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Effective heat transport of Gulf Stream to subarctic North Atlantic during Miocene cooling: evidence from "Köppen signatures" of fossil plant assemblages

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Abstract

Shallowing of the Panama Sill and the closure of the Central American Seaway initiated the modern Loop Current/Gulf Stream circulation pattern during the Miocene but no direct evidence has yet been provided for effective heat transport to the northern North Atlantic during that time. Climatic signals from 11 precisely-dated plant-bearing sedimentary rock formations in Iceland, spanning 15–0.8 million years (Myr), resolve the impacts of the developing Miocene global thermohaline circulation on terrestrial vegetation in the subarctic North Atlantic region. "Köppen signatures" were implemented to express climatic properties of fossil plant taxa and their potential modern analogues using the principal concept of the generic Köppen–Geiger climate system, which is based on plant distribution patterns. Using Köppen signatures and the correlation between Köppen climate zones and major global vegetation zones, fossil assemblages were used to trace major vegetation shifts. This evidence was combined with evidence from tectonics and palaeoceanography. In contrast to the global climatic trend, the vegetation record reveals no cooling between ~ 15 and 12 Myr, whereas periods of climatic deterioration between 12–10 Myr, 8–4 Myr, and in the Pleistocene are in phase with increased pulses of ice-rafted debris in the Northern Hemisphere. The observed sequence of climate change in the northern North Atlantic can only be explained by an effective Gulf Stream-mediated heat transport from the middle Miocene onwards.

1 Introduction

The Mid-Miocene Climatic Optimum (MMCO) at 17–15 Myr was the last phase of markedly warm climate in the Cenozoic (Zachos et al., 2001). The MMCO was followed by the Mid-Miocene Climate Transition (MMCT) at 14.2–13.8 Myr correlated with the growth of the East Antarctic ice-sheet (Shevenell et al., 2004). In the Northern Hemisphere this cooling is reflected by continuous sea ice in the central Arctic Ocean since ~ 12 Myr (Frank et al., 2008). Further south, the exposed northern Barents Sea shelf was already glaciated by ~ 15–14 Myr and was the main source of glacial detritus to the Fram Strait area (Knies and Gaina, 2008), where the first pulses of ice rafted debris (IRD) are recorded at ~ 14 Myr (Wolf-Welling et al., 1996) and at ~ 12.6 Myr in the Norwegian Sea (Wolf-Welling et al., 1996; Thiede et al., 1998). The dramatic change in Earth's climate from the MMCO to the MMCT is well documented in marine and terrestrial sedimentary records from both hemispheres. Abrupt cooling after the MMCO recognized globally in marine isotope records (Zachos et al., 2001; Shevenell et al., 2004; Knies and Gaina, 2008) is also documented in the palaeobotanical records of Antarctica (Lewis et al., 2008) and Alaska (Wolfe, 1994; White et al., 1997). This change was accompanied by major oceanographic reorganisations. The timing of the MMCO coincided with the opening of the North Atlantic–Arctic gateway (Jakobsson et al., 2007) that permitted water and ice exchange between the Arctic and Atlantic oceans and established a steeper oceanic thermal gradient. Contemporaneously, global deep-sea unconformities indicate that circumequatorial circulation via the Central American Seaway was disrupted ~ 16–15 Myr (Keller and Barron, 1983) and seismic stratigraphic investigations in the eastern Gulf of Mexico also suggest a major change in ocean circulation (Keller and Barron, 1983; Mullins et al., 1987; Duque-Caro, 1990; Flower and Kennett, 1995; Nisancioglu et al., 2003). Due to the rise of the Panama sill (Mullins et al., 1987) and closure of the Central American Seaway (Montes et al., 2012), the Equatorial Current and weak proto-Gulf Stream of the early Miocene were replaced by the more intense Caribbean-Loop Current/Gulf Stream system between 15 and 12 Myr (Mullins et al., 1987). The northward deflection of deep currents and the initiation of modern Loop Current/Gulf Stream patterns in conjunction with an open North Atlantic–Arctic gateway likely intensified the pre-existing weak thermohaline circulation in the Nordic Seas (Knies and Gaina, 2008) and might have led to surface-temperature deviations in the subarctic North Atlantic that were similar to today (Kaspi and Schneider, 2011). Direct observations of the effect of Gulf Stream-mediated heat transport to the subarctic North Atlantic during the Neogene have long been hindered by the apparent lack of a continuous terrestrial sedimentary record in the northern North Atlantic, Norwegian Sea and Greenland Sea areas.

Here, we use an extensive palaeobotanical record from Neogene and Quaternary sediments in Iceland spanning 15 to 0.8 Myr (Denk et al., 2011) to evaluate climate development in this region and to compare this to global climate patterns (Zachos et al., 2001). We used Köppen climate types (Köppen, 1936; Kottek et al., 2006; Peel et al., 2007) and major vegetation zones (Walter, 1973; Schroeder, 1998) covered by the geographical and altitudinal distribution ranges of potential modern analogues (PMA) of the fossil plant taxa to infer climate shifts for the late Cenozoic of Iceland.

2 Material

In a recent monographic work (Denk et al., 2011) on late Cenozoic plant fossils of Iceland, 342 taxa comprising macro- and microfossils were described, and their systematic affinities determined (Table A1). The material investigated originates from 11 plant-bearing sedimentary formations exposed at 46 localities (Table 1) and combines material from historical collections stored in the Swedish Museum of Natural History, Stockholm, the Icelandic Institute (Museum) of Natural History, Reykjavík, and the Geological Museum, Copenhagen, with material collected during several new field campaigns (1998–2010).

The age of the sedimentary formations (Table 1), and hence of the fossil assemblages, is well constrained due to their position between basalts (Denk et al., 2011). Absolute ages are available for most bracketing basalts, for the remainder ages have been constrained by means of palaeomagnetic correlation (McDougall et al., 1984; Hardarson et al., 1997; Kristjansson et al., 2003). The oldest sedimentary formation exposed in Iceland, the Selárdalur-Botn Fm. is of early middle Miocene age ($\sim$ 15 Myr), the youngest sedimentary formation covered by the monograph is of late Pleistocene age ($\sim$ 800 kyr; Denk et al., 2011). Iceland is the only known terrestrial place in the

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subarctic North Atlantic providing a continuous sedimentary and plant fossil record for the past 15 Myr.

3 Methods

The present paper is introducing a new method to infer climate evolution from plant fossil proxies. The method and its background is explained in detail in the following.

3.1 The Köppen–Geiger climate classification

The climate classification by Wladimir Köppen (Köppen, 1884, 1936; Kottek et al., 2006; Peel et al., 2007) is currently the most widely used. It is a generic classification that is based chiefly on two complex criteria, the degree and seasonal distribution of precipitation and of warmth (Barry and Chorley, 2003). The main climate types except for the arid ("dry") climates (Köppen climate type B) are based on monthly mean temperatures (Table 2). The temperature limits in Köppen's classification were originally chosen based on several observations: The 10 °C summer isotherm roughly correlates with the poleward limit of tree growth defining the southern (on the Northern Hemisphere) or northern limit (Southern Hemisphere) of the polar (arctic and antarctic) climates ("ice climates"; Köppen climate type E). The 18 °C winter isotherm provides a threshold for a broad range of tropical plants and defines the boundary of the "equatorial" (tropical) climates (Köppen climate type A). The −3 °C January (July) isotherm corresponds to a short and regularly occurring period of snow cover at mid-latitudes, and defines the border between the "warm temperate" (Köppen climate type C) vs. the "snow climates" (Köppen climate type D) (Köppen, 1936; Barry and Chorley, 2003).

The second and third letters of the Köppen climate consider precipitation and air temperature (Table 2). In the case of the A, C and D climates the second letter differentiates between humid (f), winter dry (w), summer dry climates (s), and monsoonal (m; used for A-climates only) climates. The third letter indicates hot (a), warm (b), cool (c),

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and cold (d) summers. In the case of B climates, the differentiation is between steppe (S) and desert (W) climates, each with two variants: hot (h) and cool (k). Within the E climates, one distinguishes between the tundra climate (ET) and the frost climate (EF). Recently, the Köppen system has been revised (Kottek et al., 2006) in order to allow exact quantitative distinction between all climate types and to map their global distribution (Kottek et al., 2006; Peel et al., 2007; see http://koeppen-geiger.vu-wien.ac.at and http://www.hydrol-earth-syst-sci.net/11/1633/2007/hess-11-1633-2007-supplement.zip for updated Köppen–Geiger world maps).

