

We thank the reviewer for their constructive comments on this article. Our responses to individual comments are highlighted in blue, with any proposed changes highlighted in red.

General

Reviewer comment 1 (R1): There is a need for assessing past forest cover change from pollen regionally and the REVEALS model requiring knowledge on pollen productivity may not be the method of choice where that information is lacking or incomplete. Thus it is useful to explore other avenues and the manuscript by Sweeney et al. does that. It also adds interesting comparisons between the European estimates produced applying the REVEALS model and the modern analogue technique. While I welcome the attempt of applying a regression, I have my doubts on the choice of predictor variables. The authors should demonstrate how % needle leave and the Shannon index improve a regression model for overall tree cover. I can see how elevation improves the model in the current situation but have my doubt that this variable will improve past reconstructions. Instead using information on over and underrepresented pollen could perhaps make this a real winner.

The choice of predictor variables was explained in the paper (lines 168-177), but we agree that it would be useful to show how the inclusion of variables contributes to improve the model. We will include an additional table - Table 2 (see below)- highlighting the change in model AIC value when excluding specific variables (and their interactions).

Elevation is a significant variable describing the present level of tree cover, both in itself and in terms of the interactions with variables. Whilst we agree that the influence of elevation may have changed through time with changes in climate being expressed more strongly at higher elevations, the same could be said of each of our explanatory variables to some extent. This is perhaps a general point that should be emphasised within the Discussion section: reconstructing the past relies on an assumption that present day relationships are applicable to past situations. This point is equally applicable to the other reconstruction techniques. We agree that it would be interesting to include information on over- or under-represented taxa but this is difficult to do given the limited number of taxa for which RPP values are available, as well as raising questions regarding the appropriate RPP values for species across Europe (as with the REVEALS approach).

We will modify the text to cover these points as follows:

<L.255>. The influence of each variable on the quality of the statistical model is shown in Table 2, with the change in AIC value based on the removal of each variable. These values include the removal of interaction, polynomial and precision terms associated with each variable as applicable. Although AP and SP might be expected to be the most important explanatory variables, the model

only using AP and SP has an AIC value 568 greater than the final model, and Cox-Snell R² of only 0.27 (Table 2). Thus the inclusion of the other variables is important in fitting the final model.

Table 2: Change in modern model AIC values and Cox-Snell R² model values when excluding specific variables (exclusion includes interactions, polynomials and precision variables) and for a model with only arboreal and shrub pollen percentage

Model	Δ AIC	Cox-Snell R²
Final model	0	0.60
excluding AP	165	0.51
excluding SP	31	0.58
excluding %needleshare	121	0.55
excluding AP Shannon index	396	0.41
excluding lake or bog site	56	0.57
excluding elevation	204	0.48
AP and SP model	568	0.27

<L.426>. Our simple modelling approach yields a reasonably robust picture of changes in tree cover through the Holocene, largely consistent with known changes in climate. As with other statistical reconstruction techniques, it is predicated on the assumption of stationarity between tree cover and the explanatory variables. This may be problematic for variables such as elevation, where changes in elevational lapse rates (Mountain Research Initiative EDW Working Group, 2015) or atmospheric circulation patterns (Bartlein et al., 2017) could affect the relationship, but is less likely to be an issue for explanatory variables that reflect biophysical controls on pollen transport and deposition such as basin type or proportion of needleleaf trees. Our approach is less data-demanding...

Additional references

- Bartlein, P.J., Harrison, S.P. and Izumi, K., 2017. Underlying causes of Eurasian mid-continental aridity in simulations of mid-Holocene climate. *Geophysical Research Letters* 44, doi: 10.1002/2017GL074476.
- Mountain Research Initiative EDW Working Group. Elevation-dependent warming in mountain regions of the world. *Nature Clim Change* 5, 424–430 (2015). <https://doi.org/10.1038/nclimate2563>

R2: It is also not clear to me in which way this regression model improves upon the modern analogue technique requiring the same input information and seemingly yielding a similar performance.

As we point out in the Discussion (line 433), we cannot assess how well the MAT technique performs quantitatively because Zanon et al. (2018) do not provide reconstructions at individual sites. Although the overall pattern of tree cover changes in the two reconstructions is similar, the magnitude of the recent decline shown by Zanon et al. (2018) appears to be too large and our reconstruction appears to be more realistic (Line 335). The main advantage that we see of our approach compared to the MAT reconstructions, as we say in the Discussion, is that it obviates the necessity to make methodological choices, such as the number of analogues used, that have been shown to affect MAT-based reconstructions.

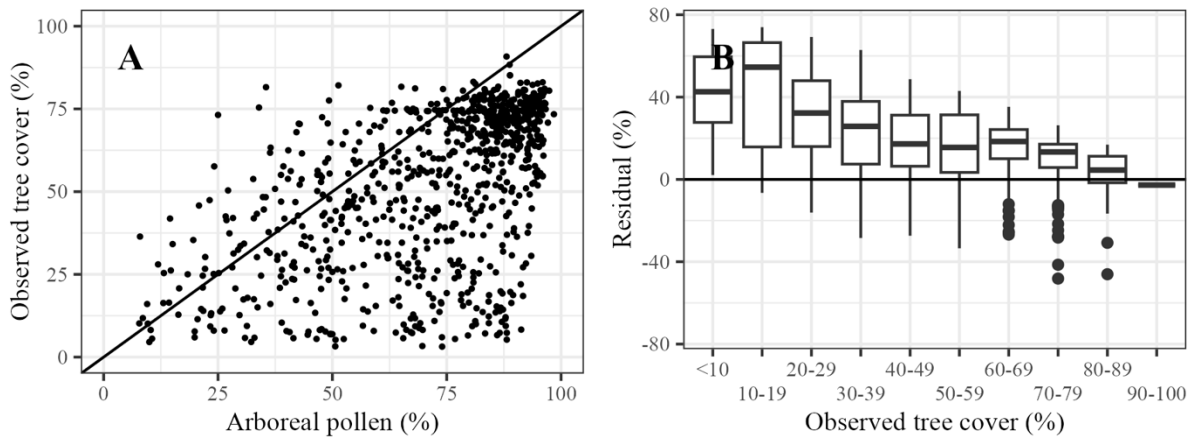
R3: The manuscript is not explaining how the proposed regression model reduces the bias of simply using arboreal percentage, which may be dominated by pine and birch versus elm and lime.

