Neotropical vegetation responses to Younger Dryas climates as analogs for future climate change scenarios and lessons for conservation

V. Rull [a, *], T. Vegas-Vilarrúbia [b], E. Montoya [c]

[a] *Palynology and Paleoecology Lab, Institut Botànic de Barcelona (IBB-CSIC-ICUB), Pg. del Migdia s/n, 08038 Barcelona, Spain.*

[b] *Department of Ecology, Univeristy of Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain.*

[c] *Department of Environment, Earth and Ecosystems, Research Centre for Physical and Environmental Sciences, The Open University, Walton Hall, Milton Keynes MK7 6AA, UK.*

* Corresponding author. *E-mail address*: vrull@ibb.csic.es (V. Rull)

Abstract

The Younger Dryas (YD) climatic reversal (12.86 to 11.65 cal ky BP), especially the warming initiated at ~12.6 cal ky BP, and the associated vegetation changes have been proposed as past analogs to forecast the potential vegetation responses to future global warming. In this paper, we applied this model to highland and midland Neotropical localities. We used pollen analysis of lake sediments to record vegetation responses to YD climatic changes, which are reconstructed from independent paleoclimatic proxies such as the Mg/Ca ratio on foraminiferal tests and Eqilibrium Line Altitude (ELA) for paleotemperature, and grayscale density and Titanium content for paleoprecipitation. Paleoclimatic reconstructions at both highlands and midlands showed a clear YD signal with a conspicuous warming extending into the early Holocene. A small percentage of taxa resulted to be sensitive to these YD climate changes. Response lags were negligible at the resolution of the study. However, changes in the sensitive taxa were relevant enough to determine changes in biodiversity and taxonomic composition. Highland vegetation experienced mainly intra-community reorganizations, whereas midland vegetation underwent major changes leading to community substitutions. This was explained in terms of threshold-crossing non-linear responses in which the coupling of climatic and other forcings (fire) was proposed as the main driving mechanism. Paleoecology provides meaningful insights on the responses of highland and midland Neotropical vegetation to the YD climatic reversal. Biotic responses at both individual (species) and collective (assemblage) levels showed patterns and processes of vegetation change useful to understand its ecological dynamics, as well as the mechanisms and external drivers involved. The use of paleoecological methods to document the biotic responses to the YD climate shifts can be useful to help forecasting the potential consequences of future global warming. Due to its quasi-global character, the YD reversal emerges as a well suited candidate for providing useful insights of global scope by analyzing the corresponding biotic responses virtually at any geographical and biological setting.

Keywords: global warming; biotic responses; past analogs; Younger Dryas; paleoclimates; Neotropics

1. Introduction

This paper uses the "ecological paleoecology" approach and aims to show to the general paleoecological audience the usefulness of this approach in ecology and conservation using selected case studies. When analyzed from an ecological perspective, paleoecological records provide unique evidence not available from short-term ecological observations. In this way, ecological hypotheses involving long-term processes can be tested with empirical data instead of unwarranted assumptions and extrapolations (Rull, 2012; Rull and Vegas-Vilarrúbia, 2011). This paleoecological approach has been called ecological paleoecology, by contrast with other paleoecological approaches providing only descriptive paleoclimatic and paleoenvironmental reconstructions (Seddon, 2012; Rull, 2014). The usefulness of ecological paleoecology in the study of ecological patterns and processes such as latitudinal diversity gradients, climate-vegetation equilibrium, community assembly, ecological succession or biodiversity conservation, among others, has been recently highlighted (e.g. Willis and Birks, 2006; Willis et al., 2007, 2010; Birks, 2008, 2013; Vegas-Vilarrúbia et al., 2011; Rull, 2012; Rull et al., 2013). Ecological paleoecology may significantly increase the usefulness of paleoecology in the study of relevant global warming and biodiversity conservation issues thus enhancing the contribution of our discipline in the search for a better future.

Useful paleoecological information for ecological hypothesis testing is the empirical record of biotic responses to past climate changes, which can be used as analogs for improving predictions about the potential ecological responses to climatic change estimates for this century (Rull, 2012; Rull et al., 2013). Several potential past analogs for the ongoing and near-future global warming have been proposed (Willis and MacDonald, 2011). Most of these analogs are of the same magnitude, in terms of temperature change, as those predicted for the end of this century, but they usually involve much more time thus failing to reproduce current warming rates. However, faster warming occurred between the Younger Dryas (YD) cooling and the beginning of the Holocene, which seem to have occurred at similar rates and time scales to present warming, and has been proposed as one of the best paleoanalogs available so far (Cole, 2009; Vegas-Vilarrúbia et al., 2011; Willis & MacDonald, 2011). The YD cold reversal has been dated between 12.86 and 11.65 cal ky BP in the Greenland ice cores (Rasmussen et al., 2006), and was preceded by the Bølling/Allerød (B/A) interstadial, and followed by the Early Holocene Warming (EHW) (Fig. 1). Both B/A-YD and YD-Holocene transitions occurred at centennial scales which in paleoclimatology, are usually considered as abrupt or rapid shifts (Alley et al., 2003).

This paper uses the YD model as a past analog in the study of two Neotropical Venezuelan localities situated in the Andean highlands, around 4000 m elevation, and the Gran Sabana (GS) midlands, around 1000 m elevation. The study is focused on relevant ecological questions about: 1) the species that are sensitive or insensitive to YD climatic changes, 2) their response types and lags in relation to the drivers and ecological mechanisms involved, 3) potential changes in taxonomic composition and biodiversity due to climatic forcing, 4) eventual differential responses according to elevation, environmental setting and vegetation types, 5) possible non-linear and threshold responses, and 6) the potential for future predictions and for the optimization of conservation strategies. These types of questions have been considered especially relevant when using paleoecological data in ecological hypothesis testing and model validation (e.g., Davies and Bunting, 2010; Seddon et al., 2014), an approach that is gaining support in northern temperate areas but is still in its infancy in other regions, including the Neotropics.

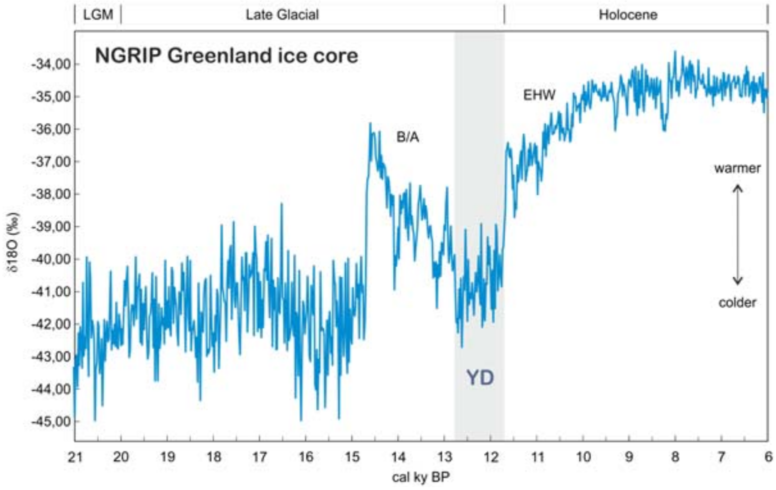

Figure 1. Late Glacial climatic trends as recorded in the NGRIP Greenland ice core. LGM – Last Glacial Maximum, B/A – Bølling/Allerød interstadial, YD – Younger Dryas, EHW – Early Holocene Warming. Raw data from Rasmussen et al. (2006).

2. YD climates in northern South America

In northern South America, the YD climatic reversal has been documented, well dated and quantified in climatic terms, in lake sediments from the Andean highlands (Van der Hammen & Hooghiemstra, 1995; Van't Veer et al., 2000; Groot, et al., 2011); Stansell et al., 2010) and in marine sediments from the Cariaco Basin (Fig. 3) (Hughen et al., 2000; Haug et al., 2001; Lea et al., 2003). At both sites, the YD was characterized by cold and dry climates (Fig. 2), which coincides with speleothem paleoclimatic reconstructions from the Amazon Basin (Cheng et al., 2013) suggesting trends of more regional amplitude.

