# Neogene aridification of the Northern Hemisphere

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## ABSTRACT

Neogene cooling and aridification in the Northern Hemisphere have long been recognized, but there are no studies comparing patterns of aridity gradients or differences between North America and Eurasia. Large herbivorous mammals are an excellent source for understanding large-scale environmental and climatic patterns because their molar crown height (hypsodonty) reflects both habitat and precipitation. The temporal development of hypsodonty in the North American Great Plains is well studied, but both spatial detail and comparisons with patterns in Eurasia are lacking. Here we use a methodology based on community levels of hypsodonty to estimate precipitation during the Neogene (the past 23 Ma). We show that aridification was more profound and occurred ~5 Ma earlier in North America than in Eurasia. By combining our results with existing climate model output and new sensitivity experiments, we show how these changes were influenced by ocean heat transport and atmospheric circulation patterns. We further suggest that asymmetric dispersal of large mammals between Eurasia and North America was related to the contrasting humidity regimes between the continents.

## INTRODUCTION

The global climate was warm and humid in the early Cenozoic, but starting ca. 45 Ma, the climate became increasingly cooler in the higher latitudes. An early-middle Miocene warming phase resulted in the higher latitudes being warmer and more humid than today, but cooling in the later Miocene resulting in increasingly modern climatic regimes (Zachos et al., 2001). In previous studies (Fortelius et al., 2002; Eronen et al., 2010a) we demonstrated that community levels of hypsodonty (tooth crown height) in ungulates (hoofed mammals) correlate with patterns of precipitation in modern faunas, and used models based on hypsodonty levels in the mammalian paleofaunas to examine climatic changes over the Eurasian Neogene. Here we use this same methodology (see the Appendix for a detailed description) to estimate past precipitation levels in both Eurasia and North America. We discuss the possible processes responsible for changes in precipitation, and combine the hypsodonty models from the mammalian paleofaunas with results from climate models and new climate sensitivity experiments to present a possible scenario of Neogene climate evolution across the middle latitudes of the Northern Hemisphere.

## NORTHERN HEMISPHERE ARIDITY PATTERNS

According to our fossil mammal data, the Early Miocene climate was humid in both North America and Eurasia (Fig. 1A), with esti-mated precipitation (EP) of >1000 mm/yr in most areas. Europe showed little spatial variation, but in North America, lower values (EP of 500–700 mm/yr) were apparent at some western localities. Eurasia retained this humidity into the early Middle Miocene; North America showed more arid conditions at this time, but most areas had EPs of >800 mm/yr (Fig. 1B). Figure DR1 in the GSA Data Repository[1] shows similar patterns obtained with a slightly different metric, the mean hypsodonty pattern (MHP), and Figures DR2 and DR3 show both EP and MHP in high resolution.

A shift toward greater aridity occurred in North America in the late Middle Miocene (Fig. 1C). Western localities mainly had EPs of 500–700 mm/yr or less, although parts of the Great Plains and the eastern region of the continent were more mesic. Eurasian conditions remained constant, with humid conditions prevailing. During the early Late Miocene (Fig. 1D), arid conditions intensified and spread throughout North America. The spatial pattern changed from an east-west humidity gradient to a north-south one. Eastern Eurasia also became more arid at that time, while western Europe still remained humid, with an east-west aridity gradient. (For a more detailed analysis of Eurasia, see Fortelius et al., 2002; Eronen et al., 2010a).

The late Late Miocene EP (Fig. 1E) indicates even more arid conditions in North America. Eurasia became arid in the western part, but humid conditions returned in the east, possibly due to the establishment of the summer monsoon (Fortelius et al., 2002). The aridity pattern in western Eurasia changed to a north-south direction, possibly relating to changes in the storm track patterns (Eronen et al., 2009; Micheels et al., 2011).

During the Pliocene in North America the Great Plains remained dry, while the western coast was more humid than in the Miocene (Fig. 1F). The MHP values (Fig. DR1) indicate less severe conditions than previously. The pattern in western Eurasia was mixed, with a strong north-south gradient. In the central and eastern parts of Eurasia, conditions were more arid, but there was considerable spatial variation.