We do not attempt to account for over- or under-representation of specific taxa, except in the inclusion of proportion of needleleaf as a predictor to account for gross differences between conifer and broad-leaved trees as shown by Serge et al. The new Table (see response to R1) shows that the final model is better than a model based on arboreal percentage data alone. However, we will add a new supplementary section (S6 – resulting in current S6 becoming S7 etc.) showing the AP % plotted against observed tree cover in the modern day, and we will add a comment about this issue in the main text as follows:

<L.260>. This correlation value compares favourably to the correlation between raw AP% and observed tree cover values (0.54): raw AP% values tend to overestimate observed tree cover (Supplementary information: S6).

<Within supplement> S6: Arboreal pollen percentages compared with observed tree cover percentages

Raw arboreal pollen percentages tend to overestimate tree cover, with the range in AP% greater for lower observed tree cover groups (Supp. Fig. 3).



Supplementary Figure 3: Arboreal pollen percentage compared to observed tree cover: A - AP% compared to observed tree cover for each record; B - Differences between AP% and observations (residual), in bins of observed tree cover percentage

R4: My second concern with the manuscript is the lack of appropriate recognition and citation of databases and initiatives that collected and curated the pollen data used here. Most of the modern and downcore pollen data used here was initially made available by the EPD/Neotoma or PANGAEA with a cc by 4 license requiring attribution and citation of this initial data release. Please see the recent discussion of the manuscript by Schild et al. (<https://essd.copernicus.org/preprints/essd-2023-486/#discussion>).

Much of the modern and fossil data used in this paper were derived from the EPD/Neotoma or PANGAEA, but the SMPDSv2 and the SPECIAL-EPD data sets contain additional data provided by individual palynologists (and duly acknowledged in the documentation of those data sets). Both data sets have also been cleaned to correct errors in EPD/Neotoma files. The most important improvement offered by these data sets, compared to the original files, is the construction of standardised Bayesian age models for all of the records. They also include additional metadata which is important for the interpretation and current use of these data. Thus, we think it is appropriate to refer to the SMPDSv2 and the SPECIAL-EPD as the source for the information used in this paper. However, and although the source of specific data sets is acknowledged in the documentation of those data sets, we take the point that it would be appropriate to include some further explanation about the sources in the current paper. We will therefore modify the text describing these data sources as follows (note that the inclusion of an additional Supplementary section changes S1 to S2 etc.):

<Line 114>. Modern pollen data (Fig. 2B) was obtained from version 2 of the SPECIAL Modern Pollen Dataset (Villegas-Diaz and Harrison, 2022). This data set was created from multiple different published regional datasets, from data repositories (Neotoma, PANGAEA) or directly from data collectors/authors (see Supplementary Information: S1 for sources and citations) but employs a

standardised taxonomy, and includes improvements to metadata and age models. The data set was further amended for the current analysis by including updated meta information (see *Code and data availability*).

<Within supplement> S1: Sources for SMPDSv2 data

Supplementary Table 1 provides the metadata source for the SMPDSv2 data, together with the number of entities/records and citations for each source.

Supplementary Table 1: List of SMPDSv2 data sources and references

Source (metadata table)	Number of entities	Publications
AMSS	38	Jolly et al., 1996; Julier et al., 2019, 2018; Lebamba et al., 2009
APD	90	Vincens et al., 2007
Australasian pollen	1540	Adeleye et al., 2021b, 2021a; Beck et al., 2017; Field et al., 2018; Fletcher et al., 2014; Herbert and Harrison, 2016; Luly, 1993; Luly et al., 1986; Mariani et al., 2017; McWethy et al., 2010, 2014; Pickett et al., 2004; Prebble et al., 2019
BIOME6000 Japan	94	Takahara et al., 2000
Blyakharchuk	144	Author: Tatiana A. Blyakharchuk
Bush et al., 2021	636	Bush et al., 2021
CMPD	4208	Chen et al., 2021
Dugerdil et al., 2021	48	Dugerdil et al., 2021
EMBSecBIO	149	Harrison et al., 2021
EMPDv2	3508	Davis et al., 2020
Gaillard et al., 1992	124	Gaillard et al., 1992
Harrison et al., 2022b	3	Harrison et al., 2022b
Herzschuh et al., 2019	595	Herzschuh et al., 2019
IBERIA	243	Harrison et al., 2022a
Neotoma	6702	Williams et al., 2018
Phelps et al., 2020	106	Phelps et al., 2020
SMPDSv1	6345	Harrison, 2019
Southern Hemisphere pollen	76	Black, 2006; Dodson, 1978; Dodson and Intoh, 1999; Haberle, 1993, 1996; Hope, 2009; Hope et al., 1998, 1999; Macphail, 1975, 1979, 1980; Macphail and McQueen, 1983; Macphail and Mildenhall, 1980; Norton et al., 1986; Prebble et al., 2010; Shulmeister et al., 2003

Additional References (supplement)