However, a closer look at the climatic trends reveals some differences between the Andean and the Cariaco records. The Cariaco trends are a better match to the changes recorded in the Greeland ice cores. Indeed, in Cariaco, both B/A-YD cooling and YD-

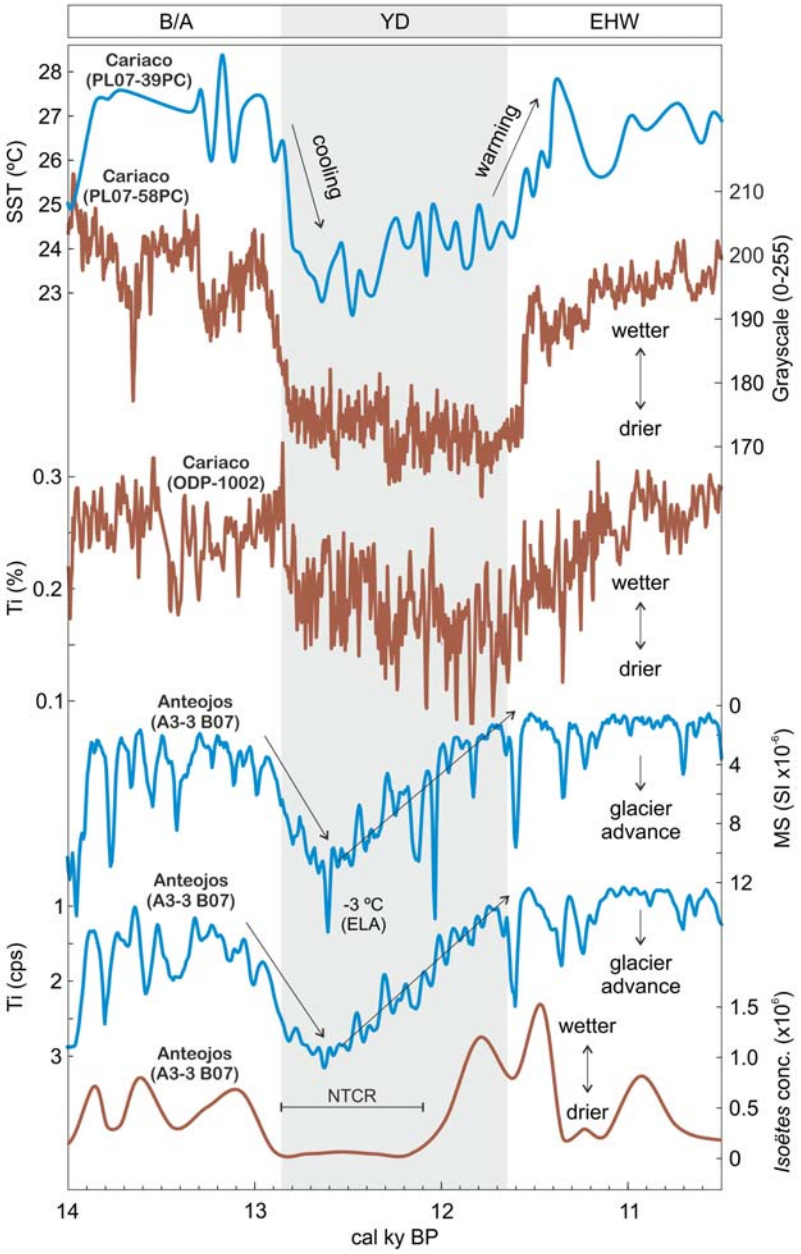

Figure 2. Summary of climatic trends during the YD in northern South America using selected records from the Cariaco Basin (cores PL07-39PC, PL07-58PC and ODP-1002) and the Mérida Andes (Lake Anteojos, core A3-3 B07). B/A – Bølling/Allerød, YD – Younger Dryas, EHW – Early Holocene Warming, NTCR – Northern Tropical Climatic Reversal, ELA – Equilibrium Line Altitude.

Holocene warming occurred in a few centuries, with an intermediate phase (~1000 years) of stable cold climates covering most of the YD. Contrastingly, the Andean records show a different pattern consisting of a rapid cooling (but slightly less abrupt than in Cariaco) attaining a thermal minimum (3 ºC below than average present temperatures, as estimated by past ELA reconstructions by Stansell et al., 2010) around 12.65 ky BP, followed by a more gradual warming of approximately 1000 years until the beginning of the Holocene (Fig. 2). Regarding precipitation and the precipitation/evaporation (P/E) balance, the Cariaco records show patterns similar to temperature, the only difference is that the Ti curve shows a more gradual precipitation increase than the grayscale record in the YD-Holocene transition. In contrast, the Andean records indicate that drier climates did not extend over the whole YD but only during the so called Northern Tropical Climate Reversal (NTCR) (Stansell et al., 2010), extending from ~12.9 to ~12.1 ky BP. A relatively abrupt P/E increase began around 12 ky BP extending to the early Holocene.

3. Study sites

The study sites (Lake Anteojos in the highlands and Lake Chonita in the GS midlands) are located in Venezuela, in the northernmost part of South America, between the Caribbean Sea to the north and the Amazon Basin to the south (Fig. 3).

3.1. Site description

Lake Anteojos (8° 32′ 18″ N, 71° 4′ 25″ W; 3920 m elevation) is a high-mountain lake situated at the Mérida Andes, the northernmost part of the Andean range. The lake is situated on a glacial cirque that is currently ice free (today, the snow line is abobe 4700 m) but was covered by ice during the LGM. Mean annual temperatures are around 3 ºC with low seasonal variations of 1-2 ºC, but high daily oscillations up to 30 ºC. Freezing occurs about 50 days per year. There is also an altitudinal dependence of temperature, which decreases at an average rate of -0.6 ºC/100 m elevation. Total annual precipitation is of 1550 mm with a short dry season (<60 mm/month) between January and March. The lake is ~900 m above the upper forest limit (~3000 m) within páramo vegetation, the highest biome of the northern Andes. The páramo is an open vegetation type dominated by columnar rosettes of several *Espeletia* (Asteraceae) species, grasses and cushion plants. Some patches of *Polylepis sericea* (Rosaceae) dwarf forests occur around the lake, on protected sites (Stansell et al., 2010; Rull et al., 2010b). The aquatic vegetation of lake shores is called azonal, as it is related to local moisture conditions, rather than to the general vegetation features arranged in an altitudinal pattern (Berg & Succhi, 2001). Human activities such as agriculture and cattle raising are, and have been historically, hindered by climatic conditions but tourism is presently active at the lake catchment.

Lake Chonita (4° 39′ 0” N, 61° 0′ 57” W; 884 m elevation) lies on the GS midlands of the Venezuelan Guayana region. The climate is warm and humid, with annual average temperatures of ~21 ºC and total annual precipitation values around 1600-1700 mm, with a weak dry season between December and March. The lake is on a floodplain characterized by extensive treeless savannas dominated by C_4 grasses (mainly *Trachypogon* and *Axonopus*) intermingled with highly diverse gallery forests along water courses. A special type of vegetation called “morichal”, consisting of monospecific palm stands of *Mauritia flexuosa*, grow around the lake on watersaturated and flooded soils. At present, the savannas and savanna-forest ecotones are usually burnt by humans thus contributing to savanna expansion at the expense of forests. The available paleoecological evidence suggests that present-day fire practices began around 2000 years ago (Montoya et al., 2011a, b; Montoya & Rull, 2011).

3.2. Regional climatic setting and vegetation dynamics

In northern South America, the main climatic parameters considered in this study, namely temperature and precipitation, are controlled by a variety of atmospheric mechanisms. Indeed, while annual average temperatures show a significant negative correlation with elevation, precipitation is largely controlled by the seasonal migration of the Intertropical Convergent Zone (ITCZ) (Poveda et al., 2006). The ITCZ is a low-pressure tropical belt of maximum cloudiness and rainfall, and its position is determined by insolation and the convergence of the northeast and southeast tropical trade winds (McGregor and Nieuwolt, 1998). During the austral summer (December to March), the ITCZ is located over the Amazon basin, around 15˚ S, whereas during the boreal summer (June to September), the ITCZ migrates to the north, reaching the southern Caribbean coasts, around 10˚ N (Fig. 3). As a result, two precipitation regimes exist: a continuous wet zone near the equator, and a zone with a dry season north of the equator. The localities of this study lie in the northern area, where the dry season extends from December to March, when the ITCZ is in its southernmost position.