3.2 Feasibility of Köppen climate types to describe complex climatic properties of plants

Köppen climate types are particularly useful for describing climatic conditions, as each climate type comprises several climate parameters that would be less or not at all informative when taken alone. For example, the warm temperate, fully humid climate with warm summers (Cfb) describes a climate that is most characteristic of temperate broadleaved deciduous forests in both hemispheres (Walter, 1973; Schroeder, 1998). A single climate parameter, such as the mean annual temperature (MAT), is not useful for describe areas hosting this particular vegetation type. MAT within Cfb climates of the Northern Hemisphere is in the range 5.5–18.9 °C (Table 3). Köppen (1936) illustrated the problem of using single climate parameters to classify climate by two examples: New Orleans (USA) and Cairo (Egypt) have roughly the same mean annual and mean monthly temperatures but New Orleans has about 50 times the mean annual precipitation (MAP) of Cairo; Khartoum (Sudan) has about the same MAP as Verkhoyansk (northeastern Siberia) but the former has a MAT of +22 °C and the latter of –50 °C (Köppen, 1936, p. C11).

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3.3 Using Köppen climate types to detect past climate change

The direct correlation of Köppen climate types (Table 2; Köppen, 1936; Kottek et al., 2006) to major vegetation types (Table 4; Walter, 1973; Schroeder, 1998) makes them useful for reconstructing past climates based on plant fossil assemblages (Köppen and Wegener, 1924; Wegener, 1929). Increasingly mild or harsh climate conditions and corresponding changes in vegetation are reflected by progression of Köppen climate types, which is also seen as a vertical gradient in mountain ranges (Table 5). Non-generalist taxa, which are restricted to particular vegetation types (Schroeder, 1998), are also restricted to certain Köppen climate types. For example, all modern species of beech trees (*Fagus*) are typical elements of the deciduous broad-leaved forests of the mid-latitudes of the Northern Hemisphere ("deciduous nemoral forests"; Table 4). Beeches are widespread across the north-temperate regions, but occur predominantly under a Cfb climate as already recognized by Köppen (Köppen, 1936), commonly forming pure stands. In the overall warmer Cfa climates (warm temperate, fully humid with hot summers, Table 2) of eastern North America, the Black Sea region, and central China, beech trees are found exclusively as accessory elements in mixed mesophytic forests (Wang, 1961; Maycock, 1994; Cao, 1995; Peters, 1997). In the more frost-prone Dfb climates (snow, fully humid with warm summers; Table 2), beech trees are co-dominants with shade-tolerant conifers such as *Abies* and *Tsuga* and few other broadleaved deciduous trees (Maycock, 1994). The genus' northern limit in North America and Japan (Maycock, 1994) coincides with the northern limit of the Dfb climate zone (Grimm and Denk, 2012). *Fagus* is not found in any other climate type (Shen, 1992; Peters, 1997).

Distribution ranges of other taxa cover different combinations of Köppen climate types. Hence, plant assemblages can be characterized and compared by scoring the Köppen climate types covered by their constituent elements. Using the actualistic principle, extinct plant assemblages can be characterized in the same way and climatic shifts detected.

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3.4 Characterisation of modern taxa using Köppen climate types ("Köppen signatures")

To establish Köppen signatures of individual plant taxa, we used distribution data from numerous sources (Hegi, 1923, 1928; Ohwi, 1965; Hegi, 1966b, a, 1974, 1981a, b; Browicz and Zieliński, 1982, 1982–1994, 1984; Hegi, 1984; Browicz, 1986; Farjon, 1990; Thompson et al., 1999a, b, 2001; Thompson et al., 2006; Fang et al., 2009; Anderberg and Anderberg, 2010; Flora of China, 2010) to identify the Köppen climate types to which they belong. The updated Köppen–Geiger World Map of Kottek et al. (2006; including a kmz-file for GoogleEarth) provided the basis for the mapping of climate types. The resolution of both, the available distribution data and the Köppen–Geiger map, necessitated some extrapolations. For taxa with a restricted altitudinal distribution, we established altitudinal progressions of Köppen climate types based on climate stations (Lieth, 1999) from the corresponding regions (ES 7 in Grimm and Denk, 2012). For example, in southern Japan (Kyushu and Shikoku islands, western part of Honshu) the predominant Cfa climate indicated in the map (Kottek et al., 2006) is replaced by a Cfb climate at ~ 1000 m a.s.l., which is not represented on the map because no climate stations are available at high elevations. In central Honshu the transition from Cfa to Cfb occurs at ~ 500 m, and at ~ 1000 m the Cfb climate is replaced by the Dfb climate, which characterizes the central high mountain range of eastern Honshu and most of the island of Hokkaido (Lieth, 1999; Kottek et al., 2006). The grid size used by Kottek et al. (2006) does not resolve the narrow strip of Cfb between the lowlands (Cfa) and mountains (Dfb) of eastern Honshu. The altitudinal distribution of *Fagus crenata* Blume in Japan (Maycock, 1994) is strongly correlated to the altitudinal distribution of the Cfb and Dfb climates, hence, this taxon was not scored for Cfa in addition to Cfb and Dfb in contrast to the North American species *F. grandifolia* Ehrh., which extends to sea-level in northern Florida and Lousiana (Cfa; Dataset S1 in Supplement). Similar extrapolations were made for high-mountain taxa of western Eurasia and East Asia. The detailed information regarding reference and scored Köppen cli-

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mate types, i.e. Köppen signatures, for all (modern) taxa are provided in the ClimGrim database (v. 0.2; www.palaeogrimm.org/data).

3.5 Representation of fossil taxa and the modern flora of Iceland by Köppen climate types

Using the actualistic principle one can infer climate conditions for a plant fossil assemblage by characterising the climate conditions under which potential modern analogues (PMA) of fossil plant taxa can thrive; here: the Köppen signatures of PMA.

Firstly, for all fossil taxa identified to genus level or below, one or several PMA were determined based on the systematic affinities of the 342 fossil taxa from Iceland with modern plant taxa (Denk et al., 2011). In the case of genera, determination of PMA is straightforward: all modern species of the genus constitute potential PMA. The number of PMA can be narrowed down in the case of large genera. Due to the geographic position and geotectonic setting of Iceland, PMA thriving in eastern North America (and Greenland), the Arctic, and (northern) Europe provide reasonable PMA for fossil taxa, in particular for the younger floras. For example, in the case of many herbaceous species, all taxa with distributions recorded in Virtuella Floran (Anderberg and Anderberg, 2010) were considered as PMA. In the older floras some taxa are found that are members of genera that went extinct in Europe and currently have a disjunct East Asian–North American distribution (e.g. *Carya, Liriodendron, Magnolia, Parthenocissus, Sassafras*). In addition, very few taxa went extinct in Europe and North America (*Ginkgo*) or in Europe and East Asia (*Comptonia*). In these cases, all Northern Hemispheric representatives of the respective genera were considered as PMA (distribution data based on Hegi, 1923; Hegi, 1928; Ohwi, 1965; Hegi, 1966b, a, 1974, 1981a, b; Browicz and Zieliński, 1982, 1982–1994, 1984; Hegi, 1984; Browicz, 1986; Farjon, 1990; Thompson et al., 1999a, b, 2001; Thompson et al., 2006; Fang et al., 2009; Anderberg and Anderberg, 2010; Flora of China, 2010).

Below the genus level, the determination of PMA followed Denk et al. (2011). For only a few cases are phylogenetic frameworks available to establish relationships be-

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tween fossil and particular modern species or intrageneric groups, i.e. *Acer* sect. *Acer* (Grimm et al., 2007), *Fagus* (Denk et al., 2005a; Denk and Grimm, 2009a), *Quercus* (Denk and Grimm, 2009b, 2010). In some cases, exact affinities can be established by means of epidermal features of the leaves, e.g. *Acer* (Walther, 1972; Friedrich and Símonarson, 1982), *Cathaya* (Denk et al., 2011), *Cryptomeria* (Denk et al., 2005b), or pollen ornamentation, *Quercus* Groups Quercus and Lobatae (Denk and Grimm, 2009b; Denk et al., 2010), *Rhododendron* subsect. *Pontica* (Denk et al., 2011). In all other cases, affinities rely on similarities of leaf morphology and morphology of reproductive structures (Denk et al., 2011). In some cases, more than one PMA was determined for a fossil taxon. If so, all Köppen climate types covered by these PMA were used to establish the Köppen signature of the fossil taxon (Dataset S1, sheet no. 3).

