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CORRESPONDENCE



A critical evaluation of the Oscillayers methods and datasets

Abstract

Here we evaluate Oscillayers, a new method that aims to estimate palaeoclimates for the past 5.4 Myr, and discuss the associated theoretical and methodological issues. We show that the theoretical foundation of Oscillayers is inherently limited, because the method cannot incorporate spatio-temporal variation and different forcing mechanisms into climate reconstructions. In addition, several methodological weaknesses are clarified that entrench the palaeoclimatic reconstruction of Oscillayers to patterns of climate change observed between the Last Glacial Maximum and current climates. We test the utility of the Oscillayers method to produce palaeoclimatic reconstructions that are similar to general circulation model (GCM)based estimates. On average, only 55.6% of values in the mean annual temperature datasets across the Pliocene and Pleistocene were within ±3°C when compared with corresponding GCM-based datasets. Furthermore, on average only 75.3% of values in the mean annual precipitation datasets across the Pliocene and Pleistocene were within ±200 mm of rainfall of the GCM-based estimates. Our results demonstrate that the Oscillayers approach does not provide a robust approximation of palaeoclimatic conditions throughout the Plio-Pleistocene. Thus, when these datasets are used for scientific analyses, the results should be interpreted with a full appreciation of their limitations, particularly for periods outside the last glacial cycle.

1 | INTRODUCTION

High-resolution, easily accessible palaeoclimatic data are essential for environmental, evolutionary and ecological studies. Recently, there has been an expansion in the number of palaeoclimatic databases produced for biological audiences (e.g., Brown, Hill, Dolan, Carnaval, & Haywood, 2018; Fordham et al., 2017; Karger et al., 2017; Lima-Ribeiro et al., 2015). A recent approach, Oscillayers (Gamisch, 2019), promises to fill the tremendous gaps in palaeoclimatic data spanning the last 5.4 Myr across the entirety of the Pleistocene and the Pliocene. A detailed understanding of these periods is important

to gain a better understanding of how past climates affected biodiversity patterns and processes (Prates et al., 2016).

Oscillayers takes benthic stable oxygen isotope ratios from deep ocean cores, an established proxy for global palaeoclimate change (δ^{18} O; Hansen, Sato, Russell, & Kharecha, 2013). These are then transformed to high-resolution spatial predictions of a broad range of temperature and precipitation climatic variables (commonly call 'bioclim' variables), based on the simulated anomalies between surface air temperatures of the Last Glacial Maximum (LGM) and the pre-industrial period. In palaeoclimatology, δ^{18} O is a measure of the ratio of the stable isotopes oxygen-18 and oxygen-16 and is frequently sampled from sediment cores to provide a proxy for deep water temperatures through time, where deeper core samples characterize older periods (Hansen et al., 2013).

Before the methods of Oscillayers, all widely available global palaeoclimate reconstructions were based on climate models called general circulation models (GCMs). These models couple oceanic and atmospheric processes with high fidelity in three dimensions, with spatially resolved surface boundary conditions and numerous parameters reflective of the period of interest, commonly called climate forcings. These forcing factors characterize the amount of energy that Earth's biomes receive from the sun (i.e., the eccentricity of the Earth's orbit and its axis of rotation) and how much energy is radiated back into space (e.g., the atmospheric composition: changes in CO_2 , CH_3 and N_2O). General circulation models have been widely used in predicting future and past climates (Haywood et al., 2013; Haywood & Valdes, 2004; Kirtman et al., 2013; Kutzbach, 1985; Singarayer & Valdes, 2010; Sloan & Rea, 1996).

Oscillayers is a hybrid method that merges the continuous palaeoclimatic temperature measurements from $\delta^{18}\text{O}$ with GCM-based palaeoclimatic reconstructions of the LGM (c. 21 kya), which is extrapolated across 539 periods during the last 5.4 Ma. In this study, we critically evaluate the approach of Oscillayers and test the utility of this method to produce palaeoclimatic reconstructions that are similar to GCM-based estimates that have been set up to simulate past climates with appropriate forcing mechanisms. We first show that the theoretical foundations of Oscillayers are severely limited, because: (a) it does not allow climate to vary spatio-temporally; and (b) it cannot incorporate important changes in palaeoclimatic forcing mechanisms, such as orbital forcing changes in palaeogeography. We also demonstrate several methodological errors that impeded the utility of generated bioclimatic variables, for example, a strict positive linear relationship is invoked between temperature and precipitation. Critically, these theoretical and methodological limitations prevent Oscillayers from characterizing meaningful temperature and precipitation reconstructions of palaeoclimatic periods outside the last glacial cycle, and thereby limit its use in scientific studies.

