

Final author comments

Both reviewers suggested some linguistic changes (technical comments), which will be done in the revised version.

Interactive referee comment, B. Tiffney (Biogeosciences Discuss., 10, C5573–C5577, 2013)

General Comments: By virtue of their static nature, plants have provided a tool for the estimation of past climates. The more closely related to living taxa, the greater the probability that “physiological uniformitarianism” may be assumed – that is, if the genetic controls of morphology are such that we can place the fossil in a living genus or perhaps even species, similarly we might assume a stable genetic control of physiology. This is the basis of the “nearest living relative” approach used by many paleobotanists to estimate Cenozoic climate. However, the nearest living relative process is a very generalized method of estimating paleoclimate. The current paper offers a continuing refinement of the nearest living relative approach by locating the nearest living relatives within their Köppen zones, permitting a more refined method of estimating the amount and annual distribution of moisture as well as annual temperature regime. The possibility that physiological uniformitarianism does not universally apply, and that some taxa may have evolved physiologically, but not morphologically, is countered by the use of a larger number of species, reducing any errors that might occur. The authors have provided their database (and linked with other data collections of a similar nature), pointing the way towards a global basis for a common methodology of estimating paleoclimates, at least within the Cenozoic where extant genera and, as one approaches the present day, species may be found in the fossil record. This is a deeply appreciated contribution to our common endeavor.

Response: We agree.

Specific Comments

[1] The title is slightly misleading, as in fact there is not extensive discussion of the heat transport via the Gulf Stream within the body of the paper. However, the data presented make the impact of the Gulf Stream clear. Perhaps an alternative might be to invert the title to read “Evidence from “Köppen signatures” of fossil plant assemblages for effective heat transport of Gulf Stream to subarctic North Atlantic during Miocene cooling”.

Response: The title will be changed as suggested.

[2] A figure comparing the decline in global temperatures in the Northern Hemisphere against those observed in Iceland would reinforce the unique aspects of the climatic changes of the last 15 Ma in the N. Atlantic.

Response: We will incorporate the Zachos et al. (2001) curve in our Figure 5 to the left of the current graph.

[3] You might specifically note that the use of this approach, as detailed as it is, still assumes that plant genera and particularly species exhibit “physiological uniformitarianism. That is, within a taxon, the climatic affinities remain fairly stable over time, and if they change, are reflected in some way in their morphology, prompting the erecting of a new species or genus.

Response: Our approach starts from the assumption of physiological uniformitarianism (Tiffney, 2008), but it is not restricted to it. If evidence is available that climatic affinities changed during time without (dramatic) morphological adaptations, the Köppen signature can be accordingly adjusted. This is not an issue for the here used Icelandic floras, but would be the case e.g. for Miocene floras of Turkey (work in progress). Two fossil *Quercus* species are abundant (*Q. drymeja*, *Q. mediterranea*), which resemble the modern Mediterranean sclerophyllous *Q. ilex* (Csa, rarely Cfa) and *Q. coccifera* (exclusively Csa) of *Quercus* Group Ilex, and have traditionally been associated with these modern taxa. However, phylogenetic studies of modern species of *Quercus* (Denk and Grimm, 2010; Simeone et al., 2013) demonstrate that most taxa of *Quercus* Group Ilex at present times are not Csa-taxa, but typically found in Cwa and Cfa climates (into Cwb; southern foothills of the Himalayas into China; Grimm and Denk, 2012). Moreover, some of these species show leaf morphotypes virtually identical to both the fossil western Eurasian *and* the modern Mediterranean species (Denk and Velitzelos, in submission). The adaptation of *Q. coccifera* and *Q. ilex* to the Csa climate (probably within the last 2–3 Ma) was not accompanied by marked morphological change. Hence, *Q. drymeja* and *Q. mediterranea* would NOT be scored as Csa, Cfa, (Cwa, Cwb) but only as Cfa, Cwa, Cwb.

Another example from Turkey is a recently described dragon tree species (*Dracaena tayfunii*, Denk et al., 2013). The fossil is virtually indistinguishable from the modern Macaronesian species *D. draco* (Csa, BSh, BWh climates) based on leaf arrangement, leaf morphology and epidermal features (and possibly infructescence axis). The associated plant assemblage as well as the depositional environment exclude any arid, or summer dry climate. Instead, a monsoon-influenced or fully humid subtropical climate is indicated (Cfa, Cwa; Denk et al., 2013; see also Güner and Denk, 2012). Hence, one would code Miocene fossil dragon trees with affinity to the *D. draco* lineage as Cfa, Cwa and not as Csa, BSh, BWh.

