Point-by-point response to referee comments (3)

We would like to thank the reviewer for their continued help in improving this manuscript.

Our responses to individual comments are highlighted in blue, with any proposed changes highlighted in red. Note that red page numbers refer to the location in the updated marked-up manuscript.

R1. I am pleased to see that the authors took many of my comments into account for the revision of the manuscript. Unfortunately no changes were made to the regression model. I accept the argument made that classifying all pollen taxa into under and overrepresented taxa may be difficult, but what would be possible is using the pollen dispersal syndrome: wind, insect, both. Also the fall speed could be obtained for all pollen taxa and this combination could really yield something new.
We tested the inclusion of dispersal syndrome instead of %needleleaf within the regression model. Categorisation of tree species as wind or biotically pollinated is a challenge, particularly for pollen only identified at the family level. We primarily used the categorisation from Tong et al. (2023), with some amendments based on expected primary dispersal methods. Models with %wind pollination and %wind and dual pollination produced a worse fit than the %needleleaf model. We also tested the inclusion of %*Pinus* rather than the %needleleaf proportion within the model. Here there was less of a difference with the %needleleaf, with the model including %*Pinus* only very marginally worse. We have included this additional analysis within the manuscript and supplement.

L228. As an additional approach to address differences in pollen production and transport, we tested the implications of including broad pollen dispersal syndromes in the model in place of %needleleaf. We calculated the percentage of the tree pollen based on wind pollination as opposed to biotic (insect, bird) or dual (wind or biotic) pollination methods, following the categorisations by Tong et al. (2023), and Kling and Ackerly (2021) (see Supplementary Information: S2). *Pinus* is the most ubiquitous pollen type recorded in the modelled data set, and is widely recognised as a potential contaminant in more open vegetation due to long-distance transport. We therefore also tested the impact of including %*Pinus* as a predictor in the regression model.

L323. Replacing %needleleaf with either %wind pollination tree species or %*Pinus* as explanatory variables related to pollen transport resulted in a poorer model fit (Supplementary Information: S3).

S3: Coefficients and model fit including %wind pollination or %Pinus

Including the %wind pollinated within the regression model instead of %needleleaf, also with a second-degree polynomial, led to a reduction in the model pseudo (Cox-Snell) R2 to 0.56 (compared to 0.60). LOOCV MAE increased to 0.12 (from 0.11), RMSE increased to 0.15 from 0.14 and the squared correlation (R2) of the predictions to the observations was reduced to 0.57 (from 0.63). The model coefficients are shown in Supplementary Table 3; although the coefficient values change compared to the model with %needleleaf, the directions of the coefficients remain the same. The slight reduction in model fit reflects the fact that %needleleaf also partially accounts for differences in pollen productivity, as well as differences in pollen transport. As well as selecting the tree species classified as wind pollinated only, we also investigated the model fit when including both those species classified as wind pollinated and those species classified as both wind and biotically pollinated. In this case the model fit was similarly worse than using %needleleaf, with the pseudo (Cox-Snell) R2 0.55, and LOOCV MAE 0.12, RMSE 0.15 and the squared correlation (R2) of the predictions to the observations 0.57.

Supplementary Table 1: Modern tree cover model coefficients, including %wind pollinated rather than %needleleaf

Coefficients (mean model with logit link)	**Estimate**	**Standard Error**	**P Value**
(Intercept)	-1.045	1.899	0.582
Tree pollen %	2.592	0.233	8.66e-29 ***
Shrub pollen %	-3.834	0.642	2.38e-09 ***
Wind pollination of AP%	-11.090	4.486	0.013 *
Wind pollination of AP%^2	7.264	2.701	0.007 **
AP Shannon index	4.413	0.481	4.61e-20 ***
AP Shannon index^2	-1.237	0.145	1.16e-17 ***
Lake or bog site	-0.034	0.139	0.807
Elevation	0.003	0.001	0.007 **
AP pollen:elevation interaction	-0.001	0.001	0.003 **
SP pollen:elevation interaction	0.004	0.001	0.003 **
AP Shannon:elevation interaction	-0.004	0.001	0.001 **
AP Shannon^2:elevation interaction	0.002	0.000	3.05e-05 ***
Lake or bog site:elevation interaction	-0.001	0.000	3.32e-04 ***
Precision submodel (log link; after variable selection^^)			
(Intercept)	-2.827	0.988	0.004 **
Wind pollination of AP%	3.382	0.978	5.41e-04 ***