2 | THEORETICAL ISSUES

2.1 | Oscillayers does not allow different forcing mechanisms and spatio-temporal variation in climates

The core spatial relationship of Oscillayers was generated by calculating the difference between the corresponding temperature layers in a "current" and an LGM (21 kya) dataset (called a "delta layer"). Then the relative change measured in benthic stable oxygen isotope ratios (δ^{18} O) is multiplied by the delta layer to scale climate change for each of the 539 time periods. Given that the calculations are based upon a single delta layer, individual pixels cannot vary independently across time periods. For example, imagine three values in our delta layer are: a = 0.1, b = 1 and c = 10. In all 539 time periods, the value in pixel "a" will always be 1/20 of pixel "b" and 1/2100 of pixel "c". Therefore, across every period in Oscillayers, the spatial relationships in temperature and precipitation covary across time in the exactly the same way and entrench all palaeoclimates to the pattern of climate change observed between the LGM and current climates. As shown in Figure 1, there has been incredible spatio-temporal

variation in temperature and precipitation during the period spanning LGM to modern times. Thus, the assumption that LGM-current climate anomalies are representative across Plio-Pleistocene climates is inaccurate, and not even consistent during the most recent glacial cycle (Figure 1; Fordham et al., 2017).

These issues became further conflated as estimates are extended deeper into the past, when the forcing values were very different. North American and European Ice sheets are one of the most important forcing mechanisms of LGM climates (Liu et al., 2009, 2012), but their influence varies considerably throughout the glacial cycles in the Pleistocene and is largely absent in the warmer Pliocene. Other forcing factors that resulted in major climate change in the Plio-Pleistocene include Milankovitch cycles/orbital forcing (Yin & Berger, 2012), glacial meltwater (Tarasov & Peltier, 2005), changes in vegetation (Foley, Kutzbach, Coe, & Levis, 1994), changes in the Antarctic ice sheet (Hill, Bolton, & Haywood, 2017). glacial erosion (Hill, 2015), mountain uplift (Ruddiman, 1997) and changes in ocean gateways (Lunt, Valdes, Haywood, & Rutt, 2008; Otto-Bleisner et al., 2016). All these forcing mechanisms are important over Plio-Pleistocene time-scales and would result in distinctly different spatio-temporal signals that are not incorporated into the Oscillayers reconstructions. To incorporate these changes fully and map the influence of these factors on the different climatological variables, a fully coupled ocean-atmosphere GCM is required.

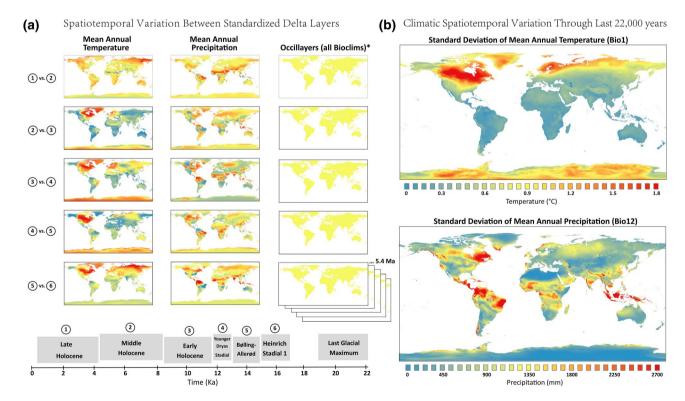


FIGURE 1 Spatio-temporal variation of palaeoclimates in periods between the Last Glacial Maximum (LGM) and the pre-industrial era. (a) Variation of standardized delta surfaces between general circulation models (GCMs) of palaeoclimates and the methods of Oscillayers. *Note that Oscillayers did not provide climate reconstructions for periods in the last 20 kyr, but these values were derived using the methods of Oscillayers to illustrate the difference in mean annual temperature and precipitation derived from the Oscillayers versus GCM modelling approaches. (b) Spatial variation in mean annual temperature and precipitation since the LGM [Colour figure can be viewed at wileyonlinelibrary.com]

3 | METHODOLOGICAL ISSUES

3.1 | Constraints associated with the scaling values

3.1.1 | Assumption of a uniform, positive linear relationship between temperature and precipitation