Secondly, for each sedimentary formation, the count of climate types realized by all its (fossil) constituents was established in order to document changes in the frequencies of particular climate types. Since a single fossil taxon may count for more than one Köppen climate type and since the total number of scorable fossil taxa differs among the sedimentary formations, absolute values, i.e. the sum of fossil taxa scored for a certain Köppen climate type per sedimentary rock formation, were scaled using the maximum number of fossil taxa scorable for a single formation, i.e. 43 taxa (Dataset S1).

The same procedure was performed for the modern flora of Iceland; monocots were not considered because they are absent or very rare and not precisely identifiable in the fossil record (Dataset S2 in Supplement). Plants that thrive both under a Cfc (warm temperate, fully humid with cool summers) and ET (tundra) climate in Iceland and along the southern coast of Greenland, but otherwise are absent from ET climates, were not scored for ET (e.g. *Bartsia alpina* L.; Fig. A1). The coastal, climatically favoured ET climates of northern Iceland and southern Greenland approach the Cfc climate type (see also Peel et al., 2007) and may, in the near future, be replaced by Cfc climates (Rubel and Kottek, 2010). The extension into a warm type of ET climate in Iceland

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reflects the overall tendency of plants to extend their ranges into neighbouring climate types under particular conditions (e.g. edaphic ones). For the Cfc climate type, several adjacent climate types (Fig. 1) are commonly shared by plant taxa, i.e. a plant species will not occur only in a Cfc climate but also in ET, Cfb, and Dfc (snow, fully humid with cool summers) climates (Dataset S2). Likewise, an altitudinal progression of Köppen climate types occurs (Table 5).

3.6 Categorisation of fossil taxa as elements of major vegetation zones

In a second step, each scored taxon was categorized as "meridio-nemoral", "nemoral", "boreal", and "arctic-alpine" (Fig. 2) using the nomenclature and vegetation maps of the world from Walter (1973) and Schroeder (1998).

Plants thriving under Cfa and/or Cwa/Cwb (warm temperate, winter dry with hot or warm summers) and Csa/Csb (warm temperate, summer dry with hot or warm summers) climate types but not under a Cfb climate or harsher climates were categorized as meridio-nemoral elements (according to Schroeder, 1998). These plants are typical elements of Northern Hemisphere broadleaved deciduous forests of the nemoral zone but may extend into the warmer laurel forests of the meridional zone (Walter, 1973; Schroeder, 1998).

Nemoral elements are plants that typically thrive under Cfb, Dfb, Cwb, Dwb (snow, winter dry with warm summers) and possibly extending into warmer 'a' variants of these climate types or Cfc climates (cool summers but mild winters). These elements dominate today's northern temperate forest regions.

Boreal elements are plants typically found in Cfc, Dfc, and Dfd (snow, fully humid with cold summers) climates (and their hygric variants Csc, Dsc, Dsd, summer dry, and Cwc, Dwc, Dwd, winter dry with cool or cold summers) and possibly extend into Cfb/Dfb and related climates but are absent from ET and Cfa, Csa, and Cwa climates. The boreal zone typically comprises regions in the world that are dominated by conifer forests (Walter, 1973; Schroeder, 1998).

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Arctic-alpine elements are plants thriving under an ET climate and extend into Cfc, Dfc and Dfd climates (and their hygric variants), but not in climates with warm or hot summers (e.g. Cfb, Dfb). This group comprises species that show the typical arctic-alpine disjunction (e.g. *Ranunculus glacialis* L.; cf. Fig. A3) whereas others may be confined to the boreal and arctic zones but have closely related species in the Alps (e.g. *Erigeron borealis* (Vierh.) Simmons and *E. neglectus* Kern. ex Nyman).

All other taxa were categorized as "generalists". These can cope with a large variety of climate types (for example, Cfa to Dfc) and include cosmopolitan herbaceous plant taxa.

For fossil assemblages from each sedimentary formation, the representation of these five ecological groups (vegetation categories; Datasets S1, S2) was established in order to observe changes over the course of the past 15 Myr.

4 Results: vegetation and climate development in Iceland during the last 15 Myr

4.1 Vegetation development

The oldest plant-bearing sedimentary rocks in Iceland were deposited 15 Myr and fall within the MMCO (Denk et al., 2011). A combined analysis of macrofossils and palynomorphs from lowland and mountainous settings indicate the presence of lowland riparian and swamp forests dominated by Cupressaceae (*Glyptostrobus*) and warm temperate angiosperms such as *Aesculus*, *Platanus*, *Pterocarya* and the woody vine *Parthenocissus* at that time. Upland forests were dominated by *Fagus* with an admixture of conifers, such as *Cathaya*, *Sequoia* and, higher up, *Cryptomeria*, and a wealth of other mesothermal tree species including evergreens such as *Ilex* and *Rhododendron* (Fig. 3a–h). In 12 Myr strata, the diversity in terms of recovered fossil plant taxa increases markedly from 35 to 66 taxa; in addition to the taxa recorded from the older formation, lianas such as *Smilax* and lowland taxa with current East Asian–North American disjunctions are recorded (e.g. *Liriodendron*, *Magnolia*, *Sassafras*).

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A major floristic change is encountered in the 10 Myr formation, which hosts the most taxon-rich flora from Iceland, comprising 99 taxa (Dataset S2). Whereas four of 66 taxa were herbaceous in the 12 Myr floras, one third of all taxa in the 10 Myr formation are herbaceous (Fig. 3i–p). This increase in herbaceous plants is accompanied by the first occurrence of small-leaved Ericaceae typical of the modern tundra vegetation in Iceland (*Vaccinium*, *Arctostaphylos*) and boreal conifers such as *Larix*. Nevertheless, several warmth-loving elements persisted, including *Platanus*, *Pterocarya* and *Tilia*, and new elements are recorded (*Ginkgo*). Floras preserved in strata between 10 Myr and 3.6 Myr reflect stepwise cooling; *Fagus* persisted until 7–6 Myr and *Quercus* until 5.5 Myr, whereas the evergreen, large-leaved *Rhododendron* aff. *ponticum* L. ranges from the oldest to the 3.8–3.6 Myr floras. At 4.4–3.6 Myr, small-leaved Salicaceae occur for the first time. The second major reorganisation of the vegetation is recorded in floras from the Pliocene–Pleistocene transition. Temperate woody elements are not found in any of the Pleistocene floras, which are essentially similar to the modern flora of Iceland.

4.2 Köppen climate type distribution and frequency in modern flowering plants of Iceland

Naturally, most climate types realized in the modern flora of Iceland are those of the present (Kottek et al., 2006; Peel et al., 2007) Cfc and ET types and the climate types to which the later are directly connected (Fig. 4, bottom line). The higher proportion of Cfc in the distribution of climate types as compared to the lower proportion of ET types is due to the fact that only one third of the modern flowering plants in Iceland (monocots excluded) are typical ET plants. At the same time, most of the ET plants are also found in milder Cfc, Cfb, and Dfc climates. By contrast, there are only a few taxa that extend their ranges into warmer climates with hot summers ("a" climates); these are generalists with vast modern distribution ranges and are more typically herbaceous rather than woody plants.

The distribution of Köppen climate types based on the modern flora of Iceland serves as a reference point for comparison with the fossil floras.

