

# Abrupt Change in Climate and Biotic Systems

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**Fifty years ago**, Willi Dansgaard and colleagues discovered several abrupt climate change events in Greenland during the last glacial period. Since then, several ice cores retrieved from the Greenland ice sheet have verified the existence of 25 abrupt climate warming events now known as Dansgaard–Oeschger events. These events are characterized by a rapid 10–15°C warming over a few decades followed by a stable period of centuries or millennia before a gradual return to full glacial conditions. Similar warming events have been identified in other paleo-archives in the Northern hemisphere. These findings triggered wide interest in abrupt climate change and its impact on biological diversity, but ambiguous definitions have constrained our ability to assign biotic responses to the different types of climate change. Here, we provide a coherent definition for different types of climatic change, including ‘abrupt climate change’, and a summary of past abrupt climate-change events. We then review biotic responses to abrupt climate change, from the genetic to the ecosystem level, and show that abrupt climatic and ecological changes have been instrumental in shaping biodiversity. We also identify open questions, such as what causes species resilience after an abrupt change. However, identifying causal relationships between past climate change and biological responses remains difficult. We need to formalize and unify the definition of abrupt change across disciplines and further investigate past abrupt climate change periods to better anticipate and mitigate the impacts on biodiversity and society wrought by human-made climate change.

## Introduction

Global warming is accelerating and provoking significant impacts on natural and anthropogenic systems [1]. In the recent geological history of our planet, climate change events of comparable magnitude to what the Intergovernmental Panel for Climate Change (IPCC) expects for the end of the century have occurred and have drastically impacted biological systems [2,3]. Scientists from earth sciences to biology are looking at past climatic changes to understand how biodiversity responded and to forecast how biodiversity will react to current global warming [4].

Biological responses to past events of climate change include migrations [5,6], ecological community turnovers [7,8], reorganization of geographical ranges [9,10], changes in population sizes [11,12] as well as extinctions [13,14]. There is, however, significant ambiguity in the scientific literature on the terms used for climatic changes concerning their origin, magnitude, and speed. This ambiguity jeopardizes our ability to assign biodiversity change to climatic changes of different nature [15]. Moreover, definitions for abrupt climate change often do not match between paleoclimatologists and biologists, and it is often loosely defined across the scientific literature, including alternative concepts such as ‘fast’ or ‘rapid change’. This lack of a clear and coherent terminology across disciplines may put the understanding of the ecological consequences of different types of climatic changes at risk [16].

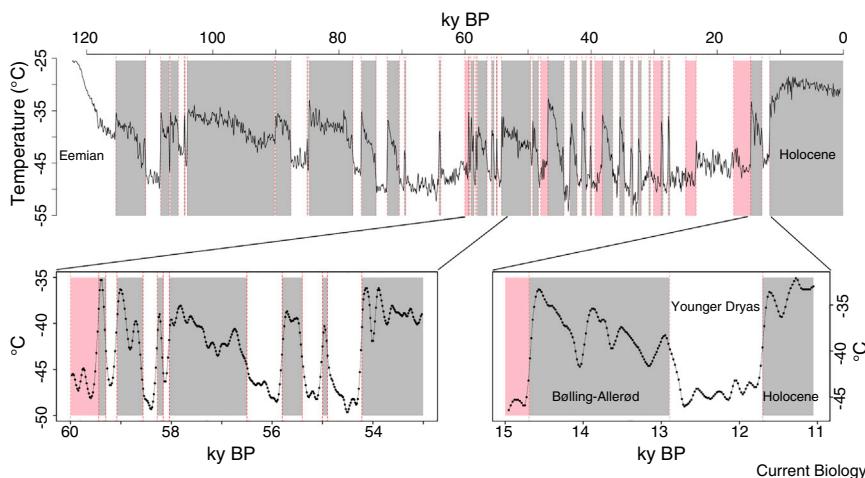
We here present an unambiguous terminology for the topic, by providing definitions of abrupt, rapid and fast climate change as well as abrupt ecological change. Thus, we aim at improving the

assignment of biological responses to events of abrupt climate change and at separating them from those introduced by gradual, fast or rapid climate change. We then summarize biological responses to periods, exclusively, of abrupt climate change, identify gaps in current knowledge, and suggest future lines of investigation to better anticipate future biodiversity dynamics.

## Discovery and Definition of Abrupt Climate Change

In Greenland ice cores,  $\delta^{18}\text{O}$  — the ratio of stable isotopes oxygen-18 ( $^{18}\text{O}$ ) and oxygen-16 ( $^{16}\text{O}$ ), a proxy for temperature — has provided evidence of 25 abrupt warming events, the Dansgaard–Oeschger (D–O) events, which occurred during the last glacial period 115–11.5 thousand years ago (kyr) [17]. The D–O events are characterized by mild climate (interstadial), lasting from a few centuries up to tens of thousands of years, which are interrupted by periods of full glacial conditions (stadials; Figure 1). High-resolution ice-core records show that D–O events begin rapidly, over typically ~50 years [18], while they end more smoothly, over centuries [19]. These temperature changes are associated with reorganizations of atmospheric circulation that may have occurred within periods of one to three years [20]. D–O events have also been identified in paleo-records in Europe, North America or Eastern Asia [21–25], suggesting that D–O events occurred at least on a hemispherical scale. At the onset of D–O events, temperatures in Greenland increased by up to 16°C [26], whereas at lower latitudes the magnitude of the temperature shift was significantly smaller.





**Figure 1. Greenland temperature through the Late Quaternary.**

Top: temperature (y-axis) at the Greenland NGRIP site [18] over the last 120 thousand years (ky BP) in 20 year resolution. Gray shaded periods highlight the Holocene and the D-O warming events (interstadials), as classified by Rasmussen and colleagues [19]. Pink shaded periods indicate Heinrich stadials, the coldest stadial periods that are characterized by events of ice-raftered debris in North Atlantic sediment cores. The red line highlights abrupt climate change, namely the transitions to and from interstadials and the Holocene onset. The Eemian refers to the previous interglacial period. Glacial temperatures are from Kindler *et al.* [26], whereas Holocene temperatures are obtained by linear regression of  $\delta^{18}\text{O}$  data with temperature data. Bottom left: detail of the 60–53,000 year period showing extreme climate variability. Bottom right: the 15–11,000 year deglacial period with indication of the Holocene, Bølling-Allerød and Younger Dryas climatic periods.

The leading hypothesis explaining D-O events is that they are caused by changes in North Atlantic deep-water formation and sea-ice extent. According to this hypothesis, stadials occur during periods of a partial or complete shutdown of the Atlantic Meridional Overturning Circulation (AMOC; Box 1), which brings warm waters towards high latitudes in the North Atlantic [27]. Other climate pulses occurred in the Late Quaternary, including the Younger Dryas cold event and the Bølling-Allerød mild events, whose classification as D-O events is still debated (Figure 1), as well as the Heinrich events that caused cooling of the North Atlantic due to massive ice stream discharges from the Laurentide ice sheet into the North Atlantic [28]. The increased freshwater influx caused by the iceberg discharge that only occurs during stadial periods may have led to a complete shutdown of the AMOC [27]. During the Holocene, minor but still significant centennial-scale perturbations of the climate system occurred at 8.2 kya and 4 kya [29,30].

Although the existence, causes and consequences of abrupt climate change in the Late Quaternary have recently received much attention, the terms ‘rapid’, ‘fast’ and ‘abrupt’ climate change are widely applied and often considered as synonyms. According to the U.S. National Research Council, an abrupt climate change “occurs when the climate system is forced to cross some threshold” [31]. Despite many formal definitions, there has been a consensus that abrupt climate change involves a switch into a new state following a tipping point [32,33]. However, given the interest in these phenomena from other fields of science, including biology, the focus has been on the effects that they unleashed in natural and human systems, hence more comprehensive definitions have been proposed [34,35]. Newer definitions of abrupt climate change also consider the nature of their consequences: for instance, the Synthesis and Assessment Report of U.S. Climate Change Science Program characterizes climate changes as abrupt based on their span and their effect on other systems [35].