The Oscillayers method uses a single scaling factor to adjust palaeoclimates across time periods that is derived from $\delta^{18}O$, which provides an estimate of bottom water temperature. The use of a single scaling factor per time period assumes that precipitation scales directly in a positive linear manner with temperature. For example, if a scaling factor of 1.5 is implemented, this would increase both precipitation and temperature values in their delta layers by 1.5 times. The final climate reconstruction would be generated by summing the rescaled delta layer and the corresponding LGM bioclim layer. Even over short time periods, the observed relationship between temperature and precipitation does not follow a simple linear relationship, and the true relationships are much more nuanced (Hutchinson, Booth, McMahon, & Nix, 1984; Madden & Williams, 1978; Trenberth & Shea, 2005). For example, in many cases, as areas increase in temperature, they often become drier, not wetter (Trenberth & Shea, 2005). Furthermore, as shown in Figure 1, areas with the highest temperature variation since the LGM do not correspond to areas that have the highest variation in precipitation. Thus, a simple scaling of the delta layers based on relative changes in temperature could not account for the observed precipitation dynamics. If they covaried perfectly, we would expect the maps depicting variation of these layers to be visually similar, which was not observed (Figure 1). An alternative to the scaling factor method used in Oscillayers is to use a GCM-based method that allows relationships between temperature and precipitation to covary across space and time at separate rates.

The use of a single scaling factor also dramatically oversimplifies climatic processes across space. As such, it is not possible to characterize global climate change patterns accurately with a single scaling value. Speleothem, fossil pollen and benthic isotope studies broadly support this (Colinvaux, De Oliveira, & Bush, 2000; Colinvaux, De Oliveira, Moreno, Miller, & Bush, 1996; Duplessy et al., 1988; Wang et al., 2004; Zachos, Quinn, & Salamy, 1996). This comment is not meant to disparage the global averages of Hansen et al. (2013), but rather to reaffirm that they were not intended to provide a precise value representative across all terrestrial ecosystems.

3.1.2 | Areas with little change between the LGM and present time are unable to change in any of the palaeoclimatic reconstructions

A second concern relates to the extent by which areas with limited differences between the current and LGM climates can change in palaeoclimate reconstructions. If there is little difference in values between these periods, the corresponding value in the delta layer will be small or zero. Given that the scaling value is multiplied by the

delta layer to affect climate changes in each reconstruction, when delta layers are small or zero, the resulting difference will always be a small value or zero, regardless of the corresponding scaling value. In contrast, areas with large climatic differences between current times and the LGM are able to change considerably in the Occillayers palaeo-reconstructions. Using the methods of Oscillayers, areas of the eastern Sahara Desert [where the Occillayers mean annual precipitation (Bio12) delta layer and corresponding LGM layers are mostly zero for the region], for instance, will never possess amounts of rainfall above zero for many months, despite the fact we know this is historically inaccurate (Tierney, Pausata, & deMenocal, 2017).

3.1.3 | Methodological errors in scaling of bioclim layers

Rather than recalculating bioclimates from monthly temperature and precipitation data, the methods of Oscillayers scale the delta layer and add it to a corresponding LGM bioclim layer. For many of the bioclim layers, the applied scaling of the delta layer is problematic (Bio8-Bio11 and Bio16-Bio19) because these layers are based on joint relationships between monthly temperature and monthly precipitation values. For example, Bio8 (mean temperature of the wettest quarter) is calculated in two steps: first, the wettest quarter is calculated based on monthly precipitation values and, second, the mean temperature of that period is calculated. Given that monthly temperature and precipitation values were not scaled in the methods of Oscillayers (rather, the derived bioclimate layer was scaled), it is possible that the real bioclim value (if calculated from monthly data) represents an entirely different month, particularly in periods when changes in forcing have a strong effect on seasonality (e.g., from different orbital parameters). Lastly, the scaling of bioclimate layers that represent ranges (mean diurnal range = Bio2 and isothermality = Bio3) is not climatologically realistic. There is limited evidence to support that diurnal range should increase as mean global temperatures increase (Hansen, Sato, & Ruedy, 1995; Lewis & Karoly, 2013; Sun et al., 2019), but rather the opposite, and warming is associated with much larger increases in minimum temperature than in maximum temperature (Easterling et al., 1997; Jhajharia & Singh, 2011; Karl et al., 1993; Vose, Easterling, & Gleason, 2005).

3.1.4 | Some areas always get colder, whereas others always get warmer

The last methodological constraint relates to how the methods of Oscillayers dictate changes in climate. Again, given that a single delta layer is used per bioclimate layer, the sign of the delta layer fixes the palaeoclimatic response relative to the climates of the LGM. If the sign of a pixel is positive in the delta layer, the resulting climate reconstruction will always be positive and will increase when compared with the LGM palaeoclimates. In contrast, if the sign of a pixel is negative in the delta layer, the resulting climatic reconstruction

will always be lower when compared with the LGM palaeoclimates. For example, in a scenario where two values in our delta layer for annual mean temperature (Bio1) are a = -2 and b = 2, a scaling value of two would change the values to a = -4 and b = 4. These scaled values would then be added to the corresponding LGM values, here $a = 24^{\circ}\text{C}$ and $b = 24^{\circ}\text{C}$, and result in reconstructed palaeoclimate values of $a = 20^{\circ}\text{C}$ and $b = 28^{\circ}\text{C}$. Given that all scaling values are positive values, the values of pixel "a" will always decrease and "b" will always increase relative to LGM mean annual temperatures.