AP Shannon index	0.938	0.116	4.84e-16 ***
Lake or bog site	0.537	0.126	1.97e-05 ***

Significance codes: 0 = '***'; 0.001 = '**'; 0.01 = '*'; 0.05 = '"' 0.1; ' ' = 1
^^Only significant covariates were included (at 5% significance)

Similarly, including %Pinus within the model instead of %Needleleaf also slightly reduced the quality of the model fit, reducing the pseudo (Cox-Snell) R2 to 0.59 (vs 0.60). Although the LOOCV MAE (0.11) and RMSE (0.14) were approximately the same as the model with %needleleaf, the squared correlation (R2) of the predictions to the observations reduced slightly to 0.62 (from 0.63). The model coefficients are shown in Supplementary Table 4. This slight reduction in model fit supports the use of %needleleaf, although this marginal difference suggests that %Pinus could also be used and tested for other geographic contexts.

Supplementary Table 2: Modern tree cover model coefficients, including %Pinus pollinated rather than %needleleaf

Coefficients (mean model with logit link)	**Estimate**	**Standard Error**	**P Value**
(Intercept)	-6.008	0.453	3.91e-40 ***
Tree pollen %	2.428	0.222	1.47e-28 ***
Shrub pollen %	-3.539	0.629	1.82e-08 ***
Pinus of AP%	-0.010	0.005	0.04272 *
Pinus of AP%^2	0.000	0.000	2.77E-07 ***
AP Shannon index	5.530	0.482	1.77e-30 ***
AP Shannon index^2	-1.497	0.144	3.62e-25 ***
Lake or bog site	-0.039	0.133	0.76985
Elevation	0.002	0.001	0.045 *
AP pollen:elevation interaction	-0.001	0.000	0.029 *
SP pollen:elevation interaction	0.004	0.001	0.002 **
AP Shannon:elevation interaction	-0.003	0.001	0.002 **
AP Shannon^2:elevation interaction	0.001	0.000	3.65e-05 ***
Lake or bog site:elevation interaction	-0.001	0.000	0.002 **
Precision submodel (log link; after variable selection^^)			
(Intercept)	0.082	0.264	0.755
Pinus of AP%	0.013	0.003	8.62e-07 *
AP Shannon index	0.959	0.128	5.98e-14 ***
Lake or bog site	0.582	0.125	3.45e-06 ***

Significance codes: 0 = '***'; 0.001 = '**'; 0.01 = '*'; 0.05 = '"' 0.1; ' ' = 1
^^Only significant covariates were included (at 5% significance)

As far as we are aware, estimates of pollen fall speeds are not readily available beyond those published by Serge et al. (2023), and will depend on pollen size and density. The REVEALS approach makes use of FS and RPP estimates, and our method is an attempt to provide reconstruction estimates that do not require quite the same level of species level information.

I continue to have the following concerns with the presented manuscript:

R2. % needleleaf: The argument made in the manuscript really only applies to Pinus so I would suggest rerunning the analysis with only Pinus. Picea and Abies will not create large biases and Larix is a problem at the other extreme. I cannot see how combining these plus Taxus Cedrus or Juniperus should improve the reconstructions.

As discussed in our response to R1, the model containing %needleleaf very slightly outperforms that with %*Pinus* instead.

R3. Shannon index: Tree pollen diversity seems to have a strong influence in the final model. More efforts should be made to explain this and evaluating how that may influence the reconstructions e.g. running a model without SI for the past and evaluating the differences.

We have performed further analysis around the use of the Shannon index in the model. We divided the modelled data into Hengl's (2017) potential natural vegetation biomes and investigated whether there was a difference between the biomes and Shannon index values. At the biome level, the difference between observed tree cover and AP% is greatest in the tundra biome, and the Shannon index value for AP lowest. This implies that the Shannon index may be helping to adjust tree cover predictions towards observations, where high AP values may reflect longer distance transport rather than localised cover. We also investigated the impact of excluding the Shannon index on the subsequent reconstructions of tree cover. Although the general pattern of mid-Holocene increase in tree cover is observable, the timing of the tree cover peak, and early Holocene tree cover values are quite different. We have included this additional analysis within the manuscript and supplement.

