11 methods, fig5 is deltaCoeff with 11 methods, fig6 is KGE with 7 methods and fig7 is deltaCoeff with 7 methods. This is quite inconsistent and we miss some comparisons (e.g. mean and smean). I would suggest to put together in a different form (e.g. as in figs10) and show all the metrics (NRMSE, KGE, deltaCoeff) for each comparison. Also, the results about distributions (Kolmogorov-Smirnov tests) are not performed for all methods and only shown in the appendix.*

- There are some reasons behind the differences in the figure design. For the first comparison, KGE is not defined for 'Mean' imputation, and therefore we chose to represent NRMSE (but KGE can be found in the supplement for those methods for which it can be calculated). The figures show different number of methods because they reflect different comparisons, as outlined in the 'Methods' section. We agree with the reviewer that some comparisons cannot be made directly, but we had to choose one way of presenting the results and this way reflects the questions that we posed in the introduction. We also chose the violin plots in the main text to better compare distributions of the different metrics across imputation methods at a given missingness level, and show a different visualisation in the supplement to focus on the trends with missingness.

*R1#32 (24)- In the whole first paragraph (l237) I am not sure that the differences highlighted by the authors are actually significant differences. For instance at 10% I only see Mean being slightly worse than the other methods for LMA and WD, and OrdKrig for WD. OrdKrig also does not seems to perform better than others for most traits. Same remark for Fig3. Maybe a test looking at the effects of the method corrected by the trait identity would provide more general results.*

- As explained before (*R1#3*), we have now performed pairwise comparisons resulting from a model including imputation method and missingness as predictors. We have also modified the first paragraph of the 'Results and discussion' section using this new approach. In this paragraph we now emphasize more  the differences between traits and convey the message that, without auxiliary variables, 'OrdKrig' performs better that the rest of the methods (in terms of NRMSE, see section 3.1):
- **In general, 'mice' and 'kNN' imputations resulted in more accurate imputations in terms of NRMSE than 'Mean' at low missingness rates (10%). However, at moderate and high missingness both 'mice' and 'kNN' were comparable or outperformed by 'Mean', and specially by 'OrdKrig' (Fig. 2, Fig. S7). 'OrdKrig' was the best-performing method, in terms of NRMSE, at missingness ≥ 50%  (P <0.05), although for three traits its performance was indistinguishable from that of 'Mean' imputations (Nmass, Hmax, LMA; P>0.05).  Even if 'Mean' imputations imply the rather naive assumption that species identity may be unknown in a given dataset, it is nonetheless useful to compare 'Mean' imputations against 'mice' and 'kNN', which use the full trait matrix for prediction. In this case, trait covariation did not improve imputations at high missingness. Recent assessments also report that the performance of MICE and kNN notably declines when missingness is ≥ 30% (Penone et al. 2014; Taugourdeau et al. 2014). Therefore, our results for 'OrdKrig', compared to those for 'mice' and 'kNN', show that  spatial structure, rather than trait covariation, may provide more accurate trait imputations when gaps are frequent (Fig. 2, Fig. S7, S8).**

*R1#33 (25)- L250: from what I see in fig s8 mice is not the method with lower NRMSE or deltaCormat: kNN is the best performing method except at around 50% of NAs, where OrdKrig seems to perform better. This seems to be the case also for KGE where kNN performs as good as the other methods (fig s7). However it performs bad when looking at distributions. I also do not see mice being better than kNN or OrdKrig in Fig.3 (as stated L.251). I would suggest revising this paragraph and carefully checking all results for similar problems.*

- We do not state that mice has the lowest NRMSE or Δcormat. For example, we say that mice and kNN seem to perform better at low missingness but that their performance seems to decline with missingness (section 3.1):

- **In general, 'mice' and 'kNN' imputations resulted in more accurate imputations in terms of NRMSE than 'Mean' at low missingness rates (10%). However, at moderate and high missingness both 'mice' and 'kNN' were comparable or outperformed by 'Mean', and specially by 'OrdKrig' (Fig. 2, Fig. S7). [...]**