Concerning vegetation dynamics, previous studies suggest that temperature (notably average annual temperature) was the main environmental driver in high-mountain areas, especially in the Andes. Moisture and CO_2 atmospheric concentration (CO_2^{atm}) have also been suggested to be significant drivers of change (Bennett & Willis, 2000; Groot et al., 2011). Temperature controls the altitudinal distribution of plants and their communities, as well as their eventual vertical displacements over time (Rull et al., 2005; Polissar et al., 2006; Rull, 2006). In the GS midlands, precipitation and available moisture, as expressed by the Precipitation/Evaporation (P/E) balance, have been proposed to have been more decisive than temperature for vegetation dynamics (Montoya et al., 2011a, b, c). The influence of human activities on vegetation dynamics seem to have been minimal in the Mérida Andes until the arrival of Europeans in the 15th century (Rull, 2006). In the GS, on the contrary, human influence, especially fires, has been proposed as one of the main drivers of vegetation change during the last 2000 years (Montoya and Rull, 2011; Montoya et al., 2011b).

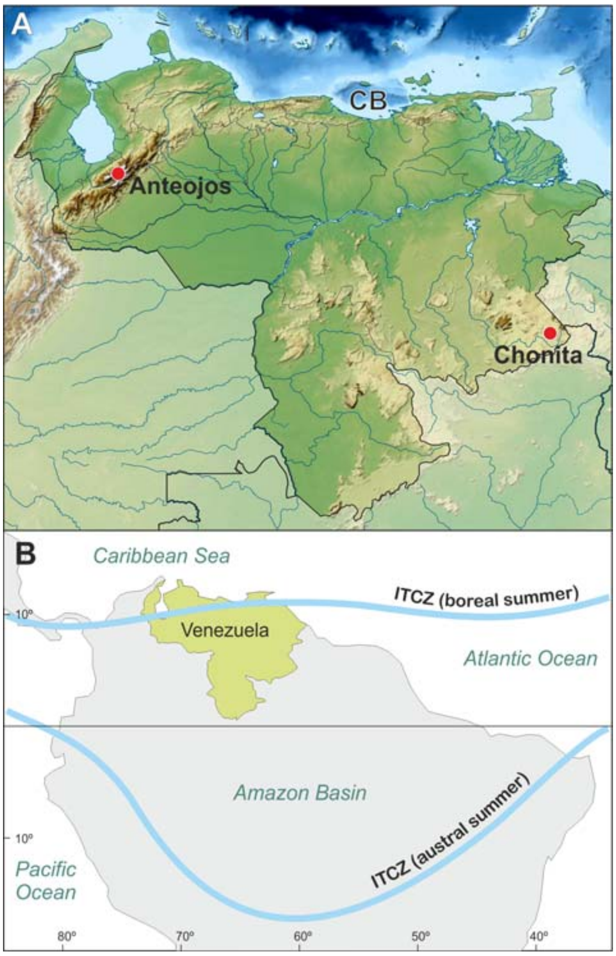

Figure 3. A) Topographic map of Venezuela indicating the sites studied and the Cariaco Basin (CB), which paleoclimatic records are used as reference. B) Map of northern South America indicating the seasonal migration of the Intertropical convergent Zone (ITCZ), which determines the precipitation regimes (see text). Redrawn from Rull et al. (2010a).

3. Methods

Key selected paleoclimatic and paleoecological records from the sites described were used to assess ecological responses to YD climate shifts. Independent paleoclimatic and paleoecological proxies were selected in order to avoid circular reasoning.

3.1. Paleotemperature proxies

Paleotemperature proxies were based on the Mg/Ca ratios of foraminiferal tests from the Cariaco Basin and the estimates of and the Equilibrium Line Altitude (ELA) from the Mérida Andes. Paleoprecipitation proxies were grayscale density (Cariaco), the Titanium content of sediments (Cariaco and Mérida Andes) and the concentration of spores from the aquatic pteridophyte *Isoëtes* (Isoëtaceae). All of these records were rebuilt from raw data and reprocessed according to the specific purposes of this study. Raw data were obtained from our own databases (Andean and GS lake cores) or were downloaded from public databases (Cariaco marine cores) available at the NOAA National Climatic Data Center (http://www.ncdc.noaa.gov/paleo/).

It has been demonstrated that the Mg/Ca relationship in foraminiferal tests is linked to temperature, as higher temperatures favor the incorporation of Mg while Ca remains relatively constant. Therefore, this ratio can be used as a paleotermometer when properly calibrated (Lear et al., 2002). In Cariaco, previous calibrations using modern samples showed that Mg/Ca values in the shells of the foraminifer *Globigerinoides ruber* could be converted to average annual Sea Surface Temperatures (SST) with high statistical reliability, by means on a simple logarithmic expression [SST = ln(Mg/Ca/0.38)0.09] (Lea et al., 2003). The ELA is the altitude at which snow melting and accumulation are equal. This point varies according to average annual temperatures, as warmer climates determine lower ELAs than colder climates. Paleo-ELAs can be reconstructed and mapped from glacier geomorphology, which allows estimating paleotemperatures using the adiabatic lapse rate. In the Mérida Andes, the YD ELA was reconstructed using aerial photos and paleotemperatures were reconstructed using the present-day temperature decrease with altitude (-0.6ºC/100 m elevation) (Stansell et al., 2010). In these highland environments, the Magnetic Susceptibility (MS) of lake sediments can also be used as an indirect climatic measure as it allows reconstruction of glacier advances, which is strongly linked with temperature drops. Indeed, increases in MS indicate higher input of clastic materials from the catchment into the lake, which is indicative of increased erosion by glacier advances (Stansell et al., 2010).

In laminated sediments, individual seasonal laminae can be identified by means of image analysis using the 8-bit photographic scale of 256 gray tones (0-255) (Ortiz and O'Connell, 2004). In Cariaco, this procedure was especially useful because of the light-dark alternation of seasonal layers. Trends towards darker grays imply the prevalence of terrigenous inorganic sediments transported from the continent, which is characteristic of wetter climates, when the ITCZ is located in the south; whereas lighter grays indicate greater contribution of *in situ* productivity, which occurs under rainy climates, when the ITCZ is over the site and upwelling is favored. The titanium record, for which the continent is the main source, has a similar behavior. Higher Ti content (measured as percentage) is linked to higher terrigenous input and, therefore, wetter climates, while lower Ti values indicate low continental runoff and drier climates (Martínez et al., 2007). In the Andean highlands, the Ti sedimentary content (measured as counts per second) is directly related to glacial erosion; hence, higher Ti values indicate increased catchment erosion due to glacier advance (Stansell et al., 2010). The amount of *Isoëtes* spores per cm^3 of sediment (concentration) was used as a proxy for water level change in Lake Anteojos (Mérida Andes). This pteridophyte is frequent along Andean lake shores, where it lives submerged down to the depth of light penetration. The occurrence of *Isoëtes* is only dependent on the existence of inundated conditions and independent from the characteristics of surrounding vegetation. Therefore, its absence is indicative of non-flooded local environments due to dry climatic conditions characterized by low P/E ratios (Rull et al., 2010b).

3.2. Paleoecological proxies

Past vegetation reconstructions were based on pollen analysis. Since its discovery, more than a century ago, pollen analysis of sediments has been widely used to reconstruct past vegetation dynamics. At present, the degree of maturity attained by this discipline makes it one of the more robust tools for paleoecological purposes (Birks and Birks, 1980; Faegri et al., 1989; Bennett and Willis, 2001). This study uses the raw pollen data from Rull et al. (2010b), from the same core of Stansell et al. (2010), for the Mérida Andes and Montoya et al., (2011a) for the Gran Sabana. In the GS, microscopic charcoal was used as proxy for fire incidence (frequency and/or intensity), but the origin of these fires, either natural or anthropogenic, is still a matter of discussion (Montoya and Rull, 2011, Rull et al., 2013). Diversity indices followed Pielou (1969). The Shannon-Weaver index (H) was chosen because it considers both taxa richness (R) and equitability or evenness (E), estimated by the ratio H/Hmax, where Hmax is the hypothetical H for a sample with the same richness but all its components evenly distributed. Pollen diversity is not considered a reliable measure of actual plant diversity but their trends in time use to be consistent and comparable (van der Knaap, 2009). The software MVSP 3.13q (http://www.kovcomp.co.uk/mvsp/index.html) was used for all these calculations.