L324. Increased tree SI is positively related to tree cover, with the effect decreasing with elevation. However, the negative correlation for the quadratic term for the SI suggests that the relationship has less of an effect on tree cover as tree SI increases. Again, this relationship may be explained in the context of open environments, where tree species diversity may be limited to species with longer distance pollen transport. For example, records in tundra tend to have a greater average disconnect between observed tree cover and AP%, as well as the lowest average tree SI values by biome (Supplementary Information: S4). Tree species diversity may then increase with tree cover, with the negative quadratic term implying that the highest levels of tree cover are represented by relatively uniform species types.

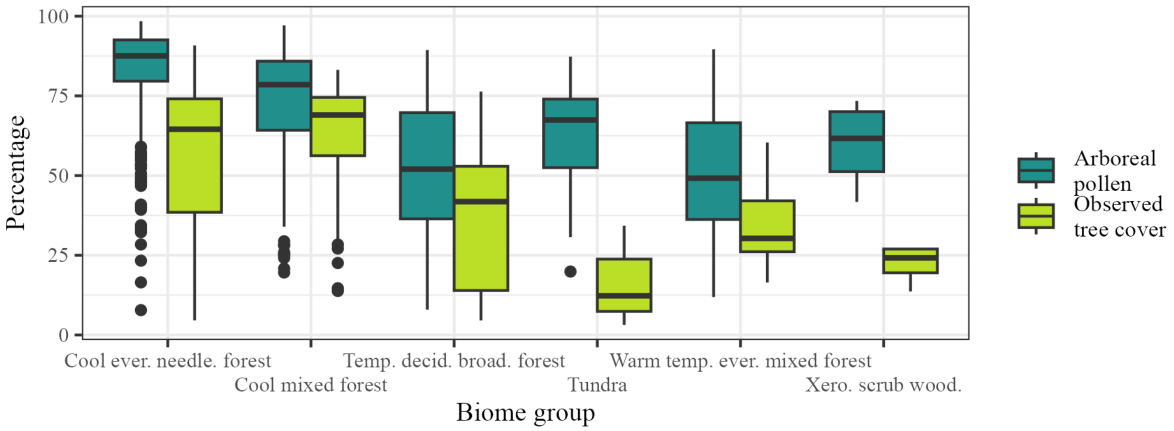
S4: Modern tree species diversity and tree cover

The tree pollen Shannon index (SI) is an important component of the regression model (Table 2). With increased tree cover, it is more likely that tree species diversity increases, although the negative second-degree polynomial (Table 1) suggests that at higher levels of tree cover this relationship becomes less important. To investigate this relationship, we divided the modelled modern data into biomes, and explore whether the SI for tree pollen varies for more open biomes. We divided the records into biomes according to Hengl's (2018) map of potential natural vegetation, extracting the modal biome with a 5km buffer around each record. We grouped some similar biomes, to simplify comparison; this grouping, and the division of modelled modern records, is shown in Supplementary Table 5.

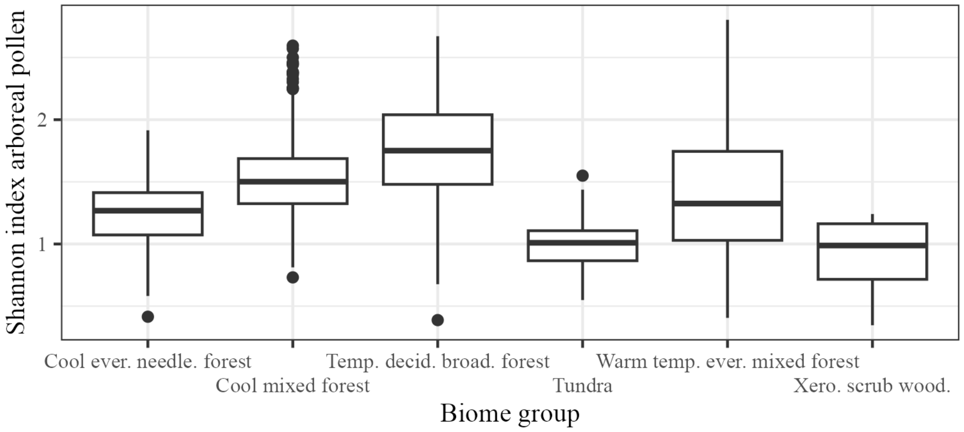
Supplementary Table 3: Biome groups for included modelled modern records. Parenthesis indicates grouped biomes