- Adeleye, M.A., Haberle, S.G., Harris, S., Hopf, F.V.-L., Connor, S., Stevenson, J., 2021a. Holocene heathland development in temperate oceanic Southern Hemisphere: Key drivers in a global context. *Journal of Biogeography* 48, 1048–1062. <https://doi.org/10.1111/jbi.14057>
- Adeleye, M.A., Haberle, S.G., McWethy, D., Connor, S.E., Stevenson, J., 2021b. Environmental change during the last glacial on an ancient land bridge of southeast Australia. *Journal of Biogeography* 48, 2946–2960. <https://doi.org/10.1111/jbi.14255>
- Beck, K.K., Fletcher, M.-S., Gadd, P.S., Heijnis, H., Jacobsen, G.E., 2017. An early onset of ENSO influence in the extra-tropics of the southwest Pacific inferred from a 14, 600 year high resolution multi-proxy record from Paddy’s Lake, northwest Tasmania. *Quaternary Science Reviews* 157, 164–175. <https://doi.org/10.1016/j.quascirev.2016.12.001>
- Black, M., 2006. The fire, human and climate nexus in the Sydney Basin, eastern Australia (Doctoral dissertation). University of New South Wales, New South Wales.
- Bush, M.B., Correa-Metrio, A., van Woesik, R., Collins, A., Hanselman, J., Martinez, P., McMichael, C.N.H., 2021. Modern pollen assemblages of the Neotropics. *Journal of Biogeography* 48, 231–241. <https://doi.org/10.1111/jbi.13960>
- Chen H-Y., Xu, D-Y., Liao M-N., Li, K., Ni, J., Cao, X.-Y., Cheng, B., Hao, X-D., Kong, Z-C., Li, S-F., Li, X-Q., Liu, G-X., Liu, P.-M., Liu, X.-Q., Sun, X-J., Tang, L.-Y., Wei, H-C., Xu, Q-H., Yan, S., Yang, X-D., Yang Z.-J., Yu, G., Zhang, Y., Zhang, Z-Y., Zhao, K-L., Zheng, Z., Herzschuh, U., 2021. A modern pollen dataset of China. *Chinese Journal of Plant Ecology* 45, 799. <https://doi.org/10.17521/cjpe.2021.0024>
- Davis, B.A.S., Chevalier, M., Sommer, P., Carter, V.A., Finsinger, W., Mauri, A., Phelps, L.N., Zanon, M., Abegglen, R., Åkesson, C.M., Alba-Sánchez, F., Anderson, R.S., Antipina, T.G., Atanassova, J.R., Beer, R., Belyanina, N.I., Blyakharchuk, T.A., Borisova, O.K., Bozilova, E., Bukreeva, G., Bunting, M.J., Clò, E., Colombaroli, D., Combourieu-Nebout, N., Desprat, S., Di Rita, F., Djamali, M., Edwards, K.J., Fall, P.L., Feurdean, A., Fletcher, W., Florenzano, A., Furlanetto, G., Gaceur, E., Galimov, A.T., Galka, M., García-Moreiras, I., Giesecke, T., Grindean, R., Guido, M.A., Gvozdeva, I.G., Herzschuh, U., Hjelle, K.L., Ivanov, S., Jahns, S., Jankovska, V., Jiménez-Moreno, G., Karpińska-Kołaczek, M., Kitaba, I., Kołaczek, P., Lapteva, E.G., Latałowa, M., Lebreton, V., Leroy, S., Leydet, M., Lopatina, D.A., López-Sáez, J.A., Lotter, A.F., Magri, D., Marinova, E., Matthias, I., Mavridou, A., Mercuri, A.M., Mesa-Fernández, J.M., Mikishin, Y.A., Milecka, K., Montanari, C., Morales-Molino, C., Mrotzek, A., Muñoz Sobrino, C., Naidina, O.D., Nakagawa, T., Nielsen, A.B., Novenko, E.Y., Panajiotidis, S., Panova, N.K., Papadopoulou, M., Pardoe, H.S., Pędziszewska, A., Petrenko, T.I., Ramos-Román, M.J., Ravazzi, C., Rösch, M., Ryabogina, N., Sabariego Ruiz, S., Salonen, J.S., Sapelko, T.V., Schofield, J.E., Seppä, H., Shumilovskikh, L., Stivrins, N., Stojakowits, P., Svobodova Svitavska, H., Święta-Musznicka, J., Tantau, I., Tinner, W.,

- Tobolski, K., Tonkov, S., Tsakiridou, M., Valsecchi, V., Zanina, O.G., Zimny, M., 2020. The Eurasian Modern Pollen Database (EMPD), version 2. *Earth System Science Data* 12, 2423–2445. <https://doi.org/10.5194/essd-12-2423-2020>
- Dodson, J.R., 1978. A vegetation history from north-east Nelson, New Zealand. *New Zealand Journal of Botany* 16, 371–378. <https://doi.org/10.1080/0028825X.1978.10425144>
- Dodson, J.R., Intoh, M., 1999. Prehistory and palaeoecology of Yap, federated states of Micronesia. *Quaternary International* 59, 17–26. [https://doi.org/10.1016/S1040-6182\(98\)00068-8](https://doi.org/10.1016/S1040-6182(98)00068-8)
- Dugerdil, L., Joannin, S., Peyron, O., Jouffroy-Bapicot, I., Vanni re, B., Boldgiv, B., Unkelbach, J., Behling, H., M enot, G., 2021. Climate reconstructions based on GDGT and pollen surface datasets from Mongolia and Baikal area: calibrations and applicability to extremely cold–dry environments over the Late Holocene. *Climate of the Past* 17, 1199–1226. <https://doi.org/10.5194/cp-17-1199-2021>
- Field, E., Tyler, J., Gadd, P.S., Moss, P., McGowan, H., Marx, S., 2018. Coherent patterns of environmental change at multiple organic spring sites in northwest Australia: Evidence of Indonesian-Australian summer monsoon variability over the last 14,500 years. *Quaternary Science Reviews* 196, 193–216. <https://doi.org/10.1016/j.quascirev.2018.07.018>
- Fletcher, M.-S., Wood, S.W., Haberle, S.G., 2014. A fire-driven shift from forest to non-forest: evidence for alternative stable states? *Ecology* 95, 2504–2513. <https://doi.org/10.1890/12-1766.1>
- Gaillard, M.-J., Birks, H.J.B., Emanuelsson, U., Berglund, B.E., 1992. Modern pollen/land-use relationships as an aid in the reconstruction of past land-uses and cultural landscapes: an example from south Sweden. *Veget Hist Archaeobot* 1, 3–17. <https://doi.org/10.1007/BF00190697>
- Haberle, S.G., 1993. Late Quaternary environmental history of the Tari Basin, Papua New Guinea (PhD Thesis). Australian National University, Canberra.
- Haberle, S.G., 1996. Explanations for palaeoecological changes on the northern plains of Guadalcanal, Solomon Islands: the last 3200 years. *The Holocene* 6, 333–338. <https://doi.org/10.1177/095968369600600307>
- Harrison, S.P., 2019. Modern pollen data for climate reconstructions, version 1 (SMPDS). <https://doi.org/10.17864/1947.194>
- Harrison, S.P., Marinova, E., Cruz-Silva, E., 2021. EMBSecBIO pollen database. <https://doi.org/10.17864/1947.309>
- Harrison, S.P., Shen, Y., Sweeney, L., 2022a. Pollen data and charcoal data of the Iberian Peninsula (version 3). <https://doi.org/10.17864/1947.000369>
- Harrison, S.P., Villegas-Diaz, R., Cruz-Silva, E., Gallagher, D., Kesner, D., Lincoln, P., Shen, Y., Sweeney, L., Colombaroli, D., Ali, A., Barhoumi, C., Bergeron, Y., Blyakharchuk, T., Bobek, P., Bradshaw, R., Clear, J.L., Czerwiński, S., Daniau, A-L., Dodson, J., Edwards, K.J.,

