



A REVIEW OF PLANT MIGRATION RATES, INDIVIDUALISM, AND PLANT COMMUNITY CONSEQUENCES IN RESPONSE TO CLIMATE CHANGE

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Abstract

Climate change in the coming century is expected to be comparable to the last deglaciation's warming. Since then, there has been no other incident of such scale. The palaeoecological evidence of animals' responses to historical temperature change, particularly plants' responses, suggests that evolutionary adaptation played only a minor role and that migration is the most common reaction to climatic change. Individualism in response has significant consequences for changes in vegetation and ecosystems. Even if the greatest realized rates of migratory response by trees may match the maximum prospective rates, they are near to the utmost that such long-lived sessile animals are thought to be capable of. Climate change is expected to accelerate 10-100 times quicker in the future than it did during the last ice age. The likelihood of widespread extinction is high unless actions are done to promote organisms' migratory responses to predicted changes. Artificial dispersal of trees and other organisms with limited dispersal and/or migratory capacity, a broadening of the legal protection currently afforded to some threatened organisms only within designated reserves, and the integration of wildlife habitat requirements and wildlife corridors into human landscape usage are all likely to be required. Stringent measures to limit the extent of future climate change by limiting emissions of greenhouse gases will also be necessary if the possibility of widespread and even catastrophic extinction is to be avoided.

Keywords: Tree, climate, extinction, habitat, vegetation

Introduction

Global system changes are not a new phenomenon; they have occurred throughout the history of the planet. A system of alternating glacial and interglacial conditions characterized the most recent Quaternary geological epoch (Zalasiewicz *et al.*, 2008, Huntley *et al.*, 1991, Bridgland and Westaway 2008, Ruddiman and Raymo, 1988). The last glacial period ended at 10000 bp, according to Start and Prell (1984). Glacial conditions existed over much of the last 0-75 Ma (Huntley 1991, Bridgland and Westaway 2008, Huntley, 1989), and it is thought that, absent human intervention, the world environment would return to glacial conditions within a few millennia at most (Huntley 1991, Bridgland and Westaway 2008, Lamb, 1982).

Human populations have increased enormously over the last two centuries, exploiting fossil fuel deposits, destroying ever wider areas of natural ecosystems, practicing more intense agriculture, and polluting their surroundings to levels that are only now becoming apparent (Schneider, 1989). Changes in the composition of the atmosphere caused by human activity have the potential to have the most devastating repercussions. During the last two centuries, the levels of a variety of so-called "greenhouse gases," both naturally occurring and those present only as presented by Pielke 1998, pollutants, have grown dramatically (Change *et al* 2006 Siegenthaler and Oeschger, 1987; Khalil and Rasmussen, 1987). The level of CO₂ has risen by 23% from 280 ppmv to > 345 ppmv, and is estimated to be rising at c. 4% per decade; the level of CH₄, which is 25 times more potent as a greenhouse gas than CO₂, has risen by c. 250 percent from 650 ppbv to 1650 ppbv, and is estimated to be rising at c. 1% per annum (Raynaud *et al.*, 1998.). A conservative consensus of predictions made using atmospheric General Circulation Models (GCMs) is c. 2-5°C for an effective doubling of atmospheric CO₂ that will be reached by about ad 2050 at current rates of increase, and estimates range as high as an 8°C rise in global mean temperature during the next century (Schneider, 1989). The Quaternary fossil record must be examined in order to uncover the biosphere's response to global and regional climate changes associated with a global warming of this magnitude. Even at the time of alleged maximum post-glacial warmth, c. 6000 bp, Webb and Wigley (1985) determined that global mean temperature was unlikely to be more than 1°C greater than it is today. We only detect larger shifts in global mean temperature when we compare glacial and interglacial circumstances. Although some regions experienced temperature increases of up to 10°C or more at the end of the last glacial period (Jouzel *et al.*, 1987), Schneider (1989) estimated that the global mean temperature change during the last glacial termination (i.e. between c. 15000 and 10000 years ago) was only about 5°C.