Biome group **(incl. biomes)**	**Number of modern records**
Cool evergreen needleleaf forest (Cold evergreen needleleaf forest; cool evergreen needleleaf forest)	363
Cool mixed forest	255
Temperate deciduous broadleaf forest	117
Warm temperate evergreen and mixed forest	84
Tundra (Low and high shrub tundra; Erect dwarf shrub tundra)	29
Xerophytic scrub and woodlands (Steppe; Xerophytic woods scrub)	4

The distribution of arboreal pollen percentages and observed tree cover percentages are shown for each biome group in Supplementary Figure 1. In general, arboreal pollen percentages are greater than observed tree cover for each biome group, but the difference is most stark for the tundra biome (and xerophytic scrub and woodlands, although there are very few records). Supplementary Figure 2 shows the arboreal pollen Shannon index values for each group. The lowest median value and distribution is for tundra, suggesting that the higher pollen values compared to observed cover reflects inputs from a few species through long-distance transport. In fact, it is generally the case that the larger the difference between arboreal pollen and observed tree cover percentages, the lower the tree SI value. This highlights the importance of including this variable in the regression model.



Supplementary Figure 1: Boxplots of arboreal pollen and observed tree cover by biome group

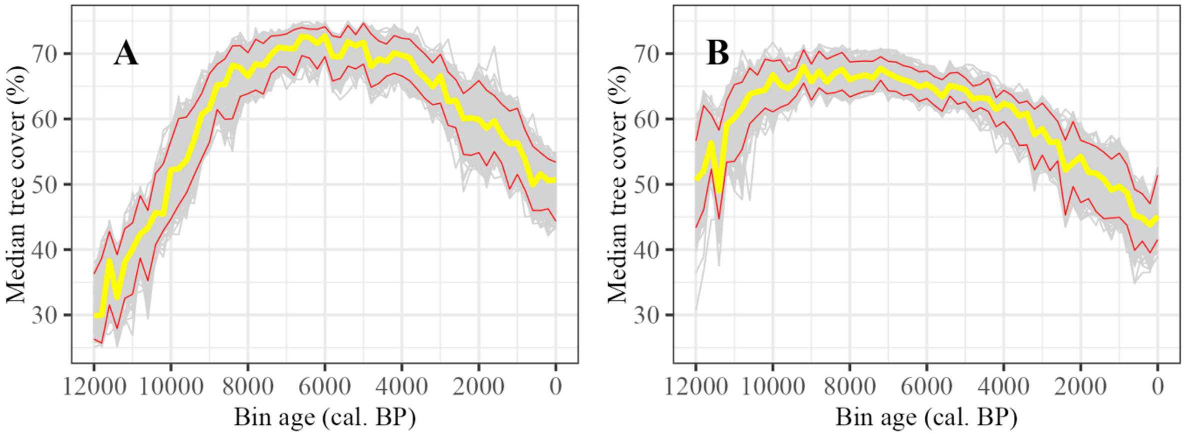


Supplementary Figure 2: Boxplots of Shannon index values for tree pollen for each biome group

L433. Given the importance of the tree SI to the regression model (Table 2), we also ran the reconstructions based on a model excluding this variable. Although the reconstruction followed the same broad mid-Holocene increase and decline in tree cover, median tree cover prior to 7,000 cal. BP was much greater than shown in Fig. 5, with a less marked increase to the mid-Holocene (see Supplementary Information: S16). As shown in Supplementary Information 16, there is a slight increase in tree SI through time, which may imply a slight underestimation in tree cover during the early part of the Holocene.

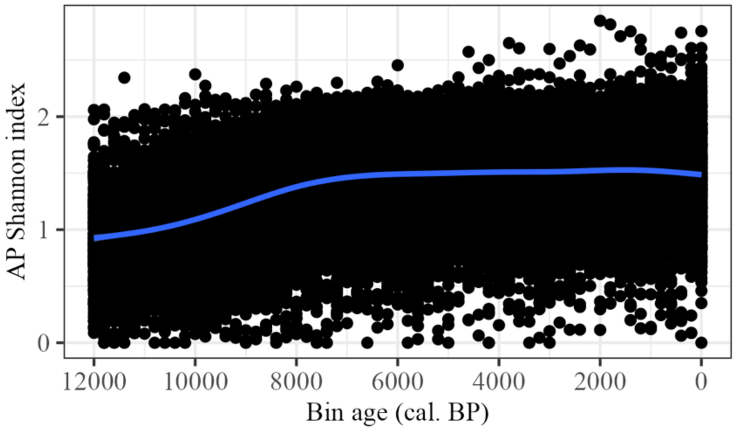
S15: AP Shannon index through time and implications for tree cover reconstructions