Although we discuss this limitation in the context of Bio1, this affects the other 18 bioclimatic variables equally.

4 | EVALUATION OF OSCILLAYERS DATASETS

To evaluate the predictive ability of the Oscillayers reconstructions, we compared the results with downscaled GCMs for the four periods

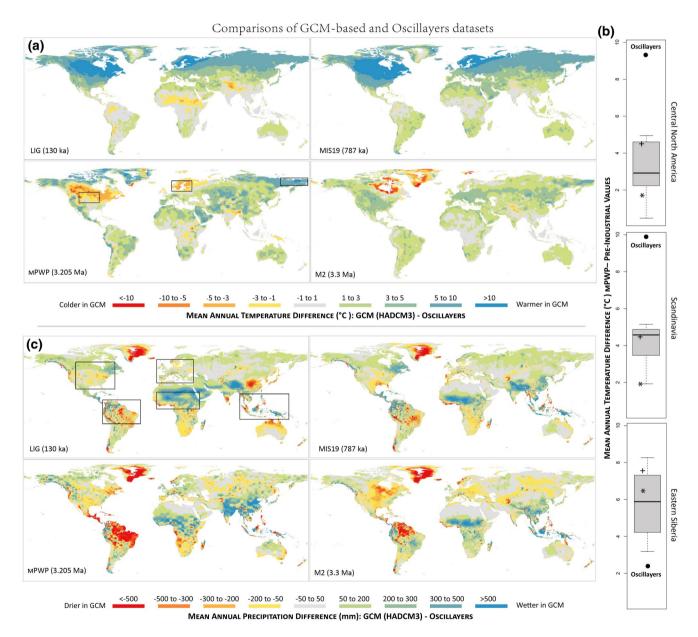


FIGURE 2 Differences between general circulation model (GCM)-based and Oscillayers climate reconstructions. (a) Comparisons of mean annual temperature values between Oscillayers climate reconstructions and downscaled HadCM3 models for four time periods. (b) Comparisons of the Oscillayers values with eight GCMs demonstrate that in several regions (black boxes in panel a), the Oscillayers differ significantly from all GCM-based values. In central North America and Scandinavia, the Oscillayers means were considered extreme outliers when compared with all GCM-based values. + and * depict the mean value HadCM3 and CCSM values, respectively (a CCSM simulation was used to create Oscillayers; HadCM3 simulations were the basis for many of the GCM-based comparisons in the paper). (c) Mean annual precipitation. Note that black boxes depict extent of regional comparisons across all time periods (Tables 2 and 3) [Colour figure can be viewed at wileyonlinelibrary.com]

by Hill (2015). Here we limit our comparisons to only Bio1 (mean annual temperature) and Bio 12 (mean annual precipitation), because both variables should be least affected by the previously mentioned errors in scaling of the bioclims and because they represent the least derived

variables and should perform the best under the methods of Oscillayers.

We performed our analysis at global and regional extents. The regional datasets were chosen to evaluate how the Oscillayers methods perform in areas of known palaeotopographical change or affected areas relative to current/LGM climates (e.g., the central and eastern USA and Europe). We focused on five regions that currently represent: the Amazon basin (82° W, 17° N; -35° W, 20° S), Europe (14° W, 63° N; -35° E, 35° N), the Island of New Guinea (93° E, 20° N; -150° E, 11° S), northern Sub-Saharan Africa (14° W, 20° N; -43° E, 0° N) and the central and eastern USA (118° W, 60° N; 67° W, 26° N). For all comparisons, we performed spatial t-tests to compare simulation means using the methods of Dutilleul, Clifford, Richardson, & Hemond (1993) to correct the degrees of freedom by spatial autocorrelation in the datasets. The t-tests were performed at 10 arc-min (c. 20 km) resolution. The Oscillayers datasets were resampled using SDMtoobox v.2.4 (Brown, Bennett, & French, 2017) using the "Advance Upscale" tool and the "mean" aggregation parameter. Correlations and significance were assessed using the modified.t.test function in the R package "SpatialPack" (Osorio & Vallejos, 2019).