The EP values for Late Miocene of North America suggest extremely arid conditions, implying levels of primary productivity that might be considered too low to support the observed high diversity of ungulate species (Janis et al., 2004). However, the relationship between precipitation, primary productivity, and species richness is complex (e.g., Olff et al., 2002). The Great Plains of North America today is potentially suitable for high large herbivore species diversity (Olff et al., 2002), and it is likely that the current low diversity reflects the end-Pleistocene megafaunal extinctions (Koch and Barnosky, 2006).

## DISCUSSION AND CONCLUSIONS

### Climatic Processes Causing Increased Seasonality

Our results show distinct continent-wide gradients in the aridification patterns through the Neogene. In North America, drying occurred first in the southwest and Great Plains, while the development of a clear north-south gradient was not established until the early Late Miocene. In Eurasia, a north-south humidity gradient developed during the late Late Miocene, especially in the western part. We present a scenario of climate processes responsible for these phenomena, making use of published data on paleogeographic changes and climate model studies, and combining these with sensitivity experiments of our own.

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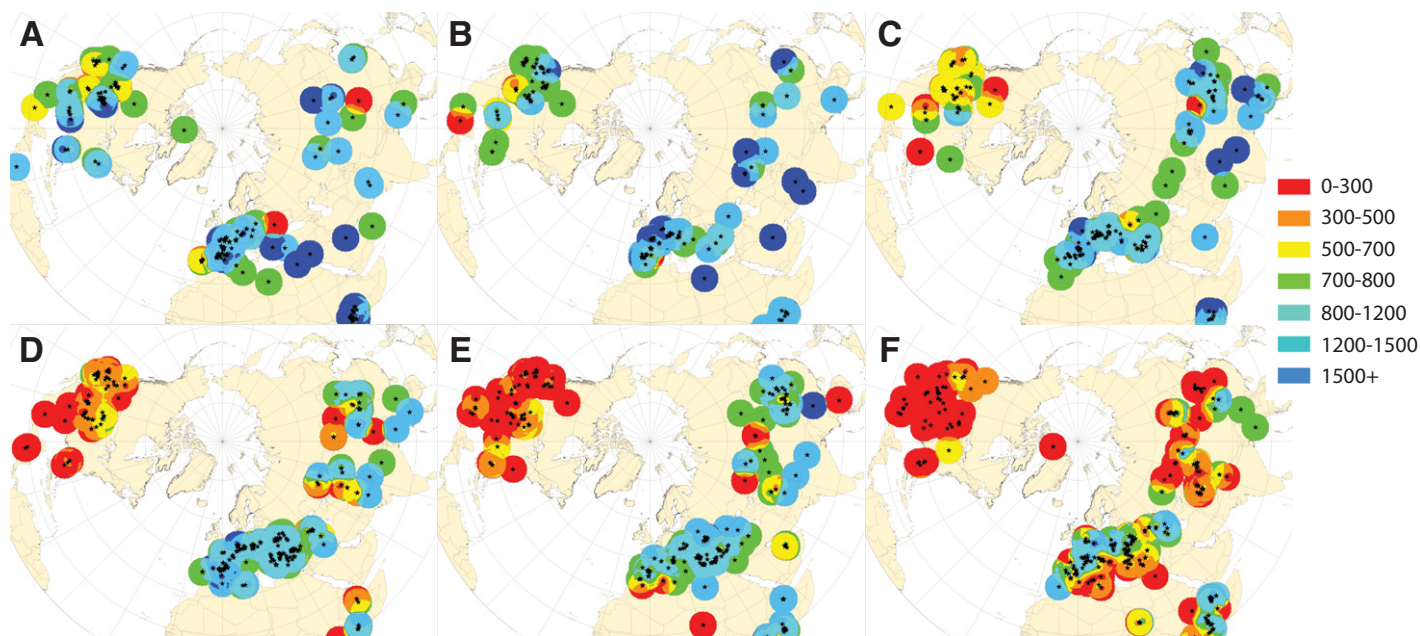
Figure 1. Estimated precipitation values (in mm/yr). A: Early Miocene (Eurasia—23–17 Ma; North America—23–17.5 Ma). B: Early Middle Miocene (Eurasia—17–15 Ma; North America—17.5–14.8 Ma). C: Late Middle Miocene (Eurasia—15–11.1 Ma; North America—14.8–12.1 Ma). D: Early Late Miocene (Eurasia—11.1–8 Ma; North America—12.1–7.6 Ma). E: Late Late Miocene (Eurasia—8–5.3 Ma; North America—7.6–4.9 Ma). F: Pliocene (Eurasia—5.3–1.8 Ma; North America—4.9–1.9 Ma).
Black stars indicate fossil localities.