The Shannon index (SI) value of arboreal pollen has a substantial impact on the quality of the model fit (Table 2). To investigate the implications of this variable for tree cover reconstructions, we re-ran the downcore reconstructions based on a model excluding tree cover SI (Supplementary Figure 9B) compared to the original model (Supplementary Figure 9A). Although the general mid-Holocene peak is visible in both reconstructions, there are differences between the two models. At the beginning of the Holocene, the median tree cover is around 20% higher when excluding tree SI. As a result, the increase in tree cover to the mid-Holocene is less dramatic. Additionally, the peak in tree cover occurs earlier, between ca. 9,000 and 7,000 cal. BP, compared to ca. 6,000 cal. BP when including the tree SI. In addition, the median tree cover values towards the present are around 5% lower when excluding tree SI.



Supplementary Figure 3: A - Median reconstructed tree cover for Europe from 12,000 to 0 cal. BP, with 95% confidence intervals for 1000 bootstrap resampling of records; B - Median reconstructed tree cover for Europe from 12,000 to 0 cal. BP excluding AP Shannon index, with 95% confidence intervals for 1000 bootstrap resampling of records

The tree SI values generally increased from the early Holocene to ca. 7,000 cal. BP (Supp. Fig. 10) and then remain relatively stable. Given that the tree SI has a positive relationship with observed tree cover in the modern regression model, this may imply that tree cover predictions for this earlier period of the Holocene are underestimated. However, since tree SI values are a means to correct for long distance transport, it is more likely that this implies there were more open environments earlier in the Holocene than is now the case.



Supplementary Figure 4: AP Shannon index for Europe from 12,000 to 0 cal. BP, average for individual records binned in 200-year bins. Blue line is a LOESS line of best fit

R4. Removal of landcover classes in the training data: may have lead to the underestimation of forest cleared for agriculture. Thus the reconstructions should be sensitive to climate induced changes in tree cover, while they may be less useful evaluating human induced deforestation. This should be more explored in the data and better communicated. If it is indeed that case that clearance for crop production is less readily detected this would render the data inappropriate for some interpretations and that should be clearly stated.

We tested the implications of not excluding cells from the tree cover map that had a majority of crop cover with the cell. There was a reasonable (negative) impact on the model fit, supporting our exclusion of these cells in the training data.

L.254. Finally, as excluding cells dominated by crop cover in the modern observed tree cover map may have implications for downcore reconstructions, we also tested the implications of removing this crop cover restriction when calculating observed tree cover on the regression model fit.

L. 371. We tested the influence of excluding cells dominated by crop cover when calculating observed tree cover values for each record location by re-running the regression using the same variables but without excluding these cells. The number of records used to train the model increased to 1050 (from 852), but the model pseudo (Cox-Snell) R^2 was reduced from 0.60 to 0.47 (Supplementary Information: S8), supporting out decision not to include these cells in the model training.

S8: Excluding crop cells from the calculation of observed tree cover

Cells dominated by crop cover (>50%) were excluded from the forest/tree cover map that was used to calculate observed tree cover for each modern pollen record. The rationale behind this methodological choice was to try to ensure that the relationship between tree cover and modern pollen was as representative as possible. Areas with high crop cover may affect the subsequent regression model, implying lower observed tree cover which is not reflected in the pollen record. To explore the implications of this exclusion, we re-ran the same regression model without excluding cells dominated by crop cover. The direction of the model coefficients (Supplementary Table 9) are the same as the standard regression model, except for whether the site was a bog or lake (which now becomes significant). However, some variables, such as the shrub pollen %, and the interactions between AP pollen and elevation, and SP pollen and elevation, are no longer significant. Note that although the needleleaf share of AP% is also insignificant, a model with orthogonal polynomials (i.e. reducing multicollinearity with the second polynomial of needle share of AP%) is significant. Additionally, the needleleaf share of AP% and whether the site is a lake or bog are no longer significant in the precision sub-model.