To determine whether the Oscillayer values were comparable to those from GCMs, we calculated the quantiles for the mean values of eight GCMs (CCSM4 (Climate Community System Model), COSMOS

spanning the Pliocene and Pleistocene: the Last Interglacial (*c.* 130 ka), Marine Isotope Stage 19 (MIS19; *c.* 787 ka), the mid-Pliocene Warm Period (mPWP; *c.* 3.205 Ma) and Marine Isotope Stage M2 (MIS M2; *c.* 3.3 Ma). These layers were downloaded from www.paleoclim.org (Brown et al., 2018). The mPWP GCM data were compared with the ensemble of 3.21 and 3.20 Ma Oscillayers palaeoclimatic reconstructions, which represented the two periods that matched the forcing values used

TABLE 1 Global results

Bio1		Pixels shared with similar values (%)			
Time	Pearson's R ²	±1°C	±3°C	±5°C	
130 ka	.966	23.3	50.2	64.8	
787 ka	.960	13.5	42.5	61.1	
3.2 Ma	.956	19.6	58.7	85.1	
3.3 Ma	.893	23.6	74.9	96.5	
Mean	.944	20.0	56.6	76.9	
		Pixels shared with similar values (%)			
Bio12		Pixels shar	red with similar	values (%)	
Bio12 Time	Pearson's R ²	Pixels share ±5 cm	red with similar ———— ±20 cm	values (%) ±30 cm	
	Pearson's R ²				
Time		±5 cm	±20 cm	±30 cm	
Time 130 ka	.882	±5 cm 27.4	±20 cm	±30 cm	
Time 130 ka 787 ka	.882	±5 cm 27.4 32.0	±20 cm 74.7 78.8	±30 cm 85.2 87.3	

TABLE 2 Regional results for mean annual temperature (Bio1)

Bio1	1		Pixels shared with similar values (%)		
Time	Extent	Pearson's R ²	±1°C	±3°C	±5°C
130 ka	Amazon	.941	62.0	99.1	99.9
	Europe	.887	.6	23.4	61.1
	Island of New Guinea	.949	85.8	100.0	100.0
	North Sub-Saharan Africa	.828	44.4	96.0	100.0
	USA	.966	.8	5.5	26.6
787 ka	Amazon	.939	38.0	94.4	99.8
	Europe	.884	.0	9.3	47.1
	Island of New Guinea	.943	29.6	99.2	100.0
	North Sub-Saharan Africa	.882	61.9	98.3	99.9
	USA	.962	.5	2.2	9.4
3.2 Ma	Amazon	.839	17.4	66.6	94.0
	Europe	.618	30.0	75.7	96.6
	Island of New Guinea	.810	57.0	95.5	99.3
	North Sub-Saharan Africa	.783	52.6	94.1	99.8
	USA	.889	21.6	56.3	93.5
3.3 Ma	Amazon	.949	20.4	88.8	99.9
	Europe	.903	7.0	42.1	98.0
	Island of New Guinea	.937	81.7	100.0	100.0
	North Sub-Saharan Africa	.880	57.3	96.6	100.0
	USA	.916	13.6	45.8	91.7

(Community Earth System Models), GISS-E2-R (Goddard Institute for Space Science), HadCM3 (Hadley Centre Coupled Model version 3), IPSLCM5A (Institut Pierre-Simon Laplace), MIROC4m (Model for Interdisciplinary Research on Climate), MRI-CGCM 2.3 (Meteorological Research Institute) and NorESM-L (Bjerknes Centre for Climate Research) in the Pliocene Model Intercomparison Project (PlioMIP; Haywood et al., 2016) and the Oscillayers dataset across three key regions: central North America (110° W, 50° N; -85° W, 35° N), Scandinavia (4° E, 72° N; -40° E, 51° N) and Eastern Siberia (130° E, 70° N; -180° E, 60° N). Pre-industrial values for Oscillayers datasets were generated using a Community Climate System Model 4-based estimate (Fordham et al., 2017; the same GCM used by Gamish, 2019). These were regions with the highest differences in values between the Oscillayers and HadCM3-based climates (the GCM used for all previous comparisons; Figure 2, mPWP). For each region, the inter-quartile range (IOR) of each GCM mean was measured. Values that exceeded 1.5 and 3 times the IQR added to the third quartile and subtracted from the first quartile were considered major and extreme outliers, respectively, thus they were data points that differed significantly from the other values.