In conclusion, physiological uniformitarianism can be the basis for establishing Köppen signatures for many but not all fossil taxa. Köppen signatures for fossil taxa will also depend on phylogenetic uniformitarianism as expressed in the two examples. We will add an according paragraph in the revised Material or Discussion section.

Interactive referee comment, S. Manchester (Biogeosciences Discuss., 10, C5582–C5582, 2013)

p. 13565, l. 10ff “The timing of the MMCO coincided with the opening of the North Atlantic–Arctic gateway (Jakobsson et al., 2007)...”

Reviewer’s question: Do you mean MMCT? Opening of this gateway and steeper gradient does not seem to explain the optimum (warmest) interval.

Response: MMCO is correct. The ventilation of the Arctic Ocean contributed to a steeper thermal gradient already during the Mid Miocene Climatic Optimum. The thermal gradient and differences in salinity among others were the prerequisites for the establishment of the thermohaline circulation.

p. 13578, l. 24ff “Nevertheless, based on association evidence, beech trees formed part of humid, warm-temperate forests typically found in modern Cfa and Cfb climates and mixed broadleaved-deciduous and conifer forests, today typically thriving under Dfb climates. Hence, scoring a *Fagus* fossil as Cfa, Cfb, and Dfb appears to be justified.”

Reviewer's comment: Or if a coexistence approach were used, the same argument could be used to reject that taxon in favor of others in the flora; those thought to be more representative (in both cases an adjustment is made based on careful evaluation of the unfiltered results).

Response: Such a filtering has occasionally been done in papers using nearest-living relatives to infer palaeoclimate. However, this has not been done in any paper using the coexistence approach (to our knowledge). The reason may be that such a filtering usually would result in (very) broad co-existence intervals. An example can be found in the Electronic Supplement to Grimm & Denk (2012, ES 9). Based on a wrong association between a fossil (*Populus*) and a (sub)arctic nearest-living relative taxon (NLR), an artificially narrow MAT interval was reconstructed for a plant assemblage otherwise dominated by warm temperate (subtropical) taxa. Based on association evidence, one could have recognised the wrong NLR association (the arctic *Populus*), and excluded this NLR taxon from the analysis. However, this would result in a broad unresolved coexistence interval (Grimm & Denk, 2012, ES 9).

References

- Denk, T. and Grimm, G. W.: The oaks of western Eurasia: traditional classifications and evidence from two nuclear markers, *Taxon*, 59, 351–366, 2010.
- Denk, T. and Velitzelos, D.: Review of the Cenozoic floras of Greece, submitted to *Rev. Palaeobot. Palynol.*
- Denk T., Güner H. T., and Grimm, G. W. From mesic to arid: Leaf epidermal features suggest preadaptation in Miocene dragon trees (*Dracaena*), *Rev. Palaeobot. Palynol.*, doi:10.1016/j.revpalbo.2013.09.009, 2013.
- Grimm, G. W. and Denk, T.: Reliability and resolution of the coexistence approach – a revalidation using modern-day data, *Rev. Palaeobot. Palynol.*, 172, 33–47, 2012.
- Güner T. H. and Denk, T. The genus *Mahonia* in the Miocene of Turkey: Taxonomy and biogeographic implications, *Rev. Palaeobot. Palynol.*, 175, 32–46, 2013.
- Simeone, M. C., Piredda, R., Papini, A., Vessella, F., and Schirone, B.: Application of plastid and nuclear markers to DNA barcoding of Euro-Mediterranean oaks (*Quercus*, Fagaceae): problems, prospects and phylogenetic implications, *Bot. J. Linn. Soc.*, 2013.
- Tiffney, B. H.: Phylogeography, fossils, and Northern Hemisphere biogeography: the role of physiological uniformitarianism, *Ann. Mo. Bot. Garden*, 95, 135–143, 2008.
- Zachos, J. C., Pagani, M., Sloan, L., Thomas, E., and Billups, K.: Trends, rhythms, and aberrations in global climate 65 Ma to present, *Science*, 292, 686–693, 2001.