We propose here a non-ambiguous terminology, stated originally by Arnell and colleagues [36], considering two relevant aspects of climate change: first, the mechanisms and dynamics of the climate change, and second their time span and magnitude. We propose the term ‘gradual climate change’ for a change

provoked by direct linear forcing, such as variation in solar insolation caused by fluctuations in Earth’s orbit, and the term ‘abrupt climate change’ for when the climate system crosses a tipping point and switches to a new state. Moreover, we propose the use of ‘rapid climate change’ for “a large-scale change in the climate system that takes place over a few decades or less, persists (or is anticipated to persist) for at least a few decades and causes substantial disruptions in human and natural systems”, as defined by the IPCC in 2013 [37]. Abrupt climate change is usually rapid, but not *vice versa*, as rapid climate changes can also be the response of a fast linear forcing [33].

Following this terminology, the Late Pleistocene stadial-interstadial transitions can be considered abrupt events. Moreover, although the current climate change is being described as rapid, it is not clear whether it will lead to an abrupt climate event during this century, although that likelihood will increase within the coming centuries [38,39]. A notable exception may be the disappearance of Arctic summer sea ice, which is likely to occur in the coming decades [37].

#### Biotic Responses to Abrupt Climate Change

The many levels of biological diversity — from genes to organisms to ecosystems — have reacted to past climatic changes by migration and phenotypic or molecular evolution, and when failing, populations and species went locally or even globally extinct (Table 1) [40,41]. It is, however, less known whether those biotic reactions were the consequence of abrupt climate change or of fast, rapid or gradual climate change. Indeed, the ability of climate change to bring about an abrupt ecological change may rely not only on the inherent properties of climate change, but also on the relationship between the climatic conditions and relevant biological thresholds, including regime shifts triggered by linear (non-abrupt) climate forcing and tipping points [42].

Marine records provide a unique window into the velocity and the modality of biotic responses to abrupt climate change. They provide evidence of significant marine species turnover during the last 20,000 years following abrupt climate change. During warm interstadial climate, marine species adapted to those conditions were dominant and reappeared consistently at the beginning of warm climate episodes. However, the exact

**Box 1. Glossary.**

**Atlantic Meridional Overturning Circulation:** the large system of ocean currents that transport warm water from the tropics northward into the North Atlantic, and also southwards colder, deep waters, back to tropical regions of the Atlantic Ocean. The AMOC contributes to the relative warmth of the Northern Hemisphere.

**Bølling-Allerød:** an interstadial period of increasing temperatures and moisture spanning from 14.7 to 12.7 kya.

**Cryptotephra:** volcanic ash sediment that can be transported to distant areas and form sedimentary layers providing isochrons for the precise comparison of paleorecords. They help to reduce the uncertainty of the dating of abrupt change and to enhance the comparability of abrupt change events across sites in different regions of the planet.

**Ice core:** a drilling sample of ice from an ice-sheet or glacier. They are the result of past snowfall accumulation that turned into ice allowing us to trace back in time the chemical composition of the atmosphere and the climatic conditions at annual time resolution over thousands of years, depending on the depth of the core.

**Last Glacial Maximum:** a cold and dry period spanning from 26.5 to 19 kya and featured by the largest extension of the ice-sheets during the Last Glacial period. The development of the ice sheets to their maximum extension happened between 33.0 and 26.5 kya.

**Spatially explicit high-resolution paleoclimatic simulations:** maps of past climatic conditions including parameters such as temperature, rainfall, moisture, winds or surface pressure, and arising from Atmospheric Ocean Circulation Models, AOGCMs, from Regional Climate Model, RCMs, or from statistical downscaling of AOGCMs and RCMs. Both AOGCMs and RCMs are systems of equations simulating the state, behaviour and interactions of the atmosphere and oceans.

**Tipping point:** the critical threshold in a dynamic process or system beyond which a substantial and persistent effect occurs, driving these dynamics or systems to a new state and, on occasion, to irreversible conditions.

**Younger Dryas:** a period of temperature cooling, from 12.8 to 11.7 kya, that was a return to glacial conditions right before the inception of the warmer Holocene.

species composition of ecological communities differed from one warming event to the other. These changes of ecological communities in response to climate warming occurred within a few decades. Benthic foraminifera assemblages shifted from oxic to dysoxic species within less than 40 years and they also experienced regional increases in species diversity within a few decades to a few centuries [43,44].

The re-organization of marine communities, including the dominance of those species best suited to the novel climate conditions without large extinction events, may imply some degree of resilience and capacity for fast adjustment to equilibrium with the environment [45]. Such resilience does not rule out, however, the possibility of biological collapse following events of abrupt climate change and significant declines of certain species. For example, during the Younger Dryas cold event, north-western Atlantic benthic ostracod communities increased in abundance over ~100y, with cold-adapted taxa reaching maximum population levels within one millennium, while the overall diversity of the ecological community decreased and recovered only several thousand years after the event [13]. Moreover, the same abrupt climate change event could provoke opposite patterns across ecological communities: in contrast to the previous example, the Younger Dryas prompted an increase in biological diversity within a tropical Atlantic diatom community, likely due to a higher nutrient supply [46]. Ostracod communities of limited dispersal ability increased in diversity during cold events (Younger Dryas, Heinrich1 and the 8.2 ka event) ashore from Iceland within about 100 years, along with other faunal reorganizations [44].

At first glance, these examples seem to suggest that responses depend on the species and geographical context, making it difficult to generalize marine biotic responses to abrupt climate change and constraining our ability to anticipate them. However, the fossil record also shows synchronous biotic responses to abrupt climate change across different, geographically distant

taxa: ostracod records and foraminifera records taken 5000 km apart show a high degree of temporal correlation in community diversity through the last 20,000 years [44]. Similarly, plankton ecological communities offshore from the Iberian Peninsula show predictable composition shifts over warming periods, in part because of the ability of some species to adapt fast to abrupt changes in sea-surface conditions [47].

Biotic responses to abrupt climate change are also evident in terrestrial environments from populations to ecological communities. Climate-driven expansion and contraction of geographical ranges provoked genetic homogenization, as observed for trees in Central America during the Heinrich events over the last 60,000 years [48], but genetic diversification was occurring as well. Populations within climate refugia were likely to have been isolated during stadial periods, leading to allopatric divergence by genetic drift or local selection. In this sense, the plant and animal diversity of Southern Europe may reflect a history of buffering and isolation from extreme climatic events [49], preventing population collapses and extinction events. Recent high-resolution studies on fossil pollen records show significant responses of plant communities to abrupt climate change [50–54], but also to gradual climate change. Also, gradual climate change has reversed or accelerated vegetation responses triggered by abrupt climate change [54,55]. Moreover, the timing of ecological responses of even geographically close ecological communities is not synchronous: while north of the Alps reforestation began at the onset of the Bølling-Allerød mild events, it occurred 1500 years earlier south of the Alps, as Mediterranean warming was followed by the spread of forests [56].