The increasing aridity throughout the Miocene of North America, especially in the Great Plains, might be connected to the uplift history of the western part of the continent and to the ocean circulation of the Pacific Ocean. The traditional view (Ruddiman and Kutzbach, 1989) is that late Neogene uplift in the western part of the North American continent resulted in a rain-shadow effect from the Middle Miocene onward, but recent evidence from isotope studies suggests that the topography of western North America has remained essentially the same since the Paleogene (Mulch et al., 2008; Mix et al., 2011). Another possible reason may be the cooling of the eastern Pacific Ocean ca. 14 Ma (Lyle et al., 2008), which would likely have resulted in decreased precipitation. Sea-surface temperatures (SSTs) in the equatorial eastern Pacific have strong effects on the precipitation in the western U.S. today (Cayan et al., 1998). This present-day link suggests that larger time-scale reorganizations of Pacific SST associated with the Miocene cooling trend could also have had a large impact on precipitation patterns (Lyle et al., 2008). Changes in the upwelling in the eastern Pacific between 14 Ma and 4 Ma would have resulted in cooler coastal waters, and changes in the seasonal pattern of rainfall, generating summer-dry conditions on the western coast of North America (Jacobs et al., 2004). The extreme drying seen in our EP values in western North America during the Late Miocene (Figs. 1D and 1E) was most likely related to the peak of upwelling in the eastern Pacific during 8–5 Ma, causing the drying of

rivers in the North American southwest (Jacobs et al., 2004).

For Eurasia, our results show a trend toward more arid conditions during the Late Miocene (Figs. 1D and 1E) (see also Eronen et al., 2010a). A possible link of the European climate to conditions in the North Atlantic region in the Late Miocene was suggested previously (Eronen et al., 2009; Micheels et al., 2011). Here we show that the main process responsible for this link is the strength of ocean heat transport from south to north, modified through the development of the Panama seaway during the Neogene.

In Europe, the fossil mammal and plant data show the development of a dry season (Agusti et al., 2003) and a trend toward lower winter temperatures (Mosbrugger et al., 2005) during the Late Miocene. The spread of more arid conditions in the eastern Mediterranean during the Late Miocene and the accompanying break-up of the open habitat-adapted mammal fauna in this area have been shown to be connected to changes in the circulation patterns in the North Atlantic Ocean (Eronen et al., 2009), implying a strong link between the western Eurasian climate and ocean circulation in the North Atlantic.

The active tectonics in Central America led to multiple changes in the depth of the Panama seaway. There were probably temporary closures of the seaway in the Middle and Late Miocene (12–8 Ma), prior to its final closure ca. 4–3 Ma (Schmidt, 2007). Sensitivity experiments shown here (Fig. 2), using an Earth system model of intermediate complexity, demonstrate a strong cyclonic anomaly in the wind

field in the North Atlantic region in response to a weaker heat transport of the ocean currents (Fig. 2; Figs. DR4–DR6). These experiments suggest that changes in Panama seaway depth led to increased climate variability in the North Atlantic and European region from the Middle to Late Miocene and onward.

The closure of the Panama seaway had profound impacts on ocean circulation and atmospheric circulation in the North Atlantic, with a shift to a cooler system from the Middle Pliocene (ca. 3 Ma) onward (e.g., Lunt et al., 2008). Our results suggest that the western coast of North America was more humid than the Great Plains during the Pliocene (Fig. 1F). In addition, previous research (Eronen et al., 2010a) shows more humid conditions in western Eurasia during the Early to Middle Pliocene. In another model experiment the Aleutian and Icelandic Middle Pliocene low-pressure systems appear to be more pronounced than today, caused by a warmer North Atlantic (Haywood et al., 2001). These trends can be related to the effects from the final closure of the Panama seaway 4–3 Ma (Fig. 2; Figs. DR4–DR6).

