



Ph.D. thesis
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The ecology of abrupt climate changes during the last glacial period



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FRONT PAGE PICTURE	Temperate coniferous forest. Source: PxHere (Creative Commons CC0 1.0 license).

Who can impress the forest, bid the tree
Unfix his earth-bound root?

— W. Shakespeare, *Macbeth*, act IV, scene I

Il vecchio diceva, guardando lontano:
«Immagina questo coperto di grano».

— F. Guccini, *Il vecchio e il bambino*

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Abstract

During the Last Glacial Period, several climate changes characterized by rapidity and broad geographical impact have occurred. In most cases, climate proxy records reveal patterns of general reorganization for atmospheric and oceanic currents, with abrupt modal switches among two or more states of equilibrium. However, no extinction event has been recorded following such dramatic environmental changes, with the notable exception of some megafauna species. This suggests that inspecting this past events might provide us of a deeper insight of the dynamics and the strategies that species and populations adopt to survive abrupt environmental change, a topic which appears to be of particular interest in the perspective of the present need to predict how nature will respond to the current climate change. Nevertheless, the short spatial and temporal scales of these events makes the study of such processes challenging. This project aims to investigate the underlying biotic mechanisms of response through analysis of paleo-archives and simulations realized by species distribution models. As such, it is divided in three parts.

The first part aims to collect and organize the existing knowledge about biotic responses to past abrupt climate changes, to achieve a general overview of the responses, and highlight the current gaps of knowledge on the topic. This is accomplished by a compilation of the published literature on the subject, with global geographic coverage and spanning the period comprising the Last Glacial Period (~120-12 ka BP) and early Holocene. The collected information is classified by habitat and organization level, in order to infer modal responses and main mechanisms of adaptation. This analysis, included in the manuscript presented in Chapter 2, exposes the importance of microrefugia and minority population presence for communities to maintain equilibrium with rapid environmental shifts.

The second part introduces a novel method of investigation of population mechanisms of adaptation to abrupt climate change, in the form of a species distribution model aiming to reproduce explicitly some of the key response dynamics. It is fully introduced in the manuscript presented in Chapter 3. The model takes climate simulation maps and paleo-archives of the taxa of interest as input; it subsequently produces a climate-driven distribution range simulation and evaluates its likelihood by comparing it against the paleo-archives. By testing the likelihood of the distribution range simulations against paleorecords of the taxa under study, the model incorporates a correlative approach to a mechanistic model. This hybrid nature aims to make the model a tool for studying and testing hypotheses about

populations response mechanism, since it reproduces explicitly some of the key response dynamics being process-based; and, at the same time, for statistically reconstructing species traits by their paleo-archives. The model is tested through a case study of *Abies* populations in North America during the transition to Holocene.

In the third part, displayed in the manuscript comprising Chapter 4, the model is applied to a fossile pollen database containing information about seven common North American tree taxa with the aim to analyse their response mechanisms to the environmental changes of last deglaciation. Simulations with different dispersal models are realized and compared to infer the colonization strategies of the taxa under rapid climate changes. The study shows a prevalent resort to long-range dispersal, with the frequency of such events inversely correlated with the ability of the taxa to maintain equilibrium with the environment.

These findings illustrate the validity to recurring to process-based models for reproducing and analysing dynamics with brief spatial and temporal resolution as rapid climate-driven distribution range responses. Explicitly spatial models allow to take into account the stochasticity in the simulated events, which are an important factor at such short time scales. The maintenance to meta-population structures appears as an important feature for successful species responses to abrupt climate changes; in particular, long-range dispersal has played a significant role in tree populations responses to Late Glacial abrupt climate changes.

Resumé

Adskillige abrupte klimaforandringer er dokumenteret i paleo-arkiver under og umiddelbart efter den sidste istid. Dette afslører mønstre af generelle reorganiseringer af atmosfæriske og oceaniske strømme med abrupte modale skift med to eller flere tilstande af ligevægtige. Dog er ingen uddøen registreret efter sådanne dramatiske klimaforandringer, med undtagelse af udslettelsen af nogle megafauna. Dette indikerer at forskning i disse abrupte klimaforandringer kan give dybere indsigt i, hvilke dynamikker og strategier arter og populationer adopterer for at overleve abrupte miljøforandringer. Set i lyset af det nutidige behov for, at forudsæ naturens respons til klimaforandringer er viden om disse fortidige abrupte klimaforandringer af høj interesse. Dog er det udfordrende at studere disse tidsmæssige korte forhistoriske klimaforandringer. Formålet af dette tre-delte projekt er at undersøge de underliggende biotiske mekanismer for arternes respons og geografiske rækkevidder gennem analyse af paleo-arkiverne og geografiske simuleringer.

Den første del har til formål, at evaluere og syntetisere den eksisterende viden om biotiske respons til forhistoriske klimaforandringer. Dette er for at opnå et generelt overblik over respons, mønstre og mekanismer og fremhæve de nuværende mangler i viden om emnet. Dette udføres ved, at samle den publicerede litteratur med global geografisk dækning i perioden fra og med den sidste istid (~120-12 ka BP) og tidlig Holocæn. Den indsamlede litteratur bliver klassificeret under habitat og organisation niveau for at udlede den modale respons og de overliggende mekanismer af adaption. Denne analyse er inkluderet i manuskriptet i Kapitel 2 og afdækker vigtigheden af adaption, spredning og mikro-refugia for populationer, arter og økologiske samfund under abrupte klimaforandringer.

Den anden del introducerer en ny metode, der benytter sig af rummelige simuleringer til, at afdække hvilke mekanismer, adaptationer in situ og spredninger, der kan forklare de observerede mønstre af geografiske habitat dynamikker under abrupte klimaforandringer. Disse simulationer er implementeret i et nyt software kaldet Radis, som er fuldt introduceret i manuskriptet præsenteret i Kapitel 3. Den gør brug af klima simulering kort og paleo-arkiver af taxa fordelinger over de forgangne tids perioder som hoved input; efterfølgende produceres en simulering af arternes spredning drevet af klima, hvorefter sandsynligheden af tolerance in situ og spredning evalueres ved sammenligning med paleo-arkiverne. Vores tilgang har til formål, at bidrage til studie og test af hypoteser i respons mekanismer. Idet tilgangen er proces baseret reproducere nogle af nøgle dynamikkerne. Modellen er testet gennem et

case studie af Abies populationer i Nord Amerika under overgangen til Holocæn.

I den tredje del af projektet, som er at finde på manuskriptet i Kapitel 4, bruges modellen med input fra databaser med fossil pollen fra syv forskellige almindelige Nord Amerikanske træ taxa, til at analysere arters respons mekanismer til de miljømæssige forandringer, der foregik under den sidste istid. Simulationer med forskellige sprednings måder, hvor lang tids sprednings events er inkluderet, og in situ tolerancer bliver sammenlignet med fortidige distributioner i Nord Amerika for at udlede rollen af nogle overlevelsesh strategier af taxa under hurtige klima forandringer. Dette studie demonstrerer en fremherskende rolle af tolerance in situ og en sekundær rolle af spredning.

Disse fund illustrerer validiteten til gentagne proces baserede modeller for reproducerbarhed og analyse dynamik af geografiske rækkevide dynamikker under abrupte klima forandringer. Udtrykkeligt de rummelige modeller tillader at indbefatte stokastiske variabler i de simulerede begivenheder, hvilket er en vigtig faktor for sådanne tids skaler. Opretholdelse af meta-population struktur fremgår som en vigtig egenskab for succesfulde arters respons til abrupte klimaforandringer. Særligt lang distance spredning har vist sig signifikant i træpopulationers respons til sidste istid abrupte klima forandringer.

1 Introduction

1.1 Climate change dynamics during last glacial period

The Pleistocene was a geological epoch consisting of several glacial periods divided by intervals of warmer global temperature, called interglacial periods. The last glacial period occurred from circa 120 ka BP to 11.7 ka BP; it starts after the Eemian interglacial period and it is succeeded by the Holocene, which is the current geological epoch. During the last glacial period, the climate of the Northern hemisphere was affected by many severe climate changes, and evidence of them has been found in several climate records around the whole Northern Hemisphere (Voelker 2002; Moreno et al. 2014).

Such rapid climate changes were first observed in ice cores from Greenland. Among paleorecords, ice cores provide some of the highest temporal resolutions: the ice is formed by layers of ice generated by snow fallen every year, therefore they have annual resolution dating back to 60 ka BP (Rasmussen et al. 2014). The isotopic composition of both oxygen and hydrogen can be used to infer the temperature history of the ice core. Evaluations for the ratio of ^{18}O over ^{16}O and deuterium over hydrogen, expressed in parts per thousand, are indicated respectively with the symbols $\delta^{18}\text{O}$ and δD . The fraction of heavier isotopes in an ice layer is dependent on the temperature of the precipitation that composed it, therefore they can be used as proxy of temperature of the ice core region for the corresponding year.

1.1.1 Dansgaard-Oeschger events

Greenland ice cores enclose data up to the last 120 ka BP. They display several transitions from stadial (i.e. periods of colder climate) to interstadial (warmer climate), before reverting back to stadial; these periods of warmer conditions are called Dansgaard-Oeschger (DO) events. The shifts towards interstadial conditions occurred on time scale of decades, to which followed a slow decline in temperature and finally a transition back to stadial spanning some hundreds of years (Fig. 1).

Other records outside Greenland display climate patterns with correspondence to DO events. One of the first and most important examples comes from the Hulu Cave, located in Eastern China. It is a main site for paleoclimate records, thanks to its stalagmites which provide for oxygen isotope records dating back to more than 70 ka BP. In this case, $\delta^{18}\text{O}$ represents a proxy for changes in the ratio of the amount of summer to winter precipitation, and therefore for intensity of the East Asian Monsoon. The general

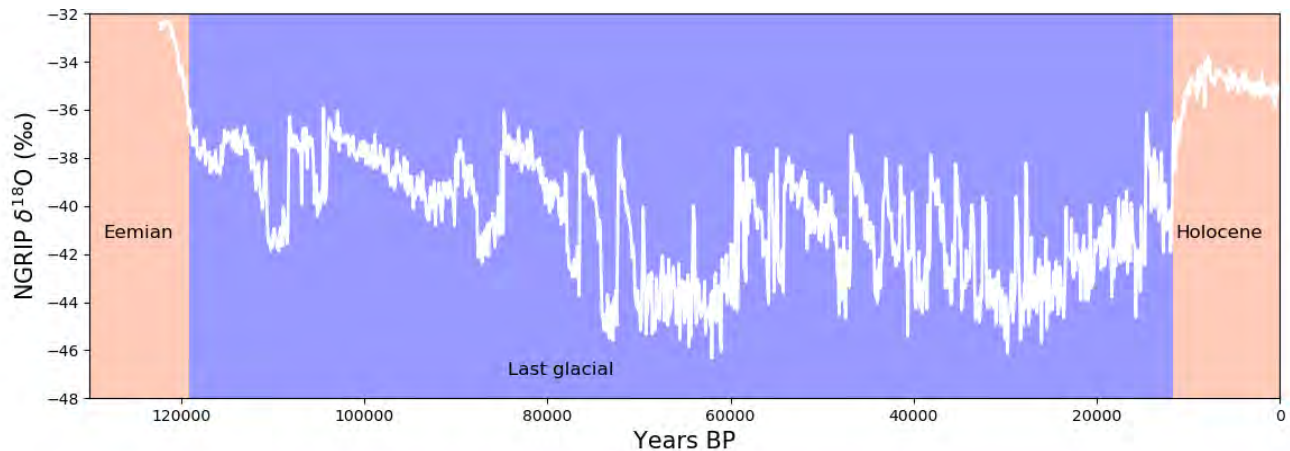


Figure 1: Profile of $\delta^{18}\text{O}$, a proxy for temperature, as from the Greenland NGRIP record. The data cover the last glacial period, which spans between the two warm interglacial periods, Eemian and Holocene. Climate variability is clearly shown throughout the whole glacial period. Data from (Andersen et al. 2004), dated with GICC05modelext chronology, as from Rasmussen et al. 2013.

pattern of such records follows, on the long term, the trend of summer insolation, but on short-term scale it shows shifts in accordance with millennial-scale events observed in Greenland paleorecords (Fig. 2). This suggests a correlations between past Greenland temperatures and intensity of summer East Asian Monsoon, with the latter increasing in periods of warmer conditions for Greenland (Wang et al. 2001).

Climatic shifts correlating with changes in Greenland temperatures have also been found in marine sediment cores in tropical North Atlantic and the Arabian sea (Deplazes et al. 2013). In these cases, the proxy used is sediment reflectance, which is a variable proportional to relative contributions of terrigenous and biogenic components and, by analogy with present-day seasonal variations, is used as proxy for latitudinal position of the Atlantic inter-tropical convergence zone (ITCZ) and monsoon intensity. Comparison of such paleorecords with ice cores shows that Greenland interstadials correspond to periods of higher precipitations of the Indian summer monsoon, and with northwards migrations of the ITCZ. Synchronicities with Greenland records have been observed repeatedly in European and North American records (Voelker 2002; Moreno et al. 2014); in Europe, stadial/interstadial transitions consisted in temperature shifts of lower amplitude but still encompassing changes of several degrees over the whole continent. Overall, this hints to the DO events consisting of

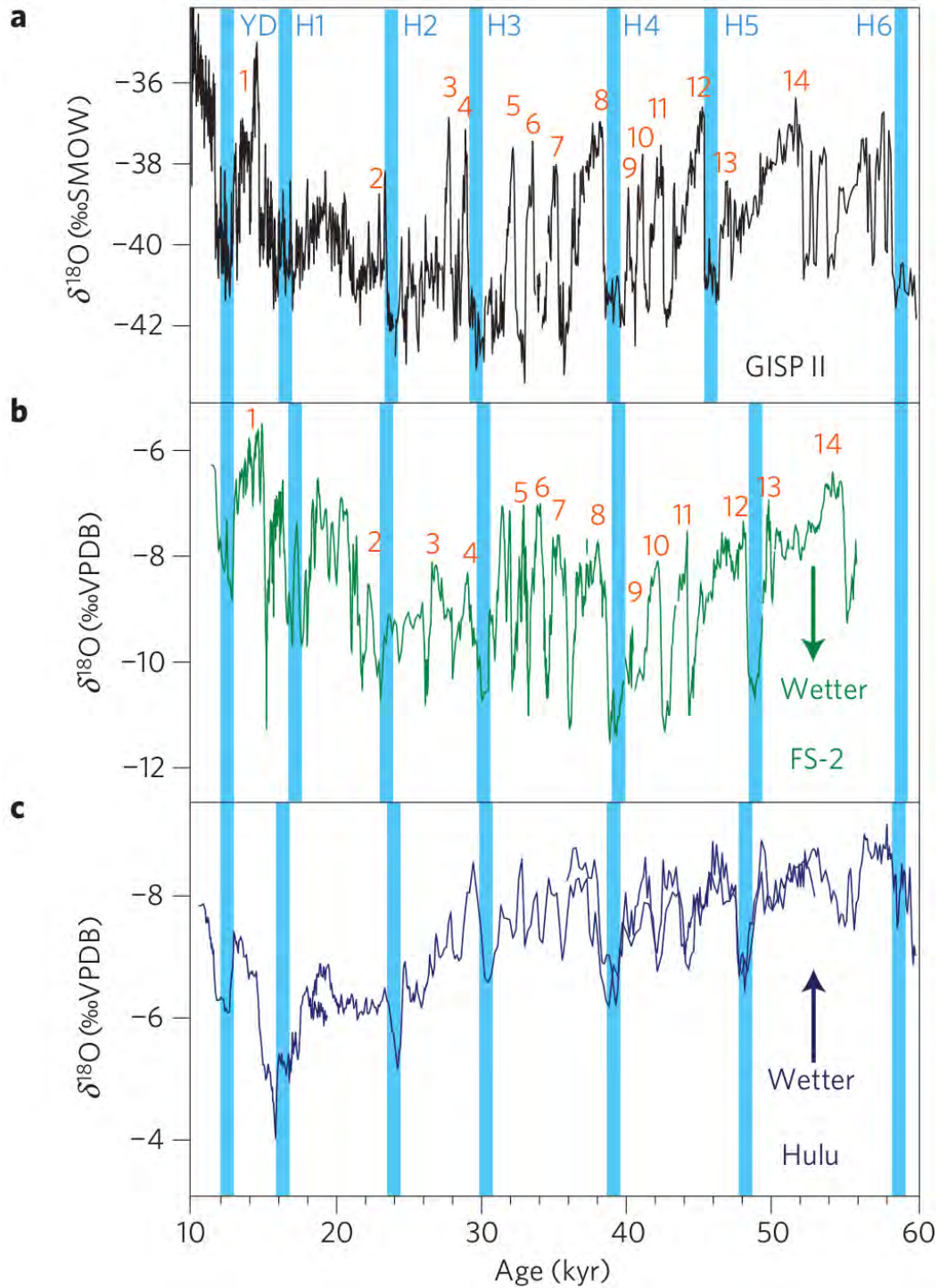


Figure 2: (a) Profile of $\delta^{18}\text{O}$ for the Greenland GISP2 ice core. (b) Profile of $\delta^{18}\text{O}$ from stalagmites of Fort Stanton cave, south-western United states. (c) Profile of $\delta^{18}\text{O}$ of the stalagmites of Hulu Cave, Eastern China. Blue bars highlight the Younger Dryas and Heinrich events, while the orange numbers indicate DO events. From Asmerom, Polyak, and Burns 2010.

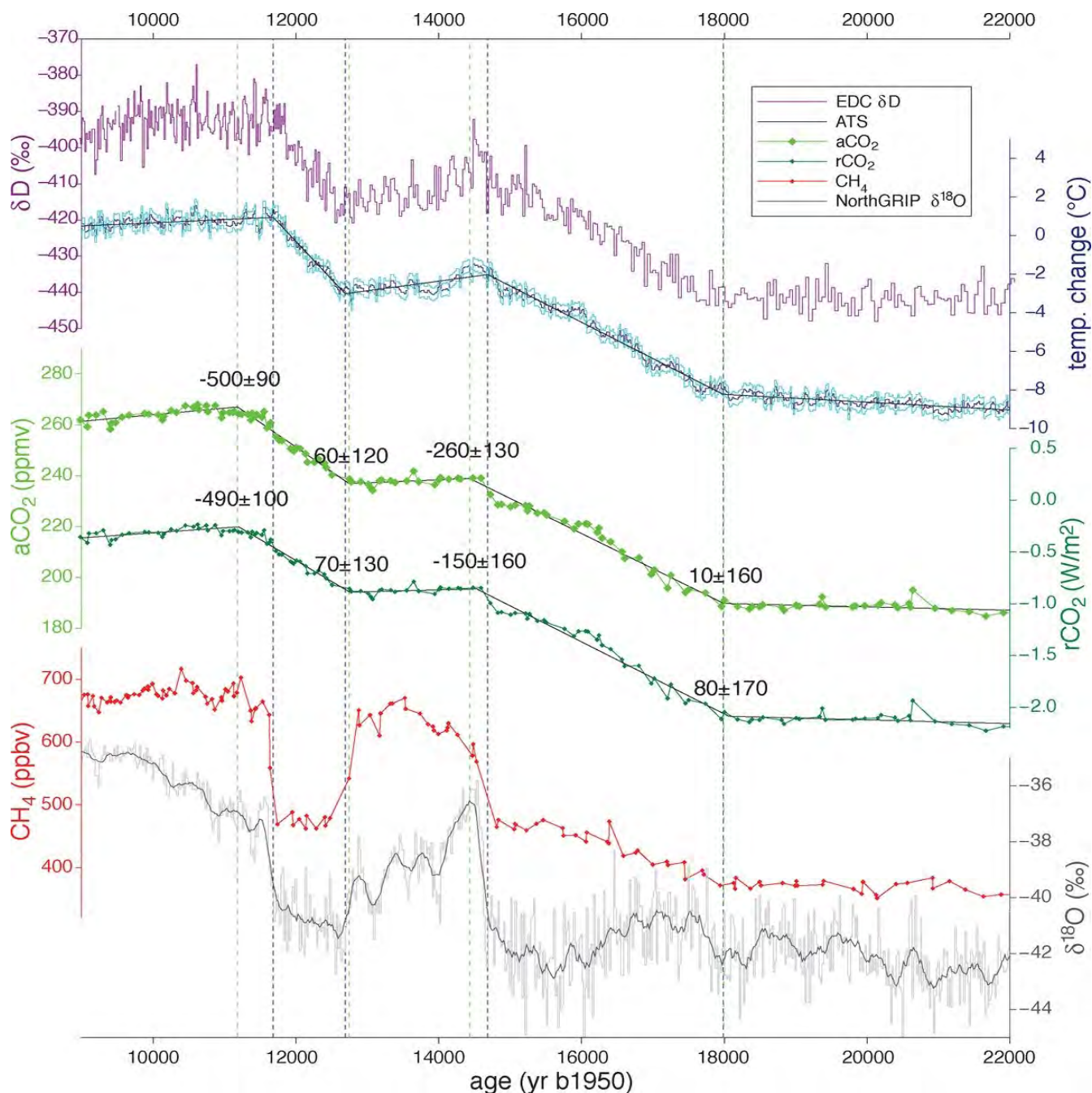


Figure 3: Purple: δD signal from EDC (an Antarctica ice core). Blue: Antarctica temperature change reconstructed from stacked ice cores records. Light green: atmospheric CO₂ from EDC. Dark green: radiative forcing of EDC atmospheric CO₂, evaluated as $5.35 \text{ W/m}^2 \cdot \ln(\text{CO}_2 / 280 \text{ parts per million by volume})$. Red: atmospheric CH₄ signal from EDC. Gray: δ¹⁸O signal from NGRIP Greenland ice core. From Parrenin et al. 2013.

complex dynamics of general reorganization of oceanic and atmospheric patterns of hemispherical scale.

1.1.2 Deglacial period

The interval between 15 and 11 ka BP encompasses the transition from the Pleistocene to the Holocene. It is widely studied both in climatology and paleoecology because of the several abrupt climate changes occurring in it and because, being relative recent, there is abundance of records with high temporal resolution for this period.

This interval, as recorded from Greenland records, is characterized by two periods: the first is called Bølling Allerød (BA), and it consists of a period of interstadial conditions spanning from 14.7 to 12.7 ka BP; then, to BA succeeded the Younger Dryas (YD), a period during which colder climates returned, lasting until 11.7 ka BP, when Holocene started. Both the BA inception and YD-Holocene transition were rapid warming events, featuring hemispherical atmospheric reorganizations occurring within 3 years, to which followed temperature changes within ~50 years (Steffensen et al. 2008).

Other high resolution paleorecords show with clarity how such warming in the northern hemisphere were preceded by a more gradual warming period in the Southern Ocean (SO), and the synchronicity of northern warming with a more gradual SO temperature drop, likely indicating a release of heat from the SO toward North Atlantic (Fig. 3). SO temperature changes occurred with a centennial scale time lag from major reorganizations of oceanic currents and SO phytoplankton productivity changes (Fischer et al. 2010).

1.1.3 Heinrich events

Heinrich events (HE) are periods of climate cooling, happening during stadial intervals and terminating with abrupt warmings. They are characterized by discharges of icebergs into North Atlantic, indicating the close interaction between ice-sheet dynamics, oceans, and atmospheric temperature changes (Bond et al. 1993).

The main signal for HEs are records of ice-rafted detritus, indicating discharges of ice from the Hudson Strait into the North Atlantic Ocean. They were accompanied by large influx of meltwater into the North Atlantic. Despite having left signals on hemispherical scale, their pattern differs from those of DO events (Hemming 2004). At low latitudes, HEs are recorded as periods of colder climates, with climate ranges of greater amplitude than DO events (Fig. 4). On the other hand, they are not recorded in Greenland ice cores, whose traces of stadial conditions appear unchanged by the occurrence of HEs at

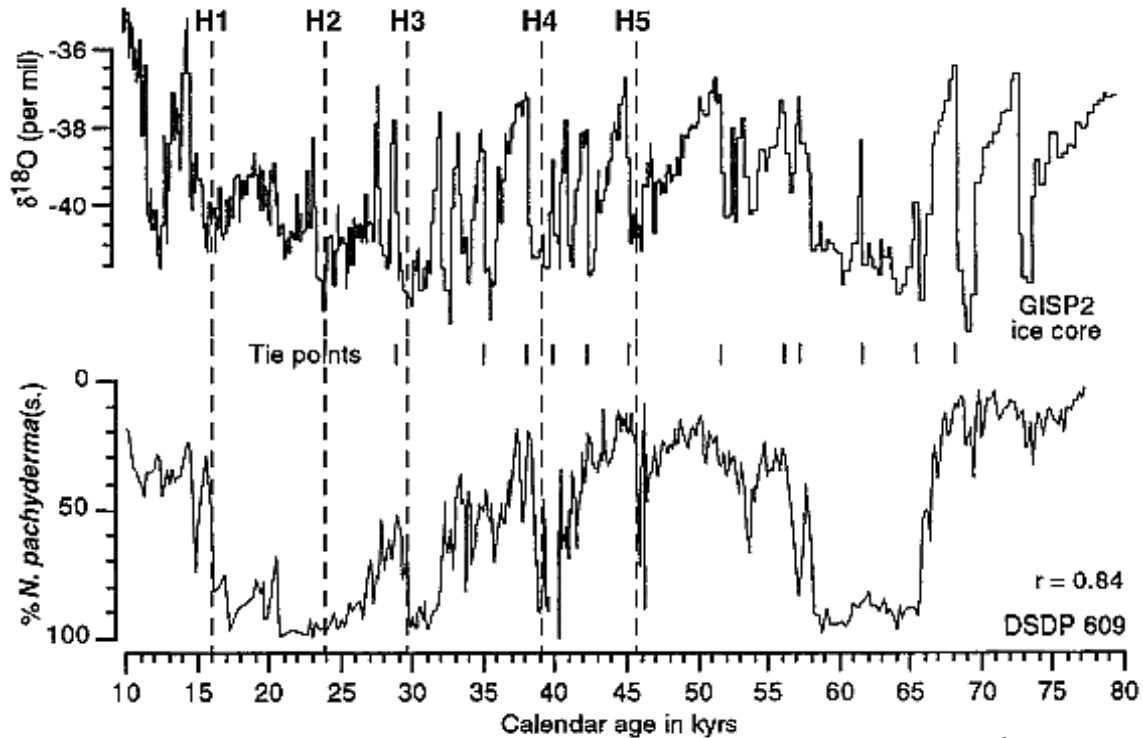


Figure 4: On top: $\delta^{18}\text{O}$ signal (proxy for temperature) of Greenland GISP core. Bottom: abundance of N. Atlantic *N. Pachyderma* (sinistral) (proxy for sea surface temperature). Vertical dashed lines indicate the last five HEs. Adapted from Hemming 2004.

lower latitudes. A possible indication for HEs, however, can be observed by comparing the difference between northern and southern Greenland records: a latitudinal gradient in the Greenland $\delta^{18}\text{O}$ signals is observable, which can be linked to changes in either the sea-ice extent or the North Atlantic sea surface temperature, as a consequence of major ice rafting events (Seierstad et al. 2014).

HE and DO events show some correlations: firstly, HE never occurred during interstadials, but usually after warm DO events, as mentioned above; moreover, after a HE, the following DO events tend to become colder until the next HE occurs, and this sequence of DO events is called a Bond cycle (Porter and Zhisheng 1995).

1.2 Theory of last glacial abrupt climate transitions

The Atlantic Meridional Overturning Circulation (AMOC) is the North Atlantic component of the global thermohaline circulation; it consists in a current of warm water coming from the tropics and flowing northwards, until becoming colder and therefore sinking. This process is known as North Atlantic deep-water formation. AMOC is an important component in the maintenance of the current

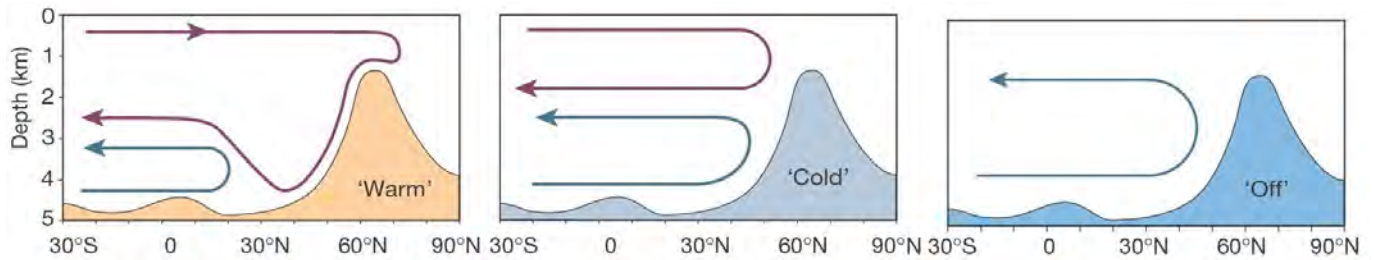


Figure 5: The three sketches schematize the different water currents along the Atlantic for three different periods; from left to right: stadial, interstadial, and HE. The bottom profile indicates the Atlantic sea bottom; the rise at $\sim 60^\circ$ of latitude indicates the shallow sill between Greenland and Scotland. Red and blue arrows represent AMOC and the bottom water current, respectively. AMOC sinks in different regions in the “warm” and “cold” states, originating different NADW regions. In the “off” state, the Atlantic currents are entirely composed by cold water coming from the Southern Ocean. From Rahmstorf 2002.

climatic conditions of the North Atlantic, as its flux of warm water contributes to the heat provision of the region.

Both DO and HE have been linked with variations in AMOC and with perturbations of the deep-water formation process. According to the presently leading theory, AMOC can switch between three stable and distinct states of circulation (Fig. 5), each corresponding to a climate condition as observed from climate paleorecords (Rahmstorf 2002). The “warm” state is analogous to the present-day state of Atlantic currents, with AMOC flowing until the Nordic Seas, warming up the region. In the “cold” state, AMOC has a shorter path as North Atlantic Deep Water (NADW) is formed at lower latitudes, in the open North Atlantic. Finally, in the “off” state, there is no deep-water formation in the Atlantic whatsoever, and the ocean comprises entirely waters from the Antarctica. Following this model, the warm state is responsible for DO events and interstadials, the cold state represents stadial conditions, and the off state the HE. In this model, feedbacks from the atmosphere and the oceans would transmit to a global scale the climate changes caused by the transitions between states (Clark et al. 2002).

This theory provides an explanation for the absence of HE at high latitude: during stadial conditions, being the warm Atlantic current already absent at those latitudes, Greenland climate would be decoupled by changes of AMOC, hence its shutting off would bear no further effect to the region’s climate. Moreover, it offers an explanation for the somewhat counter-intuitive phenomenon of ice sheet melting and discharging icebergs during cold stadial periods: it is likely that the growth of the ice sheet, as it would occur throughout a Bond cycle, would eventually make it unstable, to the point where

perturbations could trigger its breakdown and therefore causing a AMOC shut-down by the release of freshwater from the melting icebergs. A hypothesis about the nature of such perturbation has been offered by a recent model, which takes into account the isostatic uplifting of the bedrock upon which the ice sheet lies. In this model, the ice sheet is melted on the bottom by warm underwater currents. Its melting and consequent discharging of icebergs reduces its overall mass, causing its bed to uplift; this, in turn, distances the ice sheet from the warm subsurface waters, allowing eventually the ice sheet to grow again. This model offers an explanation to the smallness of the fluctuations triggering HE, and explains the timing of HE collapses, recoveries, and recurrences (Bassis, Petersen, and Mac Cathles 2017).

The exact nature of the triggers causing such freshwater variations are yet unclear. However, several climate models simulating AMOC shifts between different circulation states produced patterns similar to those of recorded abrupt climate changes. Furthermore, such simulations displayed a good fit with proxy paleorecords (Ganopolski and Rahmstorf 2001; Van Meerbeeck et al. 2011; Peltier and Vettoretti 2014). This supports the theory of DO and HE shifts in Europe being consequences of modifications of heat transport to the North Atlantic by AMOC weakening or shut-downs. HEs are indeed proven to be related to the interruption of North Atlantic deep-water formation (Keigwin and Lehman 1994).

However, simulations have also shown that changes in the thermohaline circulation alone during stadial periods were not enough to justify the degree of cooling above Greenland, which were all of similar amplitude despite displaying differences in thermohaline circulation reduction; this suggests the presence of some amplifying feedback mechanism able to extend the effects of deep-water formation reduction (Elliot, Labeyrie, and Duplessy 2002). Marine Atlantic sediments suggests that sea ice on North Atlantic insulated the atmosphere from the heat conveyed by deep currents; the abruptness of DO warmings can therefore be explained by the sudden heat release occurring when sea ice retracted (Dokken and Jansen 1999).