4. Results: vegetation responses

4.1. Andean highlands

In the Mérida Andes, pollen analysis of Lake Anteojos sediments revealed conspicuous changes in the composition of both montane forests and páramo vegetation, the biome situated between the Upper Forest Line (UFL) (~3200 m) and the snowline (~4700 m), as a response to the YD climatic reversal (Rull et al., 2010b). According to these previous results, the more sensitive taxa to the YD reversal were Poaceae, Astearaceae, *Polylepis* and *Podocarpus* (Rull et al., 2010b). It should be stressed that sensitivity to climate change is considered here in the specific context of the coring site, not in absolute terms. Poaceae, Asteraceae and *Polylepis* are elements typical of the páramo biomes, whereas *Podocarpus* grows in the uppermost layers of the montane forests close to the UFL, in the study area. The other 30 taxa showed remarkably smaller changes. All the sensitive taxa, except Asteraceae, reacted immediately (considering the average time resolution of the study, which is 170 years) to the B/A-YD cooling/drying, *Podocarpus* and *Polylepis* showed an abrupt decrease while Poaceae rapidly increased (Fig. 4). Asteraceae did not respond until some centuries after, when minimum temperatures were attained. As stated before, the YD-Holocene warming was relatively gradual in the Andean highlands, whereas moisture increase was more abrupt and occurred before the YD-Holocene boundary, at the end of the NTCR. *Polylepis* paralleled the warming trend while Poaceae exhibited an inverse, but equally gradual response. Asteraceae abruptly decreased at the end of the NTCR and initiated a gradual increase during the EHW. *Podocarpus* did not react to either post-NTCR or the YD-Holocene warming, remaining at its lower values attained during the YD temperature minimum and showing a conspicuous response asymmetry with respect to the YD climatic reversal.

Concerning diversity, H did not show any conspicuous change but it experienced a gentle decrease, attaining a minimum around the middle of the YD followed by a slight and sustained increase until the early Holocene (Fig. 4). The H minimum coincided with minima in Poaceae and maxima in Asteraceae and *Podocarpus*. During the YD, oscillations in R follow similar, though larger, variations as H: both increased when temperature started to increase and decreased to their minimal values with the ensuing moisture decline. Equitability (H/Hmax) followed somewhat opposing trends.

4.2. Gran Sabana midlands

In this case, the sensitive taxa were Poaceae, the dominant taxa of the GS savannas, and a group of tree/shrub taxa characteristic of GS shrublands (*Miconia*, *Bonyunia*, *Myrsine*,

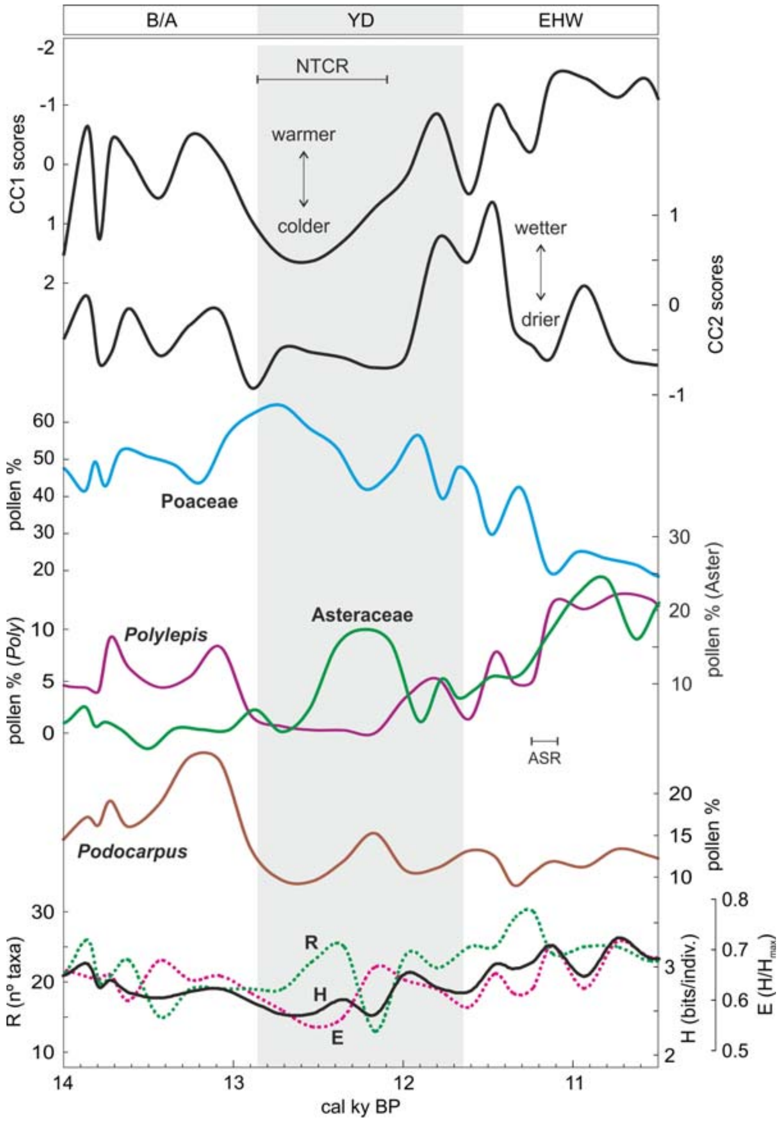

Figure 4. Comparison of paleoclimatic trends, pollen percentages from sensitive taxa and pollen diversity indices in Lake Anteojos.

Marcgraviaceae, *Myrsine* and *Odontadenia*). As in the case of the Andes, these taxa were found to be sensitive to the YD climatic shift. In the GS midlands, no independent paleoeclimatic records are available for comparison with the vegetation indicators. Instead, the Cariaco paleoclimatic trends, which are considered reliable expressions of regional climatic trends (Haug et al., 2001), were used as the paleoclimatic reference.

The studied sequence is barren of palynomoprhs until ca. 12.3 ky BP (Montoya et al., 2011a), which hinders analysis of the vegetation response to the YD cooling. However, the period in which both magnitude and rates of climatic change seem to be similar to the projected global warming for this century are in the upper part, where palynological data are available. In this case, all taxa showed a rapid (average sample resolution 98 years) and conspicuous reaction to the YD-Holocene warming; all of them except Poaceae decreased and most disappeared at the YD/Holocene boundary (Fig. 5). However, this fact cannot be attributed only to the temperature increase because fire incidence, represented by charcoal influx, shows a similar increase. A maximum in fire incidence was recorded at the end of the YD, when temperature was rising and moisture showed minimal values. The ensuing fire decrease did not produce any reaction in the taxa analyzed but another sudden and short maximum coincided with a similar Poaceae decline, during a minor temperature and moisture decrease. Among shrubs, *Myrsine* showed a slightly different behavior during the YD, as it increased and attained a maximum around 12 cal ky BP, whereas the other shrubs were already decreasing. From this point *Myrsine* followed the same trends than other shrubs.

H also decreased during the YD-Holocene warming (Fig. 5). In contrast with the Andes, this decrease is more related to E than to R. Indeed, R was relatively high until about 11 ky BP, where the sudden fire increase mentioned before took place, at the same time that temperature and moisture increased. From this point, R initiated a fluctuating trend.