Today, vegetation accounts for the vast bulk of the biomass on the planet. Understanding how vegetation responds to such changes will be critical if we are to predict how the biosphere will adapt to climatic changes of the magnitude predicted for the next centuries. Quaternary palynological data give a record of vegetation's responses to climate changes of comparable scale that have happened frequently throughout the last 0-75Ma. The past 18ka record is particularly significant since it falls within the 14C dating range and includes the most recent period of rapid global warming. The use of isopoll maps to depict late Quaternary palynological data is discussed in this work. These maps show how individual taxa have responded to past large climate shifts, allowing estimations of their reaction rates to be established (Huntley and Birks, 1983; Huntley, 1989). Pollen-climate response surfaces (Bartlein, Prentice, and Webb, 1986) demonstrate the climatic reaction of pollen taxa, and a comparative research employing these has showed

the long-term stability of the climate response of taxa (Huntley, Bartlein and Prentice, 1989). As a result, the fundamental reaction of taxa to rapid and continuous climate change has been migration (Good, 1931; Huntley and Webb, 1989), with each taxon behaving individually (Huntley and Birks, 1983; Webb, Cushing and Wright, 1983; Webb, Richard and Mott, 1983; Huntley and Webb, 1989). Palynological data can also be used to create palaeovegetation maps with the help of proper analysis (Huntley and Birks, 1983; Jacobson, Webb and Grimm, 1987; Huntley, 1990).

The characteristics revealed by such maps are explained, and the implications of taxa's individualistic reactions to climate change are explored in connection to plant community responses (Huntley, 1990). Although the scale of late-Quaternary climate changes is comparable to future predicted human-caused changes, the maximum rates of change differ by an order of magnitude (Schneider, 1989). The ramifications of this are examined in light of historical evidence of climate change responses. Huntley and Webb, 1988; Davis, 1989; Graham and Grimm, 1990; Huntley, 1991) examine the prospect that rapid human-induced climate change will result in extinction and impoverishment of populations.

Evidence from Palynological Data from the Last Quarter

Pollen diagrams have been created from late Quaternary sedimentary sequences by researchers from all around the world. Since around 1960, the majority of workers have also obtained ¹⁴C dates on sediment samples from these profiles, allowing them to be compared on a temporal scale separate from the palynological data. These statistics have been used as the foundation for several workers' syntheses (Flenley, 1979; Ritchie, 1984; Huntley and Webb, 1988). The data can be shown in a variety of ways, some of which are explained here, along with the insights and information they convey, are described below.

Isopoll maps

Isopoll maps show the distribution and abundance patterns of individual pollen taxa at specific periods for a given geographical area using contours (the 'isopolls'). Szafer (1946) was the first to utilize the approach to map the postglacial spread of diverse trees across Poland, but its utility was restricted before the availability of ¹⁴C dating (Libby, 1955). More recently, with the availability of multiple ¹⁴C-dated pollen diagrams, it has become possible to build isopoll maps for specific times on a radiocarbon time-scale, with the advantage that the dating is now completely independent of the palynological record (Huntley and Birks, 1983). The compilation of isopoll maps for Europe by Huntley and Birks (1983) was the first extensive use of this technique to examine the late and post-glacial history of many individual pollen taxa and of the vegetation of a subcontinental scale region, despite a number of more geographically, temporally, and/or taxonomically restricted studies (Birks, Deacon, and Peglar 1975; Birks and Saarnisto, 1975). The technique has now been applied to both big and small areas (Huntley and Webb, 1989). The presentation of palynology data as isopoll maps, as well as the compilation of data into databases that must precede the preparation of the maps, has revealed information and insights that could not be obtained as easily from individual pollen-stratigraphic records, and has enabled new analyses of these data that contribute to our understanding of biosphere responses to climate change (Bartlein, 1986; Jacobson *et al.*, 1987; Huntley, 1990; Huntley *et al.*, 1989). Two more types of data analysis, as well as two of the conclusions acquired directly from the isopoll maps, are particularly pertinent to discussions of vegetation's reaction to rapid climate change, and are discussed below. Surfaces of pollen-climate reaction Bartlein *et al.*, (1986) demonstrated how modern climate data might be linked with pollen surface-sample data to identify patterns of distribution and abundance of distinct pollen taxa in a climatic area. For their study of the climatic response of several eastern North American pollen taxa, they selected to use the mean temperatures of January and July, as well as the mean annual precipitation. The selection of these climatic variables is discussed by Bartlein *et al.*, (1986), and is justified by their easy availability from the conventional meteorological record, as well as their close correlation with variables that may be more clearly mechanistically implicated in determining plant, and thus pollen, distribution and abundance patterns (winter minimum temperature, growing-season temperature sum, exposure to growing-season drought). Surfaces for pollen-climate response have since been developed using these factors for a wide range of eastern North American and European pollen species, as well as utilizing only the seasonal temperature variables