4.3 Climate development inferred from Köppen signatures

In order to quantify climatic signals captured in the fossil floras, we transformed modern distribution ranges of PMA of fossil taxa into "Köppen signatures", and observed changes through time (Figs 3–5). No change is recorded between 15 Myr and 12 Myr. During this period, warm temperate, fully humid climates with hot or warm summers (Cfa, Cfb) are well represented. Meridio-nemoral and nemoral elements (Walter, 1973; Schroeder, 1998) dominated the vegetation at this time (Fig. 6). In contrast, climates with cool summers and cold winters (Cfc, Dfc), and polar tundra (ET) climates are hardly covered by the PMA suggesting that boreal and arctic-alpine elements played only a minor role during that time and were confined to highest elevations. The onset of large scale Northern Hemisphere glaciation in the Miocene as recorded from the central Arctic Ocean and the northern Barents Sea after ∼ 15 Myr (Frank et al., 2008; Knies and Gaina, 2008) and major growth of the East Antarctic Ice Sheet starting between 15 and 14 Myr (Zachos et al., 2001; Lewis et al., 2008) did not profoundly impact the subarctic North Atlantic region (Fig. 5). This is in stark contrast to the situation in subarctic North America, where vegetation changes closely mirror the MMCT (Wolfe, 1994; White et al., 1997). A clear change between the 15 and 12 Myr and the younger floras in Iceland is expressed by the marked increase of Cfc- and Dfc-tolerant taxa ("I" in Fig. 5) and the gradual loss of Cfa and Cwa taxa (Fig. 4). Three changes towards milder conditions are evident in the late Miocene between 10 Myr and 9–8 Myr ("II", Fig. 5) and in the Pleistocene and Holocene (between 1.7 and 1.1 Myr, and between 0.8 Myr and the present). Although the Miocene (9–8 Myr) shift may be influenced by the local environmental factors (fossil floras derived from vegetation flanking caldera lakes, Denk et al., 2011), the younger warming events likely reflect broader Pleistocene climate dynamics. From the late Miocene to Pliocene (7–6 Myr to 5.5 Ma; "III" in Fig. 5) marked cooling is evidenced by the further increase of Cfc, Dfc, and ET-tolerant taxa, i.e. generalist, boreal and arctic-alpine elements (Fig. 6). This correlates well with the onset of glaciation on the Iceland Plateau and off southeast Greenland (Fig. 5). The climate at this time was still significantly milder than today as evidenced by the substantial proportion of meridio-nemoral taxa, i.e. taxa chiefly restricted to subtropical, warm temperate climates (Cfa, Cwa). The most drastic shift is seen at the transition from the Pliocene to the Pleistocene (3.6 Myr to < 2.6 Myr; "IV" in Fig. 5) and corresponds to the onset of widespread Northern Hemisphere glaciations (Fronval and Jansen, 1996; St. John and Krissek, 2002). This change is expressed by a distinct drop of Cfa taxa and a marked increase of ET taxa. By this time, the modern vegetation of Iceland, dominated by boreal and arctic-alpine taxa with a few nemoral elements (Fig. 6), was established. Thus, the climatic estimates presented here largely reflect the history of IRD in the Northern Hemisphere (Fronval and Jansen, 1996; Wolf-Welling et al., 1996; Thiede et al., 1998; St. John and Krissek, 2002; Frank et al., 2008; Knies and Gaina, 2008) and of gradual cooling in the Northern Hemisphere during the late Cenozoic culminating in the Pleistocene cold phases (Zachos et al., 2001).

5 Discussion

5.1 What delayed Miocene cooling in the subarctic North Atlantic?

Northward heat transport by the Loop Current/Gulf Stream has been buffering general cooling trends in the subarctic North Atlantic since the Pliocene (Driscoll and Haug, 1998; Haug and Thiedemann, 1998; Seager et al., 2002; Kaspi and Schneider, 2011). Isotopic evidence for such an influence has previously been provided for the Pleistocene. For example, despite glacial initiation at the inception of marine isotope stage MIS 5d, ~ 115 kyr, heat transport due to an effective Gulf Stream kept the subarctic North Atlantic warm until ~ 107 kyr (McManus et al., 2002). The ameliorated climate in Iceland at ~ 12 Myr as shown by the floristic data is at odds with global climate inferences from marine isotopic records, geological data, and palaeobotanical evidence

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from elsewhere in the Northern and Southern Hemispheres that indicate global cooling after 15 Myr (Wolfe, 1994; White et al., 1997; Zachos et al., 2001; Knies and Gaina, 2008; Lewis et al., 2008). The geographical position of Iceland and an already effective Loop Current/Gulf Stream explain this discrepancy. Increased thermohaline circulation and moisture transport from low to high northern latitudes by the Loop Current/Gulf Stream after ∼ 15 Myr as a consequence of the cessation of deep marine interchange through the Central American Seaway (Mullins et al., 1987) or its closure (Montes et al., 2012), contributed to milder climates in the North Atlantic, in particular north of 60° N (Seager et al., 2002). Thus, vegetation development in Iceland provides the first direct evidence of the development and palaeoenvironmental significance (Mullins et al., 1987) of an effective Gulf Stream during the middle Miocene.

5.2 Applicability of the proposed approach – categorisation of plant taxa using Köppen climate types – to determine past climates

Taxon-based approaches to infer past-climates using plant fossil assemblages are limited by the accuracy with which fossil taxa and their modern analogues can be determined. The extent to which a PMA matches the ecological (including climatic) properties of a fossil taxon cannot be established with complete certainty. This renders actualistic approaches that use climatic tolerances of modern taxa to estimate past-climates, the so-called "nearest-living relative" approaches (Iversen, 1944; Grichuk et al., 1984; Mosbrugger and Utescher, 1997), problematic. For example, the beech trees (genus *Fagus*; see above), which have a very rich fossil record and are restricted today to Cfa, Cfb and Dfb climates had a much wider distribution during some parts of the Cenozoic including arctic areas such as Ellesmere Island (Denk and Grimm, 2009a). 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. On the other hand, it is difficult to (i) exactly determine the present climate range(s) of beeches

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(Grimm and Denk, 2012) and (ii) to establish whether or not fossil members of the genus occupied exactly the same climatic space.

A further complication is that the distribution of a taxon is affected by several, partly antagonistic biotic and abiotic parameters (see above). Köppen (1936, p. 11) already noticed that absolute climatic figures, in particular if taken independently (Wolfe, 1993; Wolfe, 1995; Mosbrugger and Utescher, 1997), are not meaningful indicators of vegetation types and general climate types. This is well illustrated by Schroeder (1998) who used Walter climate diagrams (Walter and Lieth, 1960, 1964) to document the variation of climatic conditions for particular vegetation types. In other words, any plant assemblage can only reflect a range of climatic conditions but not the exact parameters of a particular climate as for example available for climate stations.

6 Outlook

A future application of the approach proposed here may be to infer a particular Köppen climate for a plant fossil assemblage. However, several issues must be addressed first. Rich plant fossil assemblages like the ones used here often combine taxa from a larger area, hence, involve a certain altitudinal gradient. The first step, therefore, would be to divide the fossil taxa into lowland and highland groups (Denk et al., 2011). A further step would be to characterize Köppen climates by Köppen signatures of taxa thriving in these climates and the corresponding vegetation categories. Figure 7 shows the Köppen climate type frequencies for several broad-leaved deciduous (and conifer) forests of Georgia, Transcaucasia (Denk et al., 2001) thriving under Cfa to Dfb climates. The Cfa and Cfb forests show essentially the same patterns and are predominantly composed of taxa that thrive in Cfb climates. More than half of the taxa can (also) occur in Cfa and/or Dfb climates, whereas one third to one half can (also) thrive in Csa/Csb climates. In the Dfb forests the numbers of taxa occurring in Dfb climates increase and Cfa (Csa/Csb) taxa decrease. Using vegetation categories (Fig. 8), the different climates are better resolved. From Cfa to Dfb the proportion of meridio-nemoral elements decreases and that of boreal elements increases. The general high proportion of nemoral elements (Fig. 8) and number of taxa scoring for Cfa (Fig. 7) can be attributed to the particular phytogeographical position of Georgian forests, which have been providing a refuge for numerous warmth-loving taxa that went extinct in Europe during the Pleistocene (e.g. *Diospyros, Hibiscus, Osmanthus, Pterocarya, Zelkova*; Denk et al., 2001). The comparison of adequate modern reference floras to fossil ones then may enable one to infer specific Köppen climate types for the lowland and highland portions of a fossil assemblage.

Supplementary material related to this article is available online at: http://www.biogeosciences-discuss.net/10/13563/2013/ bgd-10-13563-2013-supplement.zip.

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Table 1. Age and stratigraphy of plant-bearing sedimentary rock formations from Iceland (after Denk et al., 2011).