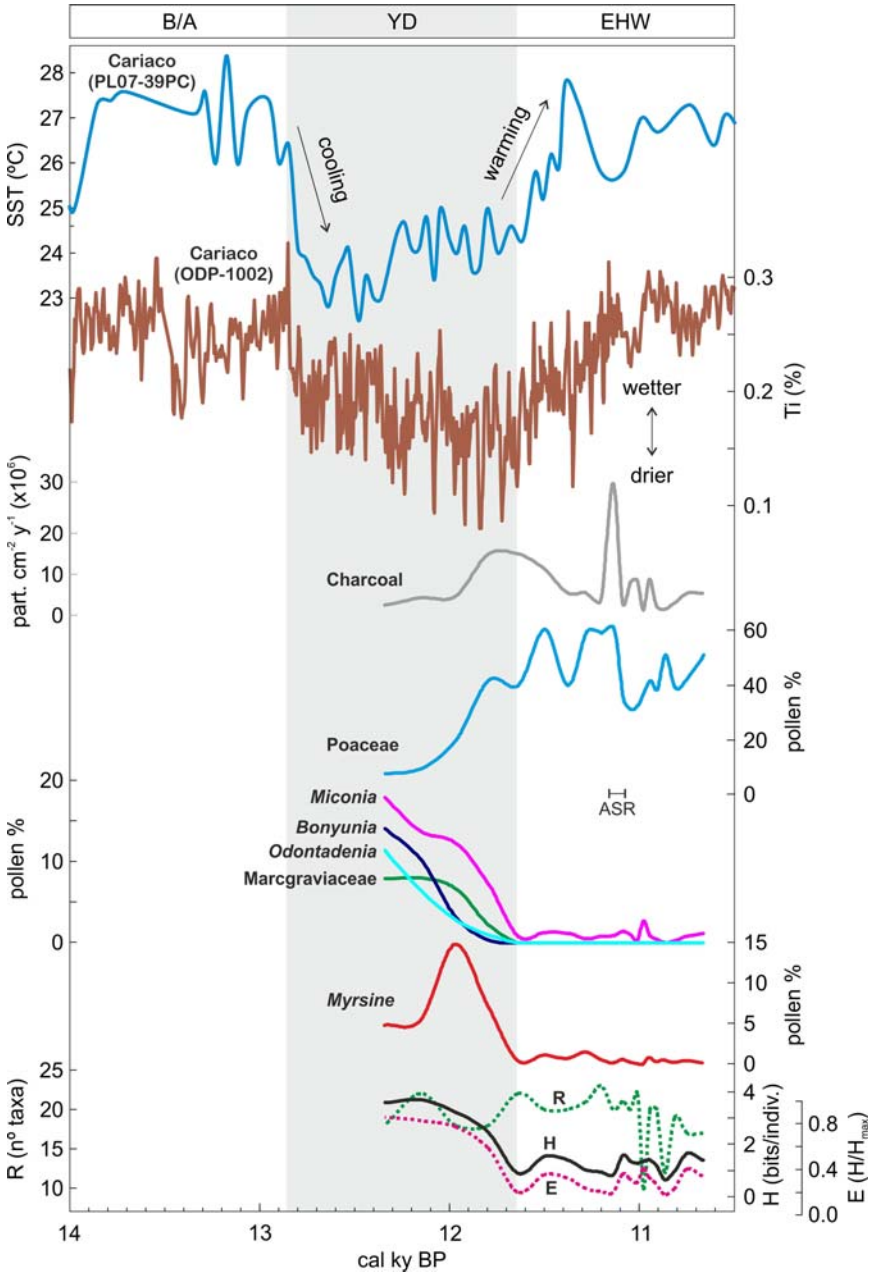

Figure 5. Comparison of paleoclimatic trends for Cariaco basin, pollen percentages from sensitive taxa and pollen diversity indices in Lake Chonita. SST and Ti curves according to Lea et al. (2003) and Haug et al. (2001), respectively.

5. Discussion and conclusions

5.1. Sensitive species

A general observation is that neither Andean nor GS vegetation responded collectively to the YD-Holocene climatic trends, only a small percentage of taxa (10-15%) proved to be sensitive to climate change. Ideally, sensitive taxa should be identified at species level but this is not always possible using only pollen. Fortunately, local and regional studies documenting in detail the flora and vegetation of both regions are available thus contributing to strengthening taxonomic resolution. Indeed, these studies have contributed to identify a number of species by their pollen, which otherwise could only be identified at genus or family level.

In the Laguna Anteojos area, the genus *Podocarpus* is represented by *P. oleifolius*, which dominates the uppermost forest ecotone up to 3200 m elevation (Berg and Suchi, 2001). *Polylepis sericea*, the only species of this genus living in the Venezuelan Andes, dominates in small and discontinuous forest patches within the páramo belt between about 3500 and 4300 m elevation, growing mostly on rocky debris (Monasterio, 1980). Concerning Poaceae and Asteraceae, despite some worthy attempts (Salgado-Labouriau, 1982; Salgado-Labouriau and Rinaldi, 1990), pollen identification at genus or species levels is still problematic. However, comparisons with the local flora of the study area may provide more detailed information. The more abundant grasses around the Anteojos lakes are *Aciachne acicularis* in the páramo and *Festuca tolucensis* in the superpáramo. Therefore, it would be expected that most of the Poaceae pollen found in the sediments correspond to these two species. However, the high dispersion power of grass pollen, in general, suggests that other species from the current regional flora could be present, as well. In the case of Asteraceae, usually pollinated by insects, the dispersion power of their pollen is lower and it can be assumed that most of the pollen recorded in lake sediments correspond to local species growing around the lake. The more characteristic elements of the páramo landscape are the columnar rosettes of the Compositae genera *Espeletia* and *Coespeletia* (Berg and Suchi, 2001).

Bonyunia minor is a shrub or a small tree living on savannas, shrublands and forest edges from 100 to 1450 m elevation (Grant, 2009). In the GS, this species dominates peculiar type of shrublands growing on ferrugineous soils restricted to the study area of this paper. *Miconia ciliata* is a minor element in the same shrub formations but another species of the same genus, *M. stephananthera*, also occurs in palm savannas growing on lake shores and along water courses (Huber, 1994, 1995). Concerning *Odontadenia*, the only reported species for the GS region is *O. puncticulosa*, a liana from evergreen forests, sometimes in secondary growth and forest edges (Hansen, 1995). *Myrsine* is a genus of small trees or shrubs with several species widespread across the GS (Pipoly and Ricketson, 2001). Marcgraviaceae is a family of climbing shrubs or woody vines, whose species are common in the GS montane rainforests (Dressler, 2001). As in the Andes, it is expected that grass pollen may have a significant regional signal but it could be assumed that most of this pollen in sediments is produced by the two major savanna dominants, namely *Trachypogon plumosus* and *Axonopus pruinosus* (Huber, 1995).

These observations contribute to improve taxonomic resolution but, in the future, it would be desirable to incorporate more specific proxies as for example DNA characterization -not only from pollen cytoplasm but also from bulk sedimentary organic matter- and chemical biomarkers, two approaches that have developed spectacularly in the recent decades (Jansen et al., 2013; Hofreiter et al., 2008). Previous experiences on aquatic sediments demonstrate that most of the sedimentary DNA is extracellular and that the analysis of this material is useful to identify species and to record their relative abundance (Bisset et al., 2005; Boere et al., 2009, 2011; Coolen et al., 2009).

5.2. Response types, drivers and potential ecological mechanisms

The fact that most of the taxa represented in the pollen diagrams analyzed proved to be insensitive to the YD and early Holocene climatic shifts may suggest that these environmental changes were insufficient to overcome the range of climatic tolerance of the taxa involved. In other words, these taxa would be considered tolerant to YD-Holocene climatic variability. The time period involved is too short to account for evolutionary changes leading to adaption (Vegas-Vilarrúbia et al., 2011). Most sensitive species displayed a decreasing trend during the YD-Holocene transition, especially in the GS. The scarcity of species with positive responses is remarkable (Table 1). Exceptions to this rule are the increases in *Polylepis* and Asteraceae in the Andean site, and Poaceae in the GS site.

The immediate decrease of *Podocarpus* coeval with the B/A-YD cooling is likely due to its intolerance to extreme cold conditions. *Podocarpus oleifolius*, the species living in the study area, is a common tree of the upper Andean forest, where it forms dense forests up to the UFL (Berg and Suchi, 2001). This species does not reach higher elevations due to its inability to support freezing conditions (Cavieres et al., 2000), which explains the absence of *P. oleifolius* in páramo vegetation where freezing temperatures are present every night (Azócar and Monasterio, 1980). Another important requirement for *P. oleifolius* is high environmental moisture which, at the Andean UFL, is furnished by dense and frequent mists (Cavieres et al., 2000). The continuous presence of a background signal (~10%) of *Podocarpus* pollen is likely due to the contribution of long-distance sources. The high buoyancy of this pollen allows transport over long distances reaching the highest peaks (Rull, 2006). The lack of apparent response of *Podocarpus* to the YD-Holocene warming is surprising because both

Table 1. Responses of sensitive species to the environmental drivers considered.