1.2.1 Bipolar seesaw

Ice cores from Antarctica contain isotopic signals of $\delta^{18}\text{O}$, as the ones from Greenland, and δD (deuterium, isotope of hydrogen); both are proxies for temperature changes. Such cores date back to 800 ka BP, longer than Greenland ice cores. Antarctica climate records display long term changes, possibly driven by astronomical changes in insolation, and variability of shorter, millennial scale. When compared to the Greenland records, these latter fluctuations show some correspondence with DO

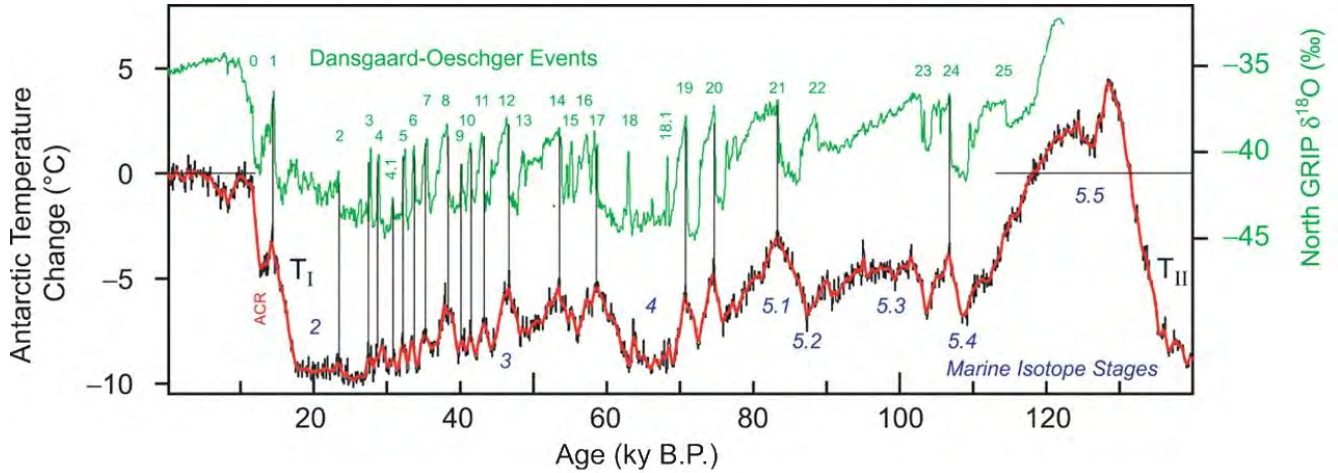


Figure 6: In green: $\delta^{18}\text{O}$ record from NGRIP Greenland ice cores. Numbers indicate DO events. In red: Antarctica temperature anomaly as from the record of EDC ice core. Vertical black lines indicate correspondences between DO and Antarctica Isotope Maxima (AIM); i.e. peaks of millennial-scale temperature variability. From Jouzel et al. 2007.

events regarding the last 100 ka BP. Antarctica temperature shifts feature smoother transitions and lower intensity than the ones from Northern hemisphere, but its peaks in amplitude correspond one-to-one to DO events as recorded in Greenland (Fig. 6). This coupling is in antiphase, i.e. warming slopes in the South occur during stadial in the North, and vice versa (Barbante et al. 2006; Jouzel et al. 2007). Greenland climatic changes lead the changes from Antarctica of ~ 200 y, hinting to the climatic signal being propagated by oceanic processes, rather than by the atmosphere (Buizert et al. 2015).

The model of the bipolar seesaw provides an explanation for this inter-hemispherical coupling. It is called after the seesaw pattern emerging from the synchronicity of Greenland abrupt warmings with Antarctica cooling events. According to this model, the climatic fluctuations are due to repeated heat transports across South and the North Atlantic, conveyed by oceanic currents. A heat supply could provoke a change in North Atlantic ocean circulation, reducing the density of surface water and therefore allowing to flow at higher latitudes before sinking (Knutti et al. 2004). Since SO is wider than the Northern Atlantic, this would explain the greater time interval needed by the former to reach a warm state, as well as the abruptness of DO warming events occurring in periods of slow heat release by the South Atlantic. In other words, the southern heat reservoir would smooth out the abrupt climate shift occurring in the North Atlantic (Stocker and Johnsen 2003). This model find support in the linear correlation of the amplitude of Antarctica interstadial temperature changes with the duration of the correspondent Northern stadial (Barbante et al. 2006).

Temperature of SO has been proposed to be the cause of AMOC changes. Timings of Northern and Southern hemisphere abrupt changes support the hypothesis of NADW formation being triggered by the Southern Ocean warming and the following Antarctica sea-ice retreat (Bianchi and Gersonde 2004). Increases in SO temperature lead to a strengthening of AMOC, which in turn make the latter less susceptible to perturbations from meltwater influx. This would explain the positive correlation between length of interstadials and temperature and warmth of the Southern hemisphere (Buizert and Schmittner 2015).

This model fails to explain the observed higher complexity of feedbacks, which requires more detailed modelling, as e.g. the correspondences between tropical atmospheric circulation changes and Antarctic temperature; however, it is able to capture and justify the general climatic patterns (Landaïs et al. 2015).

1.3 Abrupt climate changes

The raising concern about the currently occurring climate change has contributed to the growing interest that has developed in the last decades about the mechanisms able to prompt abrupt climate changes. Abrupt changes are commonly featured by systems which, if submitted to an external forcing, can switch rapidly between two stable states. Rapidity is here meant qualitatively, to characterize a transition occurring in time ranges shorter than the forcing which caused it. This kind of behaviour is also sometimes referred as threshold crossing, or tipping-point. Three features are necessary for this kind of dynamics: the aforementioned external forcing; resilience to switches, in order to give stability to each state; and thirdly, an amplifying mechanism of the external forcing, so that the latter can eventually overcome the system resilience (Alley et al. 2003; Lenton et al. 2008; Steffen et al. 2018). In the case of atmospheric and oceanic systems, tipping-point characteristics are easily identified (see e.g. Fig. 7). However, the factors responsible for the recorded wide geographical spreading of climate anomalies are often less clear. General circulation models tend for example to under-represent the extension of abrupt climate changes.

The last glacial abrupt climate changes represent a case in point of disruptive climatic switches between equilibrium states. Specifically, the NADW is a multi-stable system, since it allows for several stable states self-sustained by positive feedbacks. The two main equilibrium states, and the first historically to be identified as such, are characterized by the presence or absence of NADW formation. In this case, the positive feedback mechanism is salinity. Water from the thermohaline circulation flows

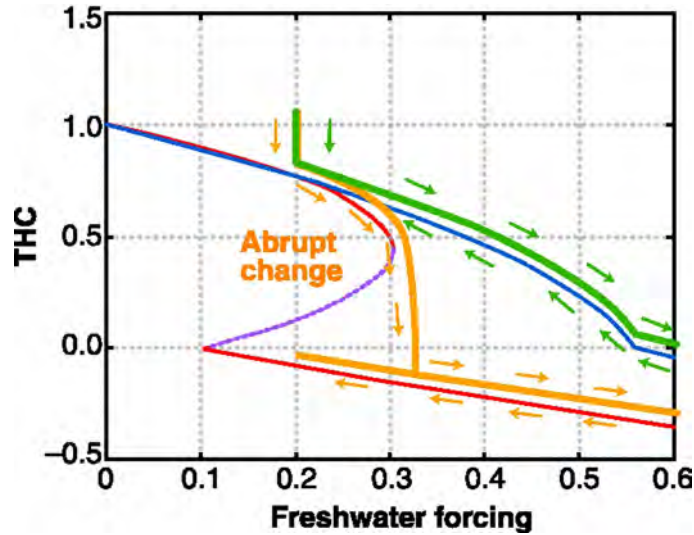


Figure 7: non-linear behaviour of the North Atlantic thermohaline circulation. Y-axis: thermohaline circulation, expressed as freshwater loss to atmosphere in subtropics. X-axis: external freshwater forcing in arbitrary units. Blue curve represents a state of strong convective mixing, red curve represents a state of weak mixing. Green and orange arrows indicate a process of increase and successive decrease of freshwater forcing, respectively with strong and weak mixing. In case of strong mixing, the current is able to return to initial state, while if mixing is weak the freshwater amount switches off the thermohaline circulation. To be noticed that, in this case, once the threshold is crossed and the systems skips to the other stable state, the system does not switch back after an equal and opposite forcing, but needs instead the latter to reduce to zero to achieve a switch of opposite sign (i.e., the system shows hysteresis). From Alley et al. 2003.

northwards from low latitude Atlantic, and is therefore warmer (and thus lighter) and with a higher component of salt in respect to the higher latitude waters. Thanks to the net effect of these two features, during interstadial conditions the warm current can flow until the North Atlantic upper latitudes and sink once there, thus increasing the net salinity of the region of deep water formation. Deep water formation, in turn, enhances the circulation, creating a positive salinity-driven feedback.

Such a system features an inner resilience to perturbation: the warming caused by AMOC induces a flux of freshwater from surrounding ice land masses, which in turn decreases salinity therefore reducing the AMOC current itself. However, a threshold can be reached if an excessive increase of freshwater in the region may decrease the salinity to the point of halting NADW and the circulation itself. Models have highlighted the existence of several other multiple equilibrium states, between which the system can switch within scales of centennial order of magnitude or less, through variations in atmospheric forcing (Lenderink and Haarsma 1994).

1.4 Paleoecology of abrupt climate change

Effects of last glacial abrupt climate changes on the biosphere have been widely recorded on a global scale. They constitute natural experiments to investigate how ecosystems reacts to those changes, and therefore gaining lessons to anticipate how they may react to the ongoing climate change (Urban et al. 2016). Three strategies are available for species responding to a rapid climate change: disperse to and colonize to more suitable areas, persist in situ or become extinct (Aitken et al. 2008). However, there are large gaps of knowledge on the role and magnitude of the mechanisms behind species responses to past climate change. We know that species responded in the past differently depending on both traits specificities and how the regional climate was affected by the global climatic dynamics (Lorenzen et al. 2011).

Paleorecords show tree taxa responding to the repeated warmings of late Quaternary by displacing their range northwards or expanding it from glacial refugia (Williams et al. 2004). However, the speed of climate and environmental changes poses a challenge to species to adapt and thrive. For example, trees tend to respond to more gradual climatic changes by adaptive differentiation and dispersal (Petit, Hu, and Dick 2008). DO warming events, some of which occurred in centennial or decennial scales, challenge this processes by triggering disequilibrium dynamics between the climate and the optimal climatic conditions for species.

Adaptation and range shifts of a species are not necessary mutually exclusive strategies; on the contrary, they can be correlated. Speed of adaptation affect invasion rate and population growth rate, which in turn affect dispersal rate and probability of extirpation (Davis, Shaw, and Etterson 2005). Indeed, adaptation to novel local conditions is inherent in migration itself. This implies that migration does not simply consist of an expansion of species distribution ranges, but as the combined effort of population individuals to establish in the new region. Therefore, the more a population features inner gene flow, the more it increases its chances to disperse and colonize new areas successfully. For this reason, habitat fragmentation and population isolation are potentially critical for populations that are subject to rapid climate change. Moreover, a rapid climate change imposing a selective pressure on a population, by extirpating the less fitting individuals, can result in genetic bottlenecks within populations (Jump and Peñuelas 2005; Hoffmann and Sgró 2011), triggering vortex dynamics of genetic inbreeding. The present adaptive differentiation in many living species is a hint of both dispersal and adaptation having played a role during last glacial climate changes (Davis and Shaw

2001). It is plausible to assume that adaptation as a response to rapid climate changes could have been relevant for taxa with short time ranges of evolutionary change (Hoffmann and Sgró 2011).

Adaptation cannot be a suitable survival strategy for taxa whose life cycle time is comparable or greater than the time scales of rapid climate changes, e.g. tree taxa; several of which appear nevertheless to have coped well during the last glacial period. In such cases, available strategies can have consisted in retreats into microrefugia (i.e. minor regions of suitable microclimates), intraspecific phenotypic variability and individual phenotypic plasticity (Hof et al. 2011). In the study of past responses, it can be challenging to tell apart microevolution and phenotypic plasticity as the feature responsible for a recorded resistance to climate change, even though recent studies suggest that phenotypic plasticity mediates most responses to climate change (Nogués-Bravo et al. 2018).

It must be noted that the traits alone of a species are not sufficient to establish its response to climate change. Studies have been unable to isolate genetic traits or dispersal dynamics distinguishing surviving to extinct species. Moreover, in some cases the climate does not appear as the only factor responsible for species' responses, as much as a contributing factor, together with interspecific interaction (Lorenzen et al. 2011).

To contribute to fill up the current gaps of knowledge on the role and magnitude of mechanisms such as dispersal or tolerance in situ in species past reactions to climate change, this research project reviews the state-of-the-art knowledge on species response mechanisms to climate change (Chapters 2), with a special emphasis on reactions to abrupt climate change, and synthesises that knowledge in theoretical predictions and simulations tested against paleoecological records (Chapters 4) implemented in a new software, Radis (Chapters 3).

1.4.1 Abrupt responses

Fossil records from the Northern Hemisphere show that vegetation responses to last glacial abrupt climate changes were, overall, spatially synchronous with both bursts and collapses of their geographical ranges, consistently with such responses being driven by external forcing (Williams, Blois, and Shuman 2011). As to the magnitude and the modality of biotic responses, they varied greatly, depending on the taxa, the ecosystem which they belonged to, and the specific climatic outcome that the global shift provoked in the region. In many cases, responses of species to abrupt climate changes were not isolated, but instead their effects propagated in the ecological networks and between trophic levels, by instance through food webs (Walther 2010). In general, responses affecting

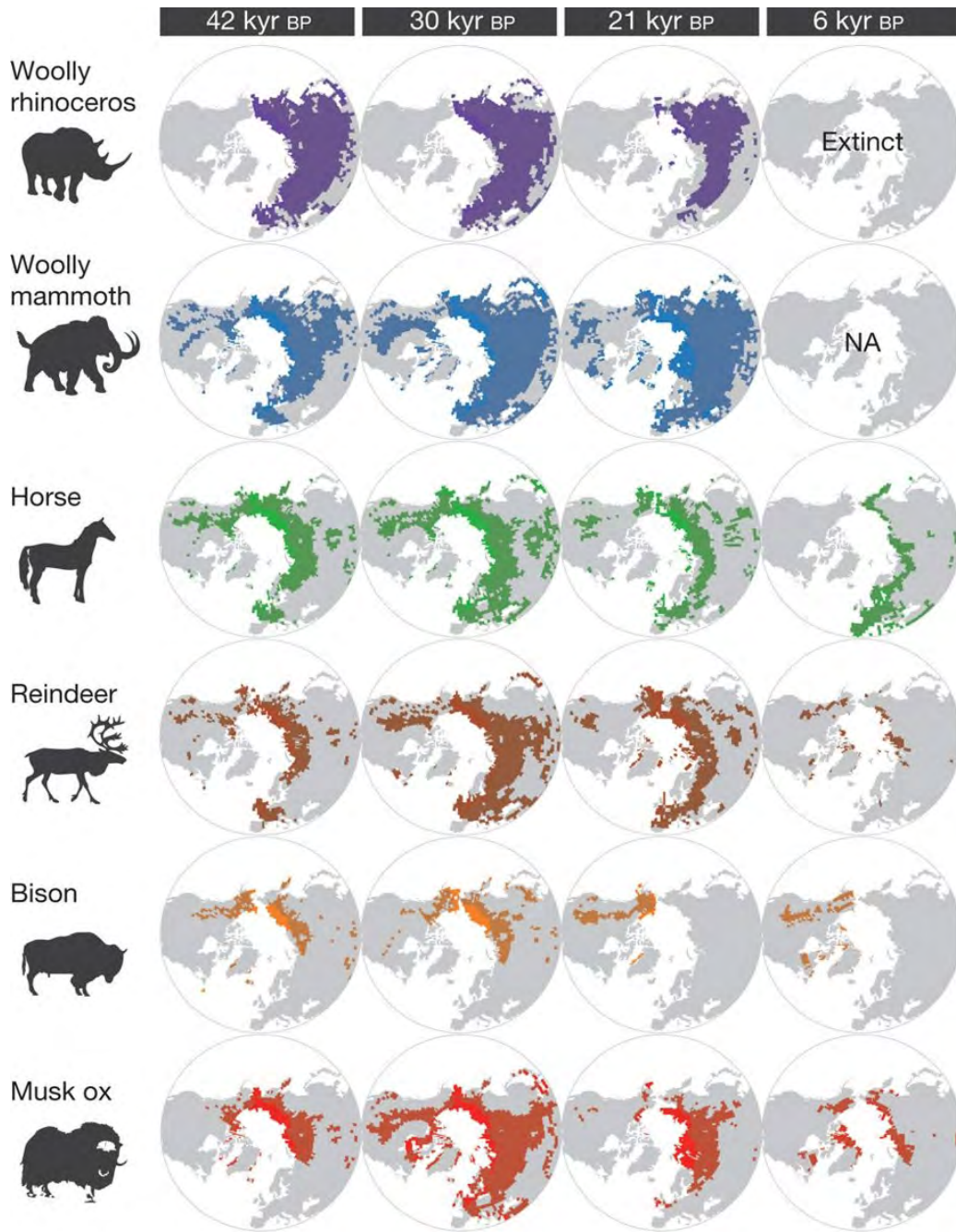


Figure 8: Potential ranges of some megafauna species at 42, 30, 21 and 6 ka BP. Range measurements are reconstructed by fossil records and paleoclimatic data. From Lorenzen et al. 2011.

not only species or individuals, but also the biotic interactions between them, may induce non-linear dynamics in ecosystems, including feedback processes. As discussed above for climatic systems, positive feedbacks can be responsible of abrupt behaviours.

Given the potentially catastrophic consequences of an abrupt change in the environment, and thus in the ecosystem services it provides, research has been focused on how to discern and approach abrupt changes in ecological systems (Steffen et al. 2018). Abrupt ecological collapses of regime shift are frequently preceded by a reduction of system noise coupled with an increased resistance to perturbation; however, such feature is in some case missing or not statistically detectable (Boettiger, Ross, and Hastings 2013). Theoretical modelling indicate, as further possible signs of early warning, specific indicators based on changes in the spatial structure of an ecosystem, e.g. increases in the spatial variance (which may signify the approaching to a bifurcation point), and size changes of the ecosystem shape pattern (Kéfi et al. 2014). Interestingly, presence of ecological tipping points appear not only related by the magnitude of the environmental change that a species has to face. Instead, a key factor to determine the likelihood of success is the permanence of the strategy, i.e. the possibility to adopt the same strategy throughout the whole period of climate change; conversely, species increase extinction chance whenever environmental changes forces them to change adaptive strategies (Botero et al. 2015).

Although the specific changes that occurred across different regions varied in rate and direction, these transitions were consistent with the behaviour expected from unimodal distributions of species along environmental gradients. Spatially coherent, abrupt climate changes are indeed expected to induce “approximately synchronous ecological responses” (Williams et al. 2004). In summary, past abrupt climatic changes have triggered biodiversity reactions from genes to ecosystem levels, providing a suitable study system to explore the mechanisms and strategies allowing species to react to those climatic events.

1.4.2 Megafauna extinctions

Abrupt climate change have pushed dynamics of local extinctions, but few taxa global extinctions may be explained as a consequence of abrupt climate change. However, there is the exception of large mammal extinctions at the end of the Pleistocene, most likely triggered by a combination of climate and other factors (Cooper et al. 2015). The complete disappearance of several of these taxa occurred on a global scale, with the exception of Africa. Such extinctions produced cascading effect in the rest of their ecosystems, by inducing alterations in the composition and structure of some of the plant communities that composed the habitat of extinct megafauna species (Johnson 2009).

Two are the main theories proposed as an explanation of this phenomenon: lack of adaptation to

environmental changes, or excessive predation (often dubbed as “overkill”) by humans. The latter, in particular, is often conceived as a so-called “blitzkrieg” model, in which extinction were briefly accomplished by early human colonizers within short intervals of intensive hunting. Mechanistic population models hint to this hypothesis, albeit no definite evidence has yet been found to its support (Brook and Bowman 2002, 2004).

Both factors – mainly climate and secondarily humans – seem to have influenced demographic history of some megafauna species (Lorenzen et al. 2011), but their exact role in the megafauna extinction is still debated: their contribution to extirpation is difficult to infer statistically, because of the scarcity of records and the dating errors of the latter. In North America, timings of extinctions event were closely correlated with those of human colonization, while in Eurasia they occurred ~20 ka after the arrival of humans. Climate changes also appear to have affected megafauna distribution ranges (Fig. 8), and extinctions usually occurred after a severe range contraction (Stuart et al. 2004). Some extinctions did occur in conjunction with abrupt climate transition, and for some species climate change alone appears a sufficient explanation for extinction (Lorenzen et al. 2011). Nevertheless, that leaves open the question of why did the extinction occurred in that particular transition, given the many analogous previous climate transitions (Stuart 1991). Generally, evidence supports the idea that both climate and human impact had a contribution, with effect varying depending on the timing of human arrival and on the habitat changes provoked by climate changes (Barnosky et al. 2004; Broughton and Weitzel 2018).

Although the extinctions of megafauna during the Late Quaternary are not object of this dissertation, the approach presented in Chapters 3 holds the potential for investigating the likely role of climate change triggering megafauna geographical range shifts and collapses of those large and iconic animals.

1.5 Reconstructing past ecosystems

This section comprises a brief overview of the most common data types adopted for paleoecological research, with a particular focus on those that will be adopted in the following chapters.

1.5.1 General circulation models

Numerical models are used to test hypotheses explaining the observed trends in past climate records. Physical climate models consist of simulations of the dynamics of the climate systems, particularly atmospheric and oceanic circulations. In a climate simulation, the physical laws governing the climate

aspect of interest are directly simulated by the internal mechanisms of the model itself.

Validity of models is usually tested by simulating present conditions, so to allow confrontation with observed data. Simulations are then realized by altering one or more characteristics (called boundary conditions) of the modern world in order to reflect past conditions. The output is then analysed and confronted against independent paleoarchives.

General circulation models (GCM) constitute the most complete representations of the climate system. They simulate atmosphere and/or ocean three-dimensionally as an amount of grid boxes, displayed horizontally over latitude and longitude and stacked vertically. Some models also incorporate ice sheets by simulating them as well as grid boxes; they are especially relevant for long time range simulations (millennial or more), which is the time scale for most ice sheet dynamics.

Such models operate by reproducing the known physical laws governing atmospheric and oceanic circulation; their start is chosen to be an equilibrium point, then a forcing (e.g. solar heating) is imposed, and the development of the system is followed until the successive state of equilibrium. This last state is used as model output. CGM's can be used for sensitivity tests, realized by altering one boundary condition to study the impact that the conditions produces on climate. Alternatively, CGM's may provide for full climate reconstructions, where all boundary conditions are set to simulate past climate.

Climatic data used as input for paleoecological simulations in Chapters 3 and 4 are obtained from the PaleoView software (Fordham et al. 2017). They, in turn, originate from TraCE21ka, a dataset which is the output from CCSM3, a global coupled atmosphere-ocean-sea ice-land GCM (Collins et al. 2006).

1.5.2 Biotic archives

Information on past species distributions can be inferred by fossil records. The most numerous amount of fossile remains originates from plants. Plants can leave also macrofossils, i.e. larger fossil remains, like fossil leaves and seeds. However, the majority of their fossil remains consists of pollen. The pollen grains they produce gets sometimes deposited in lakes, and subsequently deposited to the lake bedrock and conserved in sediments. Sediments layer can be dated, so that the relative number of a given taxon's pollen in a layer can be used as proxy for abundance in the surrounding region for the dated period. Pollen data are nowadays collected in massive databases of public use, e.g. Neotoma Paleoecological Database or the European Pollen Database (Fyfe et al. 2009; Blois et al. 2011), which

provide information about abundance, dating and geolocalization of fossile pollen records.

Ocean basins can also provide sediments. In that case, the biotic information is produced by the remains of small shell-forming species, which may deposit in layers on the rock bottom of the ocean and fossilize. They can include animal species (like planktic foraminifera and radiolaria) or plants (like diatoms and coccoliths, which are algae).

1.5.3 Species distribution models

Since macroecology deals on complex, large-scale processes, its study cannot rely on classic syntactic scientific approach, which relies on principles of falsification and strong inference. Hence, studies have therefore relied on numerical algorithms to predict ecological patterns as e.g. species geographic distributions. Originally, they have been designed with a correlative approach. Correlative models use data of observed geographical presences and absences of a given species, relate it with the environmental conditions of the region of presences, and use this information to project the likely environmental ranges of the species. This kind of approach infers conclusions by testing for associations between explanatory variables and outcome patterns.

Typical drawbacks of such models are the common lack of recorded absences (which sometimes requires the creation of statistically created “pseudo-absence” data), possible mismatches between the realized and the fundamental niche of a species, and the demand of hypothesis that the records represent the species while in state of equilibrium with the environment. The most critical downside of correlative models is their difficulty in predicting biological responses, and that is also because correlation between species ranges and climate does not take into account of the underlying mechanisms, as range dynamics, species interactions and life history (Urban et al. 2016). This is specially important when studying biotic responses to past climate change, where such mechanism played key roles (Veloz et al. 2012).

More recent models, called mechanistic or process-based models, comprise such biological mechanisms, by simulating them directly and comparing the output with the paleoarchives. In general, models are defined as process-based if they are “models that characterize changes in a system’s state as explicit functions of the events that drive those state changes” (Connolly et al. 2017). They follow therefore the same working pattern of aforementioned climate numerical models, incorporating mechanisms and testing for fitting of the predictions against data. This approach allows a deeper focus on prediction of systems parameter values, and selection of alternative models. Process-base model are

particularly apt when studying relations between biota and climate, as they commonly outperform correlative models in predicting responses to climate changes (Pagel and Schurr 2012).

1.6 Relevance and outline

Several abrupt climate change, of considerable magnitude and less than centennial scale, occurred repeatedly on hemispherical scale. Nevertheless, very few extinctions have been recorded throughout all that period. This poses an interesting question to paleoecology and conservation ecology, since it suggests a relevant lacuna in our current knowledge about ecological responses to climate change.

A significant amount of paleoecological data of species during last glacial period has been collected in the last decades, allowing to shed a light on many macroecological patterns of response to abrupt climate changes. The challenge is now to draw inferences about the mechanisms and processes that lie beneath such dynamics. Investigating the population coping strategies and community response patterns may give hindsight on fundamental ecosystem features of particular relevance in the face of dealing with the currently occurring rapid climate change.

We address here such challenge, starting by collecting the current knowledge of biotic responses to abrupt climate changes occurred in the Last Glacial and early Holocene. Such overview will allow us to summarize the ecological patterns, focusing on what constants they may display among different habitats and taxa. We aim to apply this information to design a process-based model relating paleoclimate and species distribution ranges. Purpose of the model is to be used in two ways: firstly, as a tool to analyse paleoecological data, and provide statistically inferred estimates about the mechanism that studied taxa adopted; secondly, as an object of investigation itself, by studying its behaviour under different starting assumptions.

This work is based on three article manuscripts, composing the backbone of Chapters 2, 3 and 4. The first article (Chapter 2) reviews all published literature about the topic, with the purpose of collecting all so far collected knowledge, exposing eventual general ecological patterns and identifying current gaps of knowledge. The second article (Chapter 3), exposes the development of a process-based model intended to be a method to analyse fossil record data, reproduce taxa spatial pattern of response to climate changes, and test competing ecological hypotheses. Finally, in the third article (Chapter 4) we use the presented model to simulate geographical range dynamics of seven tree taxa in North America during the transition from the Pleistocene to the Holocene, and to explore the role of tolerance *in situ* and dispersal as mechanism of response.

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2 Biotic responses to last glacial abrupt climate changes

Despite the amount of research already produced about the ecology of late Quaternary abrupt climate changes, the narrowness of this topic and the recentness of the interest that it gained in the scientific community are the reason of a lack of a comprehensive overview on the topic itself. Therefore, the first step to address our research consisted in realizing a general summary of the already existing knowledge, by collecting all the relevant literature.

The topic has started being inquired significantly only in the last decade, and the interest is rapidly growing. The majority of articles treat data coming from Europe and North America. There is consensus over the DO events affecting the whole northern hemisphere at least, while having a slower and smaller effect in the southern. According to the leading theories, climate variability was linked to changes in North Atlantic oceanic circulation. This could contribute explaining the greater number of studies concerning Northern America and Europe, which are the world regions closer to North Atlantic ocean and therefore more affected by any changes in its circulation. Interestingly, little to none literature was found covering South America; this may represent a current gap of knowledge, which could be interesting to fill given the high biodiversity of that particular region.

While it is presumable that abrupt climate changes affected every kind of species, not all taxa have been equally studied, mainly because of the variable difficulty of getting fossils with a sufficiently high temporal resolution. This might create gaps of knowledge in our understanding to these paleoecological phenomena. Plants, whose activities are traceable by high-resolutions paleorecords as fossil pollens in lake or marine cores, are vastly studied. For the same reason, small or microscopic animals, as *Ostracoda*, *Foraminifera* and so forth, whose fossilized shells can sediment in marine records, have been the object of studies on responses of marine ecosystems. Such leanings on the choice of taxa might bias the conclusions we tried to draw below about how general ecosystem responds to abrupt climate change. *Homo Sapiens* is the only mammal widely chosen as subject for these studies, because of the intersection of fields inclined to an interest on it (archeology, anthropology, biology). Such studies, however, rely often on proxies (artefacts, archeological sites) with a lower temporal resolution in respect of the time scales of the climatic events under exam.

The analysis on published literature about ecology of abrupt climate change is further discussed in the following manuscript, currently under review at Current Biology and reported here with a few minor edits.

Biotic responses to last glacial abrupt climate changes

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In 1969, Dansgaard and colleagues identified for the first time several climate changes occurring in Greenland during the last glacial period. Since then, a number of deep ice cores retrieved from the Greenland ice sheet have verified the existence of several abrupt climate change (ACC) events. Among them, the most prominent are 25 major and several minor climate events now known as Dansgaard-Oeschger (D-O) events; they are characterized by a rapid 10-15 degrees warming followed by a mild period of century to millennium duration before a more gradual return to full glacial conditions. Similar rapid warming events have been identified in a number of other paleoarchives in the Northern Hemisphere. These findings have provoked wide interest in how abrupt climate change impacts biological diversity, and understanding of past biotic responses will be essential to predict how nature will respond to ongoing climate change. We provide here a coherent set of definitions for different types of fast climatic and ecological change, including ACC, and a summary of past ACC events. We synthesize and provide examples of biotic responses from genetic to ecosystem level, to identify and discuss modal responses and main mechanisms of adaptation. These abrupt climatic and ecological changes may well have shaped the past, and likely in the future, fate of human civilizations across the planet. We identify large gaps of knowledge, including the mechanisms triggering species' resilience after an abrupt change, or changes in ecosystem functioning. However, assigning crucial causal relationships between past ACC and biological responses due to constraints in temporal resolution for biological proxies dating is still a daunting challenge. We advocate for formalizing and unifying the meaning of abrupt climate change across disciplines, and call for specific research on past ACC periods to improve future biodiversity scenarios.

2.1 Introduction

It is the year 2300 and the Atlantic Meridional overturning circulation (AMOC) finally collapses after 200 years of weakening. Within few decades, Europe experiences frozen winters, meanwhile droughts

are more frequent in the Sahel. Potential impacts of a future ACC in natural and anthropogenic systems are worrying (Steffen et al. 2018), and they have occurred in the recent geological history of our planet (Mulitza et al. 2008; Buizert and Schmittner 2015). Scientists from different disciplines spanning from earth to biological sciences nowadays are looking at the past to find how these changes have impacted biodiversity (Nogués-Bravo et al. 2018), and to understand and anticipate how future biodiversity, ecosystems services and the human societies upon which they rely may be impacted from future ACC (Steffen et al. 2015).

There is, however, significant ambiguity in the scientific literature on the terms used for such climate changes. Definitions for “abrupt” change do not frequently match between paleoclimatology and biological communities, and it is often loosely defined across the scientific literature, including alternative concepts like fast or rapid change. This lack of clear terminology of these concepts across studies may jeopardize the current understanding of the ecological and human consequences of different types of climatic changes, the integration of disciplines and the assignation of biodiversity responses to periods of “abrupt” change, neither fast or rapid, as defined in recent reports (IPCC 2013a).

Herein we aim firstly to set an unambiguous terminology for the topic, by providing firstly definitions of abrupt, rapid and fast climate change as well as abrupt ecological change to clarify the panchreston of definitions. Then, we summarize abrupt paleoclimatic changes from a climatological perspective and the ecological responses to late Quaternary abrupt climate changes. Previous studies looking at biological responses to previous events of climate change have found that migration (Müller, Pross, and Bibus 2003; Lothrop et al. 2011), ecological community turnover (Jackson et al. 2014; Ampel et al. 2010), reorganization of geographical ranges (Anderson et al. 2011; Tinner and Kaltenrieder 2005), changes in population sizes (Pérez-Folgado et al. 2003; Peros, Gajewski, and Viau 2008), local extinctions (Yasuhara et al. 2008; Schmeisser, Loope, and Wedin 2009) are among the most recurrent responses. We review relevant literature across marine and terrestrial systems and, across the hierarchy of life organization, from individuals, to populations to communities, to find biological responses generalizable only during periods fitting the definition of “abrupt climate change” (see Definitions section). Those climatic and ecological shifts had also significant consequences to our own species, as the result of the natural resources and services that ecosystems provide us. We therefore synthesize and discuss how abrupt climate change have shaped the biological history of *Homo Sapiens sapiens*, and the demise and collapse of iconic human civilizations, to place the role of

abrupt climatic changes in the recent history of the biosphere and of our own species. Finally, we identify gaps in current knowledge, and suggest fruitful future lines of investigation.