The survival of species in microrefugia following abrupt climate change was a key resilience mechanism during the last glacial period. South African birds have been shown to have survived Heinrich events by contracting in the Cape region [57], and

**Table 1. Biodiversity change examples under abrupt climate change from individual to ecosystem levels.**

Biological level	Dynamics	Taxa	Marine/lacustrine	Terrestrial plants	Terrestrial animal	<i>Homo sapiens</i>
Genetic	Divergence			[49]**		
Individual	Productivity change	[45]				
	Behavioural change		[99]		[14,100]	[101,102]
Population	Adaptation	[47]				
	Replacement				[63]	
	Abundance variation	[11]	[12,54,103,104]		[62]	[9,105–108]
	Extirpation				[63,109]	[110]
	Range expansion or contraction		[56,60,111,112]			[113]
	Dispersal		[59,60]**, [5,99]		[109]	[6,107,114–118]
	Socio-cultural change					[78,83,106,108,117,119–121]
Species	Extinction				[64,65,122]*	
Community	Turnover	[8,13,43]	[48,50–52,54,55,69,70]		[73]	[110]
	Composition shift	[45,46]	[10,53,55,59,68,123]		[66,67]	
	Competition		[72]			[118]
Ecosystem	Richness fluctuation	[46]			[57]	
	Diversity fluctuation	[44,124]				

\*Contributory effect

\*\*Hypothesized

plants in central Europe endured in small areas with local favourable climatic conditions. [58] From such refugia, species expanded again, in some cases rapidly, such as the altitudinal shifts occurring both in Central Scandinavia and in the north-western Alps [59,60], highlighting the potential of mountains for favouring fast migrations along altitudinal belts and favouring species' survival [61]. Although refugia facilitated the survival of species, abrupt climate change triggered large decimation of terrestrial animal and plant populations, and on occasion extinction dynamics. There is ample evidence of population decimations across paleo-records. In tropical and subtropical regions, abrupt changes in temperature and rainfall provoked large collapses of vertebrate populations, for example a 50-fold population size reduction of two tomato frog populations in Madagascar [62]. The decimation of populations in other systems like in mammal megafauna across temperate and cold regions led to regional replacements of populations by conspecific species, and regional and global extinctions following D-O events. However, it is still debated, as in the case of the woolly mammoth, whether such extinctions were triggered by the events themselves [63,64] or whether humans were the main extinction force [65]. Smaller mammals, on the contrary, were more resilient to extinction because they are able to adapt faster by having shorter generation times or higher reproductive rates, and yet they were also highly sensitive to abrupt climate changes [66,67].

Following abrupt climate change, large shifts occurred in the taxonomic diversity, composition and structure of ecological communities [68,69]. These impacts are recorded across the globe, from the arctic to the tropics, and across plants and animals. In the cold regions of the planet, open tundra shifted to boreal forest in Western Europe during stadial-interstadial transitions and *vice versa*, while in mid-Atlantic North America forest assemblages responded to Heinrich and D-O events by shifting

from subtropical to boreal compositions [50,51,70]; in temperate regions, like in Southern Italy, the onset of the Bølling-Allerød interstadial prompted a switch of a small mammal community from a low diversity state, with the dominance of one species (*Microtus arvalis*), to a higher diversity state [67]. In the tropical lowlands of central America, the dominant climate driver of community turnover was water availability instead of temperature, leading to more severe assemblage variation during droughts caused by Heinrich events [48].

In some cases, ecological communities were able to maintain viable populations under changing climatic conditions and reaching dynamic equilibrium within 100 years after an abrupt climate change [10,69,71], suggesting some degree of resilience. These equilibrium states were maintained through community turnover in favour of species more suited to the novel climate conditions [59], as was the case of fast colonizers and early-successional taxa [10,48]. For instance, *Populus* populations (poplar, aspen, cottonwood) in North America expanded both after the transitions from the Bølling-Allerød interstadial to the Younger Dryas and from the Younger Dryas-to the Holocene; in both cases, they were favoured by the climate-induced decline of competitor taxa [12]. Abrupt environmental changes in the future may generate similarly abrupt changes in interspecific interactions, with ecological communities shifting during climate transition from a temporary period of unstable competition to stable coexistence [72].

Biodiversity has experienced profound changes within a few decades or centuries after events of abrupt climate change. These footprints of abrupt climate change in biodiversity are evident across marine and terrestrial systems, from population to ecosystem level and from the arctic to the tropics. Many of those biodiversity changes were not synchronous and they did not seem to follow regular patterns across biotic systems or

temporal and geographical context, suggesting that there are significant challenges ahead to accurately predict future states of nature under abrupt climate change.

### The Unknowns of Ecosystem Functioning and Tipping Points

We know most about responses to abrupt climate change at the population and community levels, but there are still significant gaps in our knowledge on how ecosystems and their functions, e.g. the sum of energy flows among individuals and species, respond to abrupt climate change. There are some lines of evidence suggesting that even if ecological communities, as for small mammals in the Great Basin, drastically changed during the last 12,000 years, the energy flow in the ecosystems stayed constant, indicating the resilience of energy fluxes to abrupt climate change [73]. However, a further understanding of past ecosystem functioning, including responses of biomass production and nutrient cycling in terrestrial ecosystems, as determined by animal and plant communities, and of the relative role and impact of each ecosystem component is of utmost importance [74], not least to predict future states of the biosphere. In this context, paleo metagenomics and sedimentary ancient DNA [75] may help to fill the gaps in the fossil record when estimating the occurrence, abundance, and biomass of plant and animal taxa. This is likely to yield a more accurate picture of the functioning of past ecosystems under abrupt climate change.

Furthermore, and given the dependence of humans on the resources and services that ecosystems provide, we would expect that abrupt climate changes may have impacted the emergence and demise of societies across history. Certainly, climate change triggered human migrations and abrupt climate change has been proposed to have caused the extinction of Neanderthals [76,77]. There is also robust evidence of the contribution of abrupt climate change to the demise and spread of civilizations [78–84], highlighting the need for modern societies to anticipate and adapt. Recent climate change, even of less worrying nature than past abrupt climate change, has even contributed to armed conflicts (e.g. scarcity of water [85]). As these changes spread across Earth, the services that ecosystems provide may compromise the sustainability of our societies. Moreover, changes in ecosystem functioning due to abrupt climate change may trigger feedbacks between climate and the biosphere. Shifts in the functioning of plankton ecosystems, for instance, may jeopardize the role of oceans as biological pumps, reducing the potential for carbon sequestration in deep waters. Such feedbacks could trigger an accelerating and continued warming, a ‘hothouse Earth’ [1], provoking tipping points and the reinforcement of abrupt changes in climate and the biosphere.

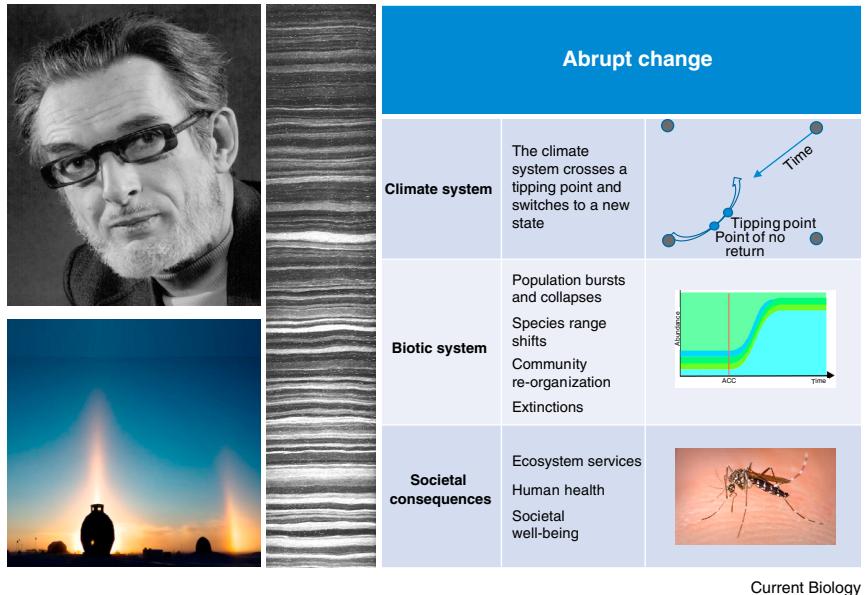
To disentangle the network of reactions across the main components of the Earth System – biosphere, climate, and human societies – during past, recent or upcoming periods of abrupt climate change, we need to accurately estimate the timing of climatic and biological events. Whereas abrupt climate change is well documented in high temporal resolution records, such as ice cores and stalagmites [20,86,87], those archives generally lack proxies of biotic responses. Biotic responses to abrupt climate change since the last glacial maximum are typically documented in records of pollen or foraminifera from terrestrial or marine archives that are often dated by radiocarbon [23,88].