- Edwards, M.E., Feurdean, A., Foster, D., Gajewski, K., Galka, M., Garneau, M., Giesecke, T., Gil Romera, G., Girardin, M.P., Hoefler, D., Huang, K., Inoue, J., Jamrichová, E., Jasiunas, N., Jiang, W., Jiménez-Moreno, G., Karpińska-Kołaczek, M., Kołaczek, P., Kuosmanen, N., Lamentowicz, M., Lavoie, M., Li, F., Li, J., Lisitsyna, O., López-Sáez, J.A., Luelmo-Lautenschlaeger, R., Magnan, G., Magyari, E.K., Maksims, A., Marcisz, K., Marinova, E., Marlon, J., Mensing, S., Miroslaw-Grabowska, J., Oswald, W., Pérez-Díaz, S., Pérez-Obiol, R., Piilo, S., Poska, A., Qin, X., Remy, C.C., Richard, P.J.H., Salonen, S., Sasaki, N., Schneider, H., Shotyck, W., Stancikaite, M., Šteinberga, D., Stivrins, N., Takahara, H., Tan, Z., Trasune, L., Umbanhowar, C.E., Väiliranta, M., Vassiljev, J., Xiao, X., Xu, Q., Xu, X., Zawisza, E., Zhao, Y., Zhou, Z., Paillard, J., 2022b. The Reading Palaeofire database: an expanded global resource to document changes in fire regimes from sedimentary charcoal records *Earth System Science Earth System Science Data* 14: 1109-1124
<https://doi.org/10.5194/essd-14-1109-2022>
- Herbert, A.V., Harrison, S.P., 2016. Evaluation of a modern-analogue methodology for reconstructing Australian palaeoclimate from pollen. *Review of Palaeobotany and Palynology* 226, 65–77.
<https://doi.org/10.1016/j.revpalbo.2015.12.006>
- Herzschuh, U., Cao, X., Laepple, T., Dallmeyer, A., Telford, R.J., Ni, J., Chen, F., Kong, Z., Liu, G., Liu, K.-B., Liu, X., Stebich, M., Tang, L., Tian, F., Wang, Y., Wischniewski, J., Xu, Q., Yan, S., Yang, Z., Yu, G., Zhang, Y., Zhao, Y., Zheng, Z., 2019. Position and orientation of the westerly jet determined Holocene rainfall patterns in China. *Nat Commun* 10, 2376.
<https://doi.org/10.1038/s41467-019-09866-8>
- Hope, G., 2009. Environmental change and fire in the Owen Stanley Ranges, Papua New Guinea. *Quaternary Science Reviews* 28, 2261–2276. <https://doi.org/10.1016/j.quascirev.2009.04.012>
- Hope, G., Gillieson, D., Head, J., 1988. A Comparison of Sedimentation and Environmental Change in New Guinea Shallow Lakes. *Journal of Biogeography* 15, 603–618.
<https://doi.org/10.2307/2845439>
- Hope, G., O’Dea, D., Southern, W., 1999. Holocene vegetation histories in the Western Pacific: alternative records of human impact, in: *The Pacific from 5000 to 2000 BP: Colonisation and Transformations*. Paris, pp. 387–404.
- Jolly, D., Bonnefille, R., Burcq, S., Roux, M., 1996. Représentation pollinique de la forêt dense humide du Gabon, tests statistiques, in: *Comptes rendus de l’Académie des sciences*. Presented at the Sciences de la terre et des planètes, Paris, pp. 63–70.
- Julier, A.C.M., Jardine, P.E., Adu-Bredu, S., Coe, A.L., Duah-Gyamfi, A., Fraser, W.T., Lomax, B.H., Malhi, Y., Moore, S., Owusu-Afryie, K., Gosling, W.D., 2018. The modern pollen–vegetation relationships of a tropical forest–savannah mosaic landscape, Ghana, West Africa. *Palynology* 42, 324–338. <https://doi.org/10.1080/01916122.2017.1356392>

- Julier, A.C.M., Jardine, P.E., Adu-Bredu, S., Coe, A.L., Fraser, W.T., Lomax, B.H., Malhi, Y., Moore, S., Gosling, W.D., 2019. Variability in modern pollen rain from moist and wet tropical forest plots in Ghana, West Africa. *Grana* 58, 45–62. <https://doi.org/10.1080/00173134.2018.1510027>
- Lebamba, J., Vincens, A., Jolly, D., Ngomanda, A., Schevin, P., Maley, J., Bentaleb, I., 2009. Modern pollen rain in savanna and forest ecosystems of Gabon and Cameroon, Central Atlantic Africa. *Review of Palaeobotany and Palynology* 153, 34–45. <https://doi.org/10.1016/j.revpalbo.2008.06.004>
- Luly, J.G., 1993. Holocene palaeoenvironments near Lake Tyrrell, semi-arid northwestern Victoria, Australia. *Journal of Biogeography* 20, 587–598. <https://doi.org/10.2307/2845516>
- Luly, J.G., Bowler, J.M., Head, M.J., 1986. A radiocarbon chronology from the playa Lake Tyrrell, Northwestern Victoria, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology, Palaeoenvironments of Salt Lakes* 54, 171–180. [https://doi.org/10.1016/0031-0182\(86\)90123-9](https://doi.org/10.1016/0031-0182(86)90123-9)
- Macphail, M.K., 1975. The history of the vegetation and climate in southern Tasmania since the late Pleistocene (ca. 13,000–0 BP) (Doctoral dissertation). University of Tasmania.
- Macphail, M.K., 1979. Vegetation and Climates in Southern Tasmania since the Last Glaciation. *Quaternary Research* 11, 306–341. [https://doi.org/10.1016/0033-5894\(79\)90078-4](https://doi.org/10.1016/0033-5894(79)90078-4)
- Macphail, M.K., 1980. Fossil and modern *Beilschmiedia* (Lauraceae) pollen in New Zealand. *New Zealand Journal of Botany* 18, 453–457. <https://doi.org/10.1080/0028825X.1980.10425165>
- Macphail, M.K., McQueen, D.R., 1983. The value of New Zealand pollen and spores as indicators of Cenozoic vegetation and climates. *Journal of the Biological Society* 26, 37–59.
- Macphail, M.K., Mildenhall, D.C., 1980. *Dactylanthus taylori*: in North-West Nelson, New Zealand? *New Zealand Journal of Botany* 18, 149–152. <https://doi.org/10.1080/0028825X.1980.10427242>
- Mariani, M., Connor, S.E., Fletcher, M.-S., Theuerkauf, M., Kuneš, P., Jacobsen, G., Saunders, K.M., Zawadzki, A., 2017. How old is the Tasmanian cultural landscape? A test of landscape openness using quantitative land-cover reconstructions. *Journal of Biogeography* 44, 2410–2420. <https://doi.org/10.1111/jbi.13040>
- McWethy, D.B., Whitlock, C., Wilmshurst, J.M., McGlone, M.S., Fromont, M., Li, X., Dieffenbacher-Krall, A., Hobbs, W.O., Fritz, S.C., Cook, E.R., 2010. Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. *Proceedings of the National Academy of Sciences* 107, 21343–21348. <https://doi.org/10.1073/pnas.1011801107>
- McWethy, D.B., Wilmshurst, J.M., Whitlock, C., Wood, J.R., McGlone, M.S., 2014. A High-Resolution Chronology of Rapid Forest Transitions following Polynesian Arrival in New Zealand. *PLOS ONE* 9, e111328. <https://doi.org/10.1371/journal.pone.0111328>