	Temperature and moisture decrease	Temperature and moisture increase	Fire increase
Abundance increase	Poaceae (Andes)	***Polylepis*** Asteraceae Poaceae (GS)	Poaceae (GS)
Abundance decrease	***Polylepis*** *Podocarpus*	Poaceae (Andes) *Miconia* *Bonyunia* *Odontadenia* Marcgraviaceae *Myrsine*	*Miconia* *Bonyunia* *Odontadenia* Marcgraviaceae *Myrsine*
No response	Asteraceae	*Podocarpus*	-

temperature and moisture conditions were presumably suitable for its development and an increase to values like those recorded for the B/A may be expected. A similar situation was observed in another locality from the Venezuelan Andes, where the pollen of *Podocarpus*, together with the spores of other UFL elements (tree ferns of the family Cyatheaceae), experienced a significant decrease at the beginning of the YD and did not get back to their B/A values anymore throughout the Holocene (Rull et al., 2005). This was interpreted in terms of the changing intensity of upslope winds but this remains unproved, so far. Poaceae also displayed a decreasing trend during the YD-Holocene warming. *Aciachne* and *Festuca* species might be expected to be present in the pollen assemblage but it is also possible that the grass composition of the YD páramos were different from today due to the influence of CO_2^{atm} variations on the altitudinal distribution of C_4 plants. Working in the Colombian Andes, Boom et al. (2001, 2002) showed that the reduced CO_2^{atm} during the last LGM favored the dominance of C_4 Poaceae and Cyperaceae over the modern C_3 taxa in the páramos. During the Younger Dryas, CO_2^{atm} was intermediate between LGM and present levels (Skinner et al., 2014) and, therefore, the proportion of C_3 and C_4 plants would have been different from both LGM and present times. In this framework, the maintained decrease of Poaceae pollen during the YD-Holocene transition would be attributed to a decline of C_4 grasses, which is consistent with the continual increase of CO_2^{atm} (Skinner et al., 2014).

As stated above, *Polylepis sericea* dwarf forests are restricted to favorable microenvironments commonly associated with rocky substrates and water bodies, which provide warmer and wetter environments than those available in the surroundings thus alleviating periglacial effects (Monasterio, 1980). Owing to its low dispersion power, the pollen of *Polylepis* has been considered a good indicator of the local presence of dwarf forests dominated by this species (Rull, 2006). The absence of *Polylepis* pollen around Lake Anteojos during most of the YD and its recovery around 12 cal ky BP could be explained by a combination of temperature and moisture shifts. Some authors have proposed that, in the Venezuelan Andes, a critical phase for *Polylepis sericea* establishment is the seedling to sapling transition, which is constrained by the frequency of extreme low temperatures during freezing nights (Hoch and Körner, 2005; Rada et al., 2009). It has been documented experimentally that freezing temperatures induce irreversible cell damage by ice crystal formation in saplings, whereas adult trees are capable of resisting ground temperatures around -6ºC (Goldstein et al., 1994; Azócar et al., 2007). Extreme below-zero temperatures would have been much more frequent during the YD than today and this could have hampered the establishment of *P. sericea* forests. However, temperature alone cannot explain why these forests did not establish after 12.6 cal ky BP, when temperatures began to rise. Indeed, *Polylepis* did not recover until ca. 12 cal ky BP when moisture conditions returned to pre-YD values thus suggesting a significant role for moisture in the re-colonization of Lake Anteojos catchment by *Polylepis*. During the early Holocene, however, a pronounced and abrupt moisture decrease peaking around 11 cal ky BP did not result in a *Polylepis* decline but, on the contrary, in an increase parallel to the rising temperature trend. It is possible that, once established, *Polylepis* forests were less susceptible to further temperature and moisture changes due to a buffering action of canopy, which may be supported by present-day observations showing that the frequency of nights with freezing soil temperatures is significantly higher in the open páramos than in the *Polylepis* understory (Rada et al., 2009). Rather than a simplistic response to either temperature or moisture variations, the dynamics of *Polylepis* forests seem to be linked to complex interactions between these two climatic parameters, possibly influenced by the successional stage, as well.

In the case of Asteraceae pollen, mostly representing *Espeletia*, the YD-Holocene increase also follows the temperature trends but, in this case, the intra-YD patterns were remarkably different. Contrarily to *Polylepis*, this pollen conspicuously increased during the YD, peaking around the middle of this reversal and sharply declined coinciding with the sudden 12 cal ky BP moisture increase. This pattern would suggest that Asteraceae pollen represents a species or a group of species favored by cold and dry climates, which is contradictory with the early Holocene trend, in which this pollen increases with temperature and is apparently unaffected by moisture changes. As the distinction of *Espeletia* species by means of pollen morphology is not possible, the occurrence of two or more of these species within the same pollen curve, with the YD species being a representative of the cold and dry periglacial zone, should not be dismissed. The vegetation of these extreme environments has been called superpáramo or desert páramo and is dominated by several species of the *Espeletia* complex (Monasterio, 1980). In the study area, *Coespeletia moritziana* and *C. timotensis* are characteristic of the superpáramo and have special adaptations to low temperatures and environmental dryness, such as succulent leaves totally covered by a dense network of cotton-like trichomes and a complex apical bud in which the growth meristem is protected from environmental variability by a dense “dome” of leaf primordia (Monasterio, 1979). At present, these species and the associated superpáramo vegetation grow at approximately 400-500 m above Lake Anteojos but paleoecological studies suggest that the lake was surrounded by superpáramo vegetation during the YD (Rull et al., 2010b).

The case of GS is different from the Andes as it involves an additional factor: fire. Today, anthropogenic fires are a common element in the GS ecological dynamics. Fires mainly start in savanna landscapes but they usually reach the forest-savanna ecotones resulting in a net savanna expansion at the expense of forest. The same pattern seems to have been occurring for the last two millennia during which the modern GS landscape has been shaped (Montoya and Rull, 2011; Rull et al., 2013). The charcoal record of the GS during YD-Early Holocene times is similar to the last two millennia and is among the first fire records obtained so far in the Neotropics, however, no evidence of human cultures exists for this period in the GS region, so far (Gassón, 2002). These fires started during the YD and peaked slightly before the YD-Holocene transition, coinciding with the driest climates of the period studied, at the beginning of the YD-Holocene warming. Whatever the origin of fire, such a climate would have favored vegetation ignitability and, hence, fire propagation. The coeval dramatic increase in Poaceae pollen suggests a phase of savanna expansion linked to fire increase, as occurs today. So far, this is the first record of savanna vegetation for the GS region (Montoya et al., 2011a). During the early Holocene, grasses maintained their values with some oscillations roughly parallel to the charcoal curve, independently of the climatic trends, which supports a potential role for humans in fire ignition and expansion. Therefore, the response of GS Poaceae to YD-Holocene climatic shifts was likely mediated by fire incidence that, in turn, was exacerbated by YD climates and, possibly, by early-Holocene human practices.

Besides Poaceae, all the other GS taxa significantly declined during the YD-Holocene warming. As stated above, all these taxa are characteristic of today's GS shrublands and/or forests, and a negative effect of either temperature or moisture (or both) increase on them would be hard to understand. In spite of the scarcity of autoecological studies on these taxa, some data suggest that increased moisture characteristic of the YD-Holocene warming would be favorable for their development and population expansion. For example, field observations reveal that *Miconia ciliata* is relatively drought-intolerant, as experimental irrigation improved photosynthetic rates and caused flowering and fruiting during the dry season thus spreading reproductive activity across the whole year, thus contributing to population growth (Fortini et al., 2003; Aragão et al., 2005). As in the case of Poaceae, with the available evidence, fire is the more plausible explanation. In this case, however, the first fire event that occurred at the end of the YD was enough to virtually remove these taxa from the Lake Chonita catchment, around which grassland savannas established and endured until the present (Montoya et al., 2011a, b). The ensuing Holocene fire events would have maintained or expanded the savanna vegetation by precluding forest recolonization (Montoya and Rull, 2011).

5.3. Response lags

Remarkably, response lags of sensitive taxa to temperature and moisture shifts were below sampling resolution. However, the time resolution of this study is not enough to know the actual response lags of the species involved. We now know that this lag is below 170 years in Lake Anteojos (Andes) and 98 years in Lake Chonita (GS) but a higher resolution study is required to attain more precision. High-resolution palynological studies for the time period considered here are absent in the Neotropics. Studies from northern Europe show that vegetation responded to YD climatic shifts without apparent lags (sampling resolution: 8-30 years) (Ammann et al., 2000). In the Cariaco basin, studies on other time intervals showing abrupt climatic changes (Heinrich events H3 to H6, ca. 70 to 30 ky BP), indicated also rapid vegetation responses, although exact time lags were not quantified (González et al., 2008). Also in Cariaco, a high-resolution study using plant biomarkers (alkanes from the cuticular leaf waxes) as proxies for vegetation change reported a lag of ~50 years between climate changes around the YD and vegetation responses (Hughen et al., 2004). A parallel high-resolution study of Cariaco YD sediments using pollen is worth conducting for comparison. According to the results of these studies, the minimum resolution required to estimate biotic responses to YD climatic shifts in Lake Anteojos should be of less than 50 years per sampling interval.