The uncertainties of radiocarbon dating increase with age typically to several hundreds of years during the last glacial period or even more towards the limit of the dating technique at around 40 kya. Furthermore, due to low accumulation rates, many marine and terrestrial archives have a low temporal resolution, reducing the fidelity with which to date biological responses [89]. Increasing the temporal resolution of dating is a major challenge making it difficult if not impossible to obtain precise time lags associated with abrupt climate change, let alone the challenges of synchronizing records with such low dating resolution.

An alternative approach to investigate biotic responses to abrupt climate change is to apply a multi-proxy approach to target both climate and biotic responses in the same marine or terrestrial record. Even if the temporal resolution and the absolute dating uncertainties are large compared to the duration of abrupt climate change events, a well-preserved stratigraphy will ensure the preservation of the sequence of events, and the relative dating uncertainties associated with individual abrupt climate change events may be sufficiently small for estimating their relative timing. In some cases, for instance, the annual banding of lake records may allow setting precise constraints of biotic response times associated with abrupt climate change [88]. Whereas the multi-proxy approach may be applied to key records of exceptionally high temporal resolution, it is often difficult to extend the approach to a large number of records as many of them will often not have the required temporal resolution. Large volcanic eruptions may offer a solution to this challenge. After a volcanic explosion, its traces accumulate over large geographical regions, preferably within the time range of an abrupt climate change. Volcanic synchronization of archives is developing fast and now allows the linking of marine and terrestrial records to ice cores [90]. The technique may have large potential for the last glacial period, but it is time-consuming and may require the identification of cryptotephra, volcanic ash from a single eruption not visible to the naked eye, from distant sources [91].

The development of spatially explicit high-resolution paleoclimatic simulations instead of relying only on paleoclimatic reconstructions from one single site will provide deeper and more meaningful insights into the impacts of abrupt climate change on biological diversity. Such climatic simulations will contribute to explain the role of past and current paleoclimate variability into shaping biodiversity distribution patterns [92] and better forecast future scenarios of biodiversity under climate change. Moreover, paleoenvironmental reconstructions should account for careful comparison of records, and, when aiming to infer cause–effect relationships, accuracy in the dating and in the comparison of dating from different records will be crucial. Chronological uncertainties across paleo-records may impede accurate estimates of the speed at which biodiversity reacted to abrupt climate change [93]. To overcome this limitation, records can be better integrated by deriving their chronology from independent dating and by quantifying the correlation uncertainties, as in the INTIMATE paleo-climatological database [94].

Detecting past tipping points in ecosystem functioning and anticipating how ecosystem functions and services will react to different future events of climate change are of utmost importance. However, significant challenges remain to fully apprehend



**Figure 2.** Fifty years since the discovery of abrupt climate change.

Top left: Willi Dansgaard (1922–2011), who discovered the Dansgaard-Oeschger (D–O) events of the last glacial period from studying water isotopes in ice cores (photo from [125]). Bottom left: Sunset at the EastGRIP ice core drilling site in August 2019 (photo: © NEEM ice core drilling project, [www.neem.ku.dk](http://www.neem.ku.dk)). Center: visual stratigraphy of a 0.5 m long section of the 2.9 km long NGRIP ice core from Northwestern Greenland. The section shows the annual layering across the onset of D–O 19, a 14°C abrupt warming event that occurred in Greenland 73,000 years ago. White layers are related to the dust content of the ice that changes from high values before the onset (lower section) to low values after the onset some 25 years later (upper section); image re-published with permission from [126]. Top right: the Arctic and Antarctic ice sheets, the Atlantic meridional overturning circulation (AMOC) or of the Indian Monsoon are examples of key climatic elements, represented by dark circles in the upper right figure, that may provoke abrupt climate change on regional to global scales. Center right: abrupt climate change triggers biodiversity change (i.e., large changes in the abundance of populations within ecological com-

munities), accelerating on-going impacts for societal sustainability. Bottom right: Asian tiger mosquito, *Aedes albopictus*, spreading across Europe illustrating the spread of tropical diseases out of the tropics due to climate change (photo: CDC/James Gathany).

the type, magnitude and velocity of ecosystem functioning change after abrupt climate change. There is an urgent need to expand the spatio-temporal resolution and extent of multi-proxy studies recording key ecosystem parameters such as biomass, nitrogen cycle or species interactions. The relevance of the knowledge provided by paleo-records on ecosystem functioning and across other levels of biodiversity will be amplified by, first, increasing the accuracy of the dating techniques and, second, improving the temporal and spatial resolution of paleoclimatic simulations for periods of abrupt climatic events.

## Conclusions

The discovery of recent abrupt climate change by Willi Dansgaard and colleagues [95] fifty years ago has influenced our understanding of the Earth system and drawn long-lasting attention to their biotic and societal consequences (Figure 2). By identifying periods of abrupt climate change based on a coherent definition we show that previous episodes of abrupt climate change have shaped current patterns of biological diversity and affected ecological processes [44,48]. The strength of such impacts varied regionally, mirroring the significant spatial variation of past abrupt climate change [21,96], highlighting that knowledge of regional, fast-paced climate history is fundamental for the understanding of how climate controls the diversity of life. Further research should emphasize the role of ecological and evolutionary adaptation, the ability to disperse and colonize fast new regions tracking climatic shifts across fragmented landscapes, or the significance of climatic refugia and meta-population structures. The ability to maintain meta-population structure, through which populations can disperse and colonize new habitats when climatic conditions change abruptly, will be of utmost importance to prevent large losses of biodiversity. However, this adaptation strategy might be severely hampered by the current anthropogenic habitat

fragmentation [97]. Besides, ecosystems out of equilibrium with climate are more likely to experience temporary diversity loss. A continuous state of disturbance, like that induced by human domination on the biosphere, will be likely to severely reduce the resilience of ecosystems to possible abrupt climate change events in the future [98].

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## REFERENCES

1. Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M., Biggs, R., Carpenter, S.R., de Vries, W., de Wit, C.A., et al. (2015). Planetary boundaries: Guiding human development on a changing planet. *Science* 347, 1259855.
2. Mulinza, S., Prange, M., Stuut, J.-B., Zabel, M., Dobeneck, T., von Itambi, A.C., Nizou, J., Schulz, M., and Wefer, G. (2008). Sahel megadroughts triggered by glacial slowdowns of Atlantic meridional overturning. *Paleoceanography* 23, PA4206.
3. Buizert, C., and Schmittner, A. (2015). Southern Ocean control of glacial AMOC stability and Dansgaard-Oeschger interstadial duration. *Paleoceanography* 30, 1595–1612.
4. Nogués-Bravo, D., Rodríguez-Sánchez, F., Orsini, L., de Boer, E., Jansson, R., Morlon, H., Fordham, D.A., and Jackson, S.T. (2018). Cracking the code of biodiversity responses to past climate change. *Trends Ecol. Evol.* 33, 765–776.
5. Müller, U.C., Pross, J. örg, and Bibus, E. (2003). Vegetation response to rapid climate change in central europe during the past 140,000 yr based on evidence from the Füramoos pollen record. *Quaternary Res.* 59, 235–245.
6. Lothrop, J.C., Newby, P.E., Spiess, A.E., and Bradley, J.W. (2011). Paleoindians and the Younger Dryas in the New England-Maritimes Region. *Quatern. Int.* 242, 546–569.