- Norton, D.A., McGlone, M.S., Wigley, T.M.L., 1986. Quantitative analyses of modern pollen-climate relationships in New Zealand indigenous forests. *New Zealand Journal of Botany* 24, 331–342. <https://doi.org/10.1080/0028825X.1986.10412681>
- Phelps, L.N., Chevalier, M., Shanahan, T.M., Aleman, J.C., Courtney-Mustaphi, C., Kiahtipes, C.A., Broennimann, O., Marchant, R., Shekeine, J., Quick, L.J., Davis, B.A.S., Guisan, A., Manning, K., 2020. Asymmetric response of forest and grassy biomes to climate variability across the African Humid Period: influenced by anthropogenic disturbance? *Ecography* 43, 1118–1142. <https://doi.org/10.1111/ecog.04990>
- Pickett, E.J., Harrison, S.P., Hope, G., Harle, K., Dodson, J.R., Kershaw, A.P., Prentice, I.C., Backhouse, J., Colhoun, E.A., D’Costa, D., Flenley, J., Grindrod, J., Haberle, S., Hassell, C., Kenyon, C., Macphail, M., Martin, H., Martin, A.H., McKenzie, M., Newsome, J.C., Penny, D., Powell, J., Raine, J.I., Southern, W., Stevenson, J., Sutra, J.P., Thomas, I., van der Kaars, S., Ward, J., 2004. Pollen-based reconstructions of biome distributions for Australia, Southeast Asia and the Pacific (SEAPAC region) at 0,6000 and 18,000 14C yr B.P. *Journal of Biogeography* 31, 1381–1444.
- Prebble, M., Anderson, A.J., Augustinus, P., Emmitt, J., Fallon, S.J., Furey, L.L., Holdaway, S.J., Jorgensen, A., Ladefoged, T.N., Matthews, P.J., Meyer, J.-Y., Phillipps, R., Wallace, R., Porch, N., 2019. Early tropical crop production in marginal subtropical and temperate Polynesia. *Proceedings of the National Academy of Sciences* 116, 8824–8833. <https://doi.org/10.1073/pnas.1821732116>
- Prebble, M., Kennedy, J., Southern, W., 2010. Holocene lowland vegetation change and human ecology in Manus Province, Papua New Guinea, in: *Altered Ecologies*. ANU Press, pp. 299–321.
- Shulmeister, J., McLea, W.L., Singer, C., McKay, R.M., Hosie, C., 2003. Late Quaternary pollen records from the Lower Cobb Valley and adjacent areas, North-West Nelson, New Zealand. *New Zealand Journal of Botany* 41, 503–533. <https://doi.org/10.1080/0028825X.2003.9512867>
- Takahara, H., Sugita, S., Harrison, S.P., Miyoshi, N., Morita, Y., Uchiyama, T., 2000. Pollen-based reconstructions of Japanese biomes at 0, 6000 and 18,000 14C yr bp. *Journal of Biogeography* 27, 665–683. <https://doi.org/10.1046/j.1365-2699.2000.00432.x>
- Villegas-Diaz, R., Harrison, S.P., 2022. smpds: The SPECIAL Modern Pollen Data Set for Climate Reconstructions. Software. <https://doi.org/10.5281/zenodo.6598832>
- Vincens, A., Lézine, A.-M., Buchet, G., Lewden, D., Le Thomas, A., 2007. African pollen database inventory of tree and shrub pollen types. *Review of Palaeobotany and Palynology* 145, 135–141. <https://doi.org/10.1016/j.revpalbo.2006.09.004>
- Williams, J.W., Grimm, E.C., Blois, J.L., Charles, D.F., Davis, E.B., Goring, S.J., Graham, R.W., Smith, A.J., Anderson, M., Arroyo-Cabrales, J., Ashworth, A.C., Betancourt, J.L., Bills, B.W.,

Booth, R.K., Buckland, P.I., Curry, B.B., Giesecke, T., Jackson, S.T., Latorre, C., Nichols, J., Purdum, T., Roth, R.E., Stryker, M., Takahara, H., 2018. The Neotoma Paleocology Database, a multiproxy, international, community-curated data resource. *Quaternary Research* 89, 156–177. <https://doi.org/10.1017/qua.2017.105>

<Line 156>. Fossil pollen data were obtained from the SPECIAL-EPD dataset (Harrison et al., 2024), a database of pollen records from Europe, the Middle East and western Eurasia. It builds on a pollen compilation covering the Middle East (EMBSecBIO database: Cordova et al., 2009; Harrison and Marinova, 2017; Marinova et al., 2017; Harrison et al., 2021), data available from public data repositories (NEOTOMA: <https://www.neotomadb.org/>; PANGAEA: <https://www.pangaea.de/>) and data provided by the original authors for the Iberian peninsula (Liu et al., 2023) and other regions. It includes 1,758 records from 1573 sites. The data have been extensively quality-controlled and mistakes have been corrected and documented. New BACON Bayesian age models, based on the recalibration of radiocarbon ages using INTCAL2020 (Reimer et al., 2020) calibration curve as appropriate, are provided for all the records using the ‘rbacon’ R package (Blaauw et al., 2021) in the ‘AgeR’ R package (Villegas-Diaz et al., 2021).