Age	Formation/Beds/Biozone	Plant fossil localities	Stratigraphy	
0.8 Myr	Svínafellsfjall Formation	Svínafell	Pleistocene (2.588 to 0.0117 Myr)	Cenozoic (65.5 ± 0.3 Myr to Recent)
1.1 Myr	Búlandshöfði Formation	Stöð		
1.7 Myr	Víðidalur Formation	Bakkabrúnir		
2.4–2.1 Myr	Brekkukambur Formation	Miðsandsdalur, Gljúfurdalur, Litlisandsdalur		
4.4–3.8 Myr	Tjörnes Beds (Tapes and Mactra Zone)	Egilsgjóta, Reká, Skeifá	Pliocene (5.332 to 2.588 Myr)	
5.5 Myr	Fnjóskadalur Formation	Selárgil	late Miocene (11.608 to 5.332 Myr)	
7–6 Myr	Hreðavatn-Stafholt Formation	Stafholt, Laxfoss, Veiðilækur, Brekkuá, Snóksdalur, Hestabrekkur, Giljatunga, Fífudalur, Þrimilsdalur, Fanná, Langavatnsdalur		
9–8 Myr	Skarðsströnd-Mókollsdalur Formation	Tindafjall, Hrútagil, Broddanes		
10 Myr	Tröllatunga-Gautshamar Formation	Margrétarfell, Gautshamar, Belti, Torffell, Stekkjargil, Winklerfoss, Gunnustaðagróf, Nónöxl, Bæjarfell, Húsavíkurkleif, Hleypilækur, Fætlingagil, Grỳlufoss, Dettifoss, Merkjagil, Hjálparholt, Bæjarlækur, Nónlækur		
12 Myr	Brjánslækur-Seljá Formation	Seljá, Surtarbrandsgil	middle Miocene (15.97 to 11.608 Myr)	
15 Myr	Selárdalur-Botn Formation	Þórishlíðarfjall (Selárdalur), Botn		

Table 2. Key to Köppen climate types (after Kottek et al., 2006).

Köppen climate type	Description, after Kottek et al. (20) (terminology of Kö21))	Criterion
A	Equatorial climates (Tropische Regenklimate)	$T_{min} \geq 18\,^{\circ}C$
Af	Equatorial rainforest, fully humid (Tropische Regenklimate, Trockenzeit fehlt)	$P_{min} \geq 60\,mm$
Am	Equatorial monsoon	$P_{ann} \geq 25 \cdot (100–P_{min})$
As	Equatorial savannah with dry summer (Tropische Regenklimate, Trockenzeit im Sommer)	$P_{min} < 60\,mm$ in summer
Aw	Equatorial savannah with dry winter (Tropische Regenklimate, Trockenzeit im Winter)	$P_{min} < 60\,mm$ in winter
B	Arid climates (Trockenklimate)	$P_{ann} < 10 \cdot P_{th}$
BS	Steppe climate (Steppe)	$P_{ann} > 5 \cdot P_{th}$
BW	Desert climate (Wüste)	$P_{ann} \leq 5 \cdot P_{th}$
C	Warm temperate climates (Warmgemä	$–3\,^{\circ}C < T_{min} < +18\,^{\circ}C$
Cs	Warm temperate climate with dry summer (Warmgemässigtes Regenklima, Trockenzeit im Sommer)	$P_{smin} < P_{wmin}$, $P_{wmax} > 3 \cdot P_{smin}$ and $P_{smin} < 40\,mm$
Cw	Warm temperate climate with dry winter (Warmgemässigtes Regenklima, Trockenzeit im Winter)	$P_{wmin} < P_{smin}$ and $P_{smax} > 10 \cdot P_{wmin}$
Cf	Warm temperate climate, fully humid (Warmgemässigtes Regenklima, Trockenzeit fehlt)	neither Cs nor Cw
D	Snow climates (Boreale Klimate)	$T_{min} \leq –3\,^{\circ}C$
Ds	Snow climate with dry summer (Boreales Klima, Trockenzeit im Sommer)	$P_{smin} < P_{wmin}$, $P_{wmax} > 3 \cdot P_{smin}$ and $P_{smin} < 40\,mm$
Dw	Snow climate with dry winter (Boreales Klima, Trockenzeit im Winter)	$P_{wmin} < P_{smin}$ and $P_{smax} > 10 \cdot P_{wmin}$
Df	Snow climate, fully humid (Boreales Klima, Trockenzeit fehlt)	neither Ds nor Dw
E	Polar climates (Schneeklimate)	$T_{max} < +10\,^{\circ}C$
ET	Tundra climate (Tundra)	$0\,^{\circ}C \leq T_{max} < +10\,^{\circ}C$
EF	Frost climate (Frost ewig)	$T_{max} < 0\,^{\circ}C$
3rd letter temperature classification	**Description, after Kottek et al. (20) (terminology of Kö21))**	**Criterion**
for B climates:		
h	Hot steppe/desert	$T_{ann} \geq +18\,^{\circ}C$
k	Cold steppe/desert	$T_{ann} < +18\,^{\circ}C$
for C and D climates:		
a	Hot summer (sommerheisse Temperaturstufe)	$T_{max} \geq +22\,^{\circ}C$
b	Warm summer (gemässigte Temperaturstufe)	not (a) and at least 4 $T_{mon} \geq +10\,^{\circ}C$
c	Cool summer (kalte Temperaturstufe)	not (b) and $T_{min} > –38\,^{\circ}C$
d	Extremely continental (Kältepol)	like (c) but $T_{min} \leq –38\,^{\circ}C$

P = accumulated precipitation, T = near-surface (2 m) temperature;
P_{smin} = minimum monthly precipitation for the summer half-year; P_{smax} = maximum monthly precipitation for the summer half-year;
P_{wmin} lowest monthly precipitation for the winter; P_{wmax} = maximum monthly precipitation for the winter;
P_{th} = dryness threshold for B climates in mm. If $P_w \geq 2/3 \cdot P_{ann}$ then $P_{th} = 2 \cdot T_{ann}$. If $P_s \geq 2/3 \cdot P_{ann}$ then $P_{th} = 2 \cdot T_{ann} + 28$. If P_w and $P_s < 2/3 \cdot T_{ann}$ then $P_{th} = 2 \cdot T_{ann} + 14$;
T_{mon} = mean monthly near-surface (2 m) temperature.

Table 3. Ranges of individual climate parameters of selected Köppen climate types for the Northern Hemisphere.

Equatorial and dry climates								
Climate type	Af	Am	As	Aw	BSh	BSk	BWh	BWk
Number of stations	66	51	23	126	69	205	110	48
Min of Elevation [m a.s.l.]	2	1	1	1	3	−15	−15	−20
Max of Elevation [m a.s.l.]	740	1200	522	1291	2066	3650	1478	3174
Min of P_{ann} [mm a^{-1}]	1448	1284	718	773	189	108	1	16
Max of P_{ann} [mm a^{-1}]	4608	5537	1884	2482	816	559	378	230
Min of T_{ann} [°C]	23	20	23	22	18	−4	18	−2
Max of T_{ann} [°C]	27	28	28	29	28	18	30	18
Min of ΔT [°C]	1	1	2	1	2	5	5	18
Max of ΔT [°C]	11	12	13	15	30	44	26	46
Warm-temperate climates								
Climate type	Cfa	Cfb	Cfc	Csa	Csb	Csc	Cwa	Cwb
Number of stations	567	226	12	94	59	1	64	21
Min of Elevation [m a.s.l.]	−9	−4	1	−13	3	23	5	1598
Max of Elevation [m a.s.l.]	1725	2339	304	1326	2367	23	1599	3488
Min of P_{ann} [mm a^{-1}]	393	327	693	354	418	486	533	474
Max of P_{ann} [mm a^{-1}]	4019	2968	1645	2019	2274	486	2866	2843
Min of T_{ann} [°C]	10	6	3	10	8	3	11	5
Max of T_{ann} [°C]	23	19	7	26	17	3	26	17
Min of ΔT [°C]	6	4	7	8	5	13	6	4
Max of ΔT [°C]	29	24	15	29	23	13	29	20
Snow climates (warm and hot summers)								
Climate type	Dfa	Dfb	Dsa	Dsb	Dwa	Dwb		
Number of stations	165	356	1	9	30	26		
Min of Elevation [m a.s.l.]	17	3	1156	523	4	65		
Max of Elevation [m a.s.l.]	1292	2393	1156	1667	1065	3837		
Min of P_{ann} [mm a^{-1}]	347	259	368	277	407	271		
Max of P_{ann} [mm a^{-1}]	1137	1429	368	785	1634	728		
Min of T_{ann} [°C]	6	−1	11	4	3	−3		
Max of T_{ann} [°C]	12	9	11	9	12	9		
Min of ΔT [°C]	25	17	27	19	27	18		
Max of ΔT [°C]	35	40	27	27	43	48		
Snow climates (cool summers; extremely continetal) and tundra climate								
Climate type	Dfc	Dfd	Dsc	Dwc	Dwd	ET		
Number of stations	151	8	8	39	1	70		
Min of Elevation [m a.s.l.]	1	45	24	56	400	2		
Max of Elevation [m a.s.l.]	2743	858	4053	3950	400	4701		
Min of P_{ann} [mm a^{-1}]	145	153	165	193	283	67		
Max of P_{ann} [mm a^{-1}]	3515	488	1676	720	283	3450		
Min of T_{ann} [°C]	−13	−16	−11	−10	−13	−20		
Max of T_{ann} [°C]	5	−10	3	4	−13	6		
Min of ΔT [°C]	14	53	16	16	60	9		
Max of ΔT [°C]	56	63	53	53	60	45		

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Table 4. Vegetation zones of the Earth and their corresponding Köppen climate types.