7. Jackson, S.T., Booth, R.K., Reeves, K., Andersen, J.J., Minckley, T.A., and Jones, R.A. (2014). Inferring local to regional changes in forest composition from Holocene macrofossils and pollen of a small lake in central Upper Michigan. *Quat. Sci. Rev.* 98, 60–73.
8. Ampel, L., Wohlfarth, B., Risberg, J., Veres, D., Leng, M.J., and Tillman, P.K. (2010). Diatom assemblage dynamics during abrupt climate change: the response of lacustrine diatoms to Dansgaard–Oeschger cycles during the last glacial period. *J. Paleolimnol.* 44, 397–404.
9. Anderson, D.G., Goodey, A.C., Kennett, J., and West, A. (2011). Multiple lines of evidence for possible Human population decline/settlement reorganization during the early Younger Dryas. *Quatern. Int.* 242, 570–583.
10. Tinner, W., and Kaltenrieder, P. (2005). Rapid responses of high-mountain vegetation to early Holocene environmental changes in the Swiss Alps. *J. Ecol.* 93, 936–947.
11. Pérez-Folgado, M., Sierro, F.J., Flores, J.A., Cacho, I., Grimalt, J.O., Zahn, R., and Shackleton, N. (2003). Western Mediterranean planktonic foraminifera events and millennial climatic variability during the last 70 kyr. *Mar. Micropaleontol.* 48, 49–70.
12. Peros, M.C., Gajewski, K., and Vieu, A.E. (2008). Continental-scale tree population response to rapid climate change, competition and disturbance. *Global Ecol. Biogeogr.* 17, 658–669.
13. Yasuhara, M., Cronin, T.M., deMenocal, P.B., Okahashi, H., and Linsley, B.K. (2008). Abrupt climate change and collapse of deep-sea ecosystems. *Proc. Natl. Acad. Sci. USA* 105, 1556–1560.
14. Schmeisser, R.L., Loope, D.B., and Wedin, D.A. (2009). Clues to the medieval destabilization of the nebraska sand hills, usa, from ancient pocket gopher burrows. *Palaeos* 24, 809–817.
15. Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., and Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecol. Lett.* 15, 365–377.
16. Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., et al. (2014). Climate change 2013. In *The Physical Science Basis Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* Cambridge (University Press), pp. 1447–1466.
17. Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahl-Jensen, D., Gundestrup, N.S., Hammer, C.U., Hvidberg, C.S., Steffensen, J.P., Sveinbjörnsdóttir, A.E., Jouzel, J., et al. (1993). Evidence for general instability of past climate from a 250-kyr ice-core record. *Nature* 364, 218–220.
18. Andersen, K.K., Azuma, N., Barnola, J.-M., Bigler, M., Biscaye, P., Caillet, N., Chappellaz, J., Clausen, H.B., Dahl-Jensen, D., Fischer, H., et al. (2004). High-resolution record of Northern Hemisphere climate extending into the last interglacial period. *Nature* 431, 147–151.
19. Rasmussen, S.O., Bigler, M., Blockley, S.P., Blunier, T., Buchardt, S.L., Clausen, H.B., Cvijanovic, I., Dahl-Jensen, D., Johnsen, S.J., Fischer, H., et al. (2014). A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. *Quat. Sci. Rev.* 106, 14–28.
20. Steffensen, J.P., Andersen, K.K., Bigler, M., Clausen, H.B., Dahl-Jensen, D., Fischer, H., Goto-Azuma, K., Hansson, M., Johnsen, S.J., Jouzel, J., et al. (2008). High-resolution Greenland ice core data show abrupt climate change happens in few years. *Science* 321, 680–684.
21. Deplazes, G., Lückge, A., Peterson, L.C., Timmermann, A., Hamann, Y., Hughen, K.A., Röhle, U., Laj, C., Cane, M.A., Sigman, D.M., et al. (2013). Links between tropical rainfall and North Atlantic climate during the last glacial period. *Nat. Geosci.* 6, 213–217.
22. Voelker, A.H.L. (2002). Global distribution of centennial-scale records for Marine Isotope Stage (MIS) 3: a database. *Quat. Sci. Rev.* 21, 1185–1212.
23. Moreno, A., Svensson, A., Brooks, S.J., Connor, S., Engels, S., Fletcher, W., Genty, D., Heiri, O., Labuhn, I., Persouli, A., et al. (2014). A compilation of Western European terrestrial records 60–8 ka BP: towards an understanding of latitudinal climatic gradients. *Quat. Sci. Rev.* 106, 167–185.
24. Shakun, J.D., and Carlson, A.E. (2010). A global perspective on Last Glacial Maximum to Holocene climate change. *Quat. Sci. Rev.* 29, 1801–1816.
25. Cosford, J., Qing, H., Yuan, D., Zhang, M., Holmde, C., Patterson, W., and Hai, C. (2008). Millennial-scale variability in the Asian monsoon: Evidence from oxygen isotope records from stalagmites in southeastern China. *Palaeogeogr. Palaeocl.* 266, 3–12.
26. Kindler, P., Guillec, M., Baumgartner, M., Schwander, J., Landais, A., and Leuenberger, M. (2014). Temperature reconstruction from 10 to 120 kyr b2k from the NGRIP ice core. *Clim. Past* 10, 887–902.
27. Rahmstorf, S. (2002). Ocean circulation and climate during the past 120,000 years. *Nature* 419, 207–214.
28. Andrews, J.T., and Voelker, A.H.L. (2018). “Heinrich events” (& sediments): A history of terminology and recommendations for future usage. *Quaternary Sci. Rev.* 187, 31–40.
29. Walker, M.J.C., Berkelhammer, M., Björck, S., Cwynar, L.C., Fisher, D.A., Long, A.J., Lowe, J.J., Newnham, R.M., Rasmussen, S.O., and Weiss, H. (2012). Formal subdivision of the Holocene Series/Epoch: a Discussion Paper by a Working Group of INTIMATE (Integration of ice-core, marine and terrestrial records) and the Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy). *J. Quat. Sci.* 27, 649–659.
30. Cohen, K.M., Finney, S.C., Gibbard, P.L., and Fan, J.-X. (2013). The ICS International Chronostratigraphic Chart. *Episodes* 36, 199–204.
31. National Research Council. (2001). *Abrupt Climate Change: Inevitable Surprises* (National Academies Press).
32. Alley, R.B., Marotzke, J., Nordhaus, W.D., Overpeck, J.T., Peteet, D.M., Pielke, R.A., Pierrehumbert, R.T., Rhines, P.B., Stocker, T.F., Talley, L.D., et al. (2003). Abrupt climate change. *Science* 299, 2005–2010.
33. Clark, P.U., Pisias, N.G., Stocker, T.F., and Weaver, A.J. (2002). The role of the thermohaline circulation in abrupt climate change. *Nature* 415, 863–869.
34. National Research Council. (2013). *Abrupt Impacts of Climate Change: Anticipating Surprises* (National Academies Press).
35. Clark PU. Final Report, CCSP Synthesis and Assessment Product 3–4. Available at: [http://geodesy.unr.edu/hanspeterplag/library/webpages/CCSP\\_2008.htm](http://geodesy.unr.edu/hanspeterplag/library/webpages/CCSP_2008.htm). [Accessed September 3, 2019].
36. Arnell, N.W., Tompkins, E.L., and Adger, W.N. (2005). Eliciting information from experts on the likelihood of rapid climate change. *Risk Anal.* 25, 1419–1431.
37. Intergovernmental Panel on Climate Change. (2014). *Climate Change 2013 – The Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge University Press). <https://doi.org/10.1017/CBO9781107415324>.
38. Hu, A., Meehl, G.A., Han, W., and Yin, J. (2009). Transient response of the MOC and climate to potential melting of the Greenland Ice Sheet in the 21st century. *Geophys. Res. Lett.* 36, L10707.
39. Delworth, L., Clark, U., Holland, M., Johns, E., Kuhlbrodt, T., Lynch-Stieglitz, J., Morrill, C., Seager, R., Weaver, J., and Zhang, R. (2008). The potential for abrupt change in the Atlantic Meridional Overturning Circulation. *Abrupt Clim. Chan.* 258–359.
40. Lorenzen, E.D., Nogués-Bravo, D., Orlando, L., Weinstock, J., Binladen, J., Marske, K.A., Ugan, A., Borregaard, M.K., Gilbert, M.T.P., Nielsen, R., et al. (2011). Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature* 479, 359–364.
41. Davis, M.B., Shaw, R.G., and Etterson, J.R. (2005). Evolutionary Responses to Changing Climate. *Ecology* 86, 1704–1714.
42. Williams, J.W., Blois, J.L., and Shuman, B.N. (2011). Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary. *J. Ecol.* 99, 664–677.
43. Cannariato, K.G., Kennett, J.P., and Behl, R.J. (1999). Biotic response to late Quaternary rapid climate switches in Santa Barbara Basin: Ecological and evolutionary implications. *Geology* 27, 63–66.