2.2 Abrupt climate changes: discovery and definitions

In a Greenland ice core record, Dansgaard et al. (Dansgaard et al. 1993) found proof of several climate changes (the D–O events) occurred in Greenland during the last glacial period until 10 ka ago, recorded as 25 shifts of $\delta^{18}\text{O}$, a proxy for temperature. D–O events consisted of periods of mild climate (interstadials), lasting between a few centuries up to tens of thousands of years, between other periods with glacial conditions (stadials) (Fig. 1). Successive records with improved time resolution (Andersen et al. 2004) showed their inceptions to last typically ~ 50 y, while the terminations are in most cases smoother transitions, spanning hundreds of years (Rasmussen et al. 2014). These temperature changes were preceded by reorganizations of atmospheric circulation, which in the most rapid recorded case occurred within periods of 1–3 years (Steffensen et al. 2008). Signals of D–O events have been found also in paleorecords outside of Greenland (e.g. Europe, North America and Eastern Asia), with patterns similar to the ones from Greenland (Deplazes et al. 2013; Voelker 2002; Moreno et al. 2014; Shakun and Carlson 2010; Cosford et al. 2008), suggesting that D–O events had an at least hemispherical scale. At the onset of D–O events, temperature in Greenland increased up to 16 °C (Kindler et al. 2014); at lower latitudes the amplitude of the temperature shift was smaller.

The leading hypothesis explaining D–O events is that they are caused by a weakening of North Atlantic deep water formation, leading to partial shut down of Atlantic Meridional Overturning Circulation (AMOC) which brings warm waters at high latitudes in North Atlantic (Rahmstorf 2002). Other rapid climate events occurred in the Late Quaternary, the most notable being: the Younger Dryas and Bølling-Allerød events, whose classification as D–O is still debated (Fig. 1, bottom right); and the Heinrich events (HE), rapid cooling events characterized by signals of massive ice stream draining the Laurentide ice sheet into North Atlantic (Andrews and Voelker 2018). These massive iceberg discharges into North Atlantic likely caused Heinrich events by increasing the freshwater influx, therefore shutting down AMOC (Rahmstorf 2002). Other important events are the 8.2ka and 4ka cooling, occurred on a centennial scale in the comparably stable climate of Holocene (Walker et al. 2012), thus subdividing it into three stages (Cohen et al. 2013). Although it is debatable whether the two latter can be defined as “abrupt” according to our definition (see below), we will consider them in this review, given the ample literature of biotic responses to them, and their brief durations which make

them relevant in the context of this review.

Although the existence, causes and consequences of late Quaternary ACC have been receiving recently much attention, the terms “rapid”, “fast” and “abrupt” climate changes are used widely in literature to refer to the same climatic changes and are often considered as synonyms. To disentangle the different aspects and definitions of different climate change events, we here review the recent evolution of the “abrupt climate change” term, and propose a set of definitions.

According to the NRC report “Abrupt Climate Change” (National Research Council 2002), “technically, an abrupt climate change occurs when the climate system is forced to cross some threshold”; and despite multiplicity of formal definitions about ACC, there has generally been consensus about the notion of ACC as involving a switch into a new state following a tipping-point behaviour (Alley et al. 2003; Clark et al. 2002). However, given the interest arisen for these phenomena in other fields of research, the focus has been, rather than on the study of its physical causes, to the effects that they unleashed in natural and human systems, and therefore more comprehensive definitions have been proposed (National Research Council 2013; Clark 2009). Newer definitions of ACC take in account also of the nature of their consequences: by instance, the 2008 Synthesis and Assessment Report of U.S. Climate Change Science Program characterises climate changes as abrupt based on their time span and their effect on other systems (Peter U Clark 2009).

We suggest here a non-ambiguous terminology, proposed originally by Arnell et al. (Arnell, Tompkins, and Neil Adger 2005), to disentangle terms in two categories: those that aim to classify climatic events by the dynamics of the climate change, and those that refer to their time span. As for the first category, we propose the term “gradual climate change” for the “classic” type of climate change, where a change is provoked by the means of direct linear forcing. Instead, for those periods where the climate system crosses a tipping point and switches to a new state, we propose to define them as “abrupt climate change” events. The same terminology can be transposed for changes in systems other than the climatic: for example, “abrupt ecological change” as those which consist in a switch from a stable state to new state. In this sense, abrupt changes in natural and human systems can occur even if triggered by non-abrupt climate changes. As for the second category, we propose the use of “rapid climate change” (and solely that) for defining “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 from IPCC, 2013b). Abrupt climate changes are usually rapid, but not vice versa, as rapid climate changes can also be simply the

response to a fast linear forcing (Clark et al. 2002).

Following this terminology, late Pleistocene stadial-interstadial transitions can be considered abrupt. On the other hand, despite the current climate change being described as rapid, there is low confidence that it will lead to an abrupt climate event, at least in the current century (Hu et al. 2009; Delworth et al. 2008), with the notable exception of disappearance of summer Arctic sea ice, an event which has been evaluated as likely to occur in this century (IPCC 2013b). However, abrupt ecological events could stem from it, therefore analysing past ecological changes events can help explaining and predicting the future ones. Moreover, with late Quaternary climate events being more abrupt than those expected in the future, they can provide a “worst case scenario” study case, to investigate the robustness limits of ecosystems and better understand their resilience.

2.3 Biotic responses to last glacial ACC

The multitude of levels encompassing biological diversity, from genes to ecosystems, have reacted to past climatic changes by migrating, by phenotypic or molecular evolution and when failing going locally or even globally extinct (Lorenzen et al. 2011; Davis, Shaw, and Etterson 2005). A summary of most common kind of responses recorded in literature, classified by level of organization, is shown in Table 1.

It must be noted that in the majority of occasions these reactions were consequence of ACC but in other times they might have been triggered by events of rapid, gradual climate change. Williams et al. (2011) argue that the capacity to push an abrupt ecological change relies, rather than in inherent properties of climate changes themselves, in the relationships between environment and biota: were such relationships threshold-like or hysteretic, they would be able to produce regime shifts also in presence of linear (non-abrupt) climate forcing (Williams, Blois, and Shuman 2011). An ACC (as opposed to a “just” rapid climate change) could thus be signalled either by the presence of synchronous biotic responses in a geographically extended area, or by a linear or unimodal relationship between the climate and the biotic trends (Seddon 2017).

2.3.1 Marine systems

Marine records provide a unique window to understand the velocity and the modality of biotic responses to ACC. They provide evidence of significantly marine faunal turnovers during the last 20 ka following ACC; for example, turnovers to up to 75% within less than 40 years have been recorded for

benthic foraminifera assemblages, with response lag time intervals varying from decades to centuries (Cannariato and Cannariato 1999; Yasuhara et al. 2014). During warm interstadial climate conditions, marine species more adapted for interstadial climates were dominant; they reappeared consistently at the inception of warm climate episodes, but community composition showed differences in the relative abundances of species from one event to the other. This suggests species responses were individualistic. Within marine communities, ACC prompted full population recover of species best suited to novel climate conditions, suggesting marine ecosystems having resilience and a capacity of fast adjustment to equilibrium with the environment (McKay et al. 2014). This resilience does not rule out possibility of diversity decreases following ACC: during YD cold event, a north-western Atlantic benthic ostracodes community saw some of its species increase opportunistically in abundance in ~ 100 y and reach maximum population within ~ 1 k, while general community diversity decreased, and recovered only until around 8 ka BP, possibly because of the re-establishment of ventilation (Yasuhara et al. 2008). Moreover, the same ACC could provoke opposed patterns in different communities: as opposed to former example of diversity decrease, YD prompted instead an increase in diversity within a tropical Atlantic diatom community, likely due to a higher nutrient supply promoted by regional upper ocean mixing during YD (Cermeño, Maraño, and Romero 2013). Ostracod communities ashore from Iceland increased in diversity during cold events (YD, HE1, 8.2ka) with time lapses of ~ 100 y, and along with faunal reorganizations; this is ecologically more striking than responses of foraminifera, as most ostracods lack of a dispersal stage (Yasuhara et al. 2014). These and other responses are not only synchronous with ACC (e.g. with Greenland records), but also across taxa geographically distant: ostracod records and foraminifera records taken from 5000 km apart show high temporal correlation in community diversity through the last 20 ka (Yasuhara et al. 2014). The massive circulation reorganizations occurring in concurrence with DO and HE altered also the amount of oxygen and nutrients of marine ecosystems. Vegetation and sea-surface marine communities as recorded both in pollen and marine (dinocyst) records show concerted responses, in response to oceanic circulation changes and global atmospheric reorganizations (Eynaud et al. 2016).

In synthesis, fossil records of marine ecosystems show rapid, and often individualistic and opportunistic community reorganization following ACC. Such rapid responses were likely accomplished by migration from and to refugia consisting in bathymetric and geographic shifts (Fig. 2, population level). Change of marine currents such as those associated with periods of ACC, and hence changes in nutrition and oxygen supply, were the most significant factor for marine environmental

change. Water ventilation is seemingly the variable most regulating benthic ecosystems, while pelagic ecosystems appear to respond primarily to changes in nutricline depth.

2.3.2 Terrestrial systems

There is strong support to the key role of ACC controlling biological attributes across different levels of the biological organization from genes to ecosystems. At the genetic level, modern genetic homogeneity of tree populations in Central America is likely due to numerous genetic bottlenecks that were likely induced by the series of either decline or contractions into disjunct populations caused by HE during the last 60ky (Correa-Metrio et al. 2012). Moreover, and despite genetic adaptation was likely not a predominant strategy to cope with ACC, the repeated climatic turnovers and the following pulses population contractions and expansion have provoked genetic divergence: populations within refugia were likely isolated during stadial periods, leading a genetic drift, local selection of the best adapted genotypes and allopatric divergence. Flora richness of southern Europe may in this sense reflect a history of buffering and isolation from extreme climatic events (Tzedakis et al. 2002).

At the population level, fast changes following unfavourable climatic conditions leading to population declines and collapses are frequently recorded in paleoarchives. Recent high-resolution studies on pollen fossil records show significant responses of vegetation to ACC (Heikkilä, Fontana, and Seppä 2009; Litwin et al. 2013; Seddon, Macias-Fauria, and Willis 2015; Shichi et al. 2013; Shuman, Newby, and Donnelly 2009). Vegetation responses were subject to both steady and abrupt climate changes, with the latter reversing or accelerating the trends caused by the formers (Shuman, Newby, and Donnelly 2009; Alexander Correa-Metrio et al. 2012). However, responses, even for the same species, depend on context and vary by regional climate specificities: by instance, while reforestation north of the Alps occurred at the onset of Bølling-Allerød (BA), it occurred 1500 yr earlier south of the Alps, as Mediterranean warming was sufficient for forest spread (Samartin et al. 2012). A notable exception to population recovery of vegetation is hemlock (*Tsuga*). *Tsuga* population in North America suffered a rapid decline at ~5ka BP, never to fully recover, during a period of regional moisture variability (Shuman, Newby, and Donnelly 2009; Oswald and Foster 2012). Such decline does not seem to be a direct consequence of an ACC, although rapid climate variability might have acted as a disturbance source (Booth et al. 2012).

Stadial-interstadial transitions generally drove large changes in composition of and structure of vegetations communities (Nolan et al. 2018). While subject to ACC, a key feature for plant

communities is the capacity to maintain a dynamic equilibrium (i.e. to maintain viable populations under changing ecological and climatic conditions) with the environment within ≈ 1.5 ka time scales, which has been a classic assumption in the literature (Prentice, Bartlein, and Webb 1991). Plant communities have been observed to maintain dynamic equilibrium in shorter time scales, below 100y (Tinner and Kaltenrieder 2005; Tinner and Lotter 2001) and equilibrium states were maintained through community turnovers in favour of species more suited to the novel climate conditions (Paus, Velle, and Berge 2011) (Fig. 2, community level). For example, community shifts from open tundra to boreal forest occurred in Western Europe during stadial-interstadial transitions and vice versa, while in mid-Atlantic North America forest assemblages responded to HEs and D-O events by shifting from subtropical to high boreal (Heikkilä, Fontana, and Seppä 2009; Litwin et al. 2013; Fletcher, Sánchez, et al. 2010); in central American lowlands, instead, the climate driver of community turnover was moisture more than temperature, leading to more severe assemblage variation during HE-caused droughts (Correa-Metrio et al. 2012). Although many of species responses were individualistic, abrupt climate change favoured species with potential for rapid colonizing (i.e. principally climate-driven) and early-successional taxa (Tinner and Kaltenrieder 2005; Correa-Metrio et al. 2012). Another decisive factor in determining the success of a species is climate stress trend: while lowering of climate stress may favour more sensitive species (Tinner and Lotter 2001), enhancing climate stress can instead favour species which are climate resilient but less competitive. By instance, *Populus* (poplar, aspen, cottonwood) populations in North America expanded both after BA-YD cooling and YD-Holocene warming; in both cases they were favoured by the climate-induced decline of competitor sequences (Peros, Gajewski, and Viau 2008). Abrupt environmental changes may generate similarly abrupt changes in inter-specific interactions, with competing populations shifting during climate transition from a temporary period of unstable competition to stable coexistence (Jeffers et al. 2011).

At the species level, ACC events provide a series of natural experiments to understand how species may survive future climatic changes. The survival of species in microrefugia following abrupt changes in climatic conditions has also been pointed as key process to understand species ability to adapt to future climate change; for example, South African avian species have been shown to likely have survived Heinrich events by contracting in the Cape region (Huntley et al. 2016). The survival in climatic refugia implicitly also assumes the decimation of population across the species range outside those climatic refugia. This is the case of two tomato frog populations in Madagascar (*Dyscophus antongilii* and *Dyscophus guineti*), which were abundant during late glacial maximum, but suffered a

50-fold population size reduction by the end of the glacial period, possibly associated with the inception of Holocene or with the 8.2 ka event (Orozco-Terwengel et al. 2013). In plants, the rapidity of recolonization on the onset of Holocene suggests the presence of undetected (cryptic) refugia (Birks and Willis 2008). Refugia closer than expected to the ice sheets would allow them to resist climate changes without otherwise impossibly great latitudinal dispersal (Shichi et al. 2013). Moreover, reforestations have been recorded to occur in the very same region on centennial scales whenever climate declines were not severe enough to extirpate refugia, and on millennial scales otherwise. In this second case, reforestation could happen at the condition that interstadial conditions could hold long enough to permit species to disperse back into the region (Müller, Pross, and Bibus 2003). Fast migrations, like altitudinal shifts occurring both in Central Scandinavia and in north-western Alps (Paus, Velle, and Berge 2011; Blarquez et al. 2010), into climatic by conifer highlights the key role of mountain areas as “climatic heavens” for species survival.

The reorganization of species ranges due to ACC exerted dispersal and colonization events, global extinctions and local extirpations, modifying the resulting ecological communities. Megafauna community transitions (including regional replacements of populations by conspecific, or regional extinctions) followed D-O events, even though it is debated whether such transitions were triggered by the D-O themselves (Cooper et al. 2015), or by the lack thereof (Mann et al. 2018). In any case, human presence possibly disturbed megafauna meta-population responses to climate, thus promoting their extinction; this is also suggested by the high correlation of human arrivals and megafauna extinctions in a given region (Araujo et al. 2017). Small mammals showed instead an expected high resilience to extinction, especially in comparison to megafauna, and yet also a high sensitivity to abrupt climate changes (Blois, McGuire, and Hadly 2010; Berto et al. 2017). Species-species interactions had a mediating effect between ACC and animal community reorganizations. For example, in southern Italy, only the Bølling-Allerød transition among late Quaternary ACC prompted a switch into a small mammal community from a low diversity state, with dominance of one species (*Microtus arvalis*), to a higher diversity state (Berto et al. 2017). Such a difference in response is due to the fact that, of all climate changes, only Bølling-Allerød transition rearranged the vegetation composition in the area, most likely as the consequence of crossing a climatic tipping point for vegetation change.

Much of the current knowledge on animal and plant responses to abrupt climate change is at the population and community level, but there is still a significant gap of knowledge on how ecosystems and their functions, e.g. the sum of energy flows among individuals and species, respond to ACC.

However, there are some lines of evidences in the literature, showing that even if the ecological communities shifted during the last 12 ka, the energy flow on the whole ecosystem stayed constant, thus suggesting resilience of the energy fluxes in ecosystem to ACC (Terry and Rowe 2015). A further understanding of past 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 "brick" (i.e. plants versus mega-herbivores) mediating ecosystem states under ACC is of utmost importance (Jeffers et al., 2018) to develop ecosystem-based scenarios for future events of ACC.

2.3.3 Abrupt climate change, humans and societies

Given the significant impact that abrupt climatic changes have had in marine and terrestrial environments it is therefore expected to have affected also our own species, *Homo sapiens*, and human civilizations. Our review of the literature shows that humans as individuals and the societies that have emerged, and demised, along history have indeed experienced events of ACC triggering human migrations, genetic adaptation local extinctions, and civilization collapses (Stewart and Stringer 2012; DeMenocal 2001).

Humans populations, their distribution and routes of dispersal have been driven in the past by climatic conditions and ecosystem productivity (Eriksson et al. 2012; Giampoudakis et al. 2017; Wooller et al. 2018). Early human global population distributions and migrations out of Africa were affected by orbital-scale global shifts mainly during glaciation phases. However, numerical dispersal models indicate that abrupt events such as D-O did affect population distributions differently across regions despite not affecting the global distribution pattern (Timmermann and Friedrich 2016). For example, at the onset of YD, human populations in North America suffered declines or changes in settlement patterning, with declines accounting in some areas up to 50% (Anderson et al. 2011); however, in New England region, onset of YD is followed by colonization events, despite the climate conditions becoming harsher, possibly because the lowering temperature brought open favourable habitats for caribou, which may have in turn favoured human colonization (Lothrop et al. 2011). However, North American populations could rebound within ~900 years, that is, before cold climate conditions ended. In Japan, conversely, the number of settlements decreased during YD, suggesting a contraction of human distributions without trace of migration (Nakazawa et al. 2011). Later on, in central Spain, a more arid climate induced by the 8.2 ka event was followed by disappearing of human presence from that region, whereas humans appeared at about the same time in a more nearby humid

area (González-Sampériz et al. 2009).

Different lines of evidence point also to human adaptation at the genomic level, mainly to adapt to colder climatic conditions or low oxygen regions, as an alternative strategy to adapt to climatic changes. There are traces of genomic adaptation in humans when colonizing colder regions out of Africa; for example Siberian populations experienced a selection for genetic variants in fat metabolism as an adaptation to climate change (Cardona et al. 2014). Although these responses are difficult to link to specific moments of abrupt climate change, we can expect that ACC triggered significant evolutionary pressures in allele selection. Adaptive behaviour is also another potential strategy to adapt to ACC. In Beringia, the transition to Bølling-Allerød transformed the vegetation landscapes, fragmenting former steppe habitats. To adapt to this change, human population shifted dietary preferences, switching from hunting horse and mammoth to bison and wapiti, two species which climate change pushed to higher population densities into restricted patches (Lanoë et al. 2017).

In recent times, climatic changes have been linked to the thrive and demise of human civilizations, although its attribution and causality is still hotly debated. The Akkadian civilization, settled in Mesopotamia, collapsed following the 4ka event, which caused arid climate regime in its region. Northern agricultural settlements vanished and populations migrated; the empire fell shortly after, despite being provided with storage technologies of food and water (Cullen et al. 2000). Other climatic events, even of a rapid nature but not considered as ACC as defined here, have also triggered radical societal challenges. The collapse of the Maya civilization co-occurred with the most severe drought in their history (Douglas et al. 2016) and the end of the Roman civilization occurred during the Late Antique Little Age, 536-660 AD, a cold pulse triggered by intense volcanic activity (Sigl et al. 2015). Indeed, this climatic event may have also contributed to the establishment of the Justinian plague (Büntgen et al. 2011), transformations in the Eastern Roman Empire (McCormick et al. 2012), migrations in Asia and spread of Slavic tribes (Büntgen et al. 2016) and even to political upheavals in China (Fei, Zhou, and Hou 2007). These imprints of ACC should be interpreted carefully and arising generalizations subject to deep exploration when inferring causal relationships within recorded climate changes and archeological records (Armit et al. 2014). Moreover, it has been pointed out that rapid climate changes may not necessary be disruptive, but also influence human societies in more refined ways (Clarke et al. 2016).

Social and cultural advancements have also been linked to population increases due to climate-induced migrations. During late Pleistocene, abrupt wet/dry climate shifts, synchronized to

stadial/interstadial transitions of D-O of the Northern Hemisphere, occurred in southern Africa. Archeological findings on the South African coast show pulses of technological advancements during of periods of humid conditions in the region, namely stadial periods of northern hemisphere: this suggests that, during droughts periods corresponding to D-O, the South African coast acted as a refugium for humans, and the richness of ecosystem combined with the demographic pulse allowed technological advancement (Ziegler et al. 2013).

In synthesis, humans in the late Quaternary have experienced migrations, behavioural changes, extirpations of local populations, and the burst of new technologies under events of rapid and abrupt climate change. The magnitude and speed of those changes, both rapid and abrupt climate change, have also triggered or contributed to the demise and spread of civilizations, highlighting the need to prepare for the societal change of mitigating and adapting to future abrupt changes in climatic and ecological systems.

2.4 Conclusions

The discovery 50 years ago by Dansgaard and colleagues of recent ACC (Dansgaard et al. 1969) has largely influenced our understanding of the planetary systems, including its biotic component. Abrupt climate change has pushed life across the biological hierarchies, shaped current patterns of biological diversity and regulated ecological processes (Yasuhara et al. 2014; Correa-Metrio et al. 2012). Such impacts largely varied regionally, mirroring the significant spatial variation of past ACC (Deplazes et al. 2013; Jennerjahn et al. 2004), highlighting that knowledge of regional, fast-paced climate history is fundamental for the understanding of biotic responses to ACC. Research on ACC impacts in past biological diversity will benefit of paleoclimatic simulations at high resolution, both temporal and spatial, instead of one-single site paleoclimatic reconstructions. Such climatic reconstructions will contribute to explain the role of past and current paleoclimate variability into shaping biodiversity distribution patterns (Fordham et al. 2018) and better forecast future scenarios of biodiversity under climate change. Moreover, paleoenvironmental reconstructions should account for a careful comparisons of records and, when aiming to infer cause-effect relations, accuracy in the dating and in the comparison of dating from different records will be crucial. Overlooking differences in chronological uncertainties might lead to circular narrative reinforcements (Blaauw 2012). Records can be integrated together in a safer way by deriving their chronologies from independent dating and by quantifying the correlation uncertainties, as e.g. in the paleoclimatological INTIMATE database (Bronk

Ramsey et al. 2014).

Exploring the links between ACC and biological dynamics by studying paleorecords is shedding light on the type, magnitude and speed of those dynamics, and improving the mechanistic role of processes such as adaptation *in situ*, dispersal or the significance of climatic refugia or 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 reduced by current anthropogenic habitat fragmentation (Hof et al. 2011). Besides, ecosystems out of equilibrium with climate are more likely to experience temporary diversity loss, but also to resiliently recover and reach quasi-equilibrium conditions when climatic conditions improve and are stable across time. A continuous state of disturbance, as that induced by human domination on the biosphere, might therefore impede the ecosystem ability to maintain dynamic equilibrium, thus hindering their resilience to ACC (Kröel-Dulay et al. 2015). As these biological dynamics spread across entire ecosystems, the functions and ecological services they provide to human societies may radically differ to those that today provide safety planetary boundaries (Steffen et al. 2015).

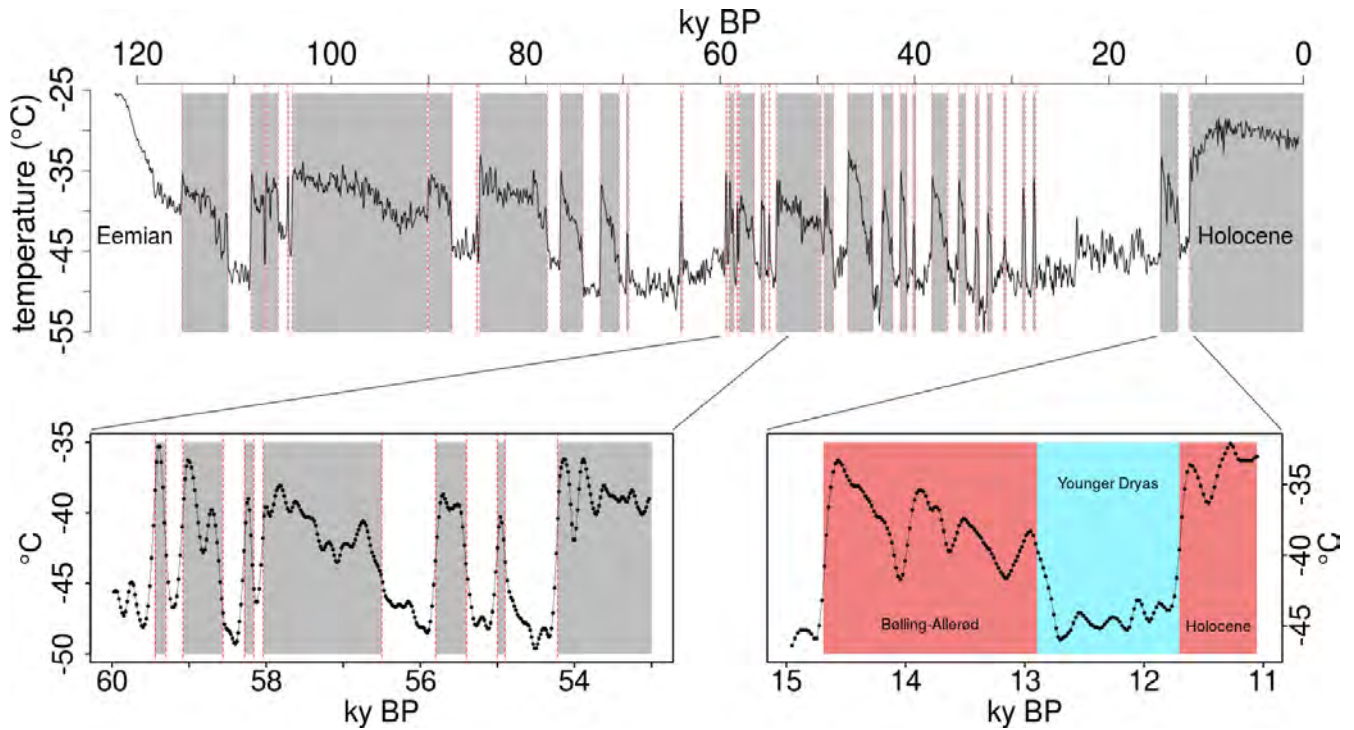


Figure 1: Greenland temperature throughout Late Quaternary. On top: annual temperature of the NGRIP site (Andersen et al. 2004) in Greenland versus time for the last 120 ky BP, i.e. before year 2000 AD. Time resolution is ~ 20 years. Gray rectangles highlight D–O events, as classified by Rasmussen et al. (Rasmussen et al. 2014), and the Holocene. Red dotted line highlight ACC, namely the transitions to and from D–O and the transition to Holocene. The label Eemian indicates the last interglacial period before Holocene. Temperature values before Holocene were reconstructed by Kindler et al. 2014; temperature values in the Holocene were obtained by linear regression of $\delta^{18}\text{O}$ data (a proxy from temperature) from Andersen et al. 2004 with aforementioned temperature data. Bottom left: detail of the top plot for the period 60–53 ka BP, showing data points as well. Bottom right: another detail of the top plot, for the period 15–11 ka BP. Data points are shown and Holocene, Bølling-Allerød and Younger Dryas are highlighted, in red or blue depending whether they are warm and cold periods, respectively; transitions to and from these events are ACC.

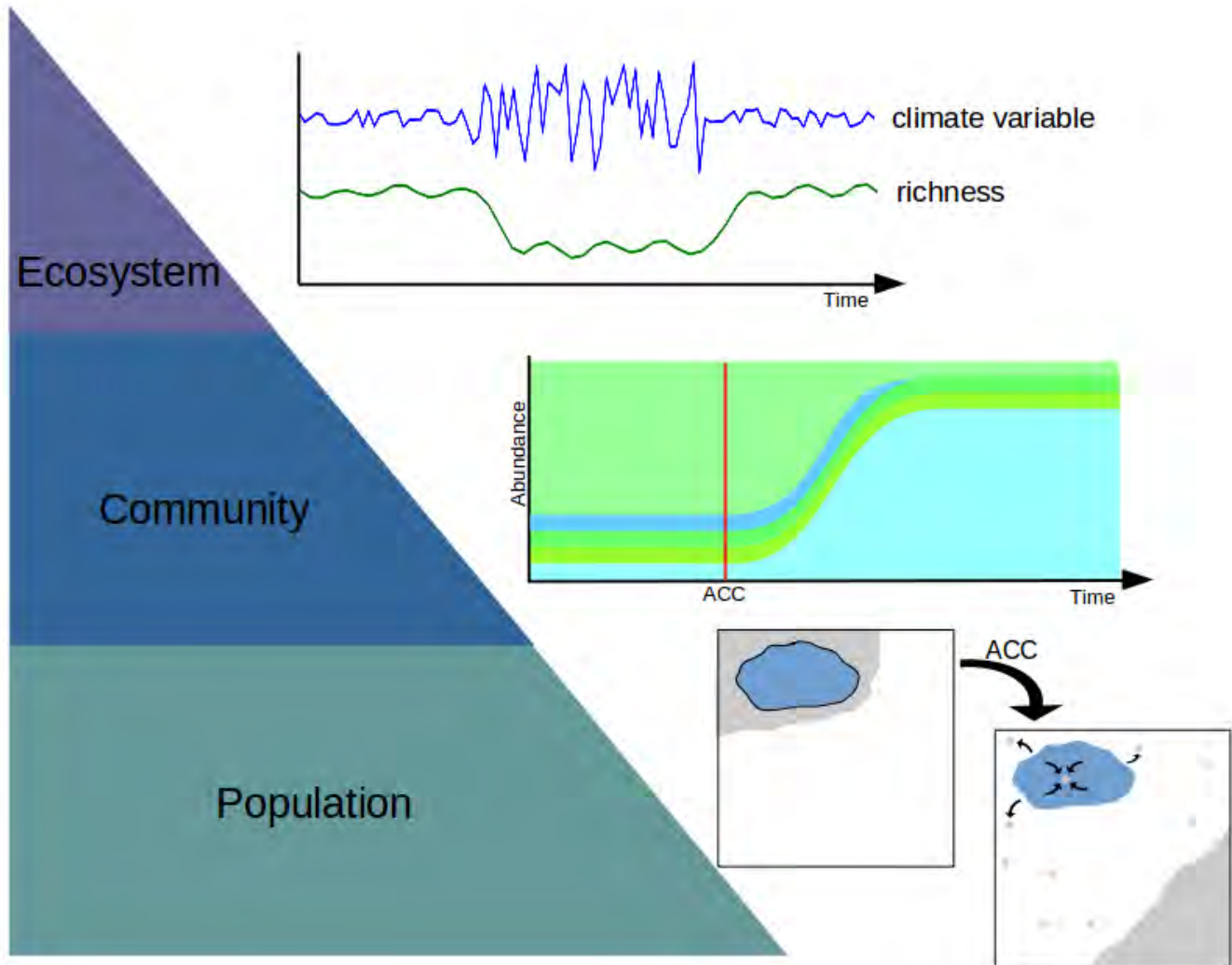


Figure 2: Sketch of general responses to ACC, ordered by level of organization. At population level: Grey represent region of environmental suitability; small grey dots are microrefugia, blue is population distribution. Before climate change, species lies within its climatic niche; after an ACC the brief time range only allows for short migrations and/or range contractions in close microrefugia. Another ACC of opposite sign would let the dispersal to invert, so that population can recover to initial distribution. At community level: an ACC may prompt the dominating species to contract or possibly to emigrate, while some former rare species can take over and others can become extirpated. At ecosystems level: climate variability, such as from ACC, extirpates some of ecosystem's species, especially if rare (Cermeño, Marañón, and Romero 2013), thus reducing richness. Species richness recovers shortly after the re-establishment of climate steadiness.