Additional References

- Blaauw, M., Christen, J. A., Lopez, M. A. A., Vazquez, J. E., Gonzalez V., O. M., Belding, T., Theiler, J., Gough, B., & Karney, C. (2021). *rbacon: Age-depth modelling using Bayesian statistics* (2.5.6) [R]. <https://CRAN.R-project.org/package=rbacon>
- Cordova, C.E., Harrison, S.P., Mudie, P.J., Riehl, S., Leroy, S.A.G., Ortiz, N., 2009. Pollen, plant macrofossil and charcoal records for palaeovegetation reconstruction in the Mediterranean-Black Sea Corridor since the Last Glacial Maximum. *Quaternary International* 197: 12-26.
- Harrison, S.P. and Marinova, E., 2017. EMBSecBIO modern pollen biomisation. University of Reading Dataset. <http://dx.doi.org/10.17864/1947.109>.
- Harrison, S.P., Marinova, E., & Cruz-Silva, E. (2021). *EMBSecBIO pollen database* [Data set]. University of Reading. <https://doi.org/10.17864/1947.309>
- Liu, M., Shen, Y., González-Sampériz, P., Gil-Romera, G., ter Braak, C.J.F. Prentice, I.C., Harrison, S.P., 2023. Holocene climates of the Iberian Peninsula. *Climate of the Past* 19: 803-834, <https://doi.org/10.5194/cp-19-803-2023>.
- Marinova, E., Harrison, S.P., Bragg, F., Connor, S., de Laet, V., Leroy, S., Mudie, P., Atanassova, J., Bozilova, E., Caner, H., Cordova, C., Djamali, M., Filipova-Marinova, M., Gerasimenko, N., Kouli, K., Kotthoff, U., Kvavadze, E., Lazarova, M., Novenko, E., Ramezani, E., Röpke, A., Shumilovskikh, L., Tantau, I., Tonkov, S., 2017. Pollen-derived biomes in the eastern Mediterranean-Black Sea-Caspian corridor. *Journal of Biogeography* 45: 484–499 DOI: 10.1111/jbi.13128

Reimer, P., Austin, W. E. N., Bard, E., Bayliss, A., Blackwell, P. G., Ramsey, C. B., Butzin, M., Cheng, H., Edwards, R. L., Friedrich, M., Grootes, P. M., Guilderson, T. P., Hajdas, I., Heaton, T. J., Hogg, A. G., Hughen, K. A., Kromer, B., Manning, S. W., Muscheler, R., ... Talamo, S. (2020). The IntCal20 northern hemisphere radiocarbon age calibration curve (0-55 cal kBP). *Radiocarbon*, 62(4), 725–757. <https://doi.org/10.1017/RDC.2020.41>

Villegas-Diaz, R., Cruz-Silva, E., & Harrison, S. P. (2021). ageR: Supervised age models [R]. *Zenodo*, <https://doi.org/10.5281/zenodo.4636716>

Specific comments

R5: L. 57: The LRA includes local reconstructions (LOVE) which has not been applied on the European scale. Only the REVEALS model was used.

We agree that this is potentially confusing. We will make the following amendment:

<Line 57>. The most recent quantitative pan-European pollen-based reconstructions of Holocene vegetation changes have been made using the REVEALS approach (Sugita, 2007b, a) or the Modern Analogue Technique (MAT) (Overpeck et al., 1985; Guiot, 1990; Jackson and Williams, 2004; Zanon et al. 2018).

R6: L. 58: You should cite Zanon et al. (2018) already here.

We agree that Zanon et al. (2018) should be cited here, given their extension of MAT to reconstruct tree cover. See response to R5.

R7: L. 63: The main focus was on reconstructing the proportion of open versus forest land cover.

We agree that we should clarify this, and will rewrite the text as follows:

<Line 63>. They produced maps showing the changing patterns of open vegetation versus forest, as well as specific plant functional types, at record-containing 1° grid cells for five time periods during the Holocene, based on 636 sites and 25 pollen taxa.

R8: L. 65: As an introductory overview this is almost too detailed while it is lacking studies to work as a good review of all that has come before: e.g. Pirzamanbein et al. (2014, *Ecological Complexity*), Roberts et al. (2018) *Scientific Reports* 8:716. Some of these appear in the discussion, but it would be good to mention them here already.

There are indeed a number of other studies applying different approaches to forest reconstruction, but we were concerned that introducing all of the techniques and approaches would make the introduction too long and so focused on the REVEALS and MAT approaches we used for quantitative comparison.

However, we agree that this paragraph could be improved by adding some additional information. We will amend the text as follows:

<L56>. Several different techniques that have been applied to reconstruct regional and sub-regional vegetation in Europe using pollen such as biomization/pseudobiomization (e.g. Fyfe et al., 2015; Binney et al., 2017) or the application of MAT using plant functional types (e.g. Davis et al., 2014). Other studies have made reconstructions combining different approaches (e.g. Roberts et al., 2018) and by combining pollen-based reconstructions with simulated potential vegetation (Pirzamanbein et al., 2014). However, the most recent quantitative pan-European pollen-based reconstructions of Holocene vegetation changes have been made using the Landscape Reconstruction Algorithm (LRA) REVEALS approach (Sugita, 2007b, a) or the Modern Analogue Technique (MAT) (Overpeck et al., 1985; Guiot, 1990; Jackson and Williams, 2004; Zanon et al., 2018). The REVEALS method calculates regional vegetation cover based on modelled relationships between pollen abundance, estimated differences in species level pollen productivity and pollen transport, and differences in site characteristics. Initially used at individual sites or small regions (e.g. Gaillard et al., 2010; Nielsen et al., 2012; Marquer et al., 2014), REVEALS was first applied at a pan-European scale by Trondman et al. (2015) and later extended with additional sites, taxa and an improved temporal resolution by Githumbi et al. (2022). The most recent analysis by Serge et al. (2023), is based on 1607 records for 500-year intervals before 700 cal. BP and for the subsequent intervals of 700-350 cal. BP, 350-100 cal. BP and 100 cal. BP- present. They tested the impact of including additional taxa (n=46) on the vegetation reconstructions, producing maps of landcover and species abundance at record-containing 1° grid cells. In contrast, the MAT approach reconstructs past vegetation based on identifying modern analogues of fossil pollen assemblages, on the assumption that samples found in the fossil record that share a similar composition to those found in present-day pollen assemblages will have similar vegetation. Zanon et al. (2018) applied MAT to 2,526 individual fossil pollen samples from Europe to generate interpolated maps at 250-year intervals at 5 arc-minute resolution through the Holocene.