44. Yasuhara, M., Okahashi, H., Cronin, T.M., Rasmussen, T.L., and Hunt, G. (2014). Response of deep-sea biodiversity to abrupt deglacial and Holocene climate changes in the North Atlantic Ocean. *Global Ecol. Biogeogr.* 23, 957–967.
45. McKay, C.L., Filipsson, H.L., Romero, O.E., Stuut, J.-B.W., and Donner, B. (2014). Pelagic–benthic coupling within an upwelling system of the subtropical northeast Atlantic over the last 35 ka BP. *Quat. Sci. Rev.* 106, 299–315.
46. Cermeño, P., Marañón, E., and Romero, O.E. (2013). Response of marine diatom communities to Late Quaternary abrupt climate changes. *J. Plankton Res.* 35, 12–21.
47. Eynaud, F., Londeix, L., Penaud, A., Sanchez-Goni, M.-F., Oliveira, D., Desprat, S., and Turon, J.-L. (2016). Dinoflagellate cyst population evolution throughout past interglacials: Key features along the Iberian margin and insights from the new IODP Site U1385 (Exp 339). *Global Plant Change* 136, 52–64.
48. Correa-Metrio, A., Bush, M.B., Hodell, D.A., Brenner, M., Escobar, J., and Guilderson, T. (2012). The influence of abrupt climate change on the ice-age vegetation of the Central American lowlands. *J. Biogeogr.* 39, 497–509.
49. Tzedakis, P.C., Lawson, I.T., Frogley, M.R., Hewitt, G.M., and Preece, R.C. (2002). Buffered tree population changes in a quaternary refugium: evolutionary implications. *Science* 297, 2044–2047.
50. Heikkilä, M., Fontana, S.L., and Seppä, H. (2009). Rapid Last Glacial tree population dynamics and ecosystem changes in the eastern Baltic region. *J. Quat. Sci.* 24, 802–815.
51. Litwin, R.J., Smoot, J.P., Pavich, M.J., Markewich, H.W., Brook, G., and Durka, N.J. (2013). 100,000-year-long terrestrial record of millennial-scale linkage between eastern North American mid-latitude paleovegetation shifts and Greenland ice-core oxygen isotope trends. *Quat. Res.* 80, 291–315.
52. Seddon, A.W., Macias-Fauria, M., and Willis, K.J. (2015). Climate and abrupt vegetation change in Northern Europe since the last deglaciation. *Holocene* 25, 25–36.
53. Shichi, K., Takahara, H., Hase, Y., Watanabe, T., Nara, F.W., Nakamura, T., Tani, Y., and Kawai, T. (2013). Vegetation response in the southern Lake Baikal region to abrupt climate events over the past 33 calkyr. *Paleogeogr. Palaeoclimatol. Palaeoecol.* 375, 70–82.
54. Shuman, B.N., Newby, P., and Donnelly, J.P. (2009). Abrupt climate change as an important agent of ecological change in the Northeast U.S. throughout the past 15,000 years. *Quat. Sci. Rev.* 28, 1693–1709.
55. Correa-Metrio, A., Bush, M.B., Cabrera, K.R., Sully, S., Brenner, M., Hodell, D.A., Escobar, J., and Guilderson, T. (2012). Rapid climate change and no-analog vegetation in lowland Central America during the last 86,000 years. *Quat. Sci. Rev.* 38, 63–75.
56. Samartin, S., Heiri, O., Lotter, A.F., and Tinner, W. (2012). Climate warming and vegetation response after Heinrich event 1 (16 000 cal yr BP) in Europe south of the Alps. *Clim. Past.* 8, 1913–1927.
57. Huntley, B., Collingham, Y.C., Singarayer, J.S., Valdes, P.J., Barnard, P., Midgley, G.F., Altweig, R., and Ohlemüller, R. (2016). Explaining patterns of avian diversity and endemism: climate and biomes of southern Africa over the last 140,000 years. *J. Biogeogr.* 43, 874–886.
58. Birks, H.J.B., and Willis, K.J. (2008). Alpines, trees, and refugia in Europe. *Plant Ecol. Div.* 1, 147–160.
59. Paus, A., Velle, G., and Berge, J. (2011). The Last Glacial and early Holocene vegetation and environment in the Dovre mountains, central Norway, as signalled in two Last Glacial nunatak lakes. *Quat. Sci. Rev.* 30, 1780–1796.
60. Blarquez, O., Carcaillet, C., Bremond, L., Mourier, B., and Radakovitch, O. (2010). Trees in the subalpine belt since 11 700 cal. BP: origin, expansion and alteration of the modern forest. *Holocene* 20, 139–146.
61. Sonne, J., Martín González, A.M., Maruyama, P.K., Sandel, B., Vizentini-Bugoni, J., Schleuning, M., Abramczyk, S., Alarcón, R., Araújo, A.C., Araújo, P.F., et al. (2016). High proportion of smaller ranged hummingbird species coincides with ecological specialization across the Americas. *Proc. R. Soc. B.* 283, 20152512.
62. Orozco-Terwengel, P., Andreone, F., Louis, E., and Vences, M. (2013). Mitochondrial introgressive hybridization following a demographic expansion in the tomato frogs of Madagascar, genus *Dyscophus*. *Mol. Ecol.* 22, 6074–6090.
63. Cooper, A., Turney, C., Hughen, K.A., Brook, B.W., McDonald, H.G., and Bradshaw, C.J.A. (2015). Abrupt warming events drove Late Pleistocene Holarctic megafaunal turnover. *Science* 349, 602–606.
64. Mann, D.H., Groves, P., Gaglioti, B.V., and Shapiro, B.A. (2019). Climate-driven ecological stability as a globally shared cause of Late Quaternary megafaunal extinctions: the Plaids and Stripes Hypothesis. *Bio. Rev.* 94, 328–352.
65. Araújo, B.B.A., Oliveira-Santos, L.G.R., Lima-Ribeiro, M.S., Diniz-Filho, J.A.F., and Fernandez, F.A.S. (2017). Bigger kill than chill: The uneven roles of humans and climate on late Quaternary megafaunal extinctions. *Quatern. Int.* 431, 216–222.
66. Blois, J.L., McGuire, J.L., and Hadly, E.A. (2010). Small mammal diversity loss in response to late-Pleistocene climatic change. *Nature* 465, 771–774.
67. Berto, C., Boscato, P., Boschin, F., Luzi, E., and Ronchitelli, A. (2017). Paleoenvironmental and paleoclimatic context during the Upper Palaeolithic (late Upper Pleistocene) in the Italian Peninsula. The small mammal record from Grotta Paglicci (Rignano Garganico, Foggia, Southern Italy). *Quat. Sci. Rev.* 168, 30–41.
68. Nolan, C., Overpeck, J.T., Allen, J.R.M., Anderson, P.M., Betancourt, J.L., Binney, H.A., Brewer, S., Bush, M.B., Chase, B.M., Cheddadi, R., et al. (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Science* 361, 920–923.
69. Tinner, W., and Lotter, A.F. (2001). Central European vegetation response to abrupt climate change at 8.2 ka. *Geology* 29, 551–554.
70. Fletcher, W.J., Sánchez Goñi, M.F., Allen, J.R.M., Cheddadi, R., Combourieu-Nebout, N., Huntley, B., Lawson, I., Londeix, L., Magri, D., Margari, V., et al. (2010). Millennial-scale variability during the last glacial in vegetation records from Europe. *Quat. Sci. Rev.* 29, 2839–2864.
71. Prentice, I.C., Bartlein, P.J., and Webb, T. (1991). Vegetation and climate change in eastern North America since the Last Glacial Maximum. *Ecology* 72, 2038–2056.
72. Jeffers, E.S., Bonsall, M.B., Brooks, S.J., and Willis, K.J. (2011). Abrupt environmental changes drive shifts in tree–grass interaction outcomes. *J. Ecol.* 99, 1063–1070.
73. Terry, R.C., and Rowe, R.J. (2015). Energy flow and functional compensation in Great Basin small mammals under natural and anthropogenic environmental change. *Proc. Natl. Acad. Sci. USA* 112, 9656–9661.
74. Jeffers, E.S., Whitehouse, N.J., Lister, A., Plunkett, G., Barratt, P., Smyth, E., Lamb, P., Dee, M.W., Brooks, S.J., Willis, K.J., et al. (2018). Plant controls on Late Quaternary whole ecosystem structure and function. *Ecol. Lett.* 21, 814–825.
75. Birks, H.J.B., and Birks, H.H. (2016). How have studies of ancient DNA from sediments contributed to the reconstruction of Quaternary floras? *New Phytol.* 209, 499–506.
76. Stewart, J.R., and Stringer, C.B. (2012). Human evolution out of Africa: the role of refugia and climate change. *Science* 335, 1317–1321.
77. deMenocal, P.B. (2001). Cultural responses to climate change during the Late Holocene. *Science* 292, 667–673.
78. Cullen, H.M., deMenocal, P.B., Hemming, S., Hemming, G., Brown, F.H., Guilderson, T., and Sirocko, F. (2000). Climate change and the collapse of the Akkadian empire: Evidence from the deep sea. *Geology* 28, 379–382.
79. Douglas, P.M.J., Demarest, A.A., Brenner, M., and Canuto, M.A. (2016). Impacts of climate change on the collapse of lowland Maya civilization. *Annu. Rev. Earth. Planet. Sci.* 44, 613–645.