When the data for taxonomically equivalent taxa from the two continents were compared, the pollen-climate response surfaces on both continents are strikingly similar (unpublished results). The seasonal temperature response surfaces for one pollen taxon were found to be almost identical and can be utilized interchangeably, according to a study (Huntley *et al.*, 1989). Because the pollen taxon represents a single species across all, or nearly all, of both continental regions, and because it is a taxon whose response to factors other than climate has been given prominence in the interpretation of its late-Quaternary history, especially in Europe, *Fagus* was chosen for investigation (Iversen, 1973). The findings of this study, which show a great deal of similarity between the climatic responses of North American and European *Fagus* spp., led to the conclusion that these taxa have a climatic response that is unique to the genus and has not evolved since the separation of *Fagus* populations on the two continents between 10 and 25Ma bp, despite the magnitude of continuous, but often rapid, climate change since then. Although similar systematic comparisons for other taxa have not yet been made, the frequency with which they show subjectively similar pollen-climate response surfaces (unpublished results) and their migratory response to postglacial climate change (Huntley and Webb, 1989) indicate that the vast majority of taxa have responded to Quaternary climatic changes by migration rather than evolution (Huntley and Webb, 1989), and that their climatic tolerances and/or adaptations are likely (Huntley *et al.*, 1989). Rates of migration Examining sequences of isopoll (Huntley and Birks, 1983) or isochrones (Davis, 1976) maps can be used to assess the rates of migratory response of taxa to climatic change.

The migration rates indicated in this method are the actual rates; the extent to which migration may have trailed behind exceptionally rapid climatic change is still a point of contention (Davis, 1984; Bennett, 2018; Birks, 1986). Most trees' maximum migration rates are in the range of 150-500m year⁻¹, and the maximum rates of migration reached by certain taxa are remarkably consistent across geographical locations (Huntley, 1989). However, the maximum rates of 1000 to 2000 m year⁻¹ achieved by a few taxa in Europe are slightly higher than those recorded in eastern North America, as Huntley and Birks (1983) have discussed. Isoline maps for events in a taxon's pollen record; the isolines connect sites where the event took place at the same time. The first rise in pollen values to a level indicating local presence of pollen-producing plants is mapped in order to assess migration.

Some aquatic plant (Iversen, 1954; Huntley and Birks, 1983) and Coleoptera (Coope, 1977) taxa, however, traveled even quicker than the trees. The evidence of these faster migrations has been used to back up the theory of migratory lag among trees (Birks, 1986; Davis, 1983; Huntley and Birks, 1983). The isopoll maps of European and eastern North American pollen data, as discussed by Huntley and Webb (1989), do not support any of the suggested sources of lag, and strongly suggest that it could not have been of any considerable significance. A simple estimation of the possible maximum migration rate also reveals that they are surprisingly comparable to the observed maximum realized migration rates. The apparent disparity between tree migration rates and aquatic plant and Coleoptera migration rates can be explained most economically by assuming that these organisms were responding to various components of the climate that altered at different rates and/or at separate times. The orbitally driven changes in solar radiation, as well as changes in the height and extent of the residual ice-sheets in North America and, to a lesser extent, Europe, were the primary forcing processes determining climatic change during the latest deglacial warming (COHMAP Members, 1988).