**Mammalian Dispersals Between Continents**

Our fossil data analysis, supported by climate modeling experiments, indicates that the effects of Neogene cooling and increased seasonality began ~5 Ma earlier and were more pronounced in North America than in Eurasia (Fig. 1). While in western Eurasia the dry season is formed by a trend toward lower winter temperatures (Agusti et al., 2003; Mosbrugger et al., 2005), in North
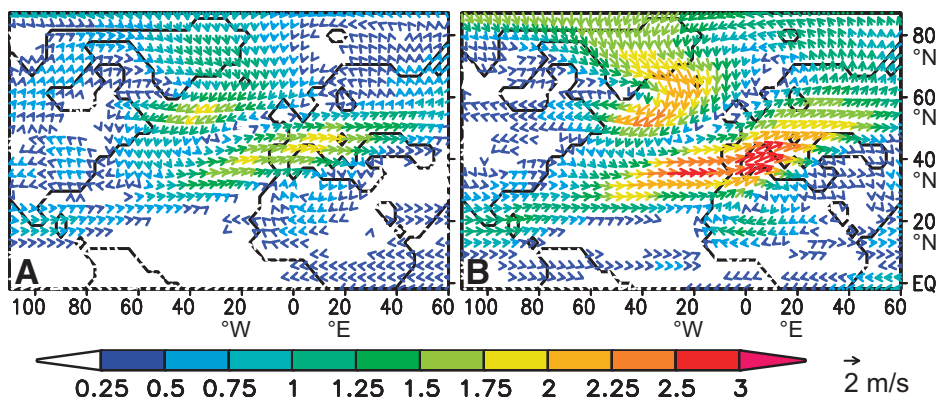
**Figure 2. Wind field anomalies at 500 hPa pressure level (~5000 m altitude) for Late Miocene (Tortonian, 11–7 Ma) climate model run for different levels of ocean heat flux in North Atlantic Ocean. Difference of wind field (vectors indicating direction and wind speed in m/s) at reduced ocean flux correction minus that at standard 100% condition. A: Ocean flux correction 75%. B: Ocean flux correction 50%.**

America it is formed by a trend of decreased summer temperatures and loss of summer rains (Wolfe, 1994; Lyle et al., 2008).

The pattern revealed by our study may explain a hitherto puzzling feature of the dispersal of large herbivorous mammals between Eurasia and North America. Compared with the steady immigration of carnivorous species from North America to Eurasia throughout the Neogene, the immigration of ungulates was more discontinuous, with a near hiatus during the later Miocene. A quick survey based on tabulation by Tedford et al. (2004, their figure 6.3) shows that of 32 large mammal genera to disperse to North America from Eurasia between 25 Ma and 15 Ma, 12 were ungulates, many of them giving rise to lineages that subsequently thrived and diversified (including proboscideans, rhinoceroses, and ruminant artiodactyls). In contrast, of 14 such large mammal dispersals between 15 Ma and 5 Ma, only four were ungulates (*Pseudoceras*, *Neotragoceros*, *Platybelodon*, and *Tapirus*). None of these taxa gave rise to a lineage diversification and, with the exception of *Tapirus*, they all had a short duration in the fossil record. Successful immigration and diversification of ungulates recommenced in the Pliocene–Pleistocene. Thus, there was a period of ~10 Ma where few ungulate taxa dispersed to North America. However, during this same interval, ungulates immigrating into Eurasia from North America (hipparionine horses and camelids) established successful lineage diversifications.