		Taxa			
		Marine/lacustrine	Terrestrial plants	Terrestrial animal	<i>Homo</i>
Genetic	Divergence		(Tzedakis et al. 2002)**		
	Productivity change	(McKay et al. 2014)			
Individual	Behavioural change		(Giampoudakis et al. 2017)	(Schmeisser, Loope, and Wedin 2009; Charmantier et al. 2008)	(Lanoë et al. 2017; Rössner et al. 2017)
	Adaptation	(Eynaud et al. 2016)			
	Replacement			(Cooper et al. 2015)	
Population	Abundance variation	(Pérez-Folgado et al. 2003)	(Shuman, Newby, and Donnelly 2009; Seppä et al. 2007; Peros, Gajewski, and Viau 2008; Oswald and Foster 2012)	(Orozco-terWengel et al. 2013)	(Timmermann and Friedrich 2016; Anderson et al. 2011; Van Geel, Buurman, and Waterbolk 1996; Ziegler et al. 2013; Lillios et al. 2016)
	Extirpation			(Cooper et al. 2015; Ukkonen et al. 2011)	(Shea 2008)
	Range expansion or contraction		(Blarquez et al. 2010; Samartin et al. 2012; Bartish, Kadereit, and Comes 2006; Patsiou et al. 2014)		(Nakazawa et al. 2011)
	Dispersal		(Blarquez et al. 2010; Paus, Velle, and Berge 2011)**; (U.C. Müller, Pross, and Bibus 2003; Giampoudakis et al. 2017)	(Ukkonen et al. 2011)	(Lothrop et al. 2011; Wooller et al. 2018; González-Sampériz et al. 2009; Van Geel, Buurman, and Waterbolk 1996; Cortés Sánchez et al. 2012; Bradtmöller et al. 2012; Ulrich C. Müller et al. 2011)
	Socio-cultural reorganization				(Ulf Büntgen et al. 2016; Cullen et al. 2000; Clarke et al. 2016; Ziegler et al. 2013; Lillios et al. 2016; Bonsall et al. 2002; Bradtmöller et al. 2012; Borrell, Junno, and Barceló 2015)
	Extinction			(Mann et al. 2018; Araujo et al. 2017; Barnosky et al. 2004)*	
Community	Turnover	(Ampel et al. 2010; Yasuhara et al. 2008; Cannariato and Cannariato 1999)	(Shuman, Newby, and Donnelly 2009; Heikkilä, Fontana, and Seppä 2009; Litwin et al. 2013; Seddon, Macias-Fauria, and Willis 2015; Tinner and Lotter 2001; Fletcher, Sánchez, et al. 2010; A. Correa-Metrio et al. 2012; Alexander Correa-Metrio et al. 2012)	(Terry and Rowe 2015)	(Shea 2008)
	Composition shift	(McKay et al. 2014; Cermeño, Marañón, and Romero 2013)	(Paus, Velle, and Berge 2011; Alexander Correa-Metrio et al. 2012; Shichi et al. 2013; Tinner and Kaltenrieder 2005; Fletcher, Goni, et al. 2010; Nolan et al. 2018)	(Blois, McGuire, and Hadly 2010; Berto et al. 2017)	
	Competition		(E.S. Jeffers et al. 2011)		(Ulrich C. Müller et al. 2011)
Ecosystem	Richness fluctuation	(Cermeño, Marañón, and Romero 2013)		(Huntley et al. 2016)	
	Diversity fluctuation	(Yasuhara et al. 2014; Kuhnt et al. 2007)			

* Contributory effect

** Hypothesized

Table 1. Literature covered. Summary of literature quoted in this review, categorised by the recorded (or hypothesised where indicated) biotic responses to ACC.

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3 Radis: Python software for simulating and analysing range dynamics in response to past climate change

By enumerating and classifying the existing knowledge, we collected an organic, coherent narrative description of ecological dynamics of response to abrupt climate changes. A step forward requires a model able to make quantitative predictions, and validate or disprove a theory.

Correlative models, a common class of models for macroecological analysis, relate statistically species distribution with environmental conditions. Such a phenomenological approach, however, may fail when applied to events of such short time range where indetermination and spatial dynamics played the important role we saw above. Besides, it is interesting to inquire not only on which effects made species survival to abrupt climate changes possible, but also how such survival relied on interactions among multiple effects.

For studying processes with these features, more utility can stem from the use of process-based model, i.e. models that directly simulate the biological process they aim to study. One of the advantages is that in a process-based model the processes under examinations are explicitly reproduced, therefore their regulating parameters have a direct biological interpretation, allowing to directly estimate species traits (Connolly et al. 2017). Moreover, they are spatially and temporally explicit, i.e. they simulate spatial dynamics through time: hence, they increase the chances to estimate complex interactions between processes, and to grasp an eventual role of stochasticity in such processes (Rangel et al. 2018). This kind of approach stresses the importance of historical processes over a simply deterministic approach (Gotelli et al. 2009).

Therefore, we developed a process-based model able to simulate the particular traits that stood out as key for coping with abrupt climate change from our previous reviewing research. Simplifications were inevitable and the most complex of the relevant interactions, namely the inter-specific community interactions, were left out for the sake of reproducibility. Consequently, the simulation does not aim to perfectly reproduce all the ecological dynamics under climate change. On the other hand, it will allow to quantitatively analyse the biological and ecological processes that could be reproduced, and to explore the nature of their interplay. This is further discussed in the following manuscript, which is intended for submission to *Ecography* and reported here with a few minor edits.

Radis: Python software for simulating and analysing range dynamics in response to past climate change

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Accelerating climate change is triggering shifts in the distribution of species, shaping ecological communities and the functioning of ecosystems. Historical and paleoecological observations, alike, indicate that those shifts are the result of the interplay between changing climatic conditions and biotic processes. Radis is a python-based software that simulates geographical range dynamics over past periods of climate change, which are validated against observed patterns in the fossil record or other sources of historical information (i.e. museum collections). The software models and estimates the relative contribution of two fundamental processes in climate-driven species' range shifts: tolerance in situ and dispersal. These processes are modelled resulting in thousands of possible distributions. Validation data is used to pinpoint the best set of modelled distributions using both Metropolis-Hastings and statistical likelihoods. In doing so, Radis estimates the specific magnitude of tolerance and dispersal needed to reliably project range shifts under past climate change. The software is very flexible, allowing users to import their own climatic and species distribution information, and to choose the time step and spatial resolution most suitable for their focal species. It provides graphical outputs to explore the spatial and temporal dynamics of observed and simulated climatic niches and geographical ranges, and offers a range of summary statistics. We showcase Radis by demonstrating how the model can i) reconstruct past changes in the distribution of fir (*Abies*) in North America during the late Pleistocene, and ii) identify the relative roles tolerance in situ and dispersal had on the species' responses to rapid climatic changes during this period. Radis can be a useful tool to investigate underlying mechanism in species' responses to environmental changes by validating models against paleorecords and to contribute to the development of biodiversity predictions rooted in past natural experiments of climate change. Paleoecologists, ecologists and scientists modelling and predicting

impacts of climate change in biodiversity will benefit from the ability of Radis to estimate and model the main mechanisms of species response to climate change.

3.1 Introduction

Several abrupt climate changes (ACC) occurred during the late Quaternary that are similar in rates and magnitudes of warming to projected climate change (Brauer et al. 2014). These included the Dansgaard-Oeschger (DO) events, where large magnitude changes in temperatures of up to 10-15°C (at some mid to high latitudes) occurred over decadal to century time-scales, affecting vast regions of the planet (Alley et al. 2003). These rapid climate change events triggered large changes in the composition of ecological communities, increased rates of species migrations, variation in the size and structure of species geographical range and the extinction of some taxa. A stronger understanding of ecological response to these rapid and large magnitude warming events has the potential to improve our capacity to anticipate and forecast how species will react to future climate change (Dawson et al. 2011); and resolve important conundrums, including why major extinctions from climate change are projected for the 21st century, despite there being rare evidence of range-wide extinctions in response to large scale climate fluctuations during the late Quaternary (Botkin et al. 2007; Hof et al. 2011). That is with the exception of megafauna, where humans and climate are likely to have combined to have devastating consequences during the late Pleistocene and early Holocene (Araujo et al. 2017). This discrepancy between observed and forecast rates of climate driven biodiversity loss suggests that our ecological understanding of the mechanisms species use to cope with these abrupt changes is likely to be incomplete, jeopardizing the potential for current ecological models to accurately predict biodiversity loss from future scenarios of climate change (Fordham et al. 2014; Nogués-Bravo et al. 2018).

Most projections of past and future distributions of biodiversity at large spatial scales are done by species distribution models (SDM) based on correlative approaches, a family of models which has provided insightful predictions on how biodiversity, from populations to species to whole communities, reacted to recent and may react to future climate change (Hugall et al. 2002; Strasburg et al. 2007). However, correlative models are of limited value for exploring the mechanisms responsible for changes in past species distributions (e.g. adaptation versus dispersal). An alternative strategy is to explicitly incorporate potential mechanisms under scrutiny. Models with this kind of approach are called mechanistic (Kearney and Porter 2009) or process-based models (Connolly et al. 2017). In process-

based models, a set of relevant mechanisms are put into action to simulate how the natural world should look like (i.e. species distributions) under specific combinations of them. The simulated patterns are then compared against observations from the field (Urban et al. 2016).

Past species distribution patterns can be useful to provide independent validations of biodiversity future projections, thus increasing robustness and their ability to provide accurate scenarios of biodiversity change and policy recommendations (Nogués-Bravo 2009; Nogués-Bravo et al. 2018). Indeed, biodiversity changes under past climatic changes are being explored with increasing frequency, to gain deeper insights in the mechanisms that allow species to survive abrupt climatic changes (Nogués-Bravo et al. 2018), and to determine how well models replicate observed species range shifts, including large expansion and collapses, as recorded in the fossil record (Nogués-Bravo et al. 2008; Lorenzen et al. 2011; Blois et al. 2013; Nogués-Bravo et al. 2016). This is being driven by open-access to curated and standardising geo-located and radio-carbon dated fossil records (Williams et al. 2018; Fordham and Nogués-Bravo 2018) and high-resolution paleoclimate simulations (Fordham et al. 2017), making it possible to reconstruct past geographical range dynamics at decadal to millennial time intervals (Fordham, Saltré, et al. 2018). Furthermore, these paleo-archives can be used as testing targets in first-principle simulation models to explain competing mechanisms for coping with climate change, including survival in situ via adaptation or dispersal and colonization of suitable areas.

To advance our understanding of the ecological mechanisms that have shaped past and current-day patterns of biodiversity, we present here Radis (simulator of RAPid DIStribution changes), a software developed in Python to conduct spatially-explicit simulations exploring the magnitude and role of the main mechanisms involved in geographical range dynamics under climate change to explain species distributions (Nogués-Bravo et al. 2018). It is rooted in a new generation of process-based models of biodiversity change in space and time, which are improving our knowledge of the mechanisms that allow species to thrive, survive or go extinct (Rangel et al. 2018), holding the potential to improve projections of future disruption to biodiversity from climate change (Fordham et al. 2016). Radis is a process-based, spatially explicit modelling framework for simulating geographical ranges in response to past climate change. It explicitly models two main ecological responses to past climatic conditions: tolerance in situ and dispersal. Being unable to tolerate in situ results in simulated local extirpations or extinctions. It differs from competing software, such as MigClim (Engler and Guisan 2009), not only because Radis accounts for the possibility of adaptation in situ, but also for rooting its evaluations in a unique validation approach of simulations using paleorecords. Specifically, Radis uses an algorithm

adapted from the Metropolis-Hastings method to explore the parameter space of response mechanisms to pin-point the specific magnitude of in situ adaptation and dispersal needed to better replicate the observed patterns in the fossil record.

There are a number of specific mechanisms to adapt in situ to changing climates. These include ecological plasticity, phenotypic change, shifts in behaviour or micro-evolutionary change (Gienapp et al. 2008; Valladares et al. 2014). Instead of simulating geographical range dynamics for each type of in situ adaptation across the entire geographic range of a species, which would be computationally challenging. Radis simulates adaptation as the ability of a species to modify and adjust its climatic niche to temporally changing climatic conditions, avoiding local extirpations. Radis simulates dispersal using a set of probabilistic kernel functions within user-defined boundaries of dispersal (Bullock et al. 2017), which account also for rare long-distance dispersal events (Clark 1998). They are parametrised to be relevant at a generational time step. Plant species, for example, from centennial to millennial scales, were, and are still today (Skov and Svenning 2004) out of equilibrium with climate (Woods and Davis 1988). This lagging is likely to increase the spatio-temporal variance of vegetation response (Prentice, Bartlein, and Webb 1991), hindering the ability of deterministic approaches for inferring responses from paleorecords. Radis allows to simulate and explore the role of rare, stochastic dispersal events, paving the route to include mechanisms that are fundamental for species to survive abrupt climate changes.

In summary, our approach and tool, Radis, allows the independent testing of two important and competing mechanisms that drive the geographic structure and dynamics of species ranges in response to different rates and magnitudes of past climatic changes, including abrupt episodes of change. Radis is available for download at the address <https://github.com/FBotta/Radis>.

3.2 Methods and features

The geographical range of species and their dynamics over time are the result of the interaction between abiotic dynamics and biological processes. Species react to climate change by tolerating climate change in situ or migrating; when these two response strategies fails, we would expect local extirpations. Radis simulates distributions of species using two important mechanistic responses to climate change, tolerance in situ and dispersal, resulting in colonization and extirpations of local populations. This is done by a process where the simulated species ranges under climate change are validated iteratively against past distributions recorded in the fossil record.

To identify the mechanisms driving geographical range dynamics under periods of past climate change. Radis requires: 1) fossil record data, with dating and coordinates; and 2) time series of maps of climatic conditions.

Radis simulates tolerance in situ by testing the species distribution range simulations against different values of breadth and position of their climatic niche. The software also simulates continuous dispersal event by implementing it on a discretely spatially fragmented lattice grid. Dispersal is modelled as a probabilistic event from one occupied cell towards an unoccupied cell; the probability of the event is mediated by a kernel function. Radis is provided with three possible shapes for the kernel well supported in the literature (Bullock et al. 2017); allowing users to choose among them before starting the simulation. In this type of modelling, the dispersal considered here is the natal dispersal, scaled up to a generational level. Accordingly, it is recommended to choose a time step length matching the generation time of the studied taxon.

The work flow of simulations in Radis starts by importing the dated and georeferenced fossil localities and the paleoclimatic maps, usually arising from atmosphere-ocean general circulation models (e.g. Fordham et al. 2017). Every raster climate map for a given climatic variable represent a climate layer, and the time steps are defined by the dating of the layer. For instance, if the climate layer represents climatic conditions spaced apart 100 years, the time steps of the simulation will be 100 y long. The duration of each time step (i.e. annual, decadal, centennial or other) and the starting and finishing times of the simulations are user-defined. In a second phase, Radis evaluates the simulation likelihood against the fossil record database provided by the user. Radis uses a Metropolis-Hastings algorithm (Mihaylova et al. 2014) to pin-point the set of simulations better explaining the observed patterns in the fossil record (Fig. 1).

Radis needs to read all the aforementioned data, which depending on their size can take a considerable amount of time. To improve computing time efficiency, Radis saves a copy of them as binary data, so that for future launches the user can choose to load them directly instead of formatting the same data a second time. Radis saves automatically two files. The first is one called “Input”, containing the climatic, fossil data given by the user; and a second one called “Dist”, containing the distance matrix of the shapefile defining the grid-cells constituting the study area (see section 3 of SI).

The output of Radis consists of a binary data file storing: 1) for every parameter, the sequence of all values that it assumed throughout the Metropolis-Hastings (see below); 2) the sequence of values likelihood assumed throughout the Metropolis-Hastings, i.e. the sequence of likelihoods of every

simulation; 3) the representation of the simulation which performed the highest likelihood. An extra script is provided in the same download page to allow for a visualization of the results, including visualizations for: likelihood and parameters versus number of iteration; kernel function of iteration with highest likelihood; best simulated niche, i.e. niche corresponding to the MH iteration with highest likelihood; distribution range maps of best simulation, i.e. simulation corresponding to the MH iteration with highest likelihood (see section 9 of SI).

3.2.1 Response processes and simulated distributions

Radis simulates both tolerance in situ and dispersal as the two main response mechanisms. Radis simulates tolerance by changing between simulations the species' climatic niche, so to persist in grid-cell under different climatic conditions than experienced before. Conceptually, the climatic niche (*sensu* the Grinnellian niche in (Soberón 2007)) is understood in Radis as the set of climatic conditions for which the intrinsic growth rate of populations are not negative. Radis estimates the climatic niche (or climatic envelope) mathematically using the Mahalanobis distance (MD) (Fig. S1), which is a computationally efficient approach for defining the suitability of climatic conditions for a species (Farber and Kadmon 2003). The approach has been shown to be successful in explaining past geographical dynamics across the Late Quaternary (Nogués-Bravo et al. 2008).

Radis allows a species to survive across varying degrees of tolerances, ranging from full niche conservatism to full niche lability (species being able to live in any kind of climatic conditions). In those grid-cells for where tolerance levels are not high enough to survive in situ, Radis will simulate local extinctions. Tolerance in situ is defined in Radis using two parameters defining the climatic niche of any species: the centroid of the Mahalanobis ellipsoid and its breadth. These two parameters allow users to simulate not only the ability of a species to shift the average conditions in which it inhabits (i.e. the centroid), but also the variability of climatic conditions that a species can persist in after an event of climate change as result of local adaptation (Richards et al. 2006). Before simulations starts, Radis evaluates the niche breadth and the centroid empirically using the georeferenced dated fossil record and the paleoclimatic simulations from user-defined period and area. Then, it allows the user to use such evaluated niche for the simulations, or alternatively to arbitrarily define any kind of climatic niche based on centroid niche positions and its breadth, allowing using Radis in a virtual species fashion. During the simulation, Radis checks whether a climate condition lies within the niche of a species, and it calculates the Mahalanobis distance of that climate condition to the centroid of the niche: if the

distance is less than the niche breadth, then the climate condition lies within the niche of that species. Both niche centre and breadth are parameters whose space is explored by the Metropolis-Hastings (see section below).

Dispersal has been shown to be a key response of plant and animals during events of climate change; regional and global plant migrations patterns have been recorded during the late glacial period, and macrofossil records document dispersal events during the same periods for populations of small mammals, megafauna, and humans (Jackson and Overpeck 2000; Ukkonen et al. 2011; Berto et al. 2017; Fordham et al. 2016; Giampoudakis et al. 2017). In Radis, the ability to disperse is modelled using a dispersal kernel function $f(x)$, from which there are three possibilities: linear, step-like and exponential (Fig. S2). These are well supported dispersal types by paleo-archives (Clark 1998; Bullock et al. 2017). When checking for a possible dispersal through a distance x . Radis picks a random number between 0 and 1; if the value is lower than $f(x)$, then dispersal occurs. Each of the kernel functions are characterized by one dispersal parameter, which is different for every of the three kernel functions but it is called α for all the three of them. Regardless of what kernel function the user chooses, α is a parameter whose space is explored by the MH (see below). The linear kernel is as follows:

$$f_{linear}(x) = \frac{-x}{\alpha M} + 1; \quad (1)$$

in this case α represents the ratio between the distance where the function reaches 0 and the maximum possible distance M . All the other parameters of the functions except α , as by instance M for kernel function (1), are fixed during simulation. M is set to 100 km, but this value can be manually changed by the user (see section 8 of SI). For the step-like kernel, α is the ratio between the position of the step and the maximum possible distance M (with, again, M being fixed but manually settable to other values).

The function for the exponential dispersal mode is as follows:

$$f_{exponential}(x) = \rho \frac{e^{\frac{-1}{2} \left(\frac{x}{\sigma}\right)^2}}{\sqrt{2\pi\sigma^2}} + (1 - \rho) \frac{e^{\sqrt{\frac{x}{\alpha}}}}{4\alpha} \quad (2)$$

namely an average, weighted on ρ , of two components: a Gaussian distribution and a “fat-tailed” distribution, which accounts for rare long-distance dispersals events. The contribution of the “fat-tail” to the kernel is governed by α , called distance parameter which can assume values in the range [0. 1] (Clark 1998). D , σ and ρ are constants; they can be set by the user but do not change during or between simulations (see section 8 of SI).

The simulated species geographical ranges are the result of the combination of a variety of magnitudes of tolerance in situ and dispersal simulated over the geographical lattice of changing

climatic conditions. At the start of a simulation, the species occupies the grid cells where climate conditions are satisfying the niche conditions. In other words, the species at the beginning is found in every grid cell having climate conditions lying within its climatic niche as defined by the Mahalanobis ellipsoid. Then, for a user-defined number of time steps, Radis updates the climate maps, and for every time step it simulates the consequent responses of the species distribution range. It locates those grid-cells with suitable climatic conditions under different magnitudes of tolerance in situ. From those grid-cells with suitable climatic conditions, the species will attempt to disperse to any other cell with a suitable climate according to its dispersal function. For every grid cell, and if the novel climate lies outside the species' niche, the species is removed from that grid cell, producing a local extirpation. The results are a time series of species distribution maps; an example of this is shown in Fig. 2d.

3.2.2 Parameter optimization and model validation

A Metropolis-Hastings (MH) algorithm is a subset of Markov chain Monte Carlo methods (MCMC) that can be used for stochastic optimization of parameters (Mihaylova et al. 2014). At the start of a Radis launch, the user can choose to have the software perform one single simulation, and evaluate its likelihood; or instead she can choose a user-defined number of iterations, where every iteration consists of one single distribution range simulation and its likelihood evaluation (see section 3 of SI). The parameters space explored is within the boundaries of three axes: α or dispersal parameter, the coordinates of the niche centroid, and the niche breadth. Therefore, through the MH, Radis searches the values of α , niche breadth and niche centroid that maximize the likelihood of predicting the patterns of species distributions observed in the fossil record.

While Radis adopts the MH algorithm, its results differ substantially from those of a usual Markov chain produced by a MH. MH algorithms usually evaluate likelihood of a step i by the use of a given function $f(x_i)$, where x_i is the vector of parameters for step i . In the case of Radis, the evaluation of likelihood is based on the result of the simulation, which is a process that may involve random processes, i.e. rare long-distance dispersal events. Therefore, for the same combination of parameters, different simulations can be produced, which will lead to different values of likelihood. Hence, differently from usual results of MH, the Markov chain of parameters produced by a Radis run does not feature a convergence in the space of parameters. Instead, it endlessly explores the parameter space, eventually finding a parameter combination corresponding to a maximum likelihood. Information about the processes determining species range dynamics under climate change can thus be inferred by

considering the parameters values producing the highest likelihood values.

At the end of a simulation i , Radis evaluates its likelihood L_i according to the following formula:

$$L_i = \min\left(\frac{p_i}{p_T}, \frac{a_i}{a_T}\right) \quad (3)$$

where p_T (a_T) is the total number of fossil presences (absences), respectively, about the given species within the region and the time interval considered by the simulation, and p_i (a_i) is the number of times that the simulation has featured a presence (absence) in a grid cell where the corresponding fossil archives records a presence (absence) (see section 5 of SI).

3.2.3 Identifying the relative contribution of tolerance and dispersal

Once a maximum likelihood, and thus an optimal combination of parameters has been found, the user may be interested into quantifying the contribution that each response strategy provides to the geographical range dynamics under climate change. For this purpose, Radis can be used to run sensitivity tests. Sensitivity test can be executed by having one or several parameters “fixed”, i.e. not letting them change throughout the MH, and thus letting only one parameter vary during the MH.

For example: if the user wishes to study the relevance of dispersal for a given taxon, she can do so by launching Radis with the niche breadth and niche centroid parameters kept fixed, therefore letting only α change value. The user can in this way verify how much the variation of α throughout all its possible values influences the total likelihood, and estimate the contribution of dispersal by the range of likelihood values obtained during the run.

Analogously, a sensitivity test can be run for each parameter, thus quantifying the relative contribution of dispersal and tolerance in situ, to explain geographical species range dynamics (see section 7 of SI for details).

3.3 Example: *Abies* under late glacial climate changes

We provide here a working example of Radis, where we considered the fir tree taxon (*Abies*) during the period 15-10 ky BP in North America. During this time interval, both the transition to Younger Dryas and to Holocene, two well studied abrupt climate changes, occurred, and their effect on regional climate was particularly intense in North America.

Paleo-archives indicate *Abies* populations in North America to be small and scattered during Late Glacial Maximum (LGM). Later, during deglacial period, *Abies* population expanded north-eastward following an increase in precipitation and temperature, and dispersing rapidly northward following the

retreat of ice sheet after 15 ka BP. It established along the Appalachians around 10 ka BP, acquiring its present-day distribution at around 8000 ka BP (Prentice, Bartlein, and Webb 1991).

Two climatic variables were chosen: average annual temperature and annual precipitation. Paleoclimatic simulated data were obtained as raster maps of 2.5° resolution from the software PaleoView (Fordham et al. 2017), and then downscaled to 10' (Fig. S3). Fossil data were compiled from the fossil pollen relative abundance database used by (Nogués-Bravo et al. 2016), whose original source was in turn the Neotoma Palaeoecology Database (<http://www.neotomadb.org>). The dataset spans the 21-10 ky BP period, and it comprises 934 recorded presences and 269 absences for *Abies* along North America; an example of its geographic extent can be seen in Fig. S1(b, c). The number of fossil data is not evenly distributed in time; on the contrary, it increases as time approximates to the present time, so that there are only 20 records for 21 ky BP, and 234 data for 10 ky BP. This might introduce a bias for niche evaluation during LGM, as it relies on a lower number of records.

A preliminary analysis, performed by crossing the climatic and pollen data, shows two different climatic niches for the two periods 21-16 ky BP and 15-10 ky BP (Fig. 2c). The first interval corresponds roughly to the period of the Late Glacial Maximum (LGM), while the second one represents circa the deglacial period; it includes periods of warmer climate, and three main rapid climate changes, namely the transitions to Bølling-Allerød, to Younger Dryas and to Holocene.

During the LGM, *Abies* was inhabiting across its geographical range areas ranging average annual temperatures between -20.5 to 8.1 °C, and average annual precipitation between 344.4 and 2047.1 mm/year. During deglacial period, *Abies* inhabited areas with warmer temperatures, ranging from -19.4 to 17.8 °C, and similar rainfall conditions ranging between 275.9 and 2415.7 mm/year. This hints to an increased tolerance to higher temperatures. The centre of the niche shifted as well between the two periods, from (-2.18 °C, 1332.2 mm/year) during LGM to (-1.06 °C, 850.4 mm/year) during deglacial period, indicating an increasing tolerance to dryer climate as well; the two niches are shown in Fig. 2c. This apparent difference of the climate niches evaluated from records of the two period raises the question on whether the niche has changed following the abrupt changes of climatic regimes. Tree species in the past has been shown to be able to inhabit different climatic conditions through time (Maiorano et al. 2013; Nogués-Bravo et al. 2016), even though it has been suggested that *Abies* taxa had a broader niche in the past (Tinner et al. 2013). Radis was thus set to start the simulations given the climatic niche of *Abies* during the LGM, and the initial MH niche parameters, centroid and breadth, were set as those for the evaluated LGM niche.

Simulations were run for each of the three different types of dispersal. A subset of the simulations of range dynamics were able to accurately predict the distribution of *Abies* under climate change events at the end of the Pleistocene. Maximum likelihood achieved were 83.7% for step-like kernel, 80.6% for linear kernel, and 84.6% for exponential kernel (first two not shown, last MH run shown in Fig. 2a). During the deglacial period, *Abies* presence is recorded at middle latitudes, mainly in eastern North America, with minor regions of presences along the Pacific coast and the Rocky Mountains. Our simulation correctly recreated the retraction of the south front and an expansion eastward for populations in eastern North America (Fig. 2d). Interestingly, the simulation represented also areas of presences on north-western regions where no presence was observed.

We evaluated also the relative role of tolerance in situ and dispersal by running sensitivity test. A sensitivity test was run for every of the four parameters, following the instructions described in section 7 of SI. In this way we could also verify whether other combinations of parameters could perform on a comparable level. For all the four parameters, the variance of top percentile values was low, hinting that all top percentile likelihood simulations explained the paleorecord pattern by the same mechanisms. Therefore, Radis finds the highest likelihood simulation aforementioned, and the parameter combinations it entails, as the most plausible explanation for the patterns of *Abies* past distributions. Radis estimated an average value of $\alpha = 0.24$. Successively, a sensitivity test was run on the α parameter, by launching again Radis with the first three parameters fixed to the optimal values found in the former launch, and letting only α vary. The sensitivity test refined the initial results, by finding a likelihood equal to 85.6% for $\alpha = 0.64$. However, the sensitivity test did not show great variance in output following differences in α : likelihood varied only of a 17.2% between the worse and best fitting simulation. The results of the evaluation suggest that *Abies* relied on long range dispersal as a survival strategy during rapid climate change, but was not as crucial as the climatic resilience hinted by its wide climatic niche. This pin-points to a larger influence of niche tolerance compared to dispersal as survival mechanism for *Abies* taxa. Moreover, Radis evaluates a niche that is considerably wider than the one that was estimated by the fossile data (Fig. 2c), and the estimated niche comprises recorded presences of LGM.

In conclusion, according to the analysis performed by Radis, a plausible explanation to the geographical range dynamics of *Abies* is that the main response of the North American fir species to deglacial abrupt climate changes was via tolerance in situ, allowing them to persist in their already occupied regions despite climate shifts. Long range dispersal was another likely necessary strategy, but

its contribution was less pivotal to the geographical range dynamics.

3.4 Conclusions

With IPCC reports projecting accelerating climatic changes within this century is more needed than ever to unveil the mechanisms that allow species to react and adapt to climate change to avoid extinctions. A necessary step for this purpose is to understand the processes that underpin species range shifts, by exploring and identifying the mechanisms allowing species to adapt to climate change. Moreover, biodiversity scenarios and quantitative forecasting are also in need of independent validations to enhance their relevance for policy guidelines and conservation approaches (Nogués-Bravo et al. 2018). Radis helps to pave the road for investigating those mechanisms using paleorecords to validate simulations of geographical range dynamics. It can therefore help investigating the climate-driven dynamics of species geographical ranges by providing a process-based approach rooted in first-principles. The spatially explicit simulation is designed with a special emphasis for the mechanisms that are relevant at the time scale for which much of the fossil record is dated, namely the last 50 ky. Radis allows also to explore the role of rare events like long-dispersals, which has been suggested to drive geographical range dynamics in trees, e.g. in the cases of colonisations of central and northern refugia in North America and Europe (Willis, Rudner, and Sümegi 2000).

Radis comes to respond recent calls on the need to validate models and explore mechanisms using paleorecords (Nogués-Bravo et al. 2018). The use of paleorecords as information source has been proven to significantly improve process-based model inferences on species dispersal and extirpation rates (Pearse et al. 2018). Despite the potential of simulations approaches as illustrated by Radis, the integration of empirical data into pure correlative species distribution models is expected to lead also to robust and validated predictions of demographic environmental responses (Fordham et al. 2014).

However, our modelling approach and tool do not come without challenges. Both the fossil record and the paleoclimatic simulations are sensitive to potential biases (i.e. fossilization potential, dating uncertainties, limited spatial resolution of paleoclimatic simulations) which are of particular relevance, considering the importance for rapid biotic responses of small-scale dynamics, both spatially (e.g. migrations to and from climatic microrefugia) and temporally (e.g. in responses to abrupt climate changes). As those uncertainties cannot be completely eliminated, they may limit the ability of our approach to fully apprehend the climatic niche of species. However, and at the same time, temporal series of climatic niches based on paleorecords are closer to the fundamental niche of species that

estimates of climatic niches based only in contemporary records (Nogués-Bravo et al. 2016). Moreover, our modelling approach does not incorporate demographics dynamics and inter-specific interactions. However, models lacking of explicit population dynamics to model species distributions have shown to perform equally good as more complex models (Fordham, Bertelsmeier, et al. 2018).

Radis has been developed using the Late Quaternary as testing ground. However, Radis is able to deal with information recording recent shifts of species ranges under recent climatic trends (i.e. the last century), allowing to explore the relevance of the main mechanisms in shorter time scales, more relevant to anticipate how species will react in the coming century to ongoing climate change. Moreover, Radis can be used by future users to simulate range dynamics under future climatic conditions based on tested predictions in the past, opening the door to provide future tested biodiversity scenarios.

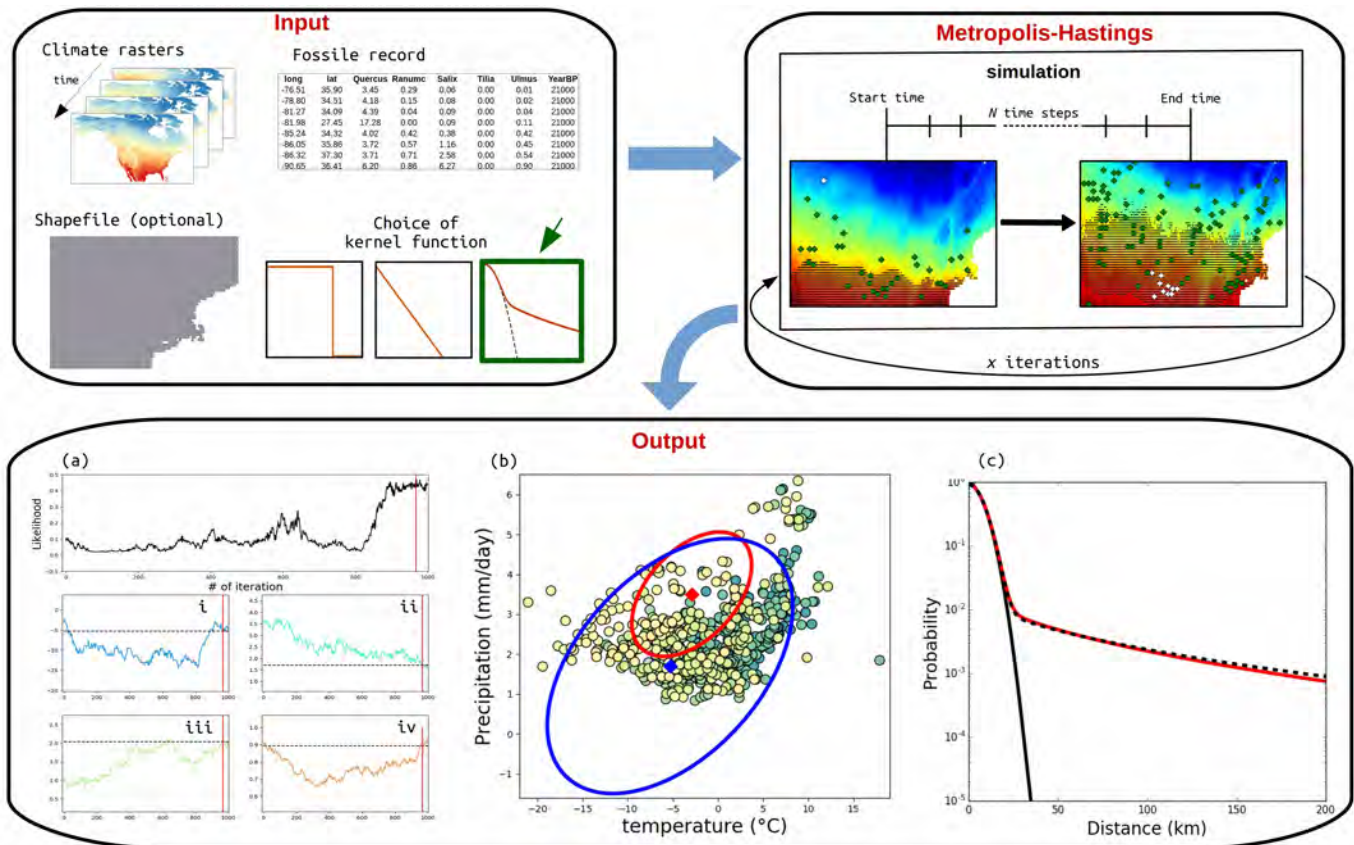


Figure 1: Diagram of Radis work flow. On the top left square the data requirements are shown, which are: rasters maps of climate variables an ASCII file containing fossil records and a shapefile (optional) for clipping the raster region. Moreover, at this step the user must choose the shape of the kernel function among the three available. Top right: sketch showing the distribution range simulation for N time steps, and a comparison of the simulated distribution range (shaded area) with fossil data (green diamonds = recorded presence; white diamonds = recorded absence). Radis iterates this x times, performing a MH algorithm (see section 6 of SI). Bottom: Radis output. At MH completion, Radis saves a binary file containing the values that likelihood and the parameters had during MH. In (a) are shown: on top, likelihood versus iteration number; below, the four plots show the four variables whose space was explored by the MH, plotted versus iteration number: (i, ii) coordinates of the niche centre, (iii) niche breadth and (iv) one the α parameter. In all these plots, the red vertical line highlights the iteration x_0 , which is the one with highest likelihood. In the plot (b) on the centre, a visual example of the parameter optimization is shown: the red and blue ovals represent the niche of iteration 0 and x_0 , respectively. Dots represent climate at grid cell occupied by fossil records, for the interval covered by the simulation. Plot (c) show kernel functions for α of iteration x_0 (red), for $\alpha=0.01$ (black continuous line), and for $\alpha=1$ (black dashed line). The last two are intended to show visually the possible range of kernel function, as α can assume values in the interval $(0,1]$.