Summer insolation in the Northern Hemisphere increased, whereas winter insolation decreased. At c. 9000 bp, when summer insolation was c. 8% higher than today and winter insolation was c. 8% lower, this enhanced seasonality of insolation reached its apex. This insolation trend started around 18000 B.P., when seasonal insolation in the northern hemisphere was close to what it is today. The volume of the major ice sheets was decreasing throughout this time, but it was still estimated to be > 50% of the maximum 18000 bp volume at 12000 bp. Only at the time of the peak seasonality of insolation, c. 9000bp, did the ice sheet volume become insignificant. While increased summer radiation would lead to higher summer temperatures, particularly over ice-free continental areas, reduced winter insolation would lead to lower winter temperatures. Any increase in winter temperatures during this time was primarily due to the ice sheets' waning effect. Kutzbach and Guetter (1986) used atmospheric GCM simulations to validate this general pattern. The July mean temperature had recovered from a M mean dip of c. 3°C at 18000 bp to a zonal mean depression of 0-5°C at 12000 bp, then rose to a zonal mean c. 2°C higher than today at 9000 bp in the northern hemisphere's mid-latitudes. For the January mean temperature zonal averages, comparable data are depressions of c. 11-5°C at 18000 BP and c. 3-5°C at 12000 BP, with little difference from the current 9000 BP 2000 bp and no difference from present at 9000 bp.

The discrepancies in migration rates and timing of trees, aquatic plants, and Coleoptera can all be explained by these variances in seasonal temperature responses. Because they are either latent in the lake-bottom muck or overwintering as eggs or in a state of hibernation throughout the winter season, the latter groups are particularly sensitive to high summer temperatures. Trees' aerial portions, on the other hand, must withstand winter exposure. As a result, the rapid return of summer temperatures to levels comparable to or even exceeding current levels allowed aquatic plants and Coleoptera to migrate more quickly at a time when winter temperatures were still much below current levels, preventing tree migration. In addition, the temperature gradient varies by season; in Europe, the summer temperature gradient is around half that of the winter. This would result in variations in possible migration rates across organisms, depending on whatever component of seasonal temperature their range margin tracked. Organisms that were more sensitive to summer temperatures migrated faster than those that were more sensitive to yearly mean temperatures or winter temperatures. Any test of this theory will require high-resolution temporal examinations of trees, aquatics, and Coleoptera from the same strata, as well as precise 14C dating of the sediments and macrofossil remains contained within them. For the time being, organisms migrate in response to climate change (Huntley and Webb, 1989), and that their actual migration rates are comparable to the potential rates required of them during deglacial warming, which is thought to be representative of the most rapid climate changes in recent geological history. It's also worth noting that there's some debate about whether longer-lived sessile organisms have a migrational lag, and that current knowledge of dispersal, vegetation dynamics, and population growth suggest that the realized migration rates of trees during déglaciation may be close to the maximum that such organisms could achieve.

Individualism among species is a common feature of the sets of isopoll and isochrones maps generated for various geographical locations. While plant ecologists have widely accepted the individualistic response of taxa to spatial variations in their current environment since the work of Whittaker (1954) and Curtis and McKintosh (1951), palaeoecologists have only recently recognized the individualism of response to temporal environmental changes. Pollen maps illustrate that taxa migrate at different times, speeds, and directions, and that no two taxa have distribution and abundance patterns that consistently correspond in space and time (Davis, 1983; Webb, 1981; Huntley and Birks, 1983; Webber al., 1983; Huntley, 1988, 1989; Huntley and Webb, 1989). Individualism in reaction has a lot of significant. Communities arise as transient assemblages of species whose constituents will dissociate as they respond individually to environmental change and form new associations under new environmental conditions, as detailed below. Even if such qualitative shifts do occur, individualism in responding has several key ramifications. Communities arise as transient assemblages of species whose constituents will dissociate as they respond individually to environmental change and form new relationships under new conditions, as detailed below. Even if such qualitative changes in community composition do not occur,

quantitative changes in relative abundance of component species do occur, which can alter the community's structural and functional characteristics. As a result, neither the history nor the evolution of communities should be discussed because they are temporary associations of taxa, each of which is responding to changes in the environment in an individualistic manner, and each of which is likely to be sensitive to different environmental variables. Second, because certain former habitats are likely to have differed from current ones, some previous communities or assemblages of species must be expected to differ from those found now. This is demonstrated by so-called "4 no-analogue" fossil assemblages, such as pollen spectra (Huntley, 1990), vertebrate remains (Stuart, 1982; Graham and Grimm, 1990), or Coleoptera remains (Graham and Grimm, 1990). (Coope, 1977). Overpeck et al. (1985) investigated quantitative measures of degree of analogy and applied them to the eastern North American pollen record. Anderson et al. (1989) used similar approaches to study the pollen record from northwestern North America, and Huntley (1990) studied the European pollen record. Since 13000 bp, Huntley (1990) has created maps illustrating patterns in the degree of analogy at millennial intervals. Most post-glacial pollen spectra in Eastern North America had modern parallels, whereas in Europe, many recent post-glacial pollen spectra lack modern analogues. Huntley (1990) has examined the causes behind this discrepancy.