80. Sigl, M., Winstrup, M., McConnell, J.R., Welten, K.C., Plunkett, G., Ludlow, F., Büntgen, U., Caffee, M., Chellman, N., Dahl-Jensen, D., et al. (2015). Timing and climate forcing of volcanic eruptions for the past 2,500 years. *Nature* 523, 543–549.
81. Büntgen, U., Tegel, W., Nicolussi, K., McCormick, M., Frank, D., Trouet, V., Kaplan, J.O., Herzig, F., Heussner, K.-U., Wanner, H., et al. (2011). 2500 years of European climate variability and human susceptibility. *Science* 331, 578–582.
82. McCormick, M., Büntgen, U., Cane, M.A., Cook, E.R., Harper, K., Huybers, P., Litt, T., Manning, S.W., Mayewski, P.A., More, A.F.M., et al. (2012). Climate change during and after the Roman Empire: reconstructing the past from scientific and historical evidence. *J. Interdiscip. Hist.* 43, 169–220.
83. Büntgen, U., Myglan, V.S., Ljungqvist, F.C., McCormick, M., Di Cosmo, N., Sigl, M., Jungclaus, J., Wagner, S., Krusic, P.J., Esper, J., et al. (2016). Cooling and societal change during the Late Antique Little Ice Age from 536 to around 660. *Nat. Geosci.* 9, 231–236.
84. Fei, J., Zhou, J., and Hou, Y. (2007). Circa a.d. 626 volcanic eruption, climatic cooling, and the collapse of the Eastern Turkic Empire. *Climatic Change* 81, 469–475.
85. Mach, K.J., Kraan, C.M., Adger, W.N., Buhagia, H., Burke, M., Fearon, J.D., Field, C.B., Hendrix, C.S., Maystadt, J.-F., O'Loughlin, J., et al. (2019). Climate as a risk factor for armed conflict. *Nature* 571, 193–197.
86. Wang, Y.J., Cheng, H., Edwards, R.L., An, Z.S., Wu, J.Y., Shen, C.-C., and Dorale, J.A. (2001). A high-resolution absolute-dated Late Pleistocene monsoon record from Hulu Cave, China. *Science* 294, 2345–2348.
87. Adolphi, F., Bronk Ramsey, C., Erhardt, T., Edwards, R.L., Cheng, H., Turney, C.S.M., Cooper, A., Svensson, A., Rasmussen, S.O., Fischer, H., et al. (2018). Connecting the Greenland ice-core and U/Th timescales via cosmogenic radionuclides: testing the synchronicity of Dansgaard-Oeschger events. *Clim. Past.* 14, 1755–1781.
88. Brauer, A., Hajdas, I., Blockley, S.P.E., Bronk Ramsey, C., Christl, M., Ivy-Ochs, S., Mosley, G.E., Nowaczyk, N.N., Rasmussen, S.O., Roberts, H.M., et al. (2014). The importance of independent chronology in integrating records of past climate change for the 60–8 ka INTIMATE time interval. *Quat. Sci. Rev.* 106, 47–66.
89. Nogués-Bravo, D., Veloz, S., Holt, B.G., Singarayer, J., Valdes, P., Davis, B., Brewer, S.C., Williams, J.W., and Rahbek, C. (2016). Amplified plant turnover in response to climate change forecast by Late Quaternary records. *Nat. Clim. Change* 6, 1115–1119.
90. Lowe, J.J., Ramsey, C.B., Housley, R.A., Lane, C.S., and Tomlinson, E.L. (2015). The RESET project: constructing a European tephra lattice for refined synchronisation of environmental and archaeological events during the last c. 100 ka. *Quat. Sci. Rev.* 118, 1–17.
91. Davies, S.M. (2015). Cryptotephra: the revolution in correlation and precision dating. *J. Quat. Sci.* 30, 114–130.
92. Fordham, D.A., Saltré, F., Brown, S.C., Mellin, C., and Wigley, T.M.L. (2018). Why decadal to century timescale palaeoclimate data are needed to explain present-day patterns of biological diversity and change. *Glob. Change Biol.* 24, 1371–1381.
93. Blaauw, M. (2012). Out of tune: the dangers of aligning proxy archives. *Quat. Sci. Rev.* 36, 38–49.
94. Bronk Ramsey, C., Albert, P., Blockley, S., Hardiman, M., Lane, C., Macleod, A., Matthews, I.P., Muscheler, R., Palmer, A., and Staff, R.A. (2014). Integrating timescales with time-transfer functions: a practical approach for an INTIMATE database. *Quat. Sci. Rev.* 106, 67–80.
95. Kröel-Dulay, G., Ransijn, J., Schmidt, I.K., Beier, C., De Angelis, P., de Dato, G., Dukes, J.S., Emmett, B., Estiarte, M., Garadnai, J., et al. (2015). Increased sensitivity to climate change in disturbed ecosystems. *Nat. Commun.* 6, 6682.
96. Dansgaard, W., Johnsen, S.J., Møller, J., and Langway, C.C. (1969). One thousand centuries of climatic record from Camp Century on the Greenland Ice Sheet. *Science* 166, 377–380.
97. Jennerjahn, T.C., Ittekkot, V., Arz, H.W., Behling, H., Pätzold, J., and Werner, G. (2004). Asynchronous terrestrial and marine signals of climate change during Heinrich events. *Science* 306, 2236–2239.
98. Hof, C., Levinsky, I., Araújo, M.B., and Rahbek, C. (2011). Rethinking species' ability to cope with rapid climate change. *Glob. Change Biol.* 17, 2987–2990.
99. Giampoudakis, K., Marske, K.A., Borregaard, M.K., Ugan, A., Singarayer, J.S., Valdes, P.J., Rahbek, C., and Nogués-Bravo, D. (2017). Niche dynamics of Palaeolithic modern humans during the settlement of the Palearctic. *Global Ecol. Biogeogr.* 26, 359–370.
100. Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B., and Sheldon, B.C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* 320, 800–803.
101. Lanoë, F.B., Reuther, J.D., Holmes, C.E., and Hodgins, G.W.L. (2017). Human paleoecological integration in subarctic eastern Beringia. *Quat. Sci. Rev.* 175, 85–96.
102. Rössner, C., Deckers, K., Benz, M., Özkan, V., and Riehl, S. (2018). Subsistence strategies and vegetation development at Aceramic Neolithic Körtik Tepe, southeastern Anatolia, Turkey. *Veget. Hist. Archaeobot.* 27, 15–29.
103. Oswald, W.W., and Foster, D.R. (2012). Middle-Holocene dynamics of *Tsuga canadensis* (eastern hemlock) in northern New England, USA. *Holocene* 22, 71–78.
104. Seppä, H., Birks, H.J.B., Giesecke, T., Hammarlund, D., Alenius, T., Antonsson, K., Bjune, A.E., Heikkilä, M., MacDonald, G.M., Ojala, A.E.K., et al. (2007). Spatial structure of the 8200 cal yr BP event in northern Europe. *Clim. Past* 3, 225–236.
105. Timmermann, A., and Friedrich, T. (2016). Late Pleistocene climate drivers of early human migration. *Nature* 538, 92–95.
106. Ziegler, M., Simon, M.H., Hall, I.R., Barker, S., Stringer, C., and Zahn, R. (2013). Development of Middle Stone Age innovation linked to rapid climate change. *Nat. Commun.* 4, 1905.
107. Geel, B.V., Buurman, J., and Waterbolk, H.T. (1996). Archaeological and palaeoecological indications of an abrupt climate change in The Netherlands, and evidence for climatological teleconnections around 2650 BP. *J. Quat. Sci.* 11, 451–460.
108. Lillios, K.T., Blanco-González, A., Drake, B.L., and López-Sáez, J.A. (2016). Mid-late Holocene climate, demography, and cultural dynamics in Iberia: A multi-proxy approach. *Quat. Sci. Rev.* 135, 138–153.
109. Ukkonen, P., Aaris-Sørensen, K., Arppe, L., Clark, P.U., Daugnora, L., Lister, A.M., Löugas, L., Seppä, H., Sommer, R.S., Stuart, A.J., et al. (2011). Woolly mammoth (*Mammuthus primigenius* Blum.) and its environment in northern Europe during the last glaciation. *Quat. Sci. Rev.* 30, 693–712.
110. Shea, J.J. (2008). Transitions or turnovers? Climatically-forced extinctions of *Homo sapiens* and Neanderthals in the east Mediterranean Levant. *Quat. Sci. Rev.* 27, 2253–2270.
111. Bartish, I.V., Kadereit, J.W., and Comes, H.P. (2006). Late Quaternary history of Hippophaë rhamnoides L. (Elaeagnaceae) inferred from chalcone synthase intron (Chsi) sequences and chloroplast DNA variation. *Mol. Ecol.* 15, 4065–4083.
112. Patsiou, T.S., Conti, E., Zimmermann, N.E., Theodoridis, S., and Randin, C.F. (2014). Topo-climatic microrefugia explain the persistence of a rare endemic plant in the Alps during the last 21 millennia. *Glob. Change Biol.* 20, 2286–2300.
113. Nakazawa, Y., Iwase, A., Akai, F., and Izuho, M. (2011). Human responses to the Younger Dryas in Japan. *Quatern. Int.* 242, 416–433.
114. Wooller, M.J., Saulnier-Talbot, E., Potter, B.A., Belmecheri, S., Bigelow, N., Choy, K., Cwynar, L.C., Davies, K., Graham, R.W., Kurek, J., et al. (2018). A new terrestrial palaeoenvironmental record from the Bering Land Bridge and context for human dispersal. *R. Soc. Open Sci.* 5, 180145.
115. González-Sampériz, P., Utrilla, P., Mazo, C., Valero-Garcés, B., Sopena, M.C., Morellón, M., Sebastián, M., Moreno, A., and Martínez-Bea, M. (2009). Patterns of human occupation during the early Holocene in the Central Ebro Basin (NE Spain) in response to the 8.2 ka climatic event. *Quat. Res.* 71, 121–132.