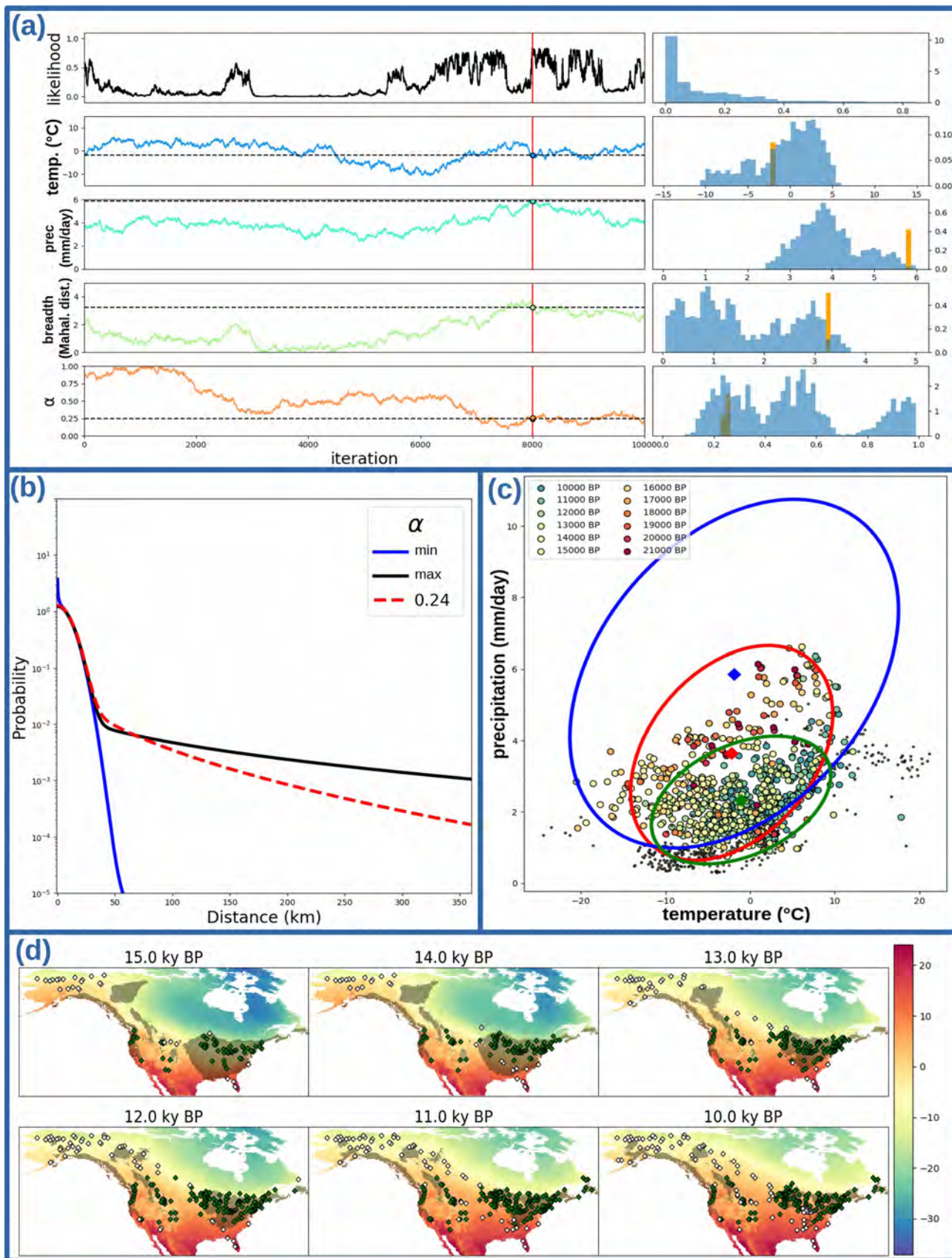


Figure 2: Results of the exemplary analysis exposed in the article. It consists of a Radis run for *Abies* (fir tree) taxon on North America for the period 15-10 ka BP, with an exponential dispersal kernel, for 10^4 iteration. Plots are generated by the ancillary script `visualize_results.py`. (a): on the left, plots of values of likelihood and parameters versus number of iteration throughout MH. In the example shown, there are two climatic variables, average annual temperature (“tmean”) and average annual precipitation per day (“prec”). Units of the y-axes are: unit-less for likelihood and α , Mahalanobis distance for niche breadth, °C for temperature, mm/day for precipitation. The vertical red line highlights the best iteration, i.e. the iteration with highest likelihood value (73.4%). On the right: in blue, normalized histograms of the values of left plots; in orange, same, but only for iterations featuring top percentile of likelihood. The latter are normalized to 0.5% for purposes of visual compatibility. Units of the x-axis are the same of y-axis for the corresponding left plot. (b): kernel function of best iteration (red), which has $\alpha=0.24$; kernel with lowest and highest possible values for α (0.01 and 1, respectively) are also shown for comparison. (c): niche of best iteration (in blue), of direct evaluation of data from period 21-16 ky BP (in red), and of direct evaluation of data from period 15-10 ky BP (in green). Ovals represent niche breadths, and diamonds the niche centres. Units on the axes are °C for average annual temperature and mm/day for the average annual precipitation. Big and small dots indicate values of climate maps in correspondence to fossil recorded presences and absences, respectively; colours indicate dating, according to the legend shown in the top left corner. (d): simulation of best iteration, i.e. the simulation with the highest likelihood. Climatic variable shown is average annual temperature (in °C); shaded areas indicate simulated presence; green and white diamonds indicate recorded fossile presences and absences, respectively. The simulation spanned the period 15-10 ky BP, with time steps of 100 y; the maps here display 1 time step out of 10.

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Radis: Python software for simulating and analysing range dynamics in response to past climate change

Supplementary information

1. Input data

Radis requires to be provided the following two input data files:

1. a text ASCII table, containing fossil record data, their dating and their coordinates. Four of its columns must have the following headers : “longitude”, “latitude”, the species’ name, and “yearBP”. Respectively, they must contain: longitude, latitude, abundance or presence/absence of the species, and dating expressed in years BP. For example (in case of pollen abundance):

longitude	latitude	Quercus	Juniper	yearBP
-60.41	30.15	2.45	0.48	15000
-60.41	30.15	1.93	4.29	14000
-60.41	30.15	0.97	3.65	15000
etc.				

In case of presence/absence data, they have to indicated with 1 and 0, respectively. For example:

long	lat	Homo_Sapiens	yearBP
43.880	11.09	0	9000
43.880	11.09	1	8000
43.880	11.09	1	7000
41.89	12.48	1	5000
etc.			

2. a time series of climatic maps in any raster format. All the rasters for one climatic variable must be contained in one folder each. The folders need to contain only climate rasters. For example, if the user wants to use three climatic variables, being “summer temperature”, “winter temperature” and “precipitation”, she needs to have the climate raster maps organized in three folders, e.g.:

```
/home/rasters/sum_t  
/home/rasters/win_t  
/home/rasters/prec
```

where the first one contains all and only rasters of displaying “summer temperature” variable, the

second one all and only rasters of “winter temperature”, and the last one all and only rasters of “precipitation” variable.

where the first one contains all and only rasters of displaying “summer temperature” variable, the second one all and only rasters of “winter temperature”, and the last one all and only rasters of “precipitation” variable.

Every raster file name must contain one number indicating its dating, expressed in years BP. E.g., in the folder `home/rasters/prec` there can be rasters named:

```
raster_prec_14200_Europe  
raster_prec_14100_Europe  
raster_prec_14000_Europe  
etc.
```

where `raster_prec_14200_Europe` must contain a climate map of 14.2 ky BP, and so on.

3. Optionally, the user may optionally choose to “clip” the region covered by the raster. This can be desirable in case the region is wider than the area of interest, and/or if the rasters cover areas where the species under study cannot disperse (e.g. bodies of water when the species are terrestrial). In this eventuality, the user can upload a shapefile, and Radis will cut off all the raster grid cells outside of it before the simulation starts. The user can also choose to use two different regions, one for simulation and one for niche evaluation; in this case, she can upload two shapefiles, one for the simulation area and the other for niche evaluation (see `niche shapefile` in the following section).

2. Setting the variables

Before launching Radis, the user has to set the variables by writing them in the file `radis_variables.txt`. They are the following:

main interval: the start and the end of the time interval within which Radis has to download climatic and fossil data, expressed in years BP, and divided by a comma. This interval must comprise the simulation interval and the niche evaluation interval (Fig. S4). For example:

```
main interval: 16000, 11000
```

niche evaluation: the start and the end, expressed in year BP and divided by a comma, of the niche evaluation time interval, i.e. the interval within which Radis will use fossil data to evaluate the initial niche (as in Fig. S4).

simulation interval: the start and the end of the simulation time interval, i.e. the interval in which the simulations run, expressed in year BP.

time step length: the time interval corresponding to one time step of the simulation, expressed in years.

climate variables: Only necessary in case a “general input data file” is not loaded, the names of the climate variables, separated by a comma. For example:

climate variables: summer_temperature, winter_temperature, mean_precipitation

rasters [climate variable1], rasters [climate variable1], etc.: Only necessary in case a “general input data file” is not loaded. The folder where the rasters containing climate maps for the given climate variable are located. There must be one “rasters [climate variable]” line for every climate variable written in the field climate variables. The field must be indicated by “raster” followed by the name of the relative climatic variable, e.g.: “rasters summer_temperature:”, For example:

rasters summer_temperature: /home/rasters/sum_t

rasters winter_temperature: /home/rasters/win_t

rasters precipitation: home/rasters/prec

fossile data: The address of the ASCII file containing all information about fossile data for the taxon of interest. Only necessary in case a “general input data file” is not loaded.

species: The species or taxon of interest. Only necessary in case a “general input data file” is not loaded. The name written here must be the same present on its column in the fossile data file, e.g. Quercus or Homo_Sapiens.

dating error: write here the error, expressed in years, over the dating in the column “yearBP” of the fossile data file. Only necessary in case a “general input data file” is not loaded.

abundance threshold: optional. The threshold below which the abundance percentage of the given species does not indicate presence. If this field is left empty or commented out, threshold is automatically set to 0. Skip this field if the fossile data file contains presence/absence data instead of abundance. Only necessary in case a “general input data file” is not loaded.

shapefile: optional. Address of the shapefile that can be used to clip the climate raster maps. If left empty or commented out, the simulation will run by using all the rasters grid cells; otherwise, it will use only the grid cells within the shapefile. Only necessary in case a “general input data file” is not loaded.

maximum distance: The maximum distance, expressed in kilometres, above which dispersal is possible. During simulations, dispersal will not occur if at a distance greater than this (see section 4).

Only necessary if the user chooses not to load a “distance matrix file” (see section 3).

niche shapefile: optional. Address of the shapefile that can be used to clip the climate rasters maps for niche evaluation. If left empty or commented out, the niche will be evaluated by using data for the whole region encompassed by the climate rasters; otherwise, it will be evaluated using only climate and pollen data from within the shapefile. Only necessary if the user chooses not to load a formatted niche evaluation input data file (see Section 5).

kernel name: the shape of the kernel function to be used for dispersal. It can be “exponential”, “linear”, or “step”, which correspond respectively to: a Gaussian distribution with “fat-tail” accounting for long dispersals, a linear distribution, a step-like function.

initial condition: this variable can assume two values: “niche” or “record”. If the former is chosen, the simulations will start with the species occupying every grid cell whose climate lies within its niche. If the latter is chosen, they will start with species occupying every grid cell within a radius of 40 kilometres from a recorded fossil presence. The value of 100 km is fixed, but can be changed manually by the user (see Section 8).

number of iterations: how many iterations the MH must comprise. Set to 0 for a single simulation. If this variable is set to 0, then Radis will run one single simulation instead of a MH comprising several.

save frequency: This variable sets how often will a “checkpoint” occur, i.e. how often do data have to be saved. If for example the user sets “number of iterations” to 10000 and “save frequency” to 10. Radis will save the results every 1000 iterations. Only necessary if `number of iterations > 0`.

range [climate variable1], range [climate variable2], etc.: the minimum and maximum values the climate variables can take during the MH. Only necessary if `number of iterations > 0`. They need to be separated by a comma, as in the following example:

```
range summer_temperature: 0, 30
range winter_temperature: -10, 10
range precipitation: 0, 20
```

range breadth: the minimum and maximum values the niche breadth can take during the MH. They need to be separated by a comma, as in the ranges for climate variables. Only necessary if `number of iterations > 0`.

range alpha: the minimum and maximum values the parameter α can take during the MH. They need to be separated by a comma, as in the ranges for climate variables. Only necessary if `number of`

iterations > 0.

general input data: Optional. address of the general input data file.

niche input data: Optional. address of the niche evaluation data file.

distance matrix: Optional. address of the file containing the distance matrix.

recovery data: the address of the partial results file, in case the users wants to recover a former MH. Only necessary if the uses chooses to recover a previously halted MH, by starting over from a partial results data file saved at a checkpoint (see Section 3).

3. Starting Radis

Radis runs on Python version 3.4 or later. It requires to have previously installed, the package GDAL/OGR, version 2.1.4 or later, besides the usual standard scientific packages (NumPy version 1.15.1 or later, SciPy). To start Radis, the user needs to have the following three files in one folder:

- `radis_launcher.py`
- `radis_functions.py`
- `radis_variables.txt`

First, the variables have to be set by writing them in `radis_variables.txt` (see Section 2). Then, Radis can be launched by running the prompt command

```
python radis_launcher.py
```

if on Linux or

```
py radis_launcher.py
```

if on Windows. The command must be executed in the folder where the scripts are.

After being launched, Radis formats the input data and saves them as binary data files, so that in future launches they can be directly loaded instead of having to be formatted again. The three data files that Radis saves automatically are:

- “general input data file”: contains all information on climate, fossile data and geography;
- “distance matrix file”: contains the distance matrix of the grid where the simulations run;
- “niche evaluation data file”: the same kind of “general input data file”; however, its data are used for niche evaluation instead of simulation.

The same file can be chosen both as “general input data file” and “niche evaluation data file”. Niche evaluation data file and general input data file must be created for the same species and with the same main interval (see “main interval” in Section 2). The user is asked at the beginning of every launch whether she wishes to load some or all of them.

Metropolis-Hastings (MH) can be time consuming. To avoid wasting time in case the run halts before the end. Radis saves at certain iterations (“checkpoints”) the partial results, i.e. the results obtained until that iteration. Frequency of checkpoints is set by the user (see “save frequency” in Section 2). The partial results file can then be loaded in a successive launch so that the MH will be rebooted from that checkpoint instead of starting over. When launched, Radis asks the user whether it has to start a new MH or recover an old one. In the latter case, it loads the partial results from the file address given by the user (see “recovery data” in Section 2).

4. Distance matrix

To evaluate dispersal probability in simulations. Radis needs the values of distances between grid cells. Distances below maximum distance are stored in a NumPy 2-dimensional array called `DQ`; greater distances are not stored. It is recommended that maximum distance is set to a value above which dispersal is very unlikely or impossible for the taxon under exam. The purpose of this cut-off is to avoid overflow errors by storing useless information.

An ancillary file called `weris` is also created and saved together with the distance matrix. It contains all the positions of every grid cell within `DQ`. It is used by Radis to have information about which grid cells are available for dispersal attempts. Both `DQ` and `weris`, as soon as they are evaluated, are automatically saved as binary data files in the distance matrix file.

5. Likelihood evaluation

After a simulation is completed, Radis evaluates its likelihood by comparing it with the provided paleorecords. Every paleorecord has a corresponding grid cell, which is the grid cell where the record lies within. To every record corresponds a dating interval, and in turn the dating interval corresponds to one or several time steps.

As an example, Fig. 5a shows a detail of a simulation having time resolution of 200 y, and records with a dating error of 400 y; therefore, to each paleorecord corresponds an interval of five time steps. In the cases where the dating error is smaller than the time step resolution, then only one time step corresponds to the paleorecord. Radis checks whether the simulation in the grid cell of the paleorecord during those five steps. In case the the paleorecord is a presence. Radis considers a correct guess if the simulation reports presence of at least on of those time steps; if the paleorecord is an absence. Radis considers a correct guess if the simulation reports presence of all the time steps.

This kind of evaluation is performed for every paleorecord, across the whole simulation, and likelihood

for the simulation is then calculated according to equation (3). Figure 5b shows an example of likelihood evaluation. It represents a sketched, simplified example where dating error is smaller than time step resolution, therefore to every paleorecord corresponds only one time step, instead than several. In this example, the simulations consists of three time steps, and there are paleorecords dating 12 ky BP and 11.6 ky BP, but there are no records dated 11.8 ky BP. The ratio of correctly guessed presences out of total number of recorded presences is $6/7 \approx 85\%$, while the ratio of correctly guessed absences out of total number of recorded absences is $4/5 = 80\%$.

6. Optimization process

The parameters optimized by the MH are: the coordinates of the niche centre, which are as many as the climate variables are, the niche breadth D and the dispersal parameter α . The users sets the value they will have for iteration 0, then during MH the optimization process will change their value. At iteration i , one parameter x with current value $p_{i,x}$ is randomly chosen, and a new value p_x^* for x is proposed as in the following:

$$p_x^* = \left(p_{i,x} \pm \epsilon \left(p_x^{\max} - p_x^{\min} \right) \right), \text{ with } \epsilon = 0.01 \quad (4)$$

where $(p_x^{\min}, p_x^{\max})$ correspond to the limits set by the user, if i is a niche centre coordinate; to (0,5), for D ; and to (0,1), for α . After the simulation, likelihood L_i for iteration i is evaluated as in formula 3 of main paper. With probability:

$$P = \min \left(1, \frac{L_i}{L_{i-1}} \right) \quad (5)$$

the proposed step p_x^* in the space of parameters is then accepted for the following iteration, i.e.

$$p_{i+1,x} = p_x^* .$$

7. Sensitivity tests

Sensitivity tests can be realized by fixing one or several of the parameters during the MH. To fix one parameter, the user has to set its range interval to 0. For example, say that that the user uses three climatic variables, `summer_temperature`, `winter_temperature` and `precipitation`, and she wants to run a sensitivity test on the α parameter. This can be done by writing the following in the `radis_variables.txt` file (see also “range” in Section 2):

```
range summer_temperature: 0, 0
range winter_temperature: 0, 0
range precipitation: 0, 0
range breadth: 0, 0
```


`range alpha: 0, 1`

In this way, the range intervals of every parameter except α are 0; therefore, α will be the only parameter varying. To be noticed that the ranges limits do not need to be 0; the same can be accomplished by setting them to any value. By instance

`range summer_temperature: 5, 5`

would work as well. All it matters for a parameter to be fixed is that its range interval has 0 length.

8. Constants

Some values are fixed and not meant to change during a run. Such constants are:

Constant	Name used in the script	Value	Meaning
—	SCALE	36 (km)	Scale value for x when using exponential kernel
M	NUL_KER	100 (km)	As used in equation (1)
ρ	RATIO	0.5	As used in equation (2)
σ	SIGMA	0.3	As used in equation (2)
ε	STEP	0.01	As used in equation (4)
—	CLUSTER	100 (km)	See “initial condition” in Section 2

If the user wishes to change such constants before a run, she can do so by re-writing the new values manually. They can be found in the `radis_functions.py` script from line 21 to line 27.

9. Output

At every checkpoint and at the end of MH (or at the end of the simulation in case `number of iterations` is set to 0). Radis saves an output file. It consists of a `.npz` archive containing the following arrays saved as binary data:

- `IniSim.npy`: a $N \times T$ array containing the simulation corresponding to the first iteration of MH, where N is the number of grid cells and T the number of time steps of the simulation. Presences are indicated with 1, absences with 0.
- `TopSim.npy`: same as `IniSim.npy`, but it contains the best simulation, i.e. the simulation corresponding to the MH iteration with highest likelihood. In case `number of iterations` is set to 0, `IniSim.npy = TopSim.npy`.
- `Vars.npy`: a $M \times I$ array containing the values assumed parameters (niche centre coordinates, D , α) during the MH, where M is the number of parameters (i.e. number of climatic variables + 2) and I the number of iterations.
- `Fit.npy`: a I -length array containing the likelihood of every simulation performed during the MH,

where I is the number of iterations.

- `SY.npy`: a 6-length array containing all interval values.

For a quick look at the data, an extra script called `visualize_results.py` is provided for download in the same web page of the other Radis scripts. It must be launched while in the same folder of the other Radis scripts. `visualize_results.py` requires Python version 3.4 or later and the package `Matplotlib`. In order to work, it requires 3 formatted data files: 1) the “general input data file” created during the run, 2) the “niche evaluation data file” created during the run, and 3) the output file. Launching `visualize_results.py` results in plots showing the results obtained in the output file (as in Fig. 2), plus a text file containing, among other recap information, the values of parameters during the iteration with highest likelihood (i.e. the parameters governing the simulation saved in `TopSim.npy`) and the average of parameters of the iterations within the top percentile of likelihood.

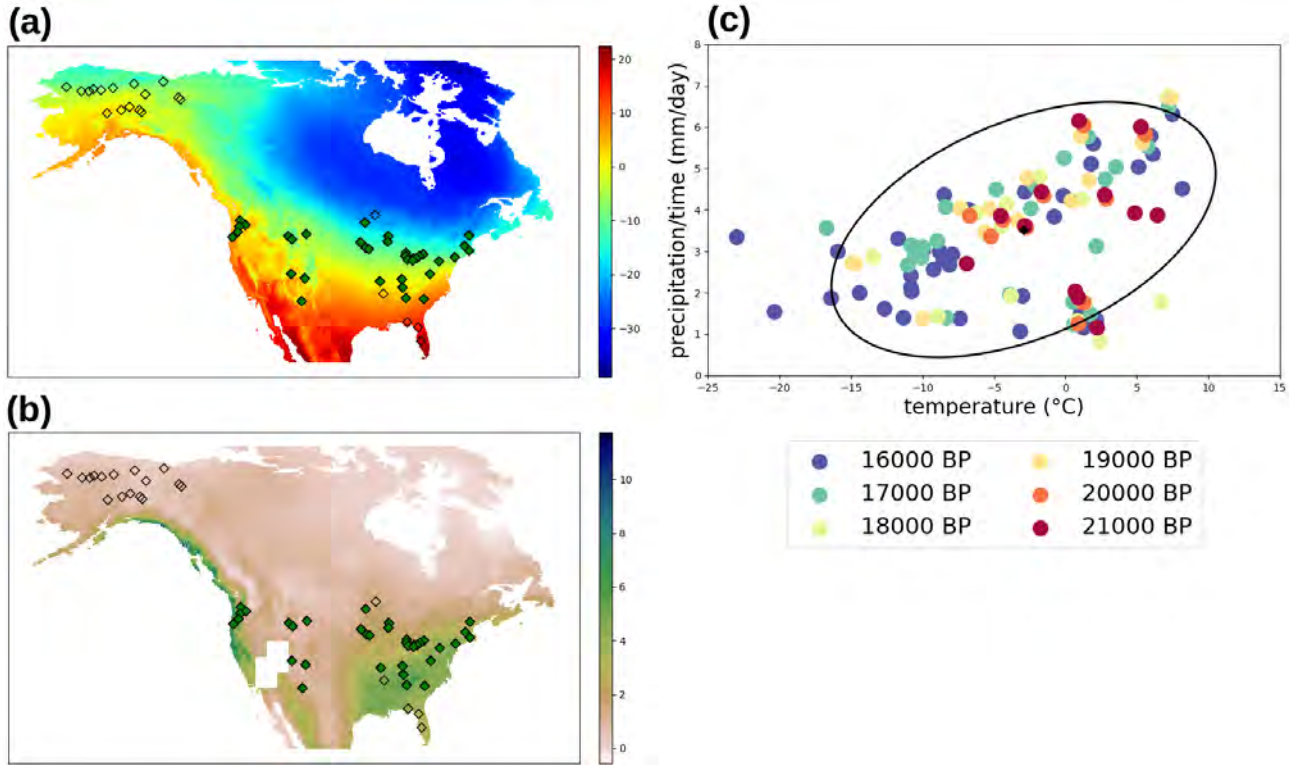


Figure S1: Example of niche evaluation, based on paleoclimate simulations and a fossil records. Plot (a) shows a 30 year mean annual temperature (°C) for 16 ky BP. Green diamonds indicate locations for *Abies* fossils recorded fossil presence dated 16 ka BP (taking in account of dating uncertainty), while empty diamonds show recorded absences. Plot (b): same as (a), but climatic variable is average precipitation per day (mm/day). Plot (c): scatter plot of climates for every grid cell where *Abies* was recorded (i.e. where a green diamond is present in the (b) and (c) plots), for six different time periods (see legend below plot); the purple points indicate a dating of 16 ky BP, i.e. they correspond to climate values of grid cells containing the green diamonds displayed in the plots on the right. The values of all the points are averaged to estimate a niche centre (black diamond) and Mahalanobis distance is calculated, so to evaluate a niche (area within the black line). The black line represents niche breadth: in the example shown, it is drawn at Mahalanobis distance equal to 2, which for the case of two variables is equivalent to 2 standard deviations from the niche centre. Radis performs such evaluation before starting the MH letting the user adopt the parameters of such evaluated niche as initial parameters for the MH run.

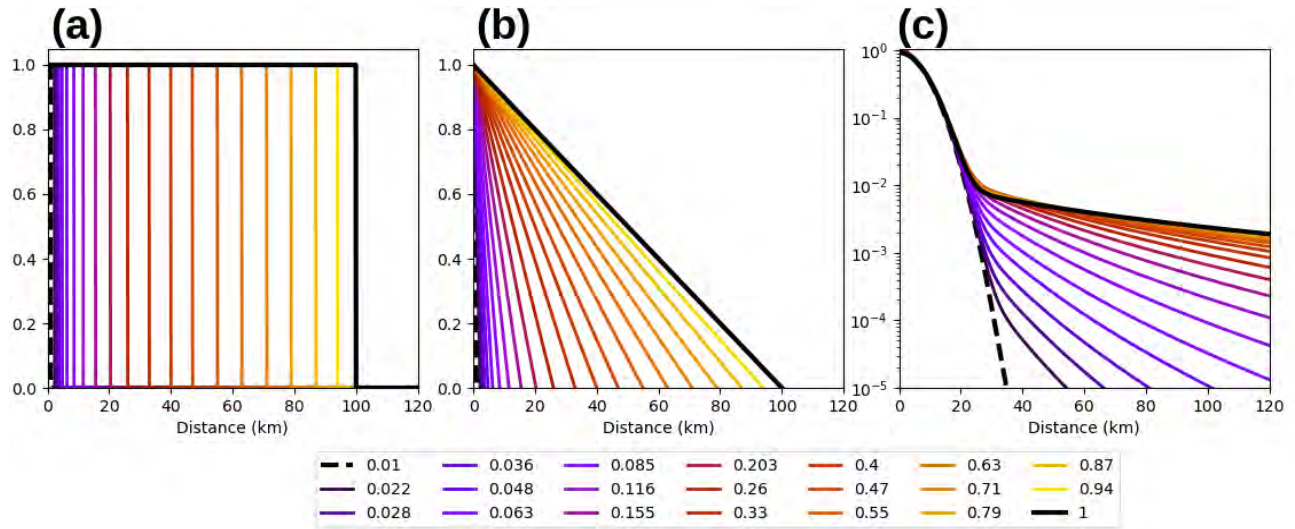


Figure S2: The three different kernel functions in Radis: (a) step-like, (b) linear, and (c) exponential. The latter is a weighted average of a Gaussian and a “fat-tail” distribution, as in (Clark 1998). For every plot, several plots of the same functions with different values of the α parameter (values in the legend on the bottom) are displayed; α is user-definable and one of the parameters of the MH. Note that, differently from the first two plots, in plot (c) the y-axis is logarithmic.

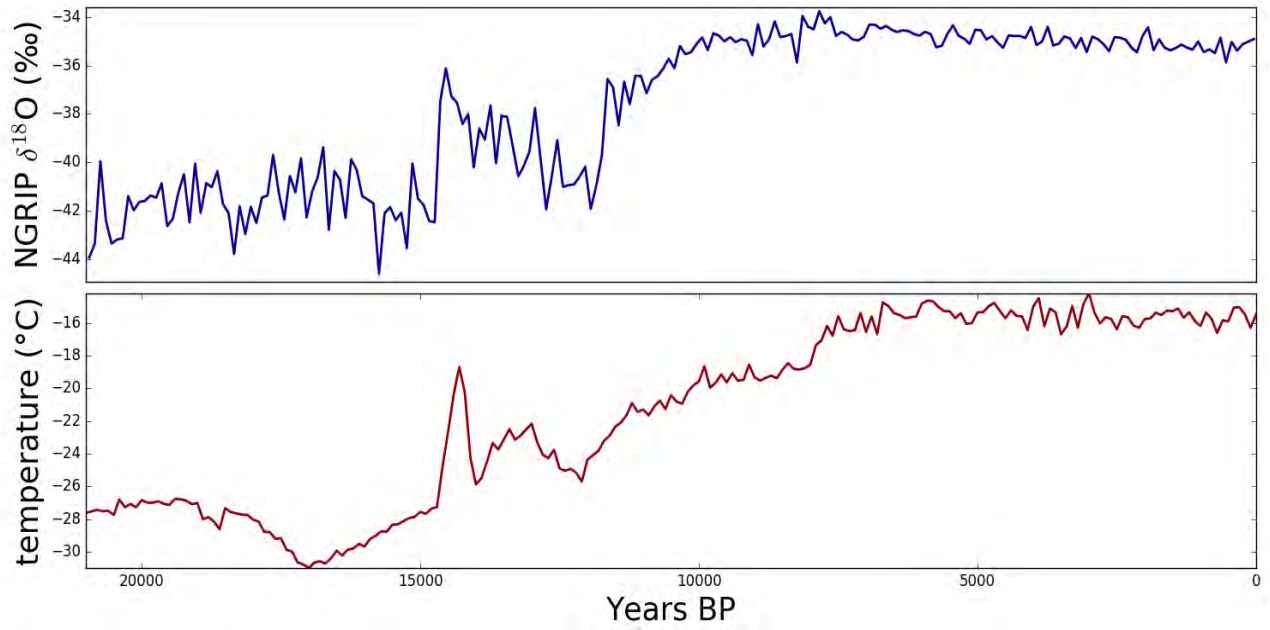


Figure S3: Comparison between experimental climatic data and the simulated climatic data from PaleoView; the latter were used for the example shown in the paper. On top: profile of $\delta^{18}\text{O}$, a proxy for temperature, from Greenland NGRIP record. Bottom: average annual temperature of Greenland, from downscaled simulated data obtained by PaleoView.