4.1 | Results

In agreement with Gamish (2019), we found moderate to high levels of correlation between the Oscillayers and the corresponding GCM-based

climatologies (Tables 1-3). However, upon deeper inspection, for every period compared, most of the corresponding climate values were notably different between the two methods. The means of the Oscillayers and GCM-based palaeoclimates were significantly different in every statistical comparison (p < .001, F = 23.37-12,111, d.f. = 5.45-667.69; both "global" and "regional"). On average, only 20.0% of values in the mean annual temperature (Bio1) datasets across the Pliocene and Pleistocene were within ±1°C when comparing the corresponding GCM-based and Oscillayers datasets (Table 1). Furthermore, 56.6% of annual temperature values were within ±3°C. Thus, across all the time periods evaluated, we observed that 43.4% of the temperature values differed by > 3°C when comparing datasets from both methods. Likewise, 30.8 and 75.3% of values in the mean annual precipitation (Bio12) datasets across the Pliocene and Pleistocene were within ±50 or ±200 mm (respectively) of rainfall when comparing the GCM-based and Oscillavers datasets (Table 1). Across all the time periods evaluated, we observed that 24.7% of the precipitation values differed by > 200 mm when comparing the two methods.

The regional datasets suggested that the methods of Oscillayers generally performed better at reconstructing the mean annual temperature (Bio1) in tropical areas (versus temperate), but this also was not unilateral (e.g., for the Amazon during the mPWP and MIS M2 and for the island of New Guinea during M19, there existed large differences between the GCM-based and Oscillayers datasets). This relationship flipped in the mean annual precipitation datasets, with temperate regions performing better and tropical regions possessing larger

TABLE 3 Regional results for mean annual precipitation (Bio12)

Bio12			Pixels shared with similar values (%)		
Time	Extent	Pearson's R ²	±5 cm	±20 cm	±30 cm
130 ka	Amazon	.882	15.6	57.2	75.1
	Europe	.814	41.6	90.2	95.7
	Island of New Guinea	.734	10.4	39.1	54.0
	North Sub-Saharan Africa	.891	10.0	39.4	61.9
	USA	.863	28.6	86.8	96.7
787 ka	Amazon	.870	14.3	52.7	71.0
	Europe	.805	44.2	90.3	95.8
	Island of New Guinea	.659	8.5	32.8	45.7
	North Sub-Saharan Africa	.869	10.2	46.3	63.9
	USA	.810	28.8	81.2	92.7
3.2 Ma	Amazon	.766	5.8	23.5	34.9
	Europe	.717	18.0	72.3	89.4
	Island of New Guinea	.677	7.7	29.4	42.2
	North Sub-Saharan Africa	.914	7.1	39.0	60.7
	USA	.852	28.6	85.2	96.0
3.3 Ma	Amazon	.801	23.3	46.3	61.0
	Europe	.819	28.6	88.5	95.4
	Island of New Guinea	.728	8.0	30.3	43.3
	North Sub-Saharan Africa	.893	18.7	52.6	67.5
	USA	.891	19.6	71.7	94.3

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differences (e.g., in the northern Sub-Saharan Africa and the Island of New Guinea). Thus, despite being highly correlated, the Oscillayers reconstructions did not reflect similar values when compared with GCM-based methods. Furthermore, high correlations do not necessarily mean that the corresponding values were similar, but instead that the relationships between the two datasets covaried in a similar manner.

4.2 | Discussion

Comparisons of the Oscillayers values with other GCMs demonstrated that in several regions, the Oscillayers results differed significantly from all GCM-based values. In central North America and Scandinavia, the Oscillayers means were considered as extreme outliers when compared with all other GCM-based values. Given a lack of GCMs for a majority of the Oscillayers datasets, it is not possible to make similar comparisons for other time periods; however, it is unlikely that these results are an anomaly. These results demonstrate the dangers of using correlation coefficients and absolute differences as the primary basis for evaluating model performance, which can lead to a false sense of high predictive performance. Overall, we conclude that the generated palaeo-bioclim layers of Oscillayers show poor agreement with independent GCMs. Hence, the Oscillayers approach does not provide a sufficiently robust approximation of palaeoclimate conditions throughout the Plio-Pleistocene. Thus, when used for scientific analyses, results should be interpreted carefully, in light of the many limitations, particularly for periods before the LGM.

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REFERENCES

- Brown, J. L., Bennett, J. R., & French, C. M. (2017). SDMtoolbox 2.0: The next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ*, 5, e4095.
- Brown, J. L., Hill, D. J., Dolan, A. M., Carnaval, A. C., & Haywood, A. M. (2018). PaleoClim, high spatial resolution paleoclimate surfaces for global land areas. *Scientific Data*, *5*, 180254.