Maps of palaeovegetation, or any other historical communities, cannot be constructed using present-day vegetation units or communities due to the individuality of taxa's responses to environmental change. There have been a number of approaches to palaeovegetation mapping from pollen data (Huntley and Birks, 1983; Jacobson *et al.*, 1987), but they have all been subjective to some degree in terms of the species and/or isopolls to combine in order to map assemblages. Huntley (1990) has recently used multivariate classification to the whole time-space dataset of European pollen data represented at millennium intervals in a database derived mostly from Huntley and Birks (1983) and Peterson (1983) databases (1983). The classification yielded a set of 32 pollen spectra clusters that were not bound by spatial proximity or temporal coincidence. These clusters have been mapped for millennia, and the resulting maps can be thought of as palaeovegetation maps down to the formation level (Huntley, 1990). Only 18 of the 32 clusters mapped are represented at this time. The nature of the compositional changes in European post-glacial forest vegetation was later studied by Huntley (Huntley, 1990). The maps show a number of general characteristics of vegetation's response to climate change (Huntley, 1990). They also point to two aspects of European and eastern North American vegetation responses that are particularly important in light of future climate change concerns. (1) The persistence of no-analogue assemblages in Europe during the postglacial, in contrast to results from eastern North America (Overpeck *et al.*, 1985), suggests that European climate may be more sensitive to insolation and other changes, and thus more variable, than the climate of eastern North America (Huntley, 1990). (2) Major changes in atmospheric circulation, such as those seen during deglaciation, result in changes in broadscale vegetation pattern and community composition, which are documented in palynological records from both Europe (Huntley and Birks, 1983; Huntley, 1988) and eastern North America (Huntley, 1990).

Discussion

Pollen data from places on a continental or at least subcontinental scale was mapped and analyzed to illustrate how vegetation, the biosphere's most important component, responds to climate change. The preceding findings lead to six major general conclusions. (1) The majority of plants and, most likely, other organisms have not adapted to Quaternary climate variations by adaptive evolutionary modifications (Coope, 1977). Since the Tertiary, at least some taxa have showed no major change in their climate sensitivity (Huntley *et al.*, 1989). (2) When faced with Quaternary climate changes, most, if not all, taxa have responded by migrating (Huntley and Webb, 1989). (3) Trees' actual maximum migration rates (Davis, 1976; Huntley and Birks, 1983; Huntley, 1989) are comparable to the anticipated maximum migration rates needed to track deglacial warming. Many researchers believe that tree migrations lagged climate change during rapid deglacial warming because such rates are near to or even constitute the absolute maximum that trees are capable of (Birks, 1986; Pennington, 1986; Bennett, 2018). (4) Taxa responded to past climate changes in an individualistic manner (Davis, 1983; Huntley and Birks, 1983; Webb, 1981; Webb et al, 1983; Huntley, 1989; Huntley and Webb, 1989), which is similar to taxa's individualism in response to aspects of their current environment (Davis, 1983; Huntley and Birks, 1983; Webb, 1981; Webb (Whittaker, 1951, 1953). (5) As a result of individualistic migratory responses, communities and vegetative units arise as transient assemblages of species that dissociate and reassemble in new assemblages as climate changes. Past climates, unlike today's, produced communities unlike today's. (6) Major re-arrangements of atmospheric circulation, such as those that occurred during deglaciation, result in changes in broadscale vegetation patterns and the orientation of major vegetation gradients and ecotones, as well as quantitative and qualitative changes in the composition of plant communities (Huntley and Birks, 1983; Webb, 1988; Huntley, 1990). How useful are these findings for predicting how vegetation will react to future climate changes caused by the release of greenhouse gases into the atmosphere as a result of human activities? Many experts now believe that an increase in global average temperature of at least 2-5 degrees Celsius by the middle of the twenty-first century is likely to occur (Schneider, 1989; Houghton, Jenkins and Ephraums, 1990).