R9: L. 80: Fall speeds are not the major issue as they can be estimated based on pollen size.

We agree that the including FS with RPP here implies they are equally challenging. We will amend the text as follows:

<L80>. For instance, landscape-level reconstructions are problematic if RPP information is not available for relatively common taxa.

R10: L. 86: Since you mention PFTs you may want to include Davis et al. (2015) here already not only in the discussion.

We agree that Davis should be cited here in relation to the use of PFTs with MAT, but that the 2003

(Quaternary Science Reviews; 22(15-17)) paper would be most appropriate given that this paper explicitly introduced this approach in relation to MAT.

<L86>. Techniques designed to minimise the number of samples for which no analogues are found, such as grouping species into plant functional types (PFTs) (see Davis, 2003), introduce further uncertainties since the allocation of pollen taxa to PFTs is often ambiguous (Zanon et al., 2018).

Additional reference

Davis, B.A.S., Brewer, S. , Stevenson, A.C. , Guiot, J.: The temperature of Europe during the Holocene reconstructed from pollen data, *Quat. Sci. Rev.*, 22, 1701-1716, [https://doi.org/10.1016/S0277-3791\(03\)00173-2](https://doi.org/10.1016/S0277-3791(03)00173-2), 2003

R11: L. 115: The SPECIAL Modern Pollen Dataset (Villegas-Diaz and Harrison, 2022) compiles samples from other data sources including Neotoma and PANGAEA which also have a CC-BY-4.0 license, hence you need to cite or acknowledge the original data source not just the data compilation. Please see response to R4 and additional text describing the data set

R12: L. 116: SMPDS needs to be introduced. It is not clear from the above that this refers to the surface sample data.

As noted, the SMPDS contains pollen samples from the post-industrial era. Records include a variety of different entity types, including surface samples, sediment samples, core tops, pollen traps etc. As indicated in L.125, we only included records from lakes and bogs in our analysis. Please see response to R4 for the additional text describing the data set.

R13: L. 119: Particularly where core tops were used this assumption is daring.

In general, the samples described simply as modern in the data set were surface samples and we have followed the authors of the various compilations in assuming that this is true.

R14: L. 122: Give a brief motivation not just a reference.

We will amend the text to provide an explanation for this as follows:

<L.122>. Depauperate samples with Hill's N2 values (Hill, 1973) of < 2 were excluded, following Wei et al. (2021). Wei et al. (2021) found that low taxa diversity produced unreliable estimates of reconstructed variables, in this case temperature via tolerance weighted partial least squares estimation.

R15: L. 122-124: Here you are referring to surface samples, core tops or Holocene records?

The data from the SMPDS that we used included lake and bog records. We included all entity types to build the modern tree cover model, except moss polsters and pollen traps which reflect very

localised pattern of pollen rain. We thank the reviewer for raising this point, as this should have been mentioned in the method and will revise the text as follows

<L.125>. Only samples from lakes and bogs were included, to ensure appropriate pollen source areas could be calculated, and samples gathered via moss polsters or pollen traps were excluded as these generally reflect only the very local pollen rain.

R16: L. 126: So you include small bogs but exclude large bogs? I cannot find this constraint discussed in Githumbi et al. (2022).

Githumbi et al. (2022) suggest that: “...*REVEALS* estimates of plant cover using pollen assemblages from large bogs should only be interpreted with great caution (Mazier et al., 2012; see also Sect. 4, “Discussion”).” (Githumbi et al., 2022). They included estimates from large bogs in their analysis but flagged these as “lower quality” estimates. Given this caution, especially regarding the issue of surface level vegetation and our inclusion of Cyperaceae, Polypodiales and Ericaceae, we decided to exclude large bog sites from our analysis. We will amend the text as follows:

<L126>. However, bog records with a radius $\geq 400\text{m}$ were excluded from the analysis. Githumbi et al (2022) indicated that caution was necessary in interpreting *REVEALS* vegetation reconstruction estimates based on large bogs and, given that we included taxa that grow on bog surfaces in our analysis (see below), we excluded large bogs to reduce the potential for these to bias the regional vegetation reconstructions.

R17: L. 135: It would be useful to mention what is included in shrub pollen: Are you including dwarf shrubs like *Calluna* or rather taller perennial woody plants like *Corylus* and *Juniperus*?

The list of species included within each grouping is included within the Table in Supplementary information: S1. *Calluna* is included within the shrub group, whereas *Colylus* and *Juniperus* (as part of amalgamated group Cupressaceae) are included as trees.

R18: L. 139: How did you deal with situations where alien tree plantations make up most forest cover: e.g. *Eucalyptus*. Also plantations of *Pseudotsuga* (0.83 million ha in Europe) may be a potential problem.

Observed tree cover is based on the Copernicus Global Land Service maps (line 105). These maps do not distinguish between alien/natural species tree cover or plantation tree cover, and so we are unable to distinguish alien tree plantations. We will clarify this in the text as follows:

<Line 107>..... permanent water, snow, and crops (Fig. 2A). However, the Copernicus maps do not distinguish between natural forests and plantations and so the tree cover target may include planted species.

R19: L. 140: Large proportions of Cyperaceae and Polypodiales are limited to bogs, excluding them would reduce the biases from including bog samples.

As we mention, the inclusion of these species was to help prevent open environments being dominated by pollen from long distance transport. Site type (bog or lake) is included as a regressor, which is meant to reflect differences between bog and lake records.

R20: L. 145: It would be good if you mentioned here the range of resulting source areas considered. We agree that it would be useful to indicate here the range of source areas considered.

<L.151>. Source area radii varied in size from 5,026 km to 418,894 km for the largest lake, with a median of 28,316 km.

R21: L. 153: What do you mean by “non-natural vegetation” here?

We agree that the terminology non-natural vegetation is somewhat ambiguous, so we will change this here, and at line 106 where the term was first used and defined, to other land-cover classes:

<Line 106>. 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 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, including bare ground, built up areas, moss or lichen, permanent water, snow, and crops (Fig. 2A).

<Line 153>. There were 263 records where more than half of the contributing grid cells were masked as land-cover classes other than vegetation; these were excluded from the model construction.

R22: L. 154: How many from bogs?

There were 133 bog records used for the development of the modern tree cover model. We will include this information:

<L.154>. A total of 852 pollen records were included in the final model training dataset, of which 133 were bog records.