5.4. Changes in taxonomic composition

In the Andean locality under study, pollen assemblage change was measured using a dissimilarity index (Euclidean distance) between a surface sample representing the present and Lateglacial samples (Rull et al., 2010b). This index was low during B/A and EHW times and displayed its maximum values during the YD, peaking at 12.6 cal ky BP, coinciding with minimum temperatures. Sensitive taxa, notably *Podocarpus*, *Polylepis* and Poaceae, were primarily responsible for these changes in taxonomic composition likely due to altitudinal reorganizations of these taxa (Rull et al., 2010b). Therefore, YD páramos around Lake Anteojos were different –i.e., more grassy and, possibly, with a higher proportion of C_4 plants (Boom et al. (2002)- and devoid of dwarf forests- from the present ones. In other words, the YD climatic reversal did not caused a vegetation replacement but the reorganization of the existing vegetation components leading to a different state of the same community. The YD páramos came back to their former composition when the climatic drivers returned to their former values thus showing reversible character of this community shift. A recent study developed in the

Colombian Andes covering the same time interval shows similar results in terms of transient community changes owing to climatically-driven individual upslope and downslope migrations (Velásquez and Hooghiemstra, 2013). In the GS, vegetation changes were more drastic as the ligneous vegetation that dominated during the YD was totally replaced by a treeless savanna (Montoya et al., 2011a), likely by the combined action of climate and fire. However, it should be highlighted that the YD shrublands were different in composition from any other GS shrubland known today. Indeed, these ligneous communities have elements from different extant GS shrubland types but in a unique combination not occurring today (Montoya et al., 2011a). Therefore, in this study, two types of non-analog plant assemblages with respect to the present ones have been documented, one in which the same elements vary their relative abundances (Andes) and another that is physiognomically similar to present-day shrublands but is composed by a different taxonomic combination (GS region).

5.5. Biodiversity trends

In the Andes, diversity does not seem to have been significantly affected by the YD climatic reversal as shown by the hammock-like curve of the H index. Perhaps the more interesting observation is the opposite trend of R and E curves, indicating that the more taxa rich an assemblage is the less equitable are the relative abundances of these taxa. For example, a maximum of R occurred around the 12.6 cal ky BP temperature minimum but H was minimal because the assemblage was dominated by grasses (coinciding with the maximum dissimilarity with respect to modern páramo communities) causing an E decline. The situation is radically different shortly after, when the increases of Asteraceae and *Polylepis* heightened E but H did not recover because of a minimum in R. These changes are not linked to any evident climatic signal and their causes remain unknown. The subsequent warming determined a general ascending trend in H, R and E reaching their maximum values during the early Holocene. Therefore, the YD-Holocene warming stimulated both the taxonomic enrichment of the páramos and the equitability of their relative abundances thus increasing the ecological diversity. In the GS, the situation is different as the H trends run parallel to E variations. These two parameters exhibit a dramatic decline coinciding with the same trend in the ligneous elements and the YD charcoal increase. R remained at high values indicating that the removed shrubland taxa were replaced by others from savanna vegetation thus retaining the total number of taxa present. The decline in E was due to the absolute dominance of Poaceae once the treeless savannas replaced the former shrublands. R did not decline until ca. 11 cal ky BP when the fires commenced.

5.6. Responses according to elevation and vegetation types

Whether highland Andean páramos and midland GS shrublands and savannas responded in a different fashion to similar climatic shifts is the main question here. This issue can be only analyzed for the YD-Holocene warming because of the lack of palynological record in the GS during the B/A and the first part of the YD. As it has been noted previously, sensitive highland taxa reacted to temperature shifts but were poorly responsive to moisture variations (but see González-Carranza et al., 2011 for a contrasting situation in the Colombian Andes). In the GS, on the contrary, the coupled action of warming and drying seem to have been decisive for fire exacerbation thus causing larger vegetation changes involving community replacement. In addition, in the GS, a potential role for human disturbance through fire should not be dismissed. In the

Venezuelan Andes, on the contrary, human disturbance has been considered to be low until the European contact. Indeed, indigenous pre-Columbian populations seem to have been small, marginal and, as a consequence, of reduced ecological significance (Wagner, 1979). Therefore, the same climatic shifts have determined different biotic responses due to disparities in the biomes involved and also in eventual anthropogenic factors.

5.7. Non-linear and threshold responses

As noted before, intra-community reorganizations have been the main changes observed in the Andean site studied here as a consequence of the climatic shifts occurring around the YD reversal. Therefore, no threshold-crossing processes seem to have occurred during that time. In the GS region, however, the significant and relatively rapid replacement of shrublands by savannas could be a potential candidate for an ecological process involving positive feedbacks leading to thresholds beyond which changes are irreversible. This confirms previous observations by Rull et al. (2013), who consider the progressive savannization of the GS region as a process of this nature, with moisture and fire as the main drivers, and grassy biomass accumulation and soil degradation as the more likely thresholds. According to the results summarized by these authors, the coupling of aridity and anthropogenic fires determine the progressive reduction of forests and the expansion of savannas. Due to the high flammability of savanna vegetation, a positive feedback soon develops exacerbating landscape burning by fuel (i.e., flammable grasses) accumulation. Present-day ecological studies carried out in the GS have demonstrated that the savannization triggers an irreversible degradation process leading to nutrient-poor soils with the accumulation of toxic aluminum and low water-retention capacity, on which only savannas grow (Dezzeo et al., 2004; Dezzeo and Chacón, 2005). As a result, forest recovery becomes impossible. It is possible that the same process occurred in the YD shrublands, which is supported by the total disappearance of these communities in the early Holocene and its absence during the whole Holocene, even in the absence of fire (Montoya et al., 2011, a, b).

5.8. Future response predictions and potential conservation strategies

The results obtained in the present paper could be useful as past analogs available for an informed forecast on the potential future biotic responses of highland and midland vegetation in the studied regions. Overall, most of the taxa present would be able to tolerate the warming projected for the end of this century, except for a small number of sensitive taxa that have been identified. We also demonstrated that vegetation responses to the same climatic factors vary according to the biome and the peculiarities of the region under study, therefore, no any survey may be generalized. Special care should be taken in the midlands (extending to the lowlands) with climatic drivers that, acting alone or coupled, may favor fire exacerbation. In the highlands, the main climatic driver is temperature, whose principal effect is the upward migration of sensitive species. Although it has not been recorded in this work, the main threat of upslope migration in mountain region is extinction by habitat loss, a possibility that should be seriously considered here and in other Neotropical mountains (Rull and Vegas-Vilarrúbia, 2006; Nogué et al., 2009; Rull et al., 2010a). Another lesson from this study is that communities different from those we know today should be expected to occur in both highlands and midlands. As a consequence, we should be prepared for changes not only in relative abundances but also in taxonomic composition. Our results provide some insights into the range of possibilities to be expected but eventual surprises should not be disregarded (Williams and Jackson, 2007; Williams et al., 2007). In light of the results obtained, a corollary is that conservation plans for the highlands and midlands studied here should focus on individual species (the sensitive species), rather than communities or biomes (Vegas-Vilarrúbia et al., 2011; Rull et al., 2013).

Acknowledgements

This work was supported by project ECOPAST, funded by the Ministry of Science and Innovation of Spain (Grant CGL2009-07069/BOS). Wesley Fraser contributed to the English improvement. We are grateful to two referees (H. Hooghiemstra and anonymous) for their detailed and insightful revision.

References

Alley, R.B., Marotzke, J., Norhaus, W.D., Overpeck, J.T., Peteet, D.M., Pielke, R.A., Pierrehumbert, R.T., Rhines, P.B., Stocker, T.F., Talley, L.D. and Wallace, J.M., 2003. Abrupt climate change. Science 299, 2005-2010.

Ammann B., Birks, H.J.B., Brooks, S.J., Eicher, U., von Grafenstein, U., Hofmann, W., Lemdahl, G., Scwander, J., Tobolski, K. and Wick, L., 2000. Quantification of biotic responses to rapid climatic changesa around the Younger Dryas-a synthesis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 159, 313-347.