This interval of little or no ungulate immigration corresponds to the time when our results indicate that the climate in North America was significantly drier than in Eurasia. Levels of aridity would affect herbivores more than carnivores, as precipitation has a direct effect on the available vegetation. We propose a causal relationship between this climatic difference between the continents and immigration patterns (previously proposed in another context; Fortelius et al., 1996). Under a trend of sustained change toward drier conditions, the animals migrating from a drier continent to a wetter one will be preadapted to future change to greater aridity, and thus will be superior competitors as immigrants. For the animals from the wetter continent, the reverse will be true: by default they will face harsher conditions after dispersal and will be weak competitors in their new environment. This may explain the imbalance in the success of Eurasian ungulates immigrating to North America, and the North American ungulates immigrating to Eurasia.

## APPENDIX: METHODS

### Fossil Mammal Data

We downloaded the data for the Northern Hemisphere from the New and Old Worlds (NOW) database (Fortelius, 2010; http://www.helsinki.fi/science/now). The North America data derive from published fossil mammal compilations (Janis et al., 1998, 2008). We used only the large herbivorous mammals (Orders Artiodactyla, Perissodactyla, Primates, and Proboscidea), and only those localities that had at least two scorings for hypsodonty and existing coordinate information. Three classes of molar tooth crown height are recorded in the NOW database: brachydont, mesodont, and hypsodont. The criterion for assigning species to classes is based on the ratio of height to length of the second molar (upper or lower). Brachydont teeth have a ratio <0.8, mesodont teeth a ratio of 0.8–1.2, and hypsodont teeth a ratio >1.2. For this study, the crown-height classes were assigned values of 1 (brachydont), 2 (mesodont), and 3 (hypsodont).

To estimate past precipitation levels, we used a method developed with present-day data from large herbivorous mammal communities and mean annual precipitation (Eronen et al., 2010b); it uses regression tree analysis on the distribution of large herbivorous mammals at the community level. With a standard error of 388 mm, it enables the interference of regime changes (arid, semiarid, semihumid, humid, extremely humid). For comparison we also calculated the mean crown height for each locality (see Fortelius et al., 2002).

We split our data in six time slices, spanning the time period from 23 to 1.8 Ma. We followed the North American biochronology (Woodburne, 2004) for division of our data, and used for Eurasia the closest corresponding Eurasian Mammalian ages (MN units). To investigate the spatial patterns, we plotted precipitation and mean hypsodonty estimates onto present-day maps using settings from Eronen et al. (2010a).

### Climate Modeling

Our climate model experiments concentrated on testing the effect of ocean heat transport through the Gulf Stream. For this we ran a series of experiments where we adjusted the monthly ocean heat flux to fractions of modern conditions for North Atlantic. We used the model Planet Simulator (Fraedrich et al., 2005a, 2005b) with a horizontal resolution of 3.75° and 10 vertical levels. Planet Simulator is a model of intermediate complexity, where atmospheric physics are simplified in comparison to complex models. The ocean model, with same T31 horizontal resolution, consists of a slab ocean with 60 m thickness, without deep-ocean circulation. The ocean-atmosphere heat transfer is represented separately for ocean and for sea ice, where the so-called flux correction represents the influence of ocean currents as an adjustment to climatic heat transfer (Stocker, 2011; for a complete description of the model, see Fraedrich et al., 2005a, 2005b). The boundary conditions of the model setup (e.g., the paleotopography, paleovegetation) refer to the Late Miocene, i.e., 11–7 Ma, and are based on previous model runs (e.g., Micheels et al., 2011). Atmospheric $CO_2$ is specified at 360 ppm. The only differences to previous model setups concern the ocean heat flux. We used present-day ocean flux correction derived from sea-surface temperatures (SSTs) for start-up runs. For the North Atlantic, the monthly ocean flux correction values were adjusted to percentage steps between 0% and 120% of present-day conditions, while the respective global average was maintained through inverse adjustments for the remainder of the ocean grid cells. We did not change the ice flux correction. We ran the model for 100 yr to reach dynamic equilibrium, and for analysis used the averages of the last 10 simulation years. For the wind field differences for 100%, 75%, and 50% flux correction (Figs. DR4, DR5, and DR6), meridional and zonal wind components were subtracted separately before composing the wind direction vector and magnitude of the anomaly. The winds at 500 hPa pressure level (~5000 m altitude) are more realistic for mountainous topography than inferred artificial sea-level winds.

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