R23: L. 156: The same problem of attribution applies to the SPECIAL-EPD. Please cite and acknowledge the EPD. See <https://www.neotomadb.org/data/data-use-and-embargo-policy>
Please see response to R4 and the additional text.

R24: L. 167ff: I like the idea, but am skeptical about the predictors used. Rather than using % needleleaf, it would have been better to classify the pollen types according to high mid and low pollen producing plants. Needleleaf trees include the high pollen producing Pines and low producing Larix

(or *Pseudotsuga*). I am not sure elevation is a good predictor when thinking about the past as vegetation belts moved up and down the mountains during the Holocene. I would perhaps rather limit the inclusion of modern and fossil sites to below 500 m. I don't understand the need of including the Shannon Index, particularly I don't understand the provided motivation.

[Please see response to R1.](#)

R25: L. 233ff: We know that % tree pollen is a strong predictor of forest cover without any transformation so it would be useful to compare the model performance to the performance of a simple regression model of % tree and shrub pollen (depending on what is in the shrubs) versus forest cover.

[Please see our response to R1.](#)

R26: L. 233: The negative correlation between %needleleaf and tree cover is interesting and unexpected. Could that be due to frequent Pine pollen in generally open areas. *Picea* pollen should however correlate with high tree cover.

[We agree that this could be an explanation for this relationship. The influence of open landscapes on the model at lower levels of needleleaf% is also potentially an explanation for the modelled relationships between SI tree cover and tree cover. For more open landscapes, tree species diversity may be limited. As these landscapes become more mixed, tree species diversity may increase. But at higher levels of tree species diversity, as evidenced by the negative quadratic term, the importance of this variable to increased tree cover values decreases and potentially could become negative for heavily wooded areas. We will add the following text:](#)

[<L.235>. This negative relationship may be a reflection of longer distance pollen transport of needleleaf species \(e.g. *Pinus*\) to open environments. As tree cover increases, this may imply an increased diversity of species, including broadleaf species. The positive quadratic term indicates that this relationship becomes positive at higher levels of tree cover, potentially reflecting higher tree cover in boreal needleleaf forests. Increased 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 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. 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.](#)

R27: L. 258: The overestimation of tree cover in northern Scandinavia is interesting and expected as pollen productivity is lower. This is also the case for higher elevations, which is why elevation is a good covariable for the present, but this relationship may not hold true in the past where temperature

changes resulted in changing pollen productivities in the mountains.

Please see our response to R1.

R28: L. 330: The difference in tree cover between the reconstructions for the last 1000 years and the early Holocene is intriguing. As Zanon et al (2018) and Serge et al (2023) use completely different methodologies, but show the same trend, my initial response would be to trust them more, even if the absolute modern cover is off for both. Here it would be interesting to explore the reasons for the deviations of the current study. Could one reason be the separation of shrub pollen from tree pollen? Within the Discussion section (L.380), we ascribe this difference as being potentially due a technical point regarding the modern map of observed tree cover. As we indicate, our model is trained on this map, which specifically excludes other land-cover classes. In contrast to the other reconstructions, we are effectively modelling tree cover without human influence, which is why our reconstructions deviate more for the later Holocene than at other periods.

R29: L. 341: Please see the recent manuscript by Schild et al.

(<https://essd.copernicus.org/preprints/essd-2023-486/#discussion>) who argue that the REVEALS method underestimates the forest cover. If that would be true then your new method would perform worse as it scores below the REVEALS estimates. If you argue that forest cover was generally lower then it would be useful to find supporting evidence and make that a point of discussion.

Thank you for highlighting this recent manuscript. However, this preprint does not appear to suggest that REVEALS underestimates forest cover, when validating modern reconstructions with satellite data. They argue that REVEALS successfully reduces the overestimation of tree cover based purely on pollen data in the modern day, with that adjustment further improved by optimising RPP values, particularly for North America (see Fig. 10, p14). Optimization of RPP values actually reduces tree cover estimates through time globally (see Figure 8, p12), which implies that the REVEALS estimates from Serge et al. (2023) would be on the higher, rather than lower side.

R30: L. 421: The main deforestation of Northwestern Europe took place during the Bronze Age and Medieval period leading to an all-time low around 1800 (see e.g. Bradshaw and Sykes 2014 Ecosystem Dynamics, Wiley).

This statement implies that we know the cause of forest loss in Europe and that it is primarily due to human destruction of the natural vegetation. Part of our reason for making forest cover reconstructions is to be able to test this assertion quantitatively. The Bronze Age is a somewhat loosely defined epoch somewhere between 5300 and 2700 BP. Since all three reconstructions show a decline in forest cover after 6ka, it could be argued that this is consistent with the idea that the main deforestation of Europe took place during the Bronze Age and is therefore potentially explained by human activities. But it is clear from our regional reconstructions and also from the REVEALS based

analysis by Roberts et al. (2017), that the timing of forest loss varied across Europe. This could, of course, be due to differences in the timing of landscape appropriation by people. But the latter part of the Holocene is also a time when climate was changing, and the timing of these changes is also non-synchronous across the continent. So, it would be equally plausible to argue that climate changes are responsible for (or have contributed to) changes in forest cover. This is the point we were trying to make, but we will take this opportunity to spell it out more clearly as follows:

<L411>. The late Holocene decline in tree cover is consistent with the orbitally-driven cooling. However, the more rapid decline in tree cover during the last millennium shown in the Boreal and Continental regions, and shown more dramatically in the Zanon et al. (2018) and Serge et al. (2023) reconstructions, is more difficult to explain as a function of climate changes - transient model simulations of the response to changes in orbital and greenhouse gas forcing (e.g. Liu et al., 2009; Zhang et al., 2016; Braconnot et al., 2019; Dallmeyer et al., 2020) generally indicate muted changes in either summer or winter temperatures during the most recent millennia. Human influence on the landscape has been identified in some regions of Europe from 6,000 cal. BP onwards (e.g. Roberts et al., 2018; Zapolska et al., 2023). Although this may have contributed to the climate-driven decline in forest cover, rapid population growth occurred only during the past 2000 years (Klein Goldewijk et al., 2010, 2017). The recent decline in tree cover may therefore reflect this rapid growth and the consequent increasing human influence on the landscape in some regions (see e.g. Marquer et al., 2017; Roberts et al., 2019). Much of the debate about the relative importance of climate and human activities on the environment during the Holocene has been based on correlations, often at a local scale. More formal modelling of these relationships, using quantitative information on climate and population size, is required to assign the impact of each on tree cover more confidently.