- The reviewer points out at the Δcormat performance of kNN at 50%, which we also mention (section 3.1):
- **'Mean' imputation severely altered trait distributions (Fig. S9), and introduced larger errors in selected trait correlations (Fig. 3). 'Mean' imputations also tended to cause larger deviations in the correlation matrix (Fig. S8). 'kNN'**

**showed the lowest Δcormat below 50% missingness (P>0.05) but its performance declined at high missingness (Fig. S8).**

- Moreover, as the reviewer comments,  we already distinguish in the text between the performance, in terms of accuracy and in terms of preserving relationships and multivariate structure (section 3.1).
- **In contrast, 'mice' closely tracked observed trait distributions (Fig. S9), introduced the least error in trait correlations under high missingness levels (Fig. 3; P<0.05) and yielded low Δcormat at extreme missingness levels (Fig. S8).**

- We have rewritten the comparison of Δcormat between 'mice' and 'OrdKrig' to better reflect the fact they tend show similar results,as noted by the reviewer (section 3.1).
- **'OrdKrig' imputations altered distributions and trait correlations more than 'mice' (Fig. 3, Fig. S9), but they performed similarly in terms of Δcormat at missingness of 80% (Fig. S8).**

*R1#34 (26)- L 266: the best performance of mice_ctsp is not really visible in fig s11. - Fig s10 is also not easily readable, I would suggest to jitter the points (geom_jitter in ggplot2). Fig s12 is better (but jittering would help as well).*

- As we explain in the reply to comment *R1#3,* and  in line with  proposed reductions in the length of supplementary materials, we actually propose to delete Fig. S10 and Fig. S12 because they're partially redundant (results are already shown in Fig. 4 and Fig. 6). As for Fig. S11, we are aware that differences can not be seen, but the point of the figure is precisely that distributions are very similar across MICE applications.

*R1#35 (27)- Mice-ctsp is discussed and presented several times (l.266, 291, 297, 306). I would suggest to merge together information. Also the 3.3 sections seems redundant with the 3.2. Maybe showing together fig6 and 7 would save some redundancy.*

- We think that it would be difficult to merge Figs. 6 and 7, because the resulting figure would have too many panels and would be difficult to read. About the section 3.3., we have made extensive changes to the entire 'Results and Discussion' section towards a better clarity.
- As for the repeated appearances of 'mice_ctsp', this is because the comparisons in the second and third objective both include this imputation method. In the second objective we compare it against MICE applications with different levels of auxiliary variables and in the third objective we compare it against other imputation methods.

*R1#36(28)- paragraph L 306 does not belong to section 3.3, which is about comparing mean, mice and knn. A separate section would be more meaningful.*

- Done. We have added a new section header: 3.4. Imputing traits for the main forest species in Catalonia.

*R1#37(29)- L328: "MICE informed by relevant ecological variables outperforms": this was not properly tested as no analyses for this are provided*

- We now provide statistical tests for the most meaningful comparisons (see replies in *R1#32, R1#33.*

**Minor comments**

*R1#38 - L165: information about kNN is missing*

- Thanks for spotting this mistake. We have rewritten the sentence (section 2.4):

- **‘Mean’ imputations used only the information on the target trait, ‘OrdKrig’ additionally used the spatial coordinates and ‘mice’ and ‘kNN’ included only the information in the trait matrix.**

*R1#39 - L234: “per missing value” should be “per missing dataset”*

- The text is actually right because in multiple imputation, >1 values are generated for each missing value.

*R1#40- L190: “statistical evaluation”, no stats are actually performed for the evaluation*

- We now provide statistical tests for the most meaningful comparisons (see examples in *R1#32, R1#33*)

*R1#41 - To facilitate the reading, please cite the exact figures of the supplementary and not only the section (e.g. do not refer to just to s5 or s6 but to fig.s7 or s10).*

- Done.

*R1#42 - All figures: please spell out the trait names or write it in the caption*

- Done in the caption.See an example in our reply to comment *R1#29.*

**References**

*Nakagawa, S. and Freckleton, R. P.2008. Missing inaction: the dangers of ignoring missing data, Trends in Ecology & Evolution, 23(11), 592–596*

*Stekhoven, D. J. and Bühlmann, P. 2012. MissForestâA ˘Tnon-parametric missing value ˘ imputation for mixed-type data. Bioinformatics 28: 112–118*

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