Vegetation zones after Walter (1973)	Climax vegetation zones after Schroeder (1998) (thermal zone and hygric variant)	Köppen climate types (Köppen, 1936; Kottek et al., 2006) (letter code: main climate type, annual distribution of precipitation and temperature)
I. Tropical and subtropical zones		
1 Evergeen, rainforests of the lowlands and mountain-sides (cloud forests)	1 Tropischer Regenwald (Tropical, humid)	Af (Equatorial, fully humid)
2 Semi-evergeen and deciduous forests	2 Regengrüner Wald (mit Savanne) (Tropical, semihumid)	Aw (Equatorial, winterdry)
2a Dry woodlands, natural savannas or grassland p.p.	3 Eurytropische Trockengehölze (Tropical, oreotropical, meridional, austral; arid)	BSh (Arid, steppe, hot arid)
2a Dry woodlands, natural savannas or grassland p.p.	8 Pampa (Austral; semiarid and arid)	BSk (Arid, steppe, cold arid), Cwb (Warm temperate, winter dry, warm summer)
3 Hot semi-deserts and deserts, polewards up to latitude of 35° N	4 Eurytropische Wüste (Halb und Vollwüste) (Tropical, oreotropical, meridional, austral; arid)	BWh (Arid, desert, hot arid)
II. Temperate and Arctic zones		
4 Sclerophyllous woodlands with winter rain	7 Hartlaubwald (Meridional and austral, semihumid)	Csa (Warm temperate, summer dry, hot summer), (Csb, Cfa, Cfb, BSh, Cwa)[a]
5 Moist warm temperature woodlands	6 Lorbeerwald (Meridional and austral, humid) p.p.	Cfa (W. temp., fully humid, hot summer), Cwa (W. temp., winter dry, hot s.), Cwb, Cfb
6 Deciduous (nemoral) forests p.p.	9 Sommergrüner Laubwald: humid/semihumid (Nemoral, humid and semihumid)	Cfa, Cfb, Dfa (Snow, fully humid, hot s.), Dfb, Cwa, Dwa, Dwb, (Csb), (Cfc)[b]
6 Deciduous (nemoral) forests p.p.	6 Lorbeerwald (Meridional and austral, humid) p.p.	Cfa, Cwa, Cwb, (Cfb)[c]
7 Steppes of the temperate zone	12 Steppe (Nemoral, boreal, semiarid and arid)	BSk
7a Semi-deserts and deserts with cold winters	13 Nemorale Wüste (Nemoral, boreal, semiarid and arid)	BWk (Arid, desert, cold arid)
8 Boreal coniferous zone p.p.	10 Nemoraler Nadelwald (Nemoral, semihumid) p.p.	Dfb → Dfc (Snow, fully humid, cool summer), Csb[5] and Cfb
8 Boreal coniferous zone p.p.	14 Dunkle Taiga (Boreal, humid)	Dfc
8 Boreal coniferous zone p.p.	15 Helle Taiga (Boreal, semihumid)	Dfc, Dfd (Snow, fully humid, extremely continental)
9 Tundra	16 Polar-Alpine Tundra/Wüste (Arctic, Antarctic, Alpine; humid to arid)	ET
10 Mountains p.p.	5 Oreotropischer Wald (Oreotropical, humid and semihumid) p.p.	Cfb, Csb, Cwb
Transitional between 4/10 and 7/7a	11 Nemorale Trockengehölze (Dry woodlands of the temperate zone)	Chiefly transiton between B and Cs climates

[a] Australia East Coast;
[b] Humid coastal broadleaved deciduous forests: subarctic birch forest of Iceland, western Norway, Kamchatka;
[c] Australia East Coast, New Zealand;
[d] Pacific North America.

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Table 5. Vertical progression of Köppen climate types in Northern Hemisphere mountain ranges.

Lowland	Mid-elevation	High-elevation	Example
Cfa	Cfb	Dfb > Dfc (ET)	S. Caucasus, Appalachian Mts.[a]
Cfb	Dfb	Dfc (ET)	E. Alps
Cfc	Dfc (ET)	ET	W. Scandinavia, Iceland
Cwa	Cwb	Dwb/Dwc (ET)	Himalaya Mts.
Csa/Cfa	Cfb	BSk	Pyrenees
Csa	Csb	? BSk	Pico Almazor (C. Spain), Atlas Mts.
Csa	Cfa	Cfb	Apennine Mts.
Csa	Dsa	Dsb	NW. Alborz Mts.
BSk	Dsa	Dsb	SC. Alborz Mts.
BSk	Dfb (Cfb)	Dfc (ET)	Rocky Mts. (Colorado, Mt. Elbert)
BSh	Csa	Csb, Csc (ET)	W. Hindukush (Tirich Mir)
BSh	Cfa/Cwa	Cfb, Dfc/ET	Nanga Parbat

[a] Highest peak: Dfb.

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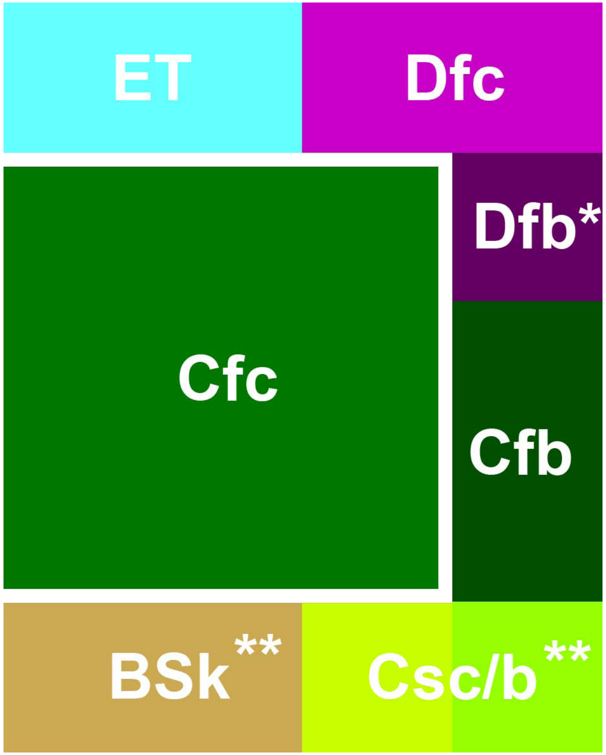

Fig. 1. Cfc Köppen climate type, typical of the coastal regions of modern Iceland, and its neighboring climate types. Note that plant taxa typical of a Cfc climate commonly occur at least in several further, adjacent climate types. (*) No direct contact, (**) direct contact only in Southern Hemisphere.