- Colinvaux, P. A., De Oliveira, P. E., & Bush, M. B. (2000). Amazonian and neotropical plant communities on glacial time-scales: the failure of the aridity and refuge hypotheses. *Quaternary Science Reviews*, 19, 141–169.
- Colinvaux, P. A., De Oliveira, P. E., Moreno, J. E., Miller, M. C., & Bush, M. B. (1996). A long pollen record from lowland Amazonia: Forest and cooling in glacial times. *Science*, 274(5284), 85–88.
- Duplessy, J. C., Shackleton, N. J., Fairbanks, R. G., Labeyrie, L., Oppo, D., & Kallel, N. (1988). Deepwater source variations during the last climatic cycle and their impact on the global deepwater circulation. *Paleoceanography*, 3, 343–360.
- Dutilleul, P., Clifford, P., Richardson, S., & Hemon, D. (1993). Modifying the t test for assessing the correlation between two spatial processes. *Biometrics*, 305–314.
- Easterling, D. R., Horton, B., Jones, P. D., Peterson, T. C., Karl, T. R., Parker, D. E., ... Folland, C. K. (1997). Maximum and minimum temperature trends for the globe. *Science*, *277*(5324), 364–367.
- Foley, J. A., Kutzbach, J. E., Coe, M. T., & Levis, S. (1994). Feedbacks between climate and boreal forests during the Holocene epoch. *Nature*, 371, 52–54.
- Fordham, D. A., Saltré, F., Haythorne, S., Wigley, T. M., Otto-Bliesner, B. L., Chan, K. C., & Brook, B. W. (2017). PaleoView: A tool for generating continuous climate projections spanning the last 21 000 years at regional and global scales. *Ecography*, 40, 1348–1358.
- Gamisch, A. (2019). Oscillayers: A dataset for the study of climatic oscillations over Plio-Pleistocene time-scales at high spatial-temporal resolution. *Global Ecology and Biogeography*, 2019, 1552–1560.
- Hansen, J., Sato, M., & Ruedy, R. (1995). Long-term changes of the diurnal temperature cycle: Implications about mechanisms of global climate change. *Atmospheric Research*, 37, 175–209.
- Hansen, J., Sato, M., Russell, G., & Kharecha, P. (2013). Climate sensitivity, sea level and atmospheric carbon dioxide. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 371(2001), 20120294.
- Haywood, A. M., Dowsett, H. J., Dolan, A. M., Rowley, D., Abe-Ouchi, A., Otto-Bliesner, B., ... Salzmann, U. (2016). The Pliocene model intercomparison project (PlioMIP) phase 2: Scientific objectives and experimental design. Climate of the Past, 12, 663–675.
- Haywood, A. M., Hill, D. J., Dolan, A. M., Otto-Bliesner, B. L., Bragg, F., Chan, W.-L., ... Zhang, Z. (2013). Large-scale features of Pliocene climate: Results from the Pliocene Model Intercomparison Project. Climate of the Past, 9, 191–209.
- Haywood, A. M., & Valdes, P. J. (2004). Modelling Pliocene warmth: Contribution of atmosphere, oceans and cryosphere. Earth and Planetary Science Letters, 218, 363–377.
- Hill, D. J. (2015). The non-analogue nature of Pliocene temperature gradients. *Earth and Planetary Science Letters*, 425, 232–241.
- Hill, D. J., Bolton, K. P., & Haywood, A. M. (2017). Modelled ocean changes at the Plio-Pleistocene transition driven by Antarctic ice sheet advance. *Nature Communications*, 8, 14376.
- Hutchinson, M. F., Booth, T. H., McMahon, J. P., & Nix, H. A. (1984). Estimating monthly mean values of daily total solar radiation for Australia. Solar Energy, 32, 277–290.
- Jhajharia, D., & Singh, V. P. (2011). Trends in temperature, diurnal temperature range and sunshine duration in Northeast India. *International Journal of Climatology*, 31, 1353–1367.
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. Scientific Data, 4, 170122.
- Karl, T. R., Jones, P. D., Knight, R. W., Kukla, G., Plummer, N., Razuvayev, V., ... Peterson, T. C. (1993). A new perspective on recent global warming: Asymmetric trends of daily maximum and minimum temperature. Bulletin of the American Meteorological Society, 74, 1007–1024.
- Kirtman, B., Power, S. B., Adedoyin, J. A., Boer, G. J., Bojariu, R., Camilloni, I., ... Wang, H. J. (2013). Near-term climate change: Projections and predictability. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, ... P. M. Midgley (Eds.), Climate