This is the largest shift in global mean temperature since the last deglaciation (i.e., since the rise of about 5 degrees Celsius between c. 15000 and 10000 years ago, which signaled the end of the last glacial period). As a result, evidence of the biosphere response to glacial warming can be used to help forecast the response to current warming. The rate of warming predicted for the next century, on the other hand, is expected to be between 10 and 100 times greater than the rate of deglacial warming. As a result, the biosphere will be responding to a rate of climate change that has never been seen before, at least in the recent geological past. Any indicator of the biosphere's ability to adjust to such rapid changes, whether positive or negative, will be extremely valuable. Given the facts presented above, the first unavoidable conclusion is that organisms would migrate in response to predicted climatic change. It is

also certain that they will do so in an individualistic manner, resulting in changes in the composition of communities and ecosystems. The amount to which they will be able to achieve this answer will be determined by a variety of things. In the case of trees, past maximum migration rates are thought to be close to the maximum rates feasible by these long-lived sessile creatures; some researchers assume that trees lagged behind deglacial climate changes due to migration rate constraints. As a result, most trees are thought to be unlikely to attain the migration rates required by predicted climate changes that are one to two orders of magnitude quicker than those seen during the last deglaciation (Davis, 1989; Huntley, 1990). Furthermore, all organisms will be forced to travel across landscapes that have been significantly transformed by human activity, and in which the habitats available to them are limited in size and fragmented (Huntley, 1991). This will put more restrictions on the amount of migration they may achieve. Many animals have had their populations significantly decreased by human activities, even in less-developed countries, and today only live in designated reserves. Although their migration may not be limited by the availability of habitat outside of the reserve areas in these cases, the legislative protection provided to many is limited to the reserves; any individuals moving outside the reserves as part of a migratory response will frequently face severe human persecution, effectively preventing their migration (Huntley and Webb, 1988; Huntley, 1991).

The prognosis for many organisms is currently bleak. If many trees are to survive, proactive actions to aid their migration in the face of future climate change may be required (Roberts, 1989; Huntley, 1991). Other animals whose small and fragmented populations limit their ability to disperse to what are frequently remote, small regions of suitable habitat may require the same artificial dispersal. Threatened taxa whose current survival is contingent on legal protection within designated reserves may only survive if their protection can be extended, allowing them to migrate to places that, in many cases, are not now protected. Few current reserves are large enough to accommodate significant migrations, and even fewer provide the option of altitudinal migrations rather than geographical migrations. If we wish to reduce the need for artificial dispersal, we must seek to integrate wildlife demands into our use of the environment rather than relying primarily on isolating them in limited designated reserves, in addition to extending legal protection to regions outside reserves. In addition, we must reassess our policy on the designation of such reserve areas (Hunter, *et al.*, 1988; Huntley, 1991). Reserves cannot be chosen only on the basis of the rarity of the creatures present inside their bounds; these organisms may migrate elsewhere in the future. Instead, in order to establish resiliency in our network of reserves, we must conserve as much land as feasible and as varied a range of physical habitats as possible. We must also place a larger emphasis on creating a connected network that facilitates migratory movements; so-called "wildlife corridors" will become increasingly important in the future and must be included in every structure or development plan. If such steps are not taken, many organisms will face extinction within the next one or two millennia if global climate change is not avoided (Roberts, 1989; Huntley, 1990). Even if strict measures to reduce greenhouse gas emissions are enacted in the near future, the return of the global system to equilibrium will require significant warming, which will induce significant migrations by many organisms (Schneider, 1989). If large-scale declines in the populations of many organisms and the extinction of others are to be avoided, policies that allow organisms to migrate will be required, regardless of future greenhouse gas emission regulations. Even if means are taken to encourage, if not artificially aid, organism migration, extinction of some species appears to be inescapable. Large-scale extinction is highly likely if these steps are not taken. If no measures are made to reduce greenhouse gas emissions, the number of extinctions will rise. It could become disastrous if potential positive feedbacks, such as those generated by the release of methane from hydrate deposits beneath permafrost zones and the oceans (Leggett, 1990), start to operate and accelerate the rate of climate change.

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