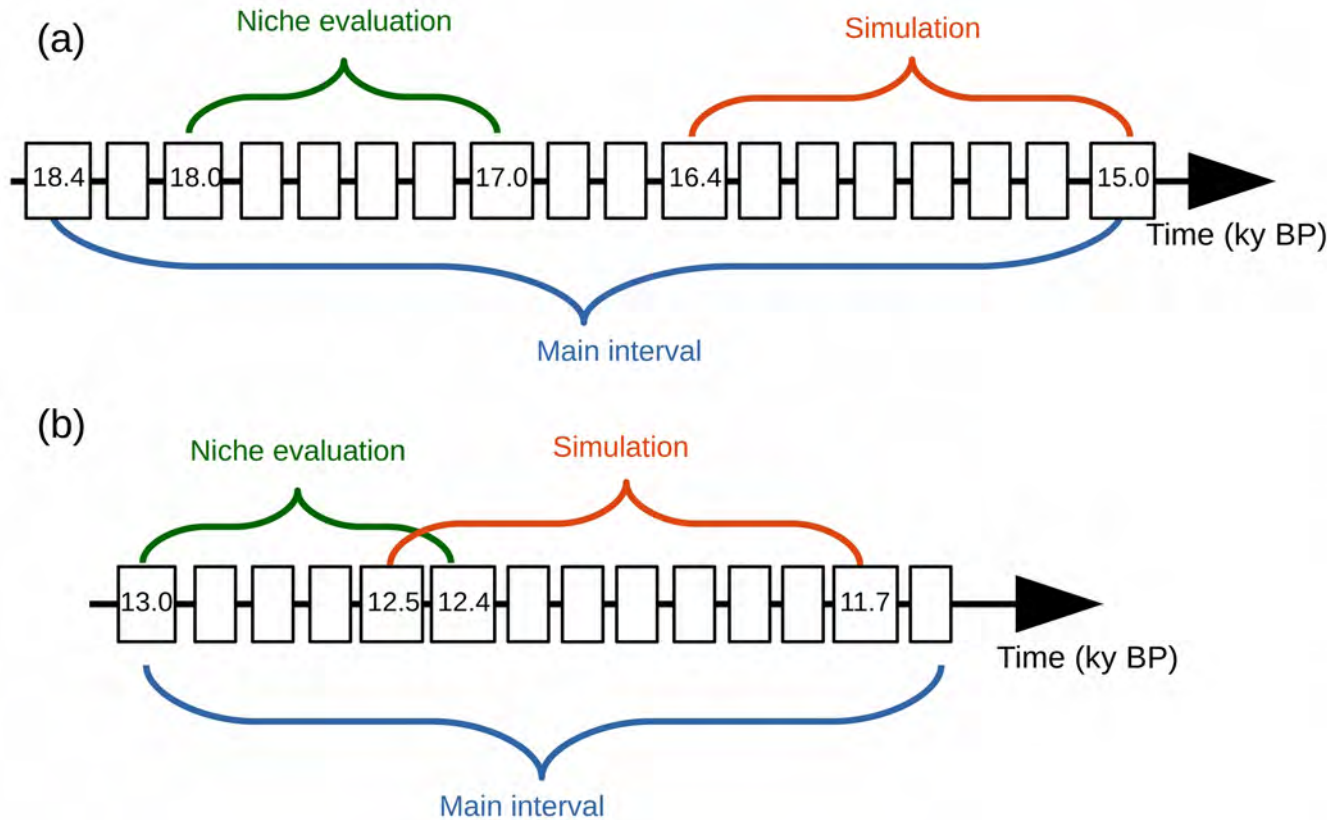


Figure S4: two sketches illustrating two possible examples of values for the three user-defined time intervals. Every rectangle represent a time step. For every time step within the main interval. Radis attempts to load both climatic and fossile data. In (a), length of a time step is 200 y; niche is evaluated between 18-17 ky BP, and the simulations run in the interval 16.4-15 ky BP; in (b), length of a time step is 100 y; niche is evaluated between 12-12.4 ky BP, and the simulations run in the interval 12.5-11.7 ky BP. The main interval must contain or be wider than the other two intervals, which may overlap. To be noted that it is not necessary to provide climate raster maps for every time step.

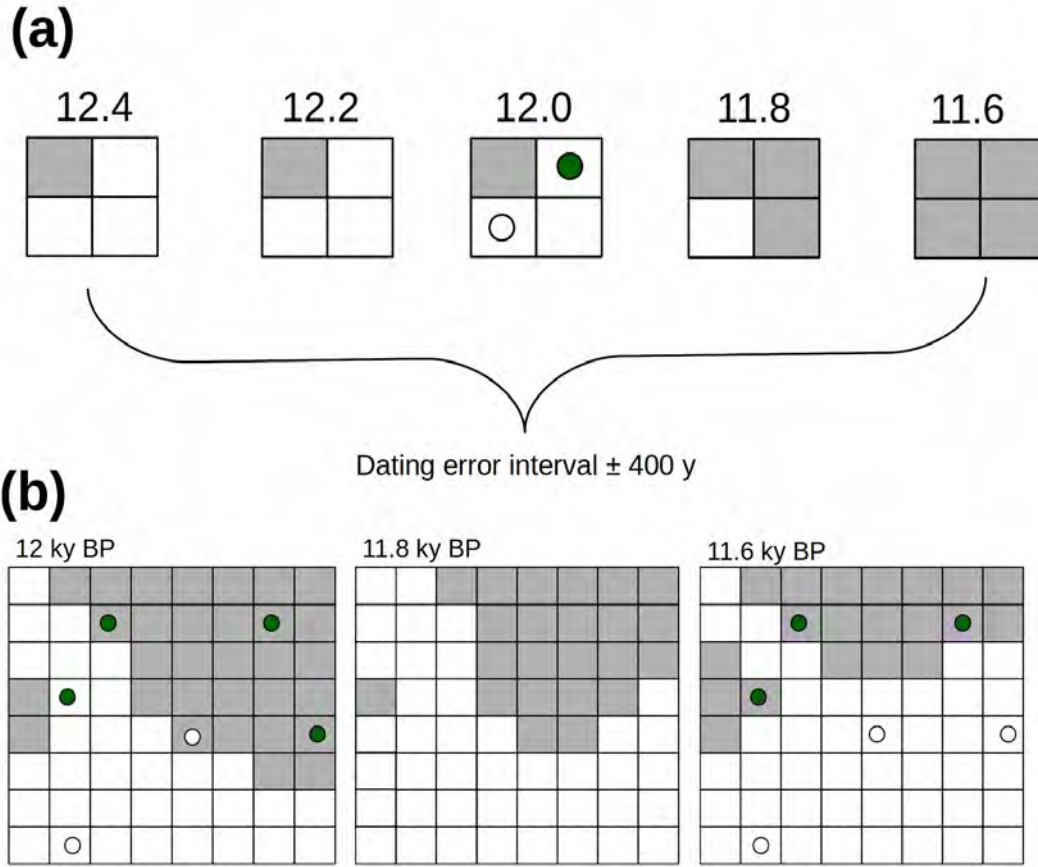


Figure S5: (a) How Radis evaluates correct guesses to paleorecords. Every of the five main squares represents a detail of a simulation grid, with the dating on top of them expressed in ky BP. Two paleorecords, one presence and one absence, are recorded at 12.0 ky BP. The dating error is 400y, which means that it cover five time steps, from 12.4 to 11.6. Radis considers the simulation to be correctly guessing a recorded presence if, in the interval defined by the dating error, the corresponding grid cell is occupied for at least one time step. In the example shown, the cell corresponding to the recorded presence is the top right, and it is occupied by the simulated taxon in the last two time steps. Therefore, Radis counts a correct guess of the recorded presence. On the other hand, Radis considers the simulation to be correctly guessing a recorded absence only if, in the interval defined by the dating error, the corresponding grid cell is empty for all time steps. In the example, the cell corresponding to the recorded presence is the bottom left, and it is occupied by the simulated taxon in the last time step. Therefore, Radis does not count a correct guess for the recorded absence. (b) How Radis calculates likelihood. The simulated distribution range is represented by the squares in grey, and the three figures represent three following time steps. In the example, the dating error on the paleorecords is <200 y, i.e. smaller than one time step. Green and white dots indicate recorded presence and absence, respectively. After having executed the simulation, Radis evaluates its likelihood by comparing it with the paleorecords. This evaluations relies on counting the correct guesses. The simulation correctly guesses 6 out of the 7 recorded presences, and 4 out of the 5 recorded absences. Thus, according equation (3): $p_i = 6$, $p_T = 7$, $a_i = 4$, $a_T = 5$, to which follows that $L = 80\%$.

4 Tolerance and dispersal influenced North American tree distributions during the deglacial period

North America provides an abundance of fossil pollen paleo-archives, while at the same time being a region heavily affected by the climate shifts of the late glacial period. In particular, the transitions from the Late Glacial Maximum to the Holocene induced reorganizations of vegetation communities and biomes of continental scale. The scale and magnitude of environmental and ecological changes, coupled with the considerable amount of fossil vegetation records, makes the continent a particularly suited region for studying the effects of past rapid climate transitions on vegetation taxa.

In this research, we focus on seven North American tree taxa, chosen for the amplex of fossil data and the reduced number of comprising species; we analyse their response mechanisms to deglacial transitions, performing the research entirely by the means of the model developed in the former chapter. This study is both intended as a testing of potentialities and limitations of the novel method, and as an inquiry of response mechanism of vegetation populations to paleoclimatic rapid transitions, through the investigation of a meaningful case study. The resulting analysis is fully presented in the following manuscript, which is intended for submission to Journal of Biogeography and reported here with a few minor edits.

Tolerance and dispersal influenced North American tree distributions during the deglacial period

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Past evidences of vegetation responses to last glacial climate changes challenge the current theories and future projections of biotic responses, suggesting that the mechanisms responsible for the observed patterns in the fossil record are yet to be clarified. On the other hand, the accumulation of knowledge and data provide the opportunity for in-depths analysis of the patterns observed in paleorecords and for tests of ecological theories. Fruitful testing of hypotheses regarding biotic processes can be realized by integrating such response mechanisms into spatially-explicit simulation models. We apply here a recently developed process-based model simulating species distribution ranges and featuring two key mechanisms, namely dispersal and tolerance in situ, to seven North American tree taxa during the deglacial period. By validating the simulation against paleorecords, we test concurring hypotheses about tree dispersal, and quantify the contribution of colonization and tolerance in situ to the resulting distribution patterns. Tolerance appears as the main strategy, except for taxa *Fagus* and *Tsuga*, for which dispersal was the main mechanisms to explain their range dynamics under climate change. Although simulations could not capture completely the observed distribution dynamics, they attained a high degree of consistency with paleo-archives, confirming the efficacy of simulating geographical range dynamics based in a reduced but general number of first-principle processes.

4.1 Introduction

Climate change is accelerating across all regions of the planet (Urban 2015) and their impacts on the distribution of species, possible extinctions, functioning of ecosystems and the services they provide are of utmost importance (Pecl et al. 2017). Scientists are coming back to the past to better understand what are the strategies or mechanisms allowing species to cope with abrupt climatic and environmental changes (Nogués-Bravo et al. 2018). Thanks to accumulation of knowledge and data by paleoecologists and scientists of related disciplines (Williams et al. 2004; Moreno et al. 2014) we do know, with an

acceptable degree of confidence, the past patterns of species distributions under climate change, mainly for those taxa and regions of the world that has been subject to a more intense scrutiny, like tree species in North America during the Late Quaternary. We are however not close yet to fully apprehend what are the mechanisms underpinning the observed patterns in the fossil record (Nogués-Bravo et al. 2018).

The recent integration of species distribution models, correlative based approaches, and paleorecords have provided already significant insights on the controlling role of climate change in species abundances, distributions or past ecological community turnovers (Nogués-Bravo et al. 2008; Lorenzen et al. 2011; Nogués-Bravo et al. 2016) and on the magnitude of geographical range shifts under different magnitudes of past climate change. They have provided also insights on the role of adaptation, tolerance or dispersal to explain species distributions (Hugall et al. 2002; Strasburg et al. 2007). However, their correlative nature reduces their potential to gain deeper insights on the role of mechanisms driving species responses to climate change. There are alternative modelling approaches rooted in the incorporation of mechanisms, and relevant species-specific data, or in the simulation or first principles, or processes, arising from theories and hypothesis on the drivers of species geographical ranges (Connolly et al. 2017; Rangel et al. 2018). We apply here a recent developed framework (Botta et al., manuscript in preparation) to simulate range dynamics under climate change based on two main mechanism: tolerance in situ (species/populations adapt to the new climatic conditions) and dispersal (species disperse to areas of suitable climatic conditions).

We simulate both tolerance in situ and dispersal as the two main response mechanisms. We define tolerance as the ability of a species to change their climatic niche to persist in grid-cell under different climatic conditions than experienced before. The climatic niche (*sensu* the Grinnellian niche in Soberón 2007) is defined as the set of climatic conditions for which the intrinsic growth rate of populations are not negative. We estimate the climatic niche (or climatic envelope) mathematically using the Mahalanobis distance (Farber and Kadmon 2003). The approach has been shown to be successful in explaining past geographical dynamics across the Late Quaternary (Nogués-Bravo et al. 2008). We define dispersal as the ability of a species to migrate and colonise a suitable climatic area. We simulate dispersal using a set of probabilistic kernel functions within user-defined boundaries of dispersal (Bullock et al. 2017), which account also for rare long-distance dispersal events (Clark 1998). Finally, simulations are tested against recorded spatio-temporal trends in the fossil record. This validation steps allow us to identify the specific contributions of tolerance in situ and dispersal to replicate, via simulations the observed patterns of species range shifts in the fossil record.

We apply this framework to six tree taxa in North America from 15 to 10 kyr BP. This time interval roughly corresponds to the last deglacial period, as it lies approximately between the Late Glacial Maximum (LGM) and Holocene; it encompasses several rapid climate shifts (Steffensen et al. 2008), thus providing a remarkable temporal frame to study species geographical range dynamic. LGM occurred between 26.5 until approximately 14.5 ka BP (Mix, Bard, and Schneider 2001; Clark et al. 2009). Climate reconstructions estimate the average global temperature during LGM to be $\sim 4.9^{\circ}\text{C}$ colder in respect to the peak interglacial conditions of Holocene (Shakun and Carlson 2010). North American continent was partially covered by two ice sheets: the Laurentide ice sheet, centred in Canada and extending as south as 38°N , and the smaller Cordilleran ice sheet, located over the Rocky Mountains (Clark and Mix 2002); the ice sheet influenced the climate of the continent by displacing atmospheric currents (Bartlein et al. 1998). During the LGM, eastern North America was dominated by forest of cold-tolerant conifers (Shuman, Bartlein, and Webb III 2005), while open forests were present in the south-west (Wagner et al. 2010; Asmerom, Polyak, and Burns 2010). Both south-eastern and north-western United States were also partly covered by open forests (Whitlock 1992; Webb III et al. 1998).

The LGM was followed by the Late Glacial period, an interval of climate warming spanning approximately between 16 and 11 ka BP. In this period, which comprises the transition to Holocene, the Northern Hemisphere, climate experienced several rapid transitions, before eventually reaching present-day climate conditions (Fig. 3 of Chapter 1). The most rapid rates of changes in North America are associated with the transition to and from the Younger Dryas period (Williams et al. 2004; Shuman, Bartlein, and Webb III 2005).

The biomes of North America tracked closely climate variability during this period, with time lags of centennial scale or shorter (Peteet 2000), and experienced general profound reorganizations (Williams et al. 2004). In eastern North America, tundra and open forest grew along the Laurentide ice sheet, extending between 30°N and 34°N . Tundra was predominant in the continent interior; in particular, taxa like *Fagus* and *Ulmus*, along with other temperate hardwood taxa, grew near the Lower Mississippi valley and; warm-temperate taxa and open vegetation occupied present-day Florida (Jackson et al. 2000). Western North America was dominated by open conifer woodlands in the south and by tundra landscape in the north-west (Jackson et al. 2005). In contrast, during the Holocene, cool and temperate conifer and hardwoods forests developed large and widespread populations in eastern North America; more northerly, taiga became the dominant biome; warm mixed forest

dominated the Florida peninsula (Prentice et al. 2000; Jackson et al. 1997).

The magnitude of late glacial climate change in North America, and the richness of paleo-archive vegetation records in the region provides therefore a remarkable system to simulate range dynamics and test the magnitude of tolerance in situ and dispersal to explain the observed patterns, and to tackling the "Quaternary conundrum" (Botkin et al. 2007), namely the seemingly paradoxical hiatus between future projections of biotic responses in species distribution models and the past evidence. In this chapter, we aim at enhancing the current knowledge on how two relevant mechanisms may played a determinant role to explain species reactions to climate change in seven tree taxa: *Abies*, *Acer*, *Betula*, *Fagus*, *Salix*, *Tsuga*, *Ulmus* (respectively fir, maple, birch, beech, willow, hemlock and elm). Using hundreds of dated and georeferenced records of pollen fossil abundance, paleoclimatic simulations and a recently launched software to simulate species range dynamics (Botta et al., manuscript in preparation) we estimate the ability of those two mechanism to replicate observed patterns, identify the contribution of tolerance and dispersal to the observed patterns, and discuss how our findings may contribute to better anticipate future reactions of species to on-going climate change and enhance forecasting modelling and future biodiversity scenarios.

4.2 Data and methods

Pollen data were provided by the database from (Nogués-Bravo et al. 2016), which features data from North America spanning the period 21-0 ka BP. These data, in turn, were obtained from the Neotoma Paleoecology Database to be spaced at 1000 years intervals, and consist of both presences and absences. From the database, seven taxa were chosen for the current analysis: *Abies*, *Acer*, *Betula*, *Fagus*, *Salix*, *Tsuga*, *Ulmus* (fir, maple, birch, beech, willow, hemlock and elm). Taxa were chosen for the abundance of both presence and absence data on the whole continent. Number of sites and number of individual recorded presences are reported in Table 1.

We have developed a new software, Radis (Botta et al., manuscript in preparation), to simulate range dynamics and pinpoint the roles of dispersal and tolerance in situ under climate change. Radis simulates tolerance in situ by simulating several breadths and positions of their climatic niche and then testing it against observations from paleo-archives. The software also simulates continuous dispersal event by implementing it on a discretely spatially fragmented lattice grid. Dispersal is modelled as a probabilistic event from one occupied cell towards an unoccupied cell; the probability of the event is mediated by a kernel function. Radis is provided with three possible shapes for the kernel well

supported in the literature (Bullock et al. 2017), allowing users to choose among them before start the simulation. In this type of modelling, the dispersal considered here is the natal dispersal, scaled up to a generational level. Accordingly, it is recommended to choose a time step length matching the generation time of the studied taxon. More details on the full methodology and protocols can be found in (Botta et al., manuscript in preparation).

The climatic niche of taxa was set as being two-dimensional, over two climatic variables: average annual temperature (in °C), and average annual precipitation per day (in mm/day). This choice is a compromise between capturing the patterns of taxa in relation to insolation and moisture, which are the most fundamental climate-driven requirements for vegetation, while at the same time keeping low the number of climate variables in order to hasten the running time. This means that runs performed with Radis will be based on four parameters: the two coordinates of the niche centre, plus the niche breadth and the dispersal parameter α .

We use paleoclimatic simulations from PaleoView software (Fordham et al. 2017). They were downloaded as 30-year averages in 100y intervals, spanning the period 16-8 ka BP. PaleoView provides raster maps with a 2.5x2.5 latitude/longitude resolution. This amounts to an average distance between one grid cell to its neighbour of ~100 km or greater. Considering the time resolution we chose, this spatial resolution would make dispersal possible only for tree dispersal velocities of one order of magnitude greater than those estimated by fossil records (Ordonez and Williams 2013). Therefore, no plausible dispersal event could occur in the simulation. To obviate the problem, climatic maps were subjected to linear statistical downscaling (Fig. 1), by linear regression with the WorldClim database (Hijmans et al. 2005). Changes in coastline profile were disregarded, as simulations show a negligible change for the period and region of interest (Fordham et al. 2017).

For every taxa, climate niche was estimated by geographically crossing pollen and climatic data for the period 16-15 ka BP. This interval is chosen for featuring glacial condition in North America, and at the same time preceding the main deglacial abrupt climate change, namely Bølling-Allerød transition (~14,700 ka BP). In this way, we aimed to estimate the realized niche of taxa before facing abrupt climate transitions; such estimated niche is the starting niche for the evaluations. The only exception to this choice was *Fagus*, whose data for that period were scarce; therefore, in this case, we chose 13-12 ka BP for the niche evaluation, a period intersecting Younger Dryas and thus mostly displaying stadial conditions.

Radis was launched for every taxa three times, each one for every kernel. Launches was set to

comprise 10^4 iterations each. Simulation period was the interval 15-10 ka BP, a period comprising the transitions to Bølling Allerød and to Holocene. For *Fagus*, simulation period was 12-8 ka BP because of a lack of data for the 15-10 ka BP.

A Radis run performs a Metropolis-Hastings algorithm, where every iteration consists of a distribution range simulation for a user-defined time interval. The parameters of the Metropolis-Hastings are niche centroid coordinates (thus, in the current research, average annual temperature and average annual precipitation), niche breadth, and the dispersal parameter α . The latter depends on which dispersal kernel function the users chooses among the three available (Botta et al., manuscript in preparation); the three kernel functions differ by shape, being one step-like, one linear, and one a mixed of normal and “fat-tail” distribution (Clark 1998). For every iteration of the Metropolis-Hastings algorithm, a particular combination of values for the parameters is chosen. That combination is then used for the simulation of the corresponding iteration.

Then, for every iteration, a likelihood evaluation of the corresponding simulation is then performed, by comparing the simulation itself to the paleo-archives (for detailed explanation of likelihood estimate see Botta et al., manuscript in preparation). Let us consider, for a given Radis run, the iteration attaining the highest likelihood value. As for every iteration, a parameters values combination will correspond to that iteration. In this analysis, we consider that specific parameter value combination as the parameter evaluation of that Radis run. Consequently, we consider the highest likelihood value obtained in the run to be the likelihood of the parameter evaluation and of the corresponding simulation.

For every taxa, three separated runs were launched, each with one of the three kernels; this was meant to evaluate, for every taxon, which kernel could best describe the paleorecord patterns. For every taxon, the highest likelihood value attained in each of the three runs was recorded. The kernel corresponding to the highest value of the three was chosen for the given taxon. We consider the simulation corresponding to such likelihood value to be the “best simulation”, and the parameter values combination to be the parameter estimate for the given taxon.

Next, a sensitivity test was performed for each of the four parameters, while the other three were fixed at the values corresponding to those of the highest likelihood run. For each of this sensitivity test, both the maximum and the minimum values were recorded. The absolute difference between these two values was calculated as an evaluation of the contribution of the relative parameter to likelihood (see SI).

4.3 Results

Results are shown in Tables 2, 3 and 4. All simulations realized a likelihood value superior to 50% (Table 2), the worst being simulation of *Acer* (52.2%) and the best being simulation of *Abies* (83.6%). The simulations could reproduce several of the known dynamics having occurred to the taxa (Fig. 2). They featured the northward *Betula* and *Abies* expansion following deglaciation on the formerly glaciated area, and the rapid north-eastward colonization of *Fagus* following Holocene, which are dynamics consistent with former studies (Prentice, Bartlein, and Webb 1991; Williams et al. 2004). However, the simulations failed to reproduce the recorded Midwest expansion of *Abies* and *Ulmus* during 15-12 ka BP. Moreover, simulations for *Betula* and *Salix* presented an obvious error as they simulated taxa distribution ranges on the north-eastern part of the continent, thus overlapping with presence of ice sheet.

The parameter evaluation performed for every taxon (values reported in Table 2) allows for a niche reconstruction for every taxa during the 15-10 ky BP (12-8 ky BP for *Fagus*); we label such estimated niche “deglacial niche”. They are shown in Fig. 3, together with niche estimate for the preceding millennium, namely the period 16-15 ky BP (13-12 ky BP for *Fagus*). Deglacial niches feature a wider breadth in respect of the estimate for the preceding millennium, with the exception of *Betula* and *Ulmus*.

The sensitivity tests showed the niche breadth being the most relevant parameter for all taxa, since its contribution to total likelihood amount for every taxa no less than 98%, with the exception of *Salix*, to which the contribution of niche breadth to likelihood was 87.52% (Table 4). Temperature niche centre contributed for more than 50% of likelihood for every taxon; precipitation niche centre contributed for more than 50% for every taxon except *Betula* (44.26%) and *Tsuga* (17.40%).

Dispersal appeared as the least relevant mechanism contributing to likelihood to paleorecords, since it amounted for less than 40% for every taxon; the two exceptions were *Fagus* (63.97%) and *Tsuga* (67.74%). Best performing kernel was linear for all taxa, except *Salix* (whose best performing kernel was step-like), and *Abies* and *Ulmus* (whose best performing kernels were exponential).

4.4 Discussion and conclusions

Our simulations of species geographical ranges over a period of abrupt climate change are able to reproduce several of the observed patterns, contractions and shifts of these 7 plant taxa in North

America based only in two processes, tolerance in situ and dispersal. Those results together suggest a past biogeographical scenario in which species experienced different climatic conditions in situ, reflecting expansions of the climatic niche breadth and changes in their average conditions, at the same time that dispersal events contributed to the re-organization of their geographical ranges.

Our simulations adequately explain overall the observed patterns of geographical range dynamics. They comprise the east-ward dispersal of *Abies*, as well as its presence patterns by the Pacific coast and the Rocky Mountains; and the rapid migration north-eastwards of *Fagus* during early Holocene. However, our simulated ranges and the observed distributions disagree in specific regions of North America. Firstly, simulations for *Acer* and *Salix* presented an obvious error as they simulated taxa distribution ranges in the north-east part of the continent, thus overlapping with the known range of the Laurentide ice sheet. Moreover, the simulations failed to reproduce the recorded Midwest expansion of *Abies* and *Ulmus* during 15-12 ka BP. Finally, the simulated ranges did not show any detectable effect of the inversion of climatic trend caused by Younger Dryas cooling.

As for the overlapping with ice sheet, the disagreements may be the consequence of the fact that ice sheets (or any other geographical obstacle to colonization) are not explicitly simulated by Radis: indeed, the software does not directly simulate climatic conditions, but instead it takes them as user-provided input. On the other hand, mismatches in the dispersal simulations of *Abies* and *Ulmus* may instead be imputable to the nature of the kernel used for both taxa, namely exponential: errors in the setting of the constants ρ and σ , components of the exponential kernel, might have resulted in underestimation of dispersal ranges. Finally, the lack of discernible effect of the Younger Dryas cooling is likely a consequence of the smoothing of climatic simulation data caused by the time step spacing; adopting time steps shorter than 100y for the simulations is likely to better expose brief climatic trends, and incorporate them in the simulations.

Tolerance in situ is overall the best supported mechanism, suggesting a priority role of the ability to survive in situ under changing climatic conditions. We observe wider deglacial niches than the ones estimated by glacial conditions for the taxa *Abies*, *Acer*, *Fagus*, and *Tsuga* (Fig. 3). This points to a shift of the realized niche for such taxa within a larger fundamental niche (Nogués-Bravo 2009). Evidence for climate-induced changes in the realized niches through time have indeed been proven for some *Abies* and *Fagus* species (Maiorano et al. 2013) but also for many other plant taxa in North America (Nogués-Bravo et al. 2016).

Between the LGM and the deglacial period, the niche breadth of *Betula*, *Salix* and *Ulmus* maintained

constant and the niche centre translated (Fig. 3), hinting to a niche shift occurred during the deglacial transition. Interestingly, the niche centre shifted towards colder conditions, despite the continental temperature increase. Such shift is accompanied with a rapid migration northwards, therefore it suggests a rapid recolonization of formerly ice sheet covered regions. The limited contribution of precipitation niche centre parameter for *Tsuga* likelihood (Table 3) is coherent with former studies of present-day *Tsuga* species niches, attributing summer temperature as the most influential factor for growth, with precipitation only playing a limiting factor regionally (Gedalof and Smith 2001). This is somewhat paradoxical, considering the well-studied mid-Holocene decline of *Tsuga* populations following period of moisture variability; however, it has already pointed out by former studies that evidence points to the *Tsuga* population trough not being directly related consequence to abrupt climate changes (Booth et al. 2012).

Whether these changes in the climatic niche of species are the result of fast adaptations to climate change via ecological plasticity or micro-evolutionary change (Gavin et al. 2014) is beyond the ability of our simulations to discern. In the case of *Ulmus*, a taxon for which dispersal was evaluated not as rapid as the other taxa, the niche shift might stem from an overestimation from the abundance threshold value chosen to translate relative pollen fossil abundances in presence/absences. Other relevant factor to understand the ability of species to survive in situ are the presence of refugia and microrefugia (specifically, in situ refugia or climate relicts, i.e. resulting from range contractions). Climatic refugia can contribute to the high influence of tolerance in situ, as persistence in refugia reduces the need of species to rapidly increase their ability to change their climatic physiological constraints via plasticity or evolutionary change (Gavin et al. 2014).

The role of dispersal as a strategy to cope with climate change has been largely acknowledged as a strategy for plants to cope with fast climatic changes. Reconstruction of past migrations rates for North America taxa report northwards individual taxa velocities up to 2.7 km/decade for the northern boundaries, with velocities being faster during periods of rapid temperature changes. Our simulations support a biogeographic scenario in which dispersal played a relevant role but of secondary order for at least 5 of the analysed taxa; the exceptions to these patterns were *Fagus* and *Tsuga*, where sensitivity tests showed dispersal contributing the 63.97% and 67.74%, respectively, to explain the observed responses. The greater amount of α value contribution to likelihood of *Fagus* and *Tsuga* distribution models suggest dispersal at great ranges whilst out of equilibrium with climate, a pattern already observed in paleo-archives for these taxa (Davis et al. 1986).

The best supported dispersal mode was linear or step-like, suggesting an scenario of species geographical ranges advancing north cohesively. The exception to this trend are *Abies* and *Ulmus*, whose α values are however equal or greater than 0.73. This equates to simulations with long range dispersal, as both the linear and the step-like kernels are of 1-2 orders of magnitude greater than the exponential for dispersal greater than 30 km. This stresses the critical impact of long distance seed travels in tree responses to global climate changes (Cain, Milligan, and Strand 2000).

By the analysis conducted with Radis, it can be concluded that the most important response of the studied taxa to deglacial abrupt climate changes has been tolerance in situ. Niche have shifted during the deglacial transitions, suggesting a wider fundamental niche. In some cases (*Abies* and *Fagus*) a wider niche was indeed estimated. Taxa appeared to have maintained equilibrium with the environment, except for *Fagus* and *Tsuga*, which relied mostly on long range dispersal. *Acer*, *Salix* and *Ulmus* featured long-range dispersal as well, although dispersal events were not a major feature to reproduce paleo-archives patterns. This is coherent with hypothesis of trees responding to Pleistocene climate changes by rare events of long distance dispersal (Powell and Zimmermann 2004). The findings suggest that taxa may in future respond effectively by rapid long-range dispersal provided that this strategy is not impaired by habitat fragmentation (Hof et al. 2011).

A possible source of error for the approach used here stems from the different methods employed for niche evaluation; LGM niche has been estimated by crossing fossil data with paleoclimatic simulation data, while the deglacial niche originates from the outcome of the simulations and validations. The validity of the comparison between the two niches can be checked by executing a Radis run where the period of niche evaluation and simulation are inverted.

Systematic error can also arise by the employment of data from a limited time interval. This may indeed lead to underestimating of a taxon's niche, as arguably realized niches at any given period denote only a subset of the climatic conditions in which the taxon can survive; such an issue has been pointed out for SDM using niche reconstructions based on contemporary data (Veloz et al. 2012). Analogously, simulating species distributions for a short time interval may lead to under-representation of the climatic niche, should the interval not feature a wide enough variety of climates. Recurring to fossil data dating to both glacial and interglacial conditions could reduce the possibility to simulate distribution ranges during no-analog climates. On the other hand, caution must be taken when using records from different periods; the amount of pollen data increases the closer to the present, therefore evaluating a niche with data spanning a long time range could lead to an overestimation of the most

recent climates.

For two of the taxa considered (*Fagus* and *Tsuga*), the high values of likelihood attained by the distribution range simulations showed to be greatly influenced by the magnitude of dispersal. It has already been pointed out that implementing population processes as dispersal and extirpation in SDM can possibly increase the quality of the projections, as it allows to incorporate variability of equilibrium between species distributions and climate (Nogués-Bravo 2009). The cases considered in this study further indicate that models including population mechanisms can better capture the distribution patterns as recorded in the paleo-archives

Since the simulations do not model species abundances, some essential dynamics might be overlooked. An example of this is given by the simulations of *Fagus*. The pollen record displays a presence concentrated in the south-west before 10 ka BP and in the north-east and Midwest after. This particular pattern is due to the choice of abundance threshold adopted for the evaluation. A possible explanation could be a massive and rapid dispersal; however, reconstructed distributions taking in account of abundance differences among sites show this pattern as the consequence of a decrease of south-western population and increase of the south-eastern population (Williams et al. 2004). Radis evaluation hints in the direction of this latter explanation, since its best simulation features a presence in both regions (Fig. 2). Future development of the method including species abundance modelling will allow to incorporate such demographic dynamics, which can improve explaining the patterns recorded in paleo-archives.

A still open question consists in how the individualistic responses here inquired resulted to the second order of responses in the vegetation communities. Future lines of research could tackle this issue by overlapping the single taxon simulations and modelling the mutual relations between coexisting species. In this way progress might be done in bridging the gap between the individualistic strategies of species and the resulting emerging patterns of biomes.