- change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (pp. 953–1028). Cambridge, UK: Cambridge University Press.
- Kutzbach, J. E. (1985). Modeling of paleoclimates. *Advances in Geophysics*, 28, 159–196.
- Lewis, S. C., & Karoly, D. J. (2013). Evaluation of historical diurnal temperature range trends in CMIP5 models. *Journal of Climate*, 26, 9077–9089.
- Lima-Ribeiro, M. S., Varela, S., González-Hernández, J., de Oliveira, G., Diniz-Filho, J. A. F., & Terribile, L. C. (2015). EcoClimate: A database of climate data from multiple models for past, present, and future for macroecologists and biogeographers. *Biodiversity Informatics*, 10, 1–21
- Liu, Z., Carlson, A. E., He, F., Brady, E. C., Otto-Bliesner, B. L., Briegleb, B. P., ... Zhu, J. (2012). Younger Dryas cooling and the Greenland climate response to CO₂. Proceedings of the National Academy of Sciences USA, 109, 11101–11104.
- Liu, Z., Otto-Bliesner, B. L., He, F., Brady, E. C., Tomas, R., Clark, P. U., ... Cheng, J. (2009). Transient simulation of last deglaciation with a new mechanism for Bølling-Allerød warming. *Science*, 325(5938), 310–314.
- Lunt, D. J., Valdes, P. J., Haywood, A., & Rutt, I. C. (2008). Closure of the Panama Seaway during the Pliocene: Implications for climate and Northern Hemisphere glaciation. *Climate Dynamics*, 30, 1–18.
- Madden, R. A., & Williams, J. (1978). The correlation between temperature and precipitation in the United States and Europe. *Monthly Weather Review*, 106, 142–147.
- Osorio, F., & Vallejos, R. (2019). Tools for assessing the association between two spatial processes. R package version 0.3-8. http://spatialpack.mat.utfsm.cl
- Otto-Bliesner, B. L., Jahn, A., Feng, R., Brady, E. C., Hu, A., & Löfverström, M. (2016). Amplified North Atlantic warming in the late Pliocene by changes in Arctic gateways. Geophysical Research Letters, 44, 957-964.

- Prates, I., Xue, A. T., Brown, J. L., Alvarado-Serrano, D. F., Rodrigues, M. T., Hickerson, M. J., & Carnaval, A. C. (2016). Inferring responses to climate dynamics from historical demography in neotropical forest lizards. Proceedings of the National Academy of Sciences USA, 113, 7978–7985.
- Ruddiman, W. F. (1997). Tectonic uplift and climate change. New York, NY: Plenum Press.
- Singarayer, J. S., & Valdes, P. J. (2010). High-latitude climate sensitivity to ice-sheet forcing over the last 120 kyr. *Quaternary Science Reviews*, 29, 43–55.
- Sloan, L. C., & Rea, D. K. (1996). Atmospheric carbon dioxide and early Eocene climate: A general circulation modelling sensitivity study. Palaeogeography, Palaeoclimatology, Palaeoecology, 119, 275–292.
- Sun, X., Ren, G., You, Q., Ren, Y., Xu, W., Xue, X., ... Zhang, P. (2019). Global diurnal temperature range (DTR) changes since 1901. *Climate Dynamics*, 52, 3343–3356.
- Tarasov, L., & Peltier, W. R. (2005). Arctic freshwater forcing of the Younger Dryas cold reversal. *Nature*, 435, 662-665.
- Tierney, J. E., Pausata, F. S., & deMenocal, P. B. (2017). Rainfall regimes of the Green Sahara. *Science Advances*, *3*, e1601503.
- Trenberth, K. E., & Shea, D. J. (2005). Relationships between precipitation and surface temperature. *Geophysical Research Letters*, 32, L14703.
- Vose, R. S., Easterling, D. R., & Gleason, B. (2005). Maximum and minimum temperature trends for the globe: An update through 2004. *Geophysical Research Letters*, 32, L23822.
- Wang, X., Auler, A. S., Edwards, R. L., Cheng, H., Cristalli, P. S., Smart, P. L., ... Shen, C. C. (2004). Wet periods in northeastern Brazil over the past 210 kyr linked to distant climate anomalies. *Nature*, 432(7018), 740–743.
- Yin, Q. Z., & Berger, A. (2012). Individual contribution of insolation and ${\rm CO_2}$ to the interglacial climates of the past 800,000 years. *Climate Dynamics*, 38, 709–724.
- Zachos, J. C., Quinn, T. M., & Salamy, K. A. (1996). High-resolution (10⁴ years) deep-sea foraminiferal stable isotope records of the Eocene-Oligocene climate transition. *Paleoceanography and Paleoclimotology*, 11, 251–266.