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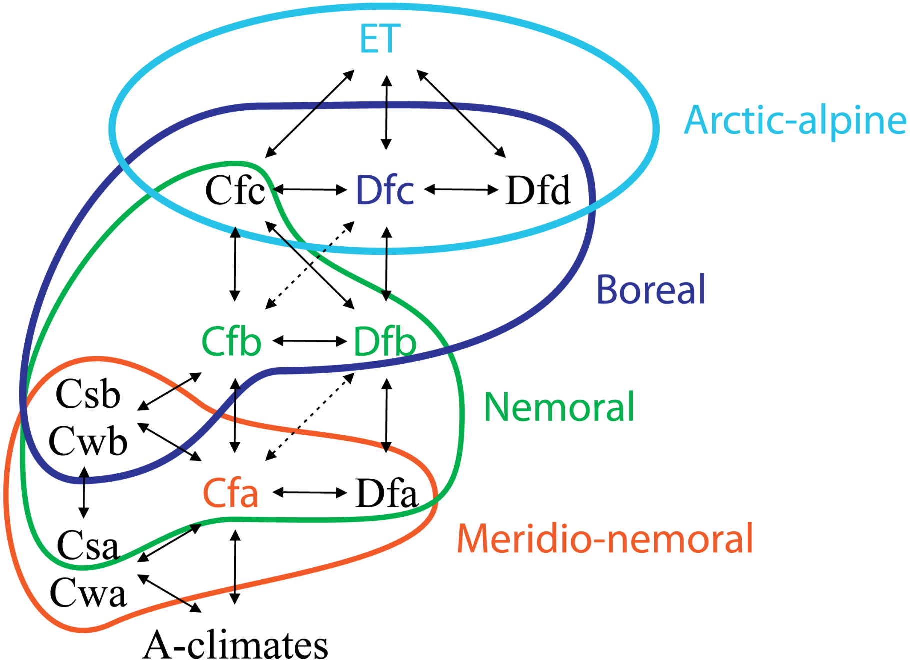

Fig. 2. Circumscription of meridio-nemoral, nemoral, boreal and arctic-alpine elements by Köppen climate types (see also Table 4).

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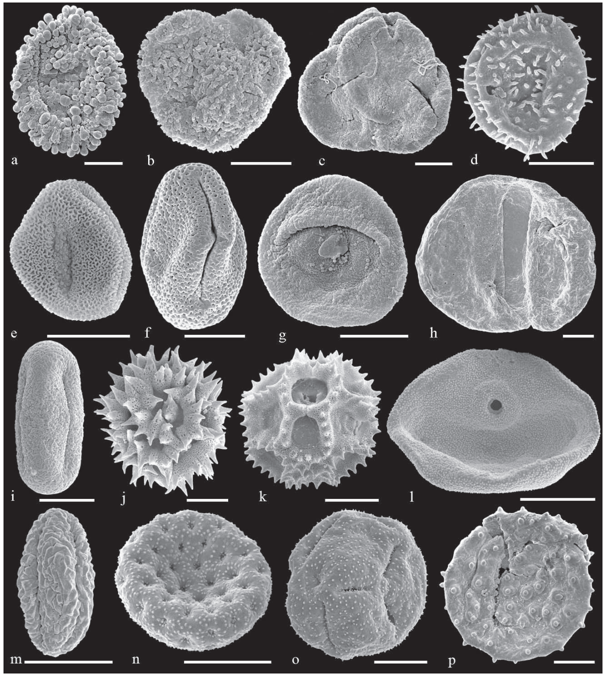

Fig. 3. Floristic turnover in Iceland as illustrated by characteristic pollen types from the 15–0.8 Myr sedimentary rock formations. **(a–h)** Pollen of predominantly woody, warmth-loving plants, 15 and 12 Myr. **(a)** *Ilex* sp., 12 Myr. **(b)** *Viburnum* sp., 12 Myr. **(c)** *Rhododendron* aff. *ponticum* L., 12 Myr. **(d)** *Lemna* sp., 12 Myr. **(e)** *Platanus* subgenus *Platanus*, 15 Myr. **(f)** *Parthenocissus* sp., 15 Myr. **(g)** *Sequoia* sp., 15 Myr. **(h)** *Cathaya* sp., 15 Myr. **(i–p)** Pollen of herbaceous plants, 10 Myr and younger formations. **(i)** Apiaceae, 10 Myr. **(j)** Asteraceae, 10 Myr. **(k)** Asteraceae, 1.1 Myr. **(l)** Poaceae, 0.8 Myr. **(m)** *Fragaria* sp., 1.7 Myr. **(n)** *Chenopodium* sp., 10 Myr. **(o)** *Ranunculus* sp., 10 Myr. **(p)** *Valeriana* sp., 3.8 Myr.

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		Sum of Csa	**Sum of Cfa**	Sum of Cwa	Sum of Csb	Sum of Cfb	Sum of Cwb	Sum of Dfa	Sum of Dwa	Sum of Dfb	Sum of Dwb	Sum of Dwc	**Sum of Cfc**	**Sum of Dfc**	Sum of Dfd	**Sum of ET**
15Ma	43	6	**28**	10	10	28	10	10	4	21	10	4	**3**	**7**	0	**1**
12Ma	43	4	**28**	8	10	27	9	7	4	19	8	4	**2**	**7**	0	**1**
10Ma	43	6	**25**	6	11	**32**	10	10	4	**26**	10	6	**10**	**13**	5	**4**
8Ma	43	2	**31**	7	8	**30**	10	5	3	**26**	8	5	**7**	**10**	2	**2**
7to6Ma	43	2	**23**	5	14	**29**	11	2	2	**27**	9	9	**9**	**16**	2	**2**
5.5Ma	43	2	**17**	2	15	**28**	9	2	0	**30**	11	9	**17**	**24**	4	**9**
4Ma	43	3	**14**	3	10	**32**	8	3	1	**28**	8	6	**20**	**24**	4	**12**
1.7Ma	43	5	**5**	3	8	**28**	3	5	3	**28**	10	5	**33**	**33**	13	**25**
1.1Ma	43	12	**6**	3	12	28	3	6	3	25	3	3	**31**	**34**	9	**22**
0.8Ma	43	3	**0**	3	3	26	3	0	3	23	7	3	**33**	**36**	10	**26**
0Ma	43	6	**3**	1	7	22	1	3	1	23	3	3	**33**	**25**	4	**16**

Fig. 4. The heat map shows the sum of fossil taxa with modern analogues occurring in certain Köppen climate types. Number of taxa scoring for particular climate types was scaled to 43 for all rock units.