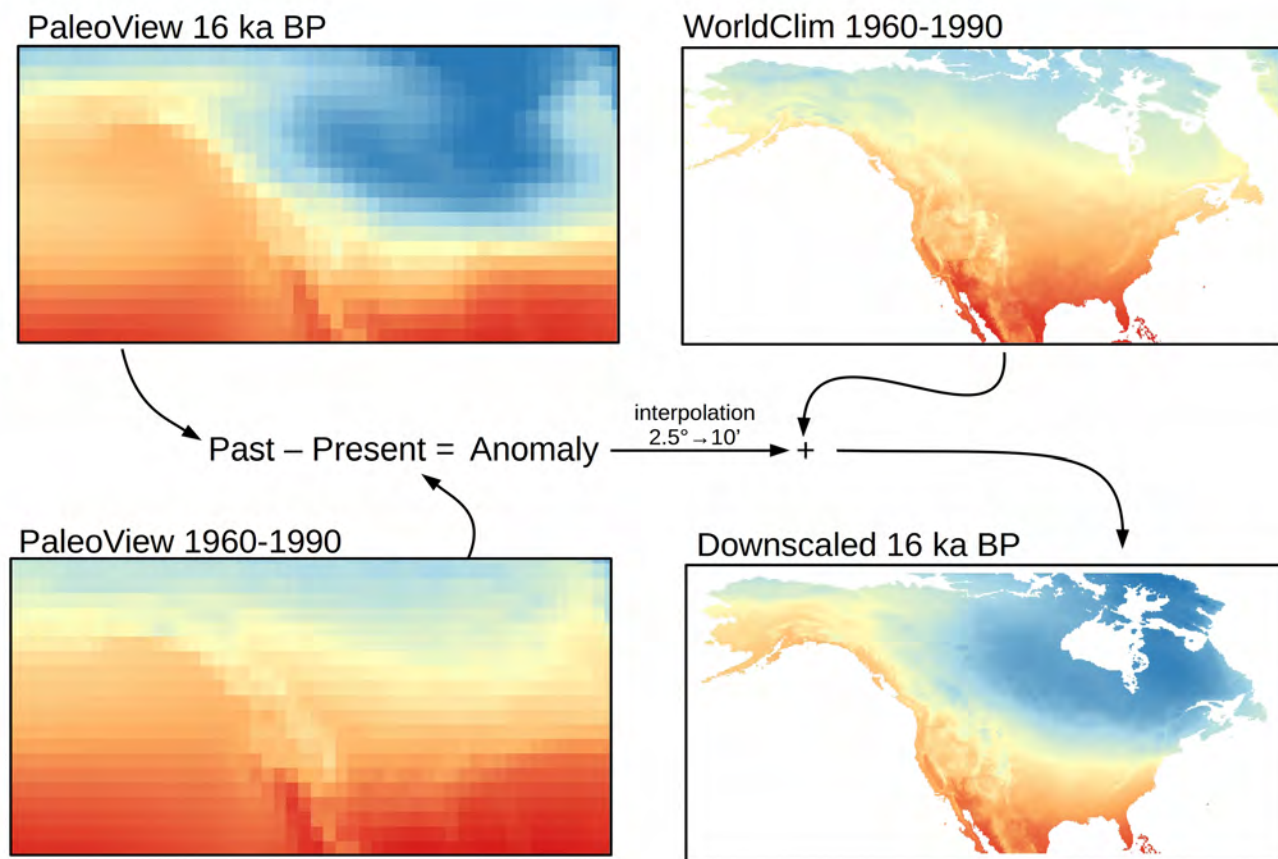


Figure 1: Example of statistical downscaling for paleoclimate raster maps. Top left: “raw” data from PaleoView, with resolution 2.5°, to be downscaled. Map show average annual temperature, averaged over 30 years around 16 ka BP. Bottom left: PaleoView simulated average annual temperature for the interval 1960-1990. Top right: recorded average annual temperature for the interval 1960-1990 from WorldClim. Bottom right: downscaled data of temperature map shown top left. It is obtained as the sum of present observed data plus the anomaly, i.e. the difference between past and present simulated climate maps, interpolated so to have same spatial resolution of top right map (anomaly map not shown here).

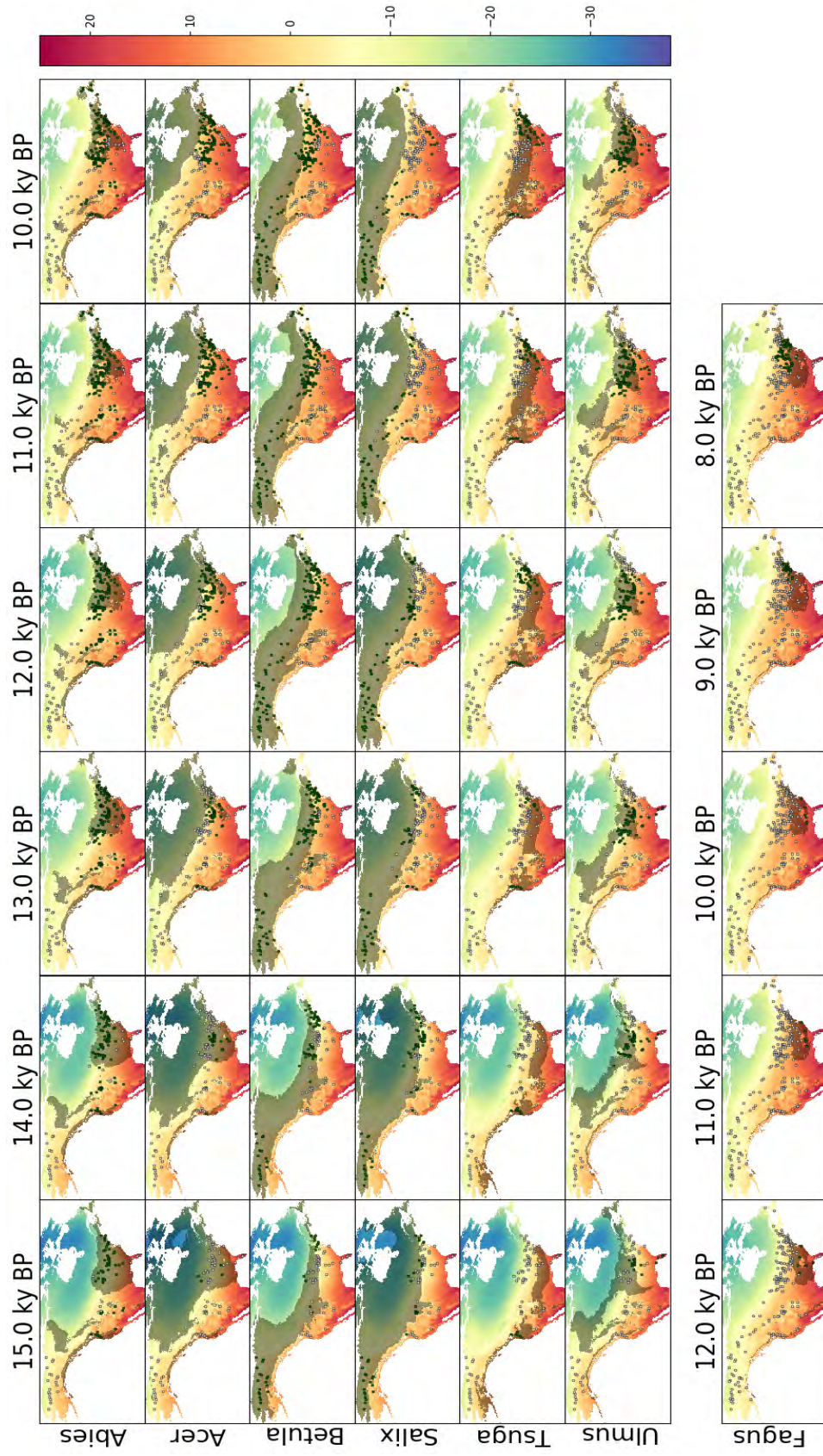


Figure 2: Best simulations, i.e. simulations obtaining the highest likelihood value, for every taxon considered. Shaded areas represent simulated presence; green and white dots indicate recorded presence and absence, respectively. Simulations are displayed over climate maps of average annual temperature. The value of likelihood obtained by every simulations corresponds to the numbers of Table 2 highlighted in red. Kernel function is exponential for *Abies* and *Ulmus*, step-like for *Salix*, and linear for all the other taxa.

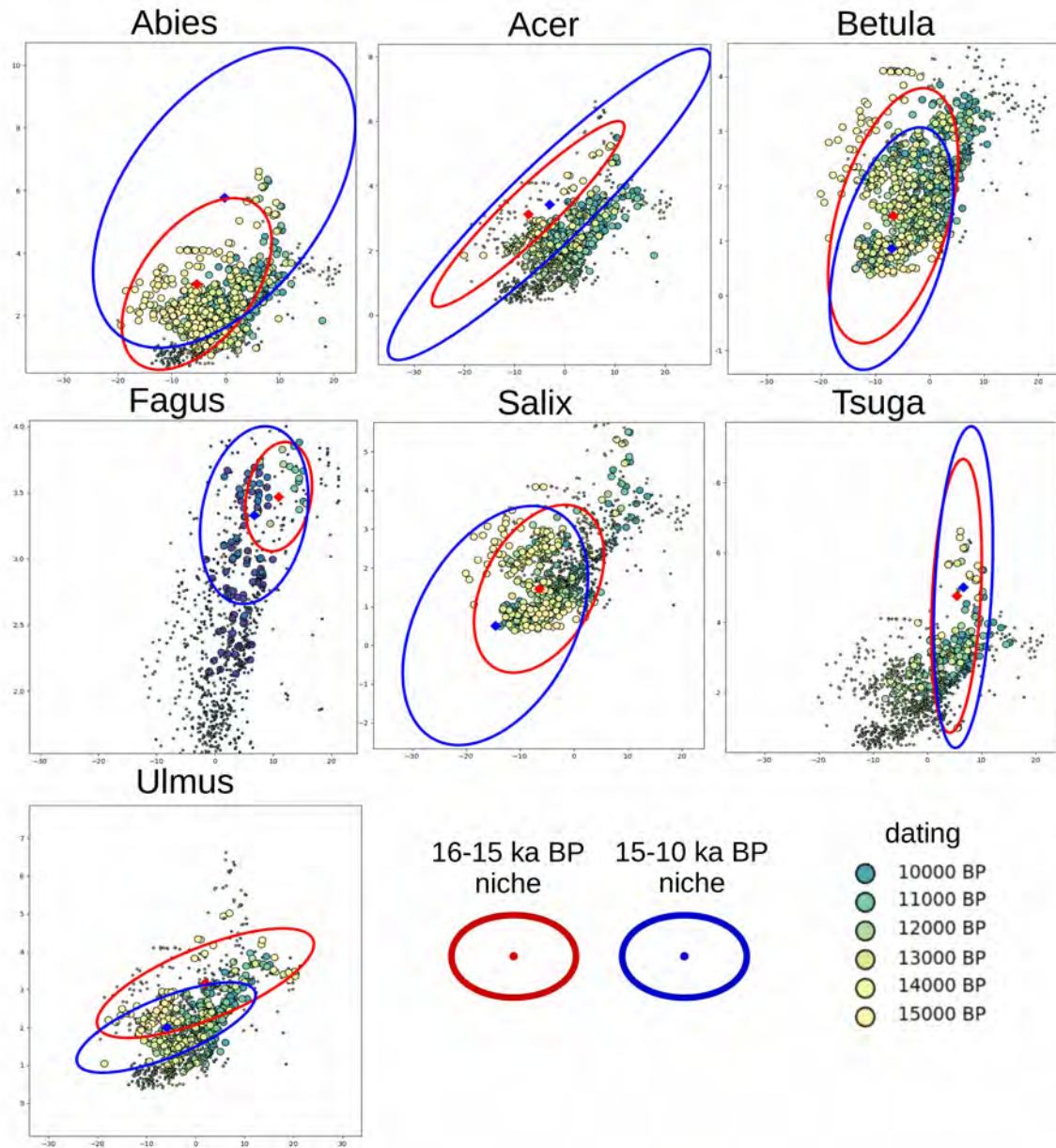


Figure 3: Niches as estimated by Radis evaluations, for all considered taxa. Niches centres are indicated by diamonds, and the corresponding niche breadths by oval line. Red niches (“LGM niches”) represent correlative evaluation performed over fossile and climate data from the period 16-15 ky BP (13-12 ky BP for *Fagus*). Blue niches (“deglacial niches”) represent the result of Radis evaluation for the period 15-10 ky BP (12-8 ky BP for *Fagus*): they are reconstructed by the taxa parameter estimate shown in Table 2. Dots indicate fossile data, and their dating is indicated by their colour, according to the bottom right legend; big and small dots indicate, respectively, presence and absence. Units are average annual temperature (in °C) for x-axis and average annual precipitation for y-axis (in mm/day).

			ky BP													
			21	20	19	18	17	16	15	14	13	12	11	10	9	8
N. of recorded presences	fir	<i>Abies</i>	16	18	16	17	27	40	61	99	128	150	175	188	209	226
	maple	<i>Acer</i>	11	9	13	15	22	37	58	95	123	135	168	176	191	201
	birch	<i>Betula</i>	17	17	18	24	36	53	77	115	153	184	219	226	259	278
	beech	<i>Fagus</i>	8	8	8	8	18	24	39	81	98	92	123	141	167	180
	willow	<i>Salix</i>	18	16	18	24	37	54	79	117	157	194	222	233	265	282
	hemlock	<i>Tsuga</i>	2	5	10	9	22	32	45	84	115	97	114	131	155	153
	elm	<i>Ulmus</i>	11	10	10	11	21	30	51	87	113	120	144	155	174	186
Total n. of sites			20	21	21	28	41	57	84	119	158	195	224	234	269	286

Table 1: Overview of the dataset used, which is taken from (Nogués-Bravo et al. 2016). The table reports the number of sites per period time, and the number of recorded presences per period of time and per taxon.

taxa	kernel			parameters			
	step-like	linear	exponential	Temperature (°C)	Precipitation (mm/day)	niche breadth (Mahalanobis distances)	dispersal parameter (α)
<i>Abies</i>	0.790	0.812	0.836	-0.27	5.77	3.50	0.81
<i>Acer</i>	0.496	0.522	0.488	-3.04	3.43	3.35	0.75
<i>Betula</i>	0.655	0.662	0.631	-6.98	0.86	1.90	0.96
<i>Fagus</i>	0.788	0.827	0.154	6.76	3.33	3.25	0.99
<i>Salix</i>	0.777	0.743	0.767	-14.55	0.51	2.85	0.98
<i>Tsuga</i>	0.761	0.767	0.665	6.67	5.01	2.35	0.99
<i>Ulmus</i>	0.683	0.659	0.734	-5.97	2.00	1.65	0.65

Table 2: Best likelihoods obtained for distribution range simulations of given taxa executed with Radis. Every taxon was tested for the three different kernels. Highlighted in red is the highest likelihood obtained for each taxon; they correspond to the best simulation (shown in Fig. 2) and to the parameter values combination displayed in in columns 4–7 of this table.

taxa	kernel		temperature	precipitation	niche breadth	dispersal (α)
<i>Abies</i>	linear					
		max	0.84	0.84	0.84	0.85
		min	0.13	0.01	0	0.69
<i>Acer</i>	linear					
		max	0.53	0.52	0.53	0.53
		min	0.02	0	0	0.47
<i>Betula</i>	linear					
		max	0.66	0.66	0.66	0.66
		min	0.11	0.37	0	0.41
<i>Fagus</i>	linear					
		max	0.83	0.83	0.83	0.83
		min	0.34	0.1	0	0.3
<i>Salix</i>	step-like					
		max	0.78	0.78	0.78	0.78
		min	0.15	0.26	0.1	0.64
<i>Tsuga</i>	linear					
		max	0.77	0.78	0.77	0.78
		min	0.12	0.64	0	0.25
<i>Ulmus</i>	exponential					
		max	0.74	0.74	0.75	0.75
		min	0	0.01	0	0.54

Table 3: Sensitivity tests for the taxa traits. First column indicates the taxon name. Second column indicates which kernel has been used for the given taxon. For each taxon, four sensitivity tests were run, one for each of the four parameters. They consisted in fixing the other three parameters, then recording the maximum and minimum likelihood so obtained. The result values are shown in columns 4–7.

taxa	contribution			
	temperature	precipitation	niche breadth	dispersal (α)
<i>Abies</i>	85.05%	98.82%	100.00%	18.09%
<i>Acer</i>	96.95%	100.00%	100.00%	11.39%
<i>Betula</i>	84.04%	44.26%	99.85%	37.65%
<i>Fagus</i>	59.25%	88.39%	100.00%	63.97%
<i>Salix</i>	80.69%	66.92%	87.52%	17.25%
<i>Tsuga</i>	84.42%	17.40%	100.00%	67.74%
<i>Ulmus</i>	100.00%	98.38%	100.00%	28.23%

Table 4: absolute differences, expressed in percentage, of the maximum and minimum likelihoods obtained in the sensitivity tests; they evaluate the contribution of dispersal in the taxa response patterns.

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Tolerance and dispersal influenced North American tree distributions during the deglacial period

Supplementary information

Once Radis has been run for a given taxon, period and geographic area, it produces an evaluation of the taxon's traits as a combination of parameter values. Let us take for example the Radis analysis for *Tsuga*, over North America, for the period 15-10 ky BP, using a linear kernel. The result of Radis analysis can be seen in Table 2: the best likelihood value obtained is 76.7%. The corresponding combination of parameter values is the following:

$$\begin{aligned} \text{tmean} &= 6.67 \\ \text{prec} &= 5.01 \\ \text{breadth} &= 2.35 \\ \alpha &= 0.99 \end{aligned} \tag{1}$$

This combination, correspondent to the highest likelihood value found by the Metropolis-Hastings run, represents the evaluation of Radis for the corresponding traits of *Tsuga*: niche centroid coordinates for average annual temperature and precipitation (labelled “tmean” and “prec”, respectively), niche breadth (“breadth”) and dispersal parameter (“ α ”).

The following question is how much the likelihood of this parameter combination owes to every single parameter. A way to answer to this is to run Radis again while keeping fixed 3 out of 4 parameters (or, more generally, $x-1$ out of x , where x is the total number of parameters) to values (1), while letting the remaining one vary. Radis will then explore all the domain interval of this remaining parameter, and evaluate all the corresponding likelihood values. In this way, it can be seen how much the likelihood changes, starting from the best likelihood value that corresponds to the (1) combination; this operation can be executed for each of the parameters. In other words, we start with the maximum likelihood parameter combination, then we “turn the knobs” of each parameter separately, and see how that affects likelihood.

An example of this analysis, performed for the aforementioned *Tsuga* example, can be seen in Fig. S1. It shows two sensitivity test; (a) is performed over dispersal parameter α and (b) is

performed over niche breadth. The result of the sensitivity test for α gives:

	Likelihood	α value	Iteration #
Max. likelihood	77.8%	0.86	2521
Min. likelihood	25.1%	0.36	6853

The Metropolis-Hastings algorithm starts with values combination (1). Then, the sensitivity test “turns the knobs” for α , so that likelihood is evaluated for the α values in the domain interval $[0, 1]$ (Fig. 1a). The maximum likelihood value obtained is 77.8%, therefore the combination

$$\begin{aligned}
 \text{tmean} &= 6.67 \\
 \text{prec} &= 5.01 \\
 \text{breadth} &= 2.35 \\
 \alpha &= 0.86
 \end{aligned} \tag{2}$$

represents a refine in respect to combination (1), since combination (2) corresponds to a higher likelihood value. The minimum likelihood value obtained in the sensitivity test is 25.1%. This means the fraction of likelihood affected by α is:

$$\frac{77.8 - 25.1}{77.8} = 67.74 \% \tag{3}$$

We dub this values as the “contribution” of α to the total likelihood, i.e. to what extent the likelihood of the evaluated parameter combination can be affected by variations of α .

All values of Table 4 are calculated with the approach of formula (3). This explains why the values of every row do not add up to 100%: as we saw in the example above, all values derive from independent sensitivity tests; the percentages simply indicate how much the corresponding parameters can affect the best likelihood value.

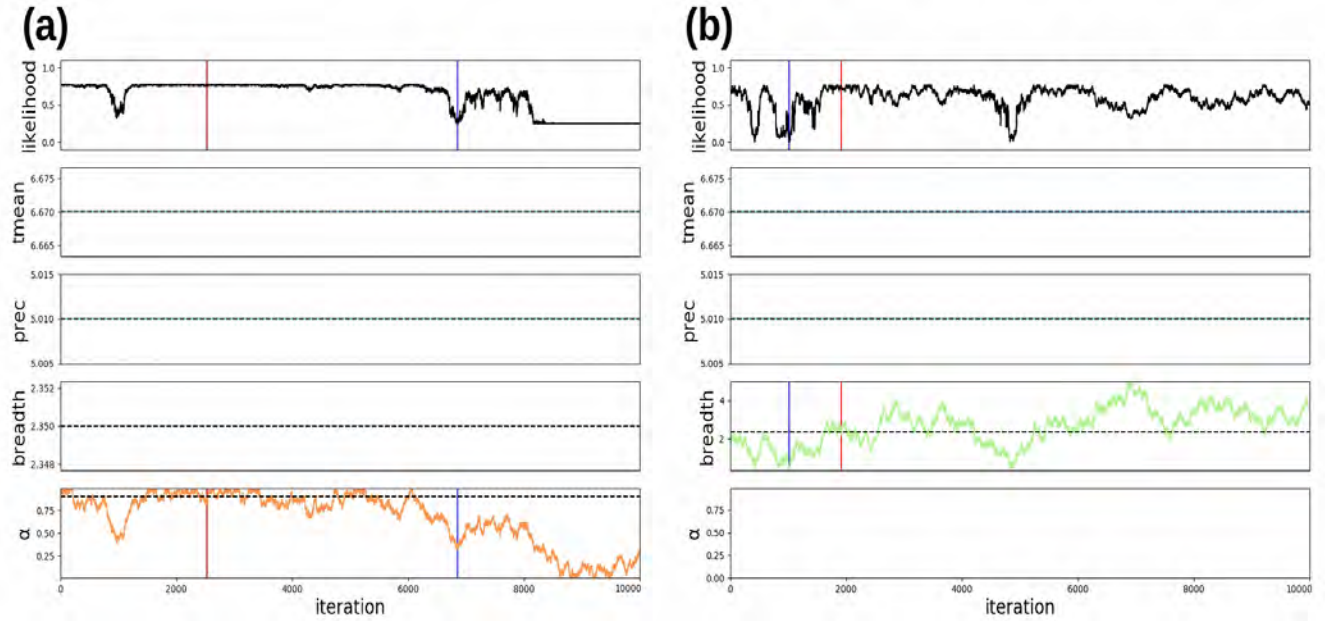


Figure S1: Two sensitivity tests conducted for *Tsuga*. In both cases, all parameters except one were fixed; in this way, the remaining parameter explored its whole domain interval. Likelihood values were, as usually, evaluated for every iteration, as shown by black plots on top. The iterations in which maximum and minimum likelihood values are obtained are highlighted with a red and blue vertical line, respectively. Plots (a) show the result of a sensitivity test for dispersal parameter α . Maximum and minimum likelihood values obtained are 77.8% and 25.1%, respectively, and they correspond to the values of 0.86 and 0.36, respectively. Plots (b) show the result of a sensitivity test for breadth niche parameter. Maximum and minimum likelihood values obtained are 76.8% and 0%, respectively, and they correspond to the values of 2.35 and 0.35, respectively.

5 Conclusions and outlook

The last glacial period was characterised by several global abrupt climate shifts, likely induced by intrinsic amplifying feedback mechanisms within atmospheric and oceanic circulations. The global transitions drove a variety of environmental changes on regional scale, whose magnitudes and modalities depended on the geographic and hydrological specificities of the various areas. Such environmental shifts affected the biosphere, inducing ramifications and cascading consequences across all ecological levels. The plethora of fossil paleorecords hints to severe ecological reorganizations, including different degrees of equilibrium/disequilibrium with climate across populations and communities.

The wide phenomenological knowledge on the biotic responses to abrupt climate changes leaves still open questions about the nature and the functioning of the response mechanism behind this outcome. This project represents an attempt to investigate on these response mechanisms, by highlighting the general response patterns and developing a mechanistic model to simulate and analyse the key mechanisms behind geographical range dynamics.

The first part of the thesis, exposed in Chapter 2, reviews and summarizes the knowledge about the biotic responses to past abrupt climate changes, focusing on Last Glacial and early Holocene. The wide variety of recorded patterns is drawn by a review of published literature comprising global coverage, where responses are analysed and classified by habitat and organization level. It is shown that the ability to maintain equilibrium with the environment is reportedly featured throughout different communities and habitats, with responses lags depending on the specificities of the interspecies relationships and the regional outcomes of the global climatic reorganizations. Such feature relies on the capacity of populations to migrate and on the variety of regional climates, which increases the possibility of presence of micro-refugia. Under abrupt climate change, rare species may become more frequent and vice versa: whenever the novel climate results advantageous for their climatic niche or causes more favourable interspecies relations, their individualistic responses may result in repopulating communities undergoing population stress and diversity loss. Nevertheless, climate variability on ecosystems exerts a jeopardizing stress, which increases probability of local extirpations if acting concomitantly with other disturbance sources.

In the second part of the thesis, corresponding to Chapter 3, a novel method for studying responses

of species geographical ranges to past abrupt climate changes is presented. Such model takes climate simulation maps and paleorecords as input, then uses the former to realize process-based distribution range simulations and the latter to validate them. Therefore, it consists of a process-based model where species mechanisms under study are explicitly modelled, hybridized with a correlative approach via confrontation of the simulated responses with recorded paleo-archives. The validity of the method was proved by testing it for the *Abies* taxa in North America during the deglacial period, in which the transitions to Bølling-Allerød, Younger Dryas and Holocene climate periods occur. This case study evaluated, with a ~85% likelihood, tolerance in situ as the main mechanism of response, and long range dispersal as secondary. The proposed method, despite representing a drastic simplifications of the mechanisms under study, succeeds in capturing some key geographical dynamics.

Lastly, in Chapter 4 the novel method is adopted to a dataset comprising seven taxa (*Abies*, *Acer*, *Fagus*, *Salix*, *Tsuga* and *Ulmus*) in order to investigate the responses of North American vegetation to the abrupt environmental changes occurring during the deglacial period. According to the analysis, tolerance in situ was overall the primary mechanism to react to abrupt climate change. Dispersal seemingly played a secondary role, except for *Fagus* and *Tsuga*.

The presented model paves the way to future elaborations of process-based models as tools to understanding the relations of species and ecosystems with a rapidly changing climate. Given the high level of variability of the population responses, and the entanglement of the ecological networks, a line of further development will consist of reproducing species-species interactions, e.g. competition for resources. This will allow to simulate the community responses as summarized in Chapter 2, which for simplicity reasons could not be taken in account in the model described in Chapter 3.

Future lines of investigations may take the inquiry further by incorporating explicit simulations of other mechanisms, for other relevant species and including population-level traits, developing the current method to an eco-evolutionary dynamic model. This would require a modelling for key processes as gene flow, mutation, as intra-specific genetic variability, as well as demographic effects. The latter, in particular, will become necessary when adopting the method of process-based modelling for studying species with short life cycles. This will make the method, that is here tested only on tree taxa, relevant and applicable to a wider number of species.

It would also be worthwhile to expand the use of the model by adopting it to simulate future distribution ranges. Such line of study is particularly relevant given the current urgency to confront the present climate change and its repercussions on the biosphere. Geographical models of species ranges

face often the issue of discrepancy of results obtained in confront to the historically reported responses. Such divergences raise questions on whether such divergence can be imputable to the anthropogenic influence, or to overlooked population dynamics. These issues highlight the need for continued development of more accurate models and further inquiries. It would be interesting, for example, to adopt the presented method to cross the results of present-day distribution range simulations with simulated processes evaluated by paleo-archives, or to double-check the likelihood of past simulations with present-day recorded distribution range changes. Such kind of analyses are a relevant future line or research in the perspective to help bridging the current gap between recorded past, and simulated future, ecological responses.

Appendix: Software code

Here are presented integrally the two scripts which comprise Radis.

radis_launcher.py

```
# -*- coding: utf-8 -*-
"""
Radis – Launching module
"""
import warnings
import numpy as np
import pandas as pd
import radis_functions as rf
warnings.filterwarnings("ignore")

# %% Read variables file
df = pd.read_csv("radis_variables.txt", index_col=0, comment="#",
                 header=None, engine='python', sep=':')
SY = np.zeros(7, dtype=int)
SY[0:2] = np.array(df.loc['main interval', 1].split(","), dtype=float)
SY[6] = float(df.loc['time step length', 1])

# %% Load data
print("\n\n#===== Loading geographical, climatic and biotic data =====#")
print('Main interval: ' + str(SY[0]) + " - " + str(SY[1]) + ' yBP')
print('Length of one time step: ' + str(int(SY[6])) + " y")
loadyn = input('Already got formatted input data file? (Y/N) ')
CHECK = False
while not CHECK:
    if loadyn == "Y":
        InpAdd = df.loc['general input data', 1].strip()
        print('Address of Input data: ' + InpAdd)
        Input = np.load(InpAdd)
        for file in Input.files:
            if file != "SY":
                vars()[file] = Input[file]
                if (str(Input[file].dtype)[0:2] == "<U"):
                    if (Input[file].shape == ()):
                        vars()[file] = str(Input[file])
        if np.any(Input["SY"][0:2] != SY[0:2]):
            print("\n\tWarning: main interval from input file " +
                  "not corresponding")
        CHECK = True
    elif loadyn == "N":
        if "shapefile" in str(df.iloc[:, 0]):
            ShpAdd = str(df.loc['shapefile', 1]).strip()
            if ((not ShpAdd == "") & (not ShpAdd == "None") &
                (not ShpAdd == "nan")):
                ShpName = ShpAdd.split("/")[-1].split(".")[0]
                print("Address of shapefile: " + ShpAdd)
            else:
                ShpAdd = ""
                ShpName = ""
        else:
            ShpAdd = ""
            ShpName = ""
        FossAdd = df.loc['fossile data', 1].strip()
        species = df.loc['species', 1].strip()
        thres = 0.
        if "abundance threshold" in df.iloc[:, 0]:
            thres = float(df.loc['abundance threshold', 1])
        error = int(df.loc['dating error', 1])
        ClimNames = np.array(df.loc['climate variables',
                                    1].strip().split(","))

        ClimFolds = []
        for i, clim in enumerate(ClimNames):
            ClimNames[i] = clim.strip()
            ClimFolds.append(df.loc['rasters ' + ClimNames[i], 1].strip())
        print("Climate variables:", ClimNames)
        print("Address of rasters:", ClimFolds)
        print('Address of fossile data: ' + FossAdd)
```

```

print('Species name: ' + species)
print('Error on the fossile data: ' + str(error))
if "abundance threshold" in df.iloc[:, 0]:
    print("Threshold on " + species + " abundance: " + str(thres))
FossName = FossAdd.split("/")[-1].split(".")[0]
(Coords, ClimMat, fos_ind, fos_ts,
 fos_ab) = rf.inp_function(ShpAdd, FossAdd, species,
                          [SY[0], SY[1], SY[6]], False, ClimNames,
                          ClimFolds, error)
InpAdd = rf.save_formatted(Coords, ClimMat, fos_ind, fos_ts,
                          fos_ab, SY, species, ShpName, FossName,
                          ClimNames, ClimFolds, FossAdd, ShpAdd,
                          thres, error, False)

CHECK = True
else:
    loadyn = input('Answer must be either "Y" or "N". ')
    CHECK = False

SY[0:2] = np.array(df.loc['main interval', 1].split(","), dtype=float)
SY[6] = float(df.loc['time step length', 1])
NumCells = Coords.shape[0]
NumClim = len(ClimNames)
nVars = NumClim + 2

# %% Make Dists and DistID
print("\n\n#===== Creating distance matrix =====#")
distyn = input('Already got a formatted distance matrix file? (Y/N) ')
CHECK = False
while not CHECK:
    if distyn == "Y":
        dis_add = df.loc['distance matrix', 1].strip()
        print('Address of distance matrix: ' + dis_add)
        DQ = weris = []
        Ds = np.load(dis_add)
        for file in Ds.files:
            vars()[file] = Ds[file]
        if DQ.shape[0] != NumCells:
            print("\nWarning: Distance matrix not compatible with input data")
            CHECK = True
    elif distyn == "N":
        cut = float(df.loc['maximum distance', 1])
        print("Maximum distance: " + str(cut) + " km")
        dis_add, DQ, weris = rf.format_dist(Coords, cut)
        print("Distance matrix saved as " + dis_add + ".npz")
        CHECK = True
    else:
        distyn = input('Answer must be either "Y" or "N". ')
        CHECK = False

# %% Initiate MH
print("\n\n#===== Simulation setting =====#")
SY[4:6] = np.array(df.loc['simulation interval', 1].split(","), dtype=float)
newyn = input('Starting a new run? (Y/N) ')
CHECK = False
while not CHECK:
    if newyn == "Y":
        print("\n\n#===== Evaluating initial niche " +
              "=====#")
        SY[2:4] = np.array(df.loc['niche evaluation interval', 1].split(","),
                          dtype=float)
        print('\tNiche evaluation interval: ' + str(SY[2]) + " - " +
              str(SY[3]) + ' y BP')
        nichyn = input('\tAlready got niche evaluation data file? (Y/N) ')
        CHECK = False
        while not CHECK:
            if nichyn == "Y":
                NicAdd = df.loc['niche evaluation data', 1].strip()
                print('\tAddress of niche evaluation data: ' + NicAdd)
                InputNiche = np.load(NicAdd)
                cmn = InputNiche["ClimMat"]
                nfi = InputNiche["fos_ind"]
                nft = InputNiche["fos_ts"]
                nfa = InputNiche["fos_ab"]
                if np.any(InputNiche["SY"][0:2] != SY[0:2]):
                    print("\nWarning: main interval from niche evaluation " +
                          "file not corresponding\n")
                CHECK = True
            elif nichyn == "N":
                if "niche shapefile" in str(df.iloc[:, 0]):