116. Cortés Sánchez, M., Jiménez Espejo, F.J., Simón Vallejo, M.D., Gibaja Bao, J.F., Carvalho, A.F., Martínez-Ruiz, F., Gamiz, M.R., Flores, J.-A., Paytan, A., López Sáez, J.A., et al. (2012). The Mesolithic–Neolithic transition in southern Iberia. *Quat. Res.* **77**, 221–234.
117. Bradtmöller, M., Pastoors, A., Weninger, B., and Weniger, G.-C. (2012). The repeated replacement model – Rapid climate change and population dynamics in Late Pleistocene Europe. *Quatern. Int.* **247**, 38–49.
118. Müller, U.C., Pross, J., Tzedakis, P.C., Gamble, C., Kotthoff, U., Schmiedl, G., Wulf, S., and Christanis, K. (2011). The role of climate in the spread of modern humans into Europe. *Quat. Sci. Rev.* **30**, 273–279.
119. Clarke, J., Brooks, N., Banning, E.B., Bar-Matthews, M., Campbell, S., Clare, L., Cremaschi, M., di Lernia, S., Drake, N., Gallinaro, M., et al. (2016). Climatic changes and social transformations in the Near East and North Africa during the ‘long’ 4th millennium BC: A comparative study of environmental and archaeological evidence. *Quat. Sci. Rev.* **136**, 96–121.
120. Bonsall, C., Macklin, M.G., Anderson, D.E., and Payton, R.W. (2002). Climate change and the adoption of agriculture in north-west Europe. *Eur. J. Archeo.* **5**, 9–23.
121. Borrell, F., Junno, A., and Barceló, J.A. (2015). Synchronous environmental and cultural change in the emergence of agricultural economies 10,000 years ago in the Levant. *PLoS One* **10**, e0134810.
122. Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L., and Shabel, A.B. (2004). Assessing the causes of Late Pleistocene extinctions on the continents. *Science* **306**, 70–75.
123. Fletcher, W.J., Sanchez Goñi, M.F., Peyron, O., and Dormoy, I. (2010). Abrupt climate changes of the last deglaciation detected in a Western Mediterranean forest record. *Clim. Past.* **6**, 245–264.
124. Kuhnt, T., Schmiedl, G., Ehrmann, W., Hamann, Y., and Hemleben, C. (2007). Deep-sea ecosystem variability of the Aegean Sea during the past 22 kyr as revealed by Benthic Foraminifera. *Mar. Micropaleontol.* **64**, 141–162.
125. Dahl-Jensen, D. (2014). Willi Dansgaard. In *Videnskabernes Selskab Oversigt 2013-2014* (Copenhagen, Denmark: Det Kongelige Danske), pp. 200–203.
126. Svensson, A., Nielsen, S.W., Kipfstuhl, S., Johnsen, S.J., Steffensen, J.P., Bigler, M., Ruth, U., and Röthlisberger, R. (2005). Visual stratigraphy of the North Greenland Ice Core Project (NorthGRIP) ice core during the last glacial period. *J. Geophys. Res. Atmos.* **110**, D02108.