Supplementary Table 4: Modern tree cover model coefficients, without exclusion of crop dominated cells when calculating observed tree cover

Coefficients (mean model with logit link)	**Estimate**	**Standard Error**	**P Value**
(Intercept)	-5.068	0.405	5.38e-36 ***
Tree pollen %	2.199	0.186	3.01e-32 ***
Shrub pollen %	-0.731	0.508	0.150
Needle share of AP%	-0.031	0.433	0.943
Needle share of AP%^2	1.480	0.499	0.003 **
AP Shannon index	3.576	0.483	1.36e-13 ***
AP Shannon index^2	-1.085	0.153	1.25e-12 ***
Lake or bog site	0.386	0.095	5.04e-05 ***
Elevation	0.002	0.001	0.046 *
AP pollen:elevation interaction	-0.001	0.000	0.110
SP pollen:elevation interaction	0.000	0.001	0.624
AP Shannon:elevation interaction	-0.003	0.001	0.012 *
AP Shannon^2:elevation interaction	0.001	0.000	6.74e-05 ***
Lake or bog site:elevation interaction	-0.001	0.000	6.70e-09 ***

Precision submodel (log link; after variable selection^^)			
(Intercept)	1.459	0.230	2.4e-10 ***
Needle share of AP%	1.191	0.205	0.351
AP Shannon index	0.406	0.108	1.74e-04 ***
Lake or bog site	-0.039	0.107	0.714

Significance codes: 0 = '***'; 0.001 = '**'; 0.01 = '*'; 0.05 = '"' 0.1; ' ' = 1
^^Only significant covariates were included (at 5% significance)

The model that does not exclude cells with >50% crops includes more records (1050 compared to 852) but the pseudo (Cox-Snell) R^2 model fit was worse than the standard model (0.47 compared to 0.60), with LOOCV values similarly worse (MAE = 0.13 vs 0.11; RMSE = 0.16 vs 0.14; R^2 of predictions to observations = 0.50 vs 0.63).

Line specific comments

R5. L. 30: For a global application the % needleleaf would need to be evaluated.

We agree that the modelling approach would have to be tested in other regions. However, we do not feel that this statement in the abstract is controversial.

R6. L. 59: All the newly added references are no or no good examples of the prior statement. Hicks 2001 uses absolute pollen, Kaplan used plant functional types and Adam used the trends of change during the Lateglacial, a period for which nobody has yet dared to try quantitative reconstructions.

We thank the referee for this. We have amended the references as follows:

L50. The relative abundance of arboreal pollen has often been used to infer changes in tree abundance at a site (e.g. Thorley, 1981; Eastwood et al. 1999; Gil-Romera et al.).

Additional references:

Eastwood, W. J., Roberts, N., Lamb, H. F., and Tibby, J. C.: Holocene environmental change in southwest Turkey: a palaeoecological record of lake and catchment-related changes, Quat Sci Rev, 18, 671–695, https://doi.org/10.1016/S0277-3791(98)00104-8, 1999.

Gil-Romera, G., García Antón, M., and Calleja, J. A.: The late Holocene palaeoecological sequence of Serranía de las Villuercas (southern Meseta, western Spain), Veg Hist Archaeobot, 17, 653–666, https://doi.org/10.1007/s00334-008-0146-x, 2008.

Thorley, A.: Pollen Analytical Evidence Relating to the Vegetation History of the Chalk, J Biogeogr, 8, 93, https://doi.org/10.2307/2844552, 1981.

R7. L. 106: I continue to not see how the MAT approach would be more complicated than what is proposed here. To my mind it even provides more information as it provides a dissimilarity measure to evaluate the trustworthiness of reconstructions.

We do not suggest that the MAT is more complicated, just that there are a number of arbitrary decisions that need to be made in the application of the technique, such as the choice of an appropriate number of analogues, the thresholds used for identifying analogues, and identifying non-analogue samples. To highlight the high-level differences between the techniques, we have included the following table:

L102. The key elements of each technique, including the approach applied within this paper, are summarised in Table 1.