```

```

        NicheShpAdd = str(df.loc['niche shapefile', 1]).strip()
        if ((not NicheShpAdd == "") & (not NicheShpAdd == "None") &
            (not NicheShpAdd == "nan")):
            NicheShpName = NicheShpAdd.split("/").split(".")[0]
            print("\tAddress of shapefile: " + NicheShpAdd)
        else:
            NicheShpAdd = ""
            NicheShpName = ""
    else:
        NicheShpAdd = ""
        NicheShpName = ""
    (nCo, cmn, nfi,
     nft, nfa) = rf.inp_function(NicheShpAdd, FossAdd, species,
                                [SY[0], SY[1], SY[6]], True,
                                ClimNames, ClimFolds, error)
    FossName = FossAdd.split("/").split(".")[0]
    NicAdd = rf.save_formatted(nCo, cmn, nfi, nft, nfa, SY,
                              species, NicheShpName, FossName,
                              ClimNames, ClimFolds, FossAdd,
                              NicheShpAdd, thres, error, True)

    CHECK = True
else:
    nichyn = input('Answer must be either "Y" or "N". ')
    CHECK = False
n_cen, n_cov = rf.make_niche(SY, cmn, thres, nfi, nft, nfa)
VarsIn = np.zeros(NumClim+2, dtype=float)
for i in range(NumClim):
    VarsIn[i] = float(input("\tCenter of " + ClimNames[i] + ": "))
VarsIn[-2] = float(input('\tNiche breadth: '))
VarsIn[-1] = float(input('\tAlpha: '))
NumIter = int(df.loc['number of iterations', 1])
Vars = np.zeros((NumIter+1, nVars), dtype=float)
tst = np.array((SY[0]-SY[0:SY.size-1])/SY[6], dtype=int)
fit = np.zeros(NumIter+1, dtype=float)
init = 0
Vars[0, :] = VarsIn
TopSim = np.zeros((NumCells, tst[1]+1))
IniSim = np.zeros((NumCells, tst[1]+1))
k_name = df.loc['kernel name', 1].strip()
i_name = df.loc['initial condition', 1].strip()
lims = np.array([[-100., 100.] for i in range(NumClim+2)])
if NumIter > 0:
    for ii, clim in enumerate(ClimNames):
        a = np.where(df.index == 'range ' + clim)[0]
        if len(a) > 0:
            lims[ii] = np.array(df.iloc[a[0], 0].split(","))
        else:
            print("\nWarning: missing range for " +
                  clim + ", imposing " + str(lims[ii]))
            lims[-2] = np.array(df.loc['range breadth', 1].split(","))
            lims[-1] = np.array(df.loc['range alpha', 1].split(","))
    CHECK = True
elif newyn == "N":
    RecAdd = df.loc['recovery data', 1].strip()
    Rec = np.load(RecAdd)
    for file in Rec.files:
        if file != "SY":
            vars()[file] = Rec[file]
            if (str(Rec[file].dtype)[0:2] == "<U"):
                if (Rec[file].shape == ()):
                    vars()[file] = str(Rec[file])
    NumIter = Vars.shape[0]-1
    SY[4:-1] = Rec["SY"][4:-1]
    init = np.where(~np.logical_and(np.all(Vars == 0, axis=1),
                                     fit == 0))[0][-1]
    print("Address of partial result: " + RecAdd)
    print("Last iteration: " + str(init))
    CHECK = True
else:
    newyn = input('Answer must be either "Y" or "N". ')
    CHECK = False

print('\nSimulation interval:', SY[4], "-", SY[5], ' y BP', end=" ")
Int = np.array(range(int(SY[5]), int(SY[4]+SY[6]), int(SY[6])))
for ii, clim in enumerate(ClimNames):
    missing = []
    for year in Int:
        tst = int((SY[0]-year)/SY[6])
        if np.all(np.isnan(ClimMat[:, ii, tst])):

```

```

        missing.append(year)
    if missing != []:
        print("\nWarning: missing " + clim + " raster for years " +
              str(missing) + " BP\n")

print('\nKernel: ' + k_name + '\nInitial distribution: ' + i_name)
if k_name not in rf.print_kers():
    print('\nWarning: kernel name must be one of', rf.print_kers(), '\n')
if i_name not in rf.print_indis():
    print('\nWarning: initial condition must be one of', rf.indis.keys(), '\n')

print('Num. iterations: ' + str(NumIter))
if NumIter > 0:
    sav_fre = int(df.loc['save frequency', 1])
    print('Frequency of saves: 1/' + str(sav_fre))
else:
    sav_fre = 0

# %% Metroplis-Hastings algoritm
print("\n\n#===== Starting Metropolis-Hastings =====#")
rf.MH(DQ, weris, ClimMat, Vars, fit, n_cov, k_name, thres, init, NumIter, lims,
      sav_fre, InpAdd, dis_add, ShpName, SY,
      error, Coords, TopSim, IniSim, i_name, species, fos_ts, fos_ind, fos_ab)
print("Metropolis-Hastings complete.\n\n")

```

radis_functions.py

```
# -*- coding: utf-8 -*-
"""
Functions to be used by Radis
"""

import re
import os
import copy as cp
import numpy as np
import random as rn
from os import listdir
from osgeo import gdal, ogr
from os.path import isfile, join
from scipy.spatial.distance import cdist

# %% Constants ===== #
"""
M: Maximum distance for step-lie and linear kernels
SCALE: Scale value for exponential kernel
RATIO, SIGMA: constants of exponential kernel
STEP: relative length of MH steps
CLUSTER: ray of presence around paleorecord for initial condition
See section 8 of SI
"""
NUL_KER = 100000
SCALE = 36000
RATIO = 0.9
SIGMA = 0.3
STEP = 0.01
CLUSTER = 100
R = 6371.0

# %% All Radis functions ===== #
def get_scale():
    return SCALE

def get_nul_ker():
    return NUL_KER

def com_nan(func, aa, thresh):
    """Eliminate NaN warnings """
    out = ~np.isnan(aa)
    out[out] = func(aa[out], thresh)
    return out

def save_dist(filename, array, distid):
    """To save csr sparse matrices in a compact way"""
    np.savez(filename, data=array.data, indices=array.indices,
             indptr=array.indptr, shape=array.shape, distid=distid)

def geodis(cord_2, cord_vec):
    """Calculate distance between geographical coordinates in metres """
    la1 = cord_vec[:, 1]
    lo1 = cord_vec[:, 0]
    lo2 = cord_2[0]
    la2 = cord_2[1]
    lat1 = np.radians(la1)
    lon1 = np.radians(lo1)
    lat2 = np.radians(la2)
    lon2 = np.radians(lo2)
    dlon = lon1 - lon2
    y = np.sqrt((np.cos(lat2) * np.sin(dlon))**2 +
                (np.cos(lat1)*np.sin(lat2) -
                 np.sin(lat1)*np.cos(lat2)*np.cos(dlon))**2)
    x = np.sin(lat1)*np.sin(lat2) + np.cos(lat1)*np.cos(lat2)*np.cos(dlon)
    c = np.arctan2(y, x)
    distance = np.round(2 * R * c * 1000)
    return distance
```



```

def format_dist(Coords, cut):
    """Make distance matrix"""
    nc = Coords.shape[0]
    distids = []
    distarr = []
    tmpmax = 0
    arr_id = np.arange(nc)
    for x in range(nc):
        print("Calculating distances... " + str(round(100*(x/nc), 1)),
              end="% \r")
        tmpdis = geodis(Coords[x], Coords)
        tmpdis[tmpdis > cut*1000] = 0
        distids.append(arr_id[np.where(tmpdis > 0)])
        distarr.append(np.array(tmpdis[np.where(tmpdis > 0)], dtype=int))
        tmp = len(distids[x])
        if tmp > tmpmax:
            tmpmax = tmp
    print("Calculating distances... done. ")
    SQ = np.full([nc, tmpmax], np.nan, dtype=float)
    DQ = np.full([nc, tmpmax], np.nan, dtype=float)
    weris = np.full((nc, tmpmax, 2), np.nan)
    for ii in range(nc):
        print("Formatting distance matrix... " + str(round(100*ii/nc, 1)),
              end="% \r")
        SQ[ii, 0:len(distids[ii])] = distids[ii]
        DQ[ii, 0:len(distarr[ii])] = distarr[ii]
        for jj in range(len(distids[ii])):
            isq = int(SQ[ii, jj])
            iw = np.where(np.all(np.isnan(weris[isq]), axis=1))[0][0]
            weris[isq, iw, 0] = ii, jj
    print("Formatting distance matrix... done. ")
    nn = 0
    for ii in range(DQ.shape[0]):
        if np.isnan(DQ[-ii, -ii]):
            nn = -ii
            break
    if nn == 0:
        an = np.where(np.isnan(DQ))
        weris[np.isnan(weris)] = [an[0][0], an[1][0]]
    else:
        weris[np.isnan(weris)] = nn
    weris = np.array(weris, dtype=int)
    save_add = ("Dist." + str(nc) + "%r" % int(cut))
    np.savez(save_add, DQ=DQ, weris=weris)
    del SQ, distids, distarr
    return save_add, DQ, weris

def save_formatted(Coords, ClimMat, fos_ind, fos_ts, fos_ab, sy, species,
                  shp_name, foss_name, clim_names, clim_folds, foss_add,
                  shp_add, thres, error, nyn):
    """Save formatted data"""
    if nyn:
        print("\t", end="")
        print("Saving formatted data... ", end="\r")
        save_add = species + "-" + foss_name
        if not shp_name == "":
            save_add += "-" + shp_name
        for climfold in clim_folds:
            save_add += "-" + climfold.split("/")[-1]
        save_add += "-%i_%i_%i" % (sy[0], sy[1], sy[6])
        if nyn:
            save_add = "niche_evaluation"
        else:
            save_add = "general_input"
    np.savez(save_add, fos_ind=fos_ind, fos_ts=fos_ts, fos_ab=fos_ab,
             ClimMat=ClimMat, Coords=Coords, SY=sy, ClimNames=clim_names,
             ClimFolds=clim_folds, species=species, FossAdd=str(foss_add),
             thres=thres, error=error, ShpName=shp_name)
    text = str(save_add + ".npz contains\n" +
               "- climate data from rasters in folders")
    for fold in clim_folds:
        text += "\n" + str(fold)
    text += "\n\n- fossile data with error " + str(error) + "y for " + \
            str(species) + " (abundance threshold " + str(thres) + \
            ") from file\n" + foss_add
    text += "\n\nformatted for Radis for the period " + str([int(sy[0]),
                                                             int(sy[1])]) + \
            " BP at a resolution of " + str(int(sy[6])) + \

```

```

        " years"
    if shp_add != "":
        text += " and adapted for the shapefile " + shp_add
    text_file = open(save_add + ".txt", "w")
    text_file.write(text)
    text_file.close()
    if nyn:
        print("\t", end="")
    print("Saving formatted data... saved as " + save_add + ".npz")
    return save_add

def make_niche(sy, cmn, thres, nfi, nft, nfa):
    """Evaluate niche"""
    tst = np.array((sy[0]-sy[0:sy.size-1])/sy[6], dtype=int)
    if len(nft.shape) == 3:
        con_fos = np.where(((np.nanmin(nft[0, :, :], axis=1) < tst[2])) |
                           ((np.nanmax(nft[0, :, :], axis=1)) > tst[3]))
        if con_fos[0].shape[0] == nft.shape[1]:
            n_cen = np.zeros(cmn.shape[1])
            n_cov = np.identity(cmn.shape[1])
            print("\tWarning: missing data in niche evaluation period. " +
                  "Imposing")
            for row in n_cov:
                print("\t", row)
            print("\tas evaluated niche covariance.")
        else:
            nft_c = cp.deepcopy(nft)
            nft_c[0, con_fos, :] = np.nan
            fosnan = np.where(np.isnan(nft_c))[1:3]
            fos_tsint = np.array(nft_c, dtype=int)
            fos_tsint[0, fosnan[0], fosnan[1]] = 0
            mask_pre = (nfa > thres)
            cmc = np.array(cmn[nfi, :, fos_tsint], dtype=float)[0]
            cmc[fosnan[0], fosnan[1], :] = np.nan
            cmc = cmc[mask_pre]
            nich_clim = np.reshape(cmc, (cmc.shape[0]*cmc.shape[1],
                                         cmc.shape[2]))
            nich_clim = nich_clim[np.all(~np.isnan(nich_clim), axis=1), :]
            n_cen = np.mean(nich_clim, axis=0)
            n_cov = np.cov(nich_clim, rowvar=0)
            print("\tEstimated Niche mean: " + str(n_cen))
    else:
        n_cen = np.zeros(cmn.shape[1])
        n_cov = np.identity(cmn.shape[1])
        print("\tWarning: missing data for niche evaluation. Imposing")
        for row in n_cov:
            print("\t", row)
        print("\tas evaluated niche covariance.")
    return n_cen, n_cov

def prepare_evaluation(fos_ts, fos_ab, tst, thres):
    if (len(fos_ts.shape)) == 3:
        con_fos = np.where((np.nanmax(fos_ts[0, :, :], axis=1) < tst[4]) |
                           ((np.nanmin(fos_ts[0, :, :], axis=1)) > tst[5]))
        ind_fos = np.where((np.nanmax(fos_ts[0, :, :], axis=1) >= tst[4]) &
                           ((np.nanmin(fos_ts[0, :, :], axis=1)) <= tst[5]))
        ...
        # Change to this for more conservative comparison (whole interval in) #
        con_fos = np.where((np.nanmin(fos_ts[0, :, :], axis=1) < tst[4]) |
                           ((np.nanmax(fos_ts[0, :, :], axis=1)) > tst[5]))
        ind_fos = np.where((np.nanmin(fos_ts[0, :, :], axis=1) >= tst[4]) &
                           ((np.nanmax(fos_ts[0, :, :], axis=1)) <= tst[5]))
        ...
        fos_ts[0, con_fos, :] = np.nan
        fosnan = np.where(np.isnan(fos_ts))[1], np.where(np.isnan(fos_ts))[2]
        fos_tsint = np.array(fos_ts, dtype=int)
        fos_tsint[0, fosnan[0], fosnan[1]] = 0
        mkp, mka = fos_ab > thres, fos_ab <= thres
        ngp, nga = sum(mkp[ind_fos]), sum(mka[ind_fos])
        if (fos_ts.shape[1] - len(con_fos[0])) == 0:
            print("\nWarning: no record data to evaluate likelihood\n")
    else:
        fosnan = np.zeros(1, dtype=int)
        fos_tsint = np.array(fos_ts, dtype=int)
        ngp = 0
        nga = 0
    return ngp, nga, mkp, mka, fosnan, fos_tsint

```

```

def MH(DQ, weris, cm, vas, fit, n_cov, k_name, thres, init, num_iter,
      lims, sav_fre, save_add, dis_add, shp_name, sy, error,
      Coords, TopSim, IniSim, i_name, species, fos_ts, fos_ind, fos_ab):
    """Metropolis - Hastings on simulation"""
    num_cells = Coords.shape[0]
    nvas = vas.shape[1]
    er_ts = int(error/sy[6])
    if cm.shape[1] > 1:
        VI = np.linalg.inv(n_cov)
    else:
        VI = n_cov**0.5
    tst = np.array((sy[0]-sy[0:sy.size-1])/sy[6], dtype=int)
    ngp, nga, mkp, mka, \
        fosnan, fos_tsint = prepare_evaluation(fos_ts, fos_ab, tst, thres)
    if i_name == "record":
        mask_init = init_rec(num_cells, fos_ab, fos_ind, fos_ts,
                             tst, thres, Coords, cp.deepcopy(DQ), weris)
    else:
        mask_init = np.zeros(num_cells, dtype=bool)
    # ===== The MH algorithm ===== #
    if init > 0:
        TopFit = max(fit)
        topit = np.where(fit == TopFit)[0][0]
    for it in range(init, num_iter+1):
        print("Iteration n." + str(it) + "... ", end="\r")
        # ===== Propose step in the variable space ===== #
        if it > 0:
            while True:
                t_vas = cp.deepcopy(vas[it-1, ])
                ind = np.random.randint(0, nvas)
                t_vas[ind] = (t_vas[ind] + rn.choice([+1, -1]) * STEP *
                             (lims[ind, 1] - lims[ind, 0]))
                floor = lims[ind, 0] < t_vas[ind]
                roof = t_vas[ind] < lims[ind, 1]
                if (floor and roof):
                    break
            else:
                t_vas = vas[0, :]
        Sim, TmpFit = simulation(num_cells, tst, DQ, weris, cm,
                                t_vas, VI, k_name, thres,
                                er_ts, Coords, i_name,
                                mask_init, fos_tsint, fosnan,
                                fos_ind, fos_ab, mkp, mka, ngp, nga)
        # ===== Accept or reject step ===== #
        if it == 0:
            TopSim = Sim
            IniSim = Sim
            fit[0] = TmpFit
            TopFit = TmpFit
            topit = 0
        else:
            if fit[it] == 0:
                sog = 1
            else:
                sog = min(1, TmpFit/fit[it-1])
            if np.random.rand() < sog:
                vas[it] = t_vas
                fit[it] = TmpFit
                if TmpFit > TopFit:
                    TopFit = TmpFit
                    TopSim = Sim
                    topit = it
            else:
                vas[it, ] = vas[it-1, :]
                fit[it] = fit[it-1]
        # ===== Checkpoint ===== #
        if (it == 0 or ((it) % np.ceil(num_iter/float(sav_fre)) == 0) and
            (init != it)):
            print("Checkpoint " + str(it) + "...", end="\r")
            if len(TopSim.shape) == 3:
                TopSim_fix = TopSim[:, 0, :]
            else:
                TopSim_fix = TopSim
            res_add = save_results(vas, fit, k_name, TopSim_fix, n_cov,
                                   IniSim, num_iter, save_add, topit, i_name,
                                   dis_add, shp_name, sy, it, species, lims)
            print("Checkpoint " + str(it), end="... ")

```

```

        if it < num_iter:
            print("Partial", end=" ")
        else:
            print("Final", end=" ")
        print("results saved at " + res_add + ".npz")

def kernel_step(dcalc, var):
    """Kernel step function"""
    var = var*NUL_KER
    ker = np.array(dcalc < var, dtype=int)
    return ker

def kernel_linear(dcalc, var):
    """Kernel linear function"""
    var = float(var*NUL_KER)
    ker = (-1/var)*dcalc+1
    return ker

def kernel_exponential(dcalc, alpha):
    """Kernel exponential function"""
    dist = dcalc/SCALE
    gau = (np.exp(-0.5*np.power(np.abs(dist/SIGMA), 2)) /
            (SIGMA*(2*np.pi)**0.5))
    fat = np.exp(-np.power(np.abs(dist/alpha), 0.5))/(4*alpha)
    ker = RATIO*gau + (1-RATIO)*fat
    return ker

kernels = {'linear': kernel_linear,
            'exponential': kernel_exponential,
            'step': kernel_step}

def print_kers():
    return list(kernels.keys())

def dispersal(Sim_step_before, dc, vas, k_name, DQ, weris):
    FR = np.where([Sim_step_before == 0])[1]
    ava = FR[com_nan(np.less_equal, dc[FR], vas[-2])]
    if len(ava) > 0:
        if len(FR) == 1:
            DQ[weris[FR][:, 0], weris[FR][:, 1]] = np.nan
        elif len(FR) > 1:
            DQ[weris[FR][:, :, 0], weris[FR][:, :, 1]] = np.nan
        ker = kernels[k_name](DQ[ava], vas[-1])
        rand = np.random.rand(ker.shape[0], ker.shape[1])
        pas = np.any(rand < ker, axis=1)
        migrated = ava[pas]
    else:
        migrated = np.array([], dtype=int)
    return migrated

def mahal(clim_map, nich_cen, VI):
    """Calculate Mahalanobis distance from niche centre for all grid cells"""
    clt = np.array(clim_map, dtype=float)
    if nich_cen.shape[1] > 1:
        dc = cdist(clt, nich_cen, 'mahalanobis', VI=VI)[: , 0]
    else:
        dc = (np.abs(clt - nich_cen)/VI)[: , 0]
    return dc

def init_niche(nc_cs, ClimMatIn, VI, br):
    """Start simulations by occupying all available grid cells"""
    dcst = mahal(ClimMatIn, nc_cs, VI)
    mask_init = com_nan(np.less_equal, dcst, br)
    return mask_init

def init_rec(num_cells, fos_ab, fos_ind, fos_ts, tst,
            thres, Coords, DQ, weris):
    """ Start simulations by occupying grid cells around records"""
    mask_pre = (fos_ab > thres)
    pi = fos_ind[mask_pre]

```

```

pt = fos_ts[:, mask_pre, :]
fil_pt = ((np.nanmin(pt[0, :, :], axis=1) <= tst[4]) &
          (tst[4] <= np.nanmax(pt[0, :, :], axis=1)))
PolAb = [pi[fil_pt, 0]]
mask_init = np.zeros(num_cells, dtype=bool)
for i in range(num_cells):
    tmp = np.intersect1d(weris[i, :, 0], PolAb)
    if len(tmp) > 0:
        j = np.in1d(weris[i, :, 0], tmp)
        a = DQ[weris[i, j, 0], weris[i, j, 1]] < CLUSTER*10000
        if np.any(a):
            mask_init[i] = True
return mask_init

indis = {'niche': init_niche, 'record': init_rec}

def print_indis():
    return list(indis.keys())

def simulation(num_cells, tst, DQ, weris, cm, vas, VI, kn,
              thres, er_ts, Coords, i_name, mask_init,
              fos_tsint, fosnan, fos_ind, fos_ab, mkp, mka, ngp, nga):
    """Simulate distribution range and evaluate likelihood"""
    nc_cs = np.array([vas[0:cm.shape[1]]])
    Sim = np.zeros([num_cells, tst[1]+1])
    if i_name == "niche":
        mask_init = init_niche(nc_cs, cm[:, :, tst[4]], VI, vas[-2])
    Sim[mask_init, tst[4]] = 1
    for t in range(tst[4]+1, tst[5]+1):
        dc = mahal(cm[:, :, t], nc_cs, VI)
        Sim[dispersal(Sim[:, t-1], dc, vas, kn, cp.deepcopy(DQ), weris), t] = 1
        Sim[(com_nan(np.less_equal, dc, vas[-2])) & (Sim[:, t-1] == 1), t] = 1
    if len(fos_tsint.shape) == 3:
        sim_check = np.array(Sim[fos_ind, fos_tsint], dtype=float)
        sim_check[0, fosnan[0], fosnan[1]] = np.nan
        bb = sim_check[0, mka][~np.all(np.isnan(sim_check[0, mka]), axis=1)]
        rgp = np.sum(np.any(sim_check[0, mka] == 1, axis=1))
        rga = np.sum(np.all((bb == 0) | (np.isnan(bb)), axis=1))
        tmp_fit = np.nanmin([rgp/ngp, rga/nga])
        if np.isnan(tmp_fit):
            tmp_fit = 0
    else:
        tmp_fit = 0
    return Sim, tmp_fit

def save_results(vas, fit, k_name, topsim, n_cov, inisim, num_iter, save_add,
                topit, i_name, dis_add, shp_name, sy, it, species, lims):
    """Save results of MH"""
    save_path = "Results/" + str(shp_name) + "_" + str(species) + "_" + \
                str(topsim.shape[0]) + "/"
    if not os.path.exists(save_path):
        os.makedirs(save_path)
    res_add = cp.deepcopy(save_path)
    for ii in range(len(vas[0, :])):
        res_add += "%s" % (vas[0, ii])
        if ii != len(vas[0, :])-1:
            res_add += "-"
    if (it < num_iter):
        res_add += "%i" % (it)
    np.savez(res_add, TopSim=topsim, IniSim=inisim, Vars=vas, fit=fit,
             SY=sy, k_name=k_name, i_name=i_name, n_cov=n_cov, lims=lims,)
    text = str(res_add + ".npz contains results from a MH of " + str(it) +
              " out of " + str(num_iter) + " iterations. It was launched" +
              " with dataset" + " stemming from:\n" + save_add + "\n" +
              dis_add + "\nKernel function: " + str(k_name) +
              "\n\n" + "Initial variables were set to: " + str(vas[0, :]) +
              "\nBest iterations was number " + str(topit) +
              " with likelihood " + str(np.round(fit[topit], 2)) +
              " and featured variables: " + str(vas[topit, :]))
    text_file = open(res_add + ".txt", "w")
    text_file.write(text)
    text_file.close()
    return res_add

```

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def inp_function(shp_add, foss_add, species, y_in, nyn,
                climnames, clim_folds, error):
    """Format input data"""
    numclim = len(climnames)
    NumSteps = int((y_in[0]-y_in[1])/y_in[2]+1)
    # ===== Read climatic data =====#
    onlyfiles = [""] * numclim
    click = 0
    for nc in range(numclim):
        click_proj = 0
        onlyfiles = [f for f in listdir(clim_folds[nc]) if
                     isfile(join(clim_folds[nc], f))]
        ras_year = []
        for fil in onlyfiles:
            ras_year.append(int((re.findall('\d+', fil))[0]))
        missing = []
        all_year = list(range(y_in[0], y_in[1]-y_in[2], -y_in[2]))
        for year in all_year:
            if year not in ras_year:
                missing.append(year)
        if missing != []:
            print("\n", end="")
            if nyn:
                print("\t", end="")
            print("Warning: missing " + climnames[nc] +
                  " raster for years " + str(missing) + " BP\n")
        for fil in onlyfiles:
            if nyn:
                print("\t", end="")
            print("Formatting " + climnames[nc] + " rasters... " +
                  str(round(100 * float(onlyfiles.index(fil) /
                                      len(onlyfiles)))) + "% \r")
            tmpyear = int((re.findall('\d+', fil))[0])
            if y_in[0] >= tmpyear and tmpyear >= y_in[1]:
                tmst = int((y_in[0]-tmpyear)/y_in[2])
                ras_add = clim_folds[nc] + "/" + fil
                raster = gdal.Open(ras_add)
                nod = raster.GetRasterBand(1).GetNoDataValue()
                if shp_add is not "":
                    if (raster.GetProjection() == ""):
                        if (click_proj == 0):
                            if nyn:
                                print("\t", end="")
                                print(" " * 60 + "\nWarning: missing "
                                      "projection of " + climnames[nc] +
                                      " rasters, using shapefile's\n")
                                click_proj = 1
                            driver = ogr.GetDriverByName('ESRI Shapefile')
                            dataSource = driver.Open(shp_add, 0)
                            layer = dataSource.GetLayer()
                            spatialRef = layer.GetSpatialRef()
                            ShpProj = spatialRef.ExportToWkt()
                            dest_geo = raster.GetGeoTransform()
                            rBandAr = raster.GetRasterBand(1).ReadAsArray()
                            xcount, ycount = rBandAr.shape[0], rBandAr.shape[1]
                            rvirt = gdal.GetDriverByName('MEM').\
                                Create('', ycount, xcount, 1, gdal.GDT_Float32)
                            rvirt.SetGeoTransform(dest_geo)
                            outband = rvirt.GetRasterBand(1)
                            outband.SetNoDataValue(nod)
                            outband.WriteArray(rBandAr)
                            rvirt.SetProjection(ShpProj)
                            raster = rvirt
                        rclip = gdal.Warp('', raster, format='MEM',
                                         cropToCutline=True,
                                         cutlineDSName=shp_add)
                        raster = rclip
                    rar = np.array(raster.ReadAsArray())
                    hr, lr = rar.shape[0], rar.shape[1]
                    (x0, xsz, _, y0, _, ysz) = raster.GetGeoTransform()
                    if click == 0:
                        NumCells = rar.shape[0] * rar.shape[1]
                        Coords = np.zeros((NumCells, 2))
                        ClimMat = np.full((NumCells, numclim, NumSteps),
                                          np.nan, dtype="float32")
                        for yy in range(hr):
                            for xx in range(lr):
                                xc = xx * xsz + x0 + xsz/2
                                yc = yy * ysz + y0 + ysz/2

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        Coords[xx+yy*rar.shape[1], :] = np.array([xc, yc])
        click = 1
    for yy in range(hr):
        ClimMat[lr*yy:lr*(1+yy), nc, tmst] = rar[yy]

    if nyn:
        print("\t", end="")
        print("Formatting " + climnames[nc] + " rasters... done.    ")
    ClimMat[ClimMat == nod] = np.nan
    # ===== Read fossile data =====#
    if nyn:
        print("\t", end="")
        print("Formatting fossile data...", end="")
    species = str(species)
    foss_index = np.loadtxt(foss_add, skiprows=0, dtype=str)[0]
    f_raw = np.loadtxt(foss_add, skiprows=1, dtype=str) # , dtype=float)
    sp_col = np.where(foss_index == np.array(species))[0][0]
    lat_col = np.where(foss_index == np.array(str("latitude")))[0][0]
    long_col = np.where(foss_index == np.array(str("longitude")))[0][0]
    ybp_col = np.where(foss_index == np.array(str("YearBP")))[0][0]
    w = np.abs(xsz)
    h = np.abs(ysz)
    x1 = rar.shape[1]*xsx + x0
    y1 = rar.shape[0]*ysz + y0
    tst = np.array((y_in[0]-y_in[0:2])/y_in[2], dtype=int)
    ls_ts = np.array(range(tst[0], tst[1]+1))
    ls_sy = np.array(range(y_in[0], y_in[1]-y_in[2], -y_in[2]))
    tmp_ind = np.zeros(f_raw.shape[0], dtype=int)
    tmp_ts = np.zeros([f_raw.shape[0], 2], dtype=int)
    tmp_ab = np.full(f_raw.shape[0], np.nan)
    ml_sit = np.ones(f_raw.shape[0], dtype=int)
    for ii, row in enumerate(f_raw):
        r_ybp = float(row[ybp_col])
        r_lon = float(row[long_col])
        r_lat = float(row[lat_col])
        r_sp = float(row[sp_col])
        if y_in[0] >= r_ybp and r_ybp >= y_in[1]:
            en_per = r_ybp-error
            in_per = r_ybp+error
            in_ind = np.where(ls_sy <= in_per)[0][0]
            en_ind = np.where(ls_sy >= en_per)[0][1]
            in_ts = ls_ts[in_ind]
            en_ts = ls_ts[en_ind]
            if ((x0 < r_lon) & (r_lat > y1) &
                (x1 > r_lon) & (r_lat < y0)):
                xx = int((r_lon - x0)/w)
                yy = int((y0 - r_lat)/h)
                ind_cel = xx+yy*rar.shape[1]
                if ~np.all(np.isnan(ClimMat[ind_cel, :, in_ts:(en_ts+1)])):
                    a = np.where(tmp_ind == ind_cel)[0]
                    b = np.where((tmp_ts[:, 0] == in_ts) &
                                (tmp_ts[:, 1] == en_ts))[0]
                    c = np.intersect1d(a, b, assume_unique=True)
                    if len(c) == 0:
                        tmp_ab[ii] = r_sp
                        tmp_ind[ii] = ind_cel
                        tmp_ts[ii] = [in_ts, en_ts]
                    else:
                        tmp_ab[c[0]] += r_sp
                        ml_sit[c[0]] += 1
    tmp_ab = tmp_ab / ml_sit
    em_ln = np.where(np.isnan(tmp_ab))[0]
    fos_ab = np.delete(tmp_ab, em_ln, axis=0)
    tmp_ind = np.delete(tmp_ind, em_ln, axis=0)
    tmp_ts = np.delete(tmp_ts, em_ln, axis=0)
    track_ind = np.array(range(NumCells))
    spf = np.where(np.all(np.all(np.isnan(ClimMat), axis=1), axis=1))[0]
    ClimMatNew = np.delete(ClimMat, spf, axis=0)
    CoordsNew = np.delete(Coords, spf, axis=0)
    track_indNew = np.delete(track_ind, spf, axis=0)
    fos_ind = np.zeros(len(tmp_ind), dtype=int)
    for ii, ni in enumerate(track_indNew):
        if ni in tmp_ind:
            fos_ind[np.where(tmp_ind == ni)[0]] = ii
    fos_ind = np.rot90(np.array([fos_ind]), k=3)
    if len(tmp_ts) > 0:
        wt_all = np.max(tmp_ts[:, 1]-tmp_ts[:, 0] + 1)
        fos_ts = np.full([1, tmp_ts.shape[0], wt_all], np.nan)
        for ii, row in enumerate(tmp_ts):
            ts_int = np.array(range(row[0], row[1]+1))

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        fos_ts[0,
            ii, range(len(ts_int))] = np.array(range(row[0], row[1]+1))
    else:
        fos_ts = tmp_ts
    print(" done.")
    if (len(tmp_ts) == 0) & (not nyn):
        print("\nWarning: missing data for likelihood evaluation\n")
    return CoordsNew, ClimMatNew, fos_ind, fos_ts, fos_ab

```