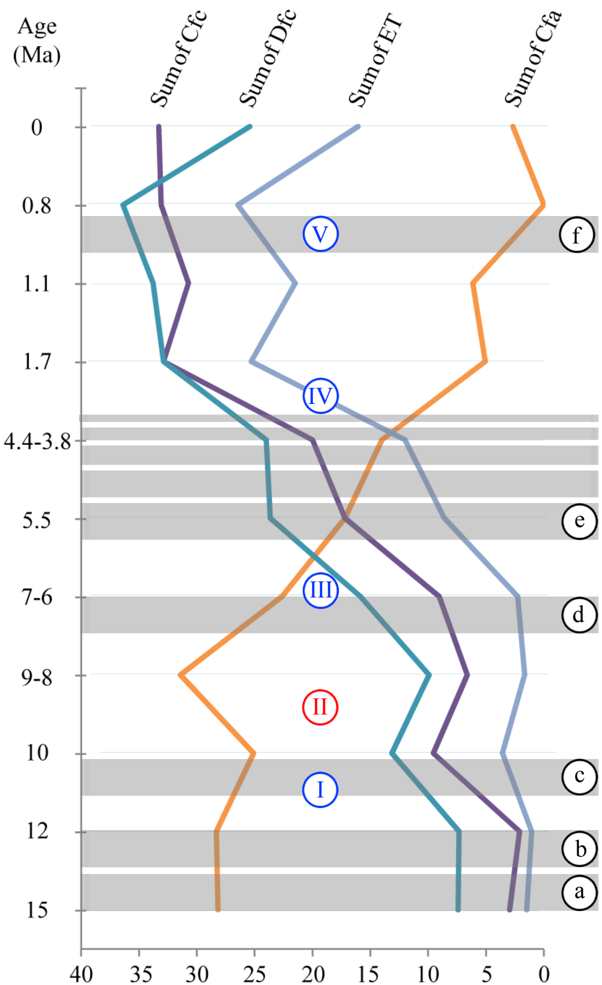

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Fig. 5. Climate change over the past 15 Myr in Iceland based on Köppen signatures of fossil taxa from Iceland (15–0.8 Myr rock units) and the modern flora of Iceland (monocots excluded). Cfa climate: warm temperate, fully humid with hot summers; Cfc: warm temperate, fully humid with cool summers; Dfc: snow climate, fully humid with cool summers; ET: polar tundra climate (Köppen, 1936; Kottek et al., 2006). Number of taxa scoring for particular climate types was scaled to 43 for all rock units. **(a–f)** denote phases of IRD pulses in the Northern Hemisphere: **(a)** glaciation in the northern Barents Sea region and Fram Strait, ODP site 909c at 15–14.5 Myr (Knies and Gaina, 2008), and at 14 Myr in the Fram Strait, ODP sites 908, 909 (Wolf-Welling et al., 1996; Thiede et al., 1998), **(b)** glaciation at 12.6 Myr on the Vöring Plateau, ODP sites 642, 643, 644 (Fronval and Jansen, 1996; Thiede et al., 1998), **(c)** various pulses of increased IRD from Vöring Plateau and Fram Strait beginning at ~ 11–10 Myr (Fronval and Jansen, 1996; Wolf-Welling et al., 1996; Thiede et al., 1998), **(d)** IRD pulses at 7.5–7 Myr off SE Greenland, ODP site 918 (Larsen et al., 1994; St. John and Krissek, 2002), Iceland Plateau, ODP site 907 and Vöring Plateau, ODP sites 642, 643, 644 (Fronval and Jansen, 1996) and Fram Strait, ODP sites 908, 909 (Wolf-Welling et al., 1996; Thiede et al., 1998), **(e)** glaciations starting between 6 and 5 Myr in all areas mentioned previously (Fronval and Jansen, 1996; Wolf-Welling et al., 1996; Thiede et al., 1998; St. John and Krissek, 2002), and **(f)** mid-Pleistocene climate transition at 0.9 Myr. **(I–V)** denote climate shifts inferred from floristic changes and changes in Köppen climate type distribution.

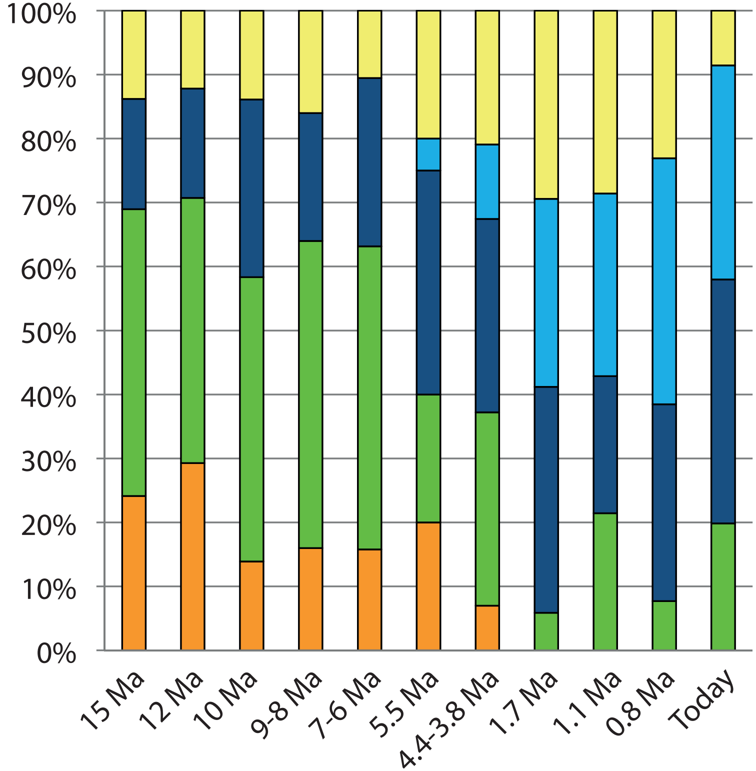

Fig. 6. Proportion of elements ascribed to major vegetation types from fossil plant assemblages and the modern flora of Iceland. Elements are categorized as meridio-nemoral (orange), nemoral (green), boreal (dark blue), arctic-alpine (light blue), and generalists (yellow) based on their specific Köppen signatures.

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		Sum of Cfa	Sum of Cfb	Sum of Cfc	Sum of Dfa	Sum of Dfb	Sum of Dfc	Sum of Cwa	Sum of Cwb	Sum of Csa	Sum of Csb
Colchic Nature Reserve, Cfa	112	76	87	14	18	59	16	11	12	52	48
Lagodekhi, lowland forest, Cfa	112	68	95	11	9	69	13	10	14	33	30
Kirnati, Cfb	112	78	94	16	9	64	16	11	14	43	46
Mt Mtiralla, Cfb	112	61	95	17	9	69	17	9	13	29	34
Borjomi, Dfb	112	63	102	12	7	86	17	7	13	38	36
Bakhmaro, Dfb	112	48	93	3	0	77	16	0	6	10	13
Lagodekhi, subalpine forest, Dfb	112	37	87	15	6	89	27	4	8	19	25

Fig. 7. Köppen climate type distribution and frequency in modern forest communities of humid temperate Georgia, Transcaucasia.

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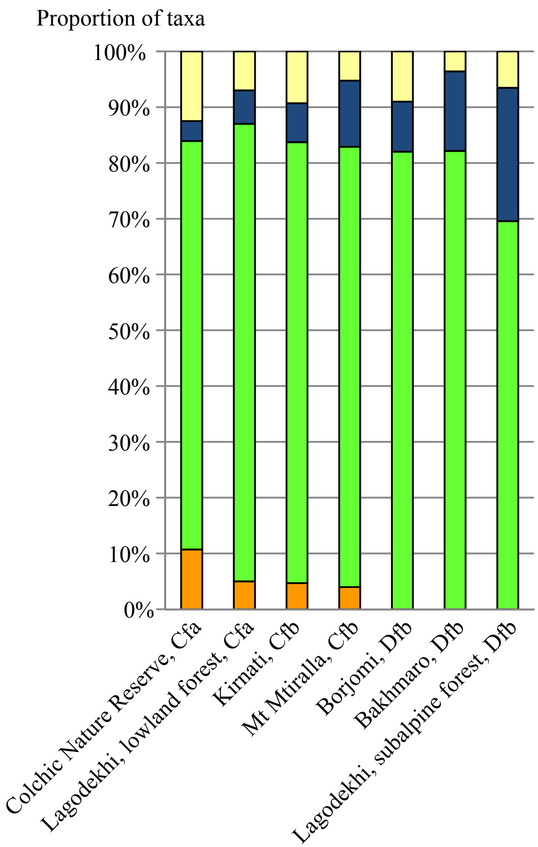

Fig. 8. Proportion of elements ascribed to major vegetation types in modern forest communities of humid temperate Georgia, Transcaucasia. Elements are categorized as meridio-nemoral (orange), nemoral (green), boreal (dark blue), and generalists (yellow) based on their specific Köppen signatures.

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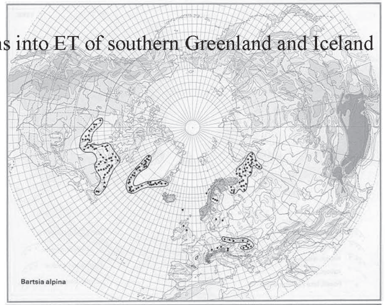
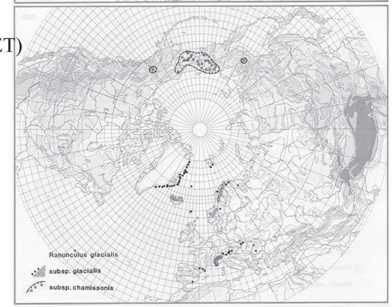
Bartsia alpina L.
Cfc, Dfc, with local extensions into ET of southern Greenland and Iceland
Scored as Cfc, Dfc



Ranunculus glacialis L.
arctic-alpine element (only ET)
Scored as ET



Salix herbacea L.
Cfc, Dfc, and ET
Scored as Cfc, Dfc, ET

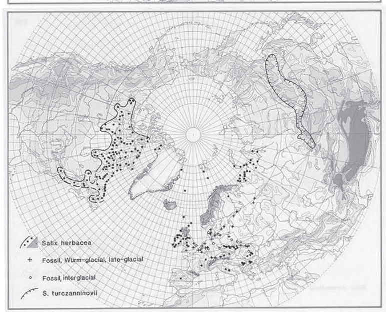


Fig. A1. Distribution maps of three Icelandic plant species with different Köppen signatures (map source: Virtuella Floran; Anderberg and Anderberg, 2010).

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