Table 1: Key elements of the reconstruction technique from this study, the REVEALS approach (i.e. Serge et al., 2023) and MAT (i.e. Zanon et al., 2018)

	This paper	**REVEALS (Serge)**	**MAT (Zanon)**
Training data	Modern pollen data Modern tree cover	NA	Modern pollen data Modern tree cover
Training model	Regression based model linking modern pollen to modern tree cover	NA	
Downcore data	Pollen data; Site characteristics	Pollen data; Site characteristics; RPP and FS per taxa	Pollen data
Main Assumptions and Challenges	Regression model applicability and included variables	Accuracy of RPP and FS values; Limited set of taxa	Number of analogues used (commonly 3-5); Threshold of similarity; Non-analogues
Scale	Site-based	Typically 1° where sites are located	Site-based; (Zanon: spatio-temporal interpolation)

R8. L. 235: These numbers go way beyond Europe please check your calculations. From my own research the area around the lake generating the signal is much smaller than the theoretical source of 70% of all pollen (e.g. Matthias & Giesecke 2014 QSR).

We thank the reviewer for pointing out this error. The distances indicated should be in m, not km.

L194. Source area radii varied in size from 5,026m to 418,894m for the largest lake, with a median of 28,316m.

R9. L. 173: It needs to be clearly stated which (all) landcover classes were removed.

We have amended to the text to clarify this.

L126. A composite map of modern tree cover for the region 12°W to 45°E and 34–73°N was generated by averaging annual percentage forest/tree cover data from Copernicus annual land cover maps from 2015 to 2019 (Buchhorn et al., 2020a, e, d, c, b), after removing cells dominated (> 50%) by other land-cover classes, which include bare ground, built up areas, moss or lichen, permanent water, snow, and crops (Fig. 2A).

R10. L. 280 ff: The motivation of why to include %needleleaf is misleading. Since Larix is included in the Needleleaf group the spread is similar to that of broadleaf trees. Moreover, Table 1 from Serge et al., 2023 only includes a small part of the here included needleleaf trees and is also not using that label.

Please see our response to R1. Additionally, we have amended the text to highlight that the %needleleaf is attempting to capture both productivity and dispersion.

L170. To take into account broadscale differences in pollen productivity and pollen transport for species at a site level, the pollen data were also used to calculate the needleleaf share of the AP (%needleleaf)…

R11. L. 288: I am still not convinced by the reasons provided for the inclusion of the Shannon Index. Please explain how this should “account of potential impacts of very localised tree cover or long-distance transport influencing” and “Increased species diversity may reflect less fragmented landscape (Hill and Curran, 2003) and the likelihood that the recorded AP% reflects regional tree cover.” Also note that the reference to Hill and Curran, 2003 is not relevant here as they were looking at trees in the landscape, while you look at a pollen count.

Please see R1 and the additional analysis performed that justifies the inclusion of this variable within the model. Additionally, we have amended the text, and removed the speculative wording around landscape fragmentation.

L244. We also included tree SI, to take account of potential impacts of very localised tree cover or long-distance transport from a single taxa or few taxon influencing the recorded AP%.

R12. L. 425: This is a result of modern forestry where even in the boreal forest you find monocultures in areas with highest forest cover. Could this parameter in the regression have caused lower tree cover in the early Holocene when tree composition was less divers?

It is true that forestry practices tend to create high cover of single species, but then some natural forest types such as beechwoods also have high cover of single species. As per R1, we acknowledge that lower Shannon tree cover values in the early Holocene could lead to somewhat lower values of tree cover than may have been the case but also point out that this could be a realistic indication of more open vegetation at this time.

R13. L. 455: The influence of the Shannon index on the final model seems important and it is therefore important to understand the relationship in order to evaluate whether this is robust though time or a potential bias when reconstructing the early Holocene tree cover.
Please see our answer to R1

R14. L. 630: Thus by ignoring areas dominated by crops in the analysis of the modern data this approach may not detect the manmade reduction in tree cover.
Please see our answer to R4.

R15. L. 766: Please add the required acknowledgment: "Much of the fossil data were obtained from the Neotoma Paleoecology Database (http://www.neotomadb.org) and its constituent databases: European Pollen Database (EPD) and The Alpine Palynological Database (ALPADABA). The work of data contributors, data stewards, and the Neotoma community is gratefully acknowledged."
We have added this acknowledgement as requested. We have also added an acknowledgement to other palynologists who have contributed to the modern data set as follows:

Much of the fossil data were obtained from the Neotoma Paleoecology Database (http://www.neotomadb.org) and its constituent databases: European Pollen Database (EPD) and The Alpine Palynological Database (ALPADABA). The work of data contributors, data stewards, and the Neotoma community is gratefully acknowledged. We also thank members of the EMBSECBIO data community and other palynologists who have contributed records to the modern and fossil data set used here.