Aragão, D.V., Fortini, L.B., Mulkey, S.S., Zarin, D.J., Araujo, M.M. and de Carvalho, C.J.R., 2005. Correlation but no causation between leaf nitrogen and maximum assimilation, the role of drought and reproduction in gas exchange in an understory tropical plant *Miconia ciliata* (Melastomataceae). Am. J. Bot. 92, 456-461.

Azócar, A. and Monasterio, M., 1980. Estudio de la variabilidad meso y microclimática en el Páramo de Mucubají, in: Monasterio, M. (Ed.), Estudios ecológicos en los páramos andinos. Universidad de Los Andes, Mérida, pp. 226-262.

Azócar, A., Rada, F. and García-Núñez, C., 2007. Functional characteristics of the arborescent genus *Polylepis* along a latitudinal gradient in the high Andes. Interciencia 32, 663-668.

Bennett, K.D. & Willis, K.J., 2000. Effect of global atmospheric carbon dioxide on glacial-interglacial vegetation change. Glob. Ecol. Biogeogr. 9, 355-361.

Bennett, K.D. and Willis, K.J., 2001. Pollen, in: Smol, J.P., Birks, H. J. B. and Last, W.M. (Eds.), Tracking Environmental Change Using Lake Sediments, Kluwer, Dordrecht, pp. 5-32.

Berg, A. and Suchi, S., 2001. La vegetación de los páramos La Aguada, La Fría y Espejo en los Andes venezolanos. Plantula 3, 47-64.

Birks, H.J B., 2008. Paleoecology, in: Jorgensen, S.E. and Fath, S.E. (Eds.), Encyclopedia of Ecology. Elsevier, Amsterdam, pp. 2623-2634.

Birks, H.J B., 2013. Ecological paleoecology and conservation biology, controversies, challenges, and compromises. Int. J. Biodiv. Sci. Ecosyst. Serv. Manag. 8, 292-304.

Birks, H.J.B. and Birks, H.H., 1980. Quaternary palaeoecology. E. Arnold, London.

Bissett, A., Gibson, J.A.E., Jaman, S.N., Swadling, K.M. and Cromer, L., 2005. Isolation,amplification, and identification of ancient copepod DNA from lake sediments. Limnol. Oceanograph. Methods 3, 533–542.

Boere, A.C., Abas, B., Rijpstra, W.I., Versteegh, G.J., Vollkman, J.K., Damsté, S. and Coolen, M.J., 2009. Late-Holocene succession of dinoflagellates in an Antarctic fjord using a multi-proxy approach, paleoenvironmental genomics, lipid biomarkers and palynomorphs. Geobiology 7, 265–281.

Boere, A.C., Damsté, J.S.S., Rijpstra, W.I.C., Volkman, J.K. and Coolen, M.J.L., 2011. Source-specific variability in post-depositional DNA preservation with potential implications for DNA based paleoecological records. Org. Geochem. 42, 1216–1225.

Boom, A., Mora, G., Cleef, A.M., Hooghiemstra, H., 2001. High altitude C4 grasslands in the northern Andes: relicts from glacial conditions? Rev. Palaeobot. Palynol. 115, 147-160.

Boom, A., Marchant, R., Hooghiemstra, H., Sinnenghe Damsté, J.S., 2002. CO_2- and temperature controlled altitudinal shifts of C4- and C3-dominated grasslands allow reconstruction of paleo-atmospheric *p*CO2. Palaeogeogr. Paloaeoclimatol. Palaeoecol. 177, 151-168.

Cavieres, L.A., Rada, F., Azócar, A., García-Núñez, C. and Cabrera, H.M., 2000. Gas exchange and low temperature resistance in two tropical high mountain species from the Venezuelan Andes. Acta Oecol. 21, 203-211.

Cheng, H., Sinha, A., Cruz, F.W., Wang, X., Edwards, R.L., d'Horta, F.M., Ribas, C.C., Vuille, M., Stott, L.D. and Auler, A.S., 2013 Climate change patterns in Amazonia and biodiversity. Nature Comm. 4, 1141, doi, 10.1038/ncomms2415.

Cole, K., 2009. Vegetation response to early Holocene warming as an analog for current and future changes. Conserv. Biol. 24, 29-37.

Coolen, M.J.L., Saenz, J.P., Giosan, L., Trowbridge, N.Y., Dimitrov, P., Dimitrov, D. and Eglington, T.I., 2009. DNA and lipid molecular stratigraphic records of haptophyte succession in the Black Sea during the Holocene. Earth Planet. Sci. Lett. 284, 610–621.

Davies, A.L. and Bunting, M.J., 2010. Applications of Palaeoecology in conservation. Open Ecol. J. 3, 54-67.

Dezzeo, N. and Chacón, N., 2005. Carbon and nutrients loss in aboveground biomass along a fire induced forest–savanna gradient in the Gran Sabana, southern Venezuela. Forest Ecol. Manag. 209, 343–352.

Dezzeo, N., Chacón, N., Sanoja, E. and Picón, G., 2004. Changes in soil properties and vegetation characteristics along a forest–savanna gradient in southern Venezuela. Forest Ecol. Manag. 200, 183–193.

Dressler. S., 2001. Marcgraviaceae, in: Berry, P.E., Yatskievych, K. and Holst, B.K. (Eds.), Flora of the Venezuelan Guayana, vol. 6, Liliaceae-Myrsinaceae, Missouri Botanical Garden Press, St. Louis, pp. 248-260.

Faegri, K., Kaland, P.E. and Krzywinski, K., 1989. Textbook of pollen analysis. Blackburn Press, Caldwell.

Fortini, L.B., Mulkey, S.S., Zarin, D.J., Vasconcelos, S.S. and de Carvalho, C.J., 2003. Drought constraints on leaf gas exchange by *Miconia ciliata* (Melastomataceae) in the understory of an eastern Amazonian regrowth forest stand. Am. J. Bot. 90, 1064-1070.

Gassón, R.A., 2002. Orinoquia, the archaeology of the Orinoco River Basin. J. World Prehist. 16, 237–311.

Goldstein, G., Meinzer, F.C. and Rada, F., 1994. Environmental biology of a tropical UFL species, *Polylepis sericea*, in: Rundel, P.W., Smith, A.P. and Meinzer, F.C. (Eds.), Tropical alpine environments. Plant form and function, Cambridge University Press, Cambridge, pp. 129-149.

González, C., Dupont, L.M., Behling, H. and Wefer, G., 2008. Neotropical vegetation response to rapid climate changes during the last glacial, Palynological evidence from the Cariaco basin. Quat. Res. 69, 217–30.

González-Carranza, Z., Hooghiemstra, H., Vélez, M.I., 2012. Major altitudinal shifts in Andean vegetation on the Amazonian flank show temporary loss of biota in the Holocene. The Holocene 22, 1227-1241.

Groot, M.H.M., Bogotá, R.G. Lourens, L.J., Hooghiemstra, H., Vriend, M., Berrio, J.C., Tuenter, E., Van der Plicht, J.H., Van Geel, B., Ziegler, M., Weber, S.L., and 14 Fúquene Project Members, 2011. Ultra-high resolution pollen record from the northern Andes reveals rapid shifts in montane climates within the last two glacial cycles. Clim. Past 7, 299-316.

Grant, J.R., 2009. A revision of neotropical *Bonyunia* (Loganiaceae,Antonieae). Ann. Missouri Bot. Gard. 96, 541-563.

Hansen, B.F., 1995. Apocynaceae, in: Berry, P.E., Holst, B.K. and Yastskievych, Y. (Eds.) Flora of the Venezuelan Guayana, vol. 2, Pterydophytes-Spermatophytes (Acathaceae-Araceae), Missouri Botanical Garden Press, St. Louis, pp. 537-571.

Haug, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.C., Röhl, U., 2001. Southward migration of the intertropical convergence zone through Holocene. Science 293, 1304-1308.

Hoch, G. and Körner, C., 2005. Growth, demography and carbon relations of *Polylepis* trees around the world's highest UFL. Funct. Ecol. 19, 941-951.

Hofreiter, M., Collins, M and Stewart, J.R., 2008. Ancient biomolecules in Quaternary paleoecology. Quat. Sci. Rev. 33, 1-13.

Huber, O., 1994. Los arbustales, in: Dezzeo, N. (Ed.), Ecología de la altiplanicie de la Gran Sabana (Guayana Venezolana). i. Investigaciones sobre la dinámica bosque-sabana en el sector SE, Subcuencas de los ríos Yuruaní, Arabopó y Alto Kukenán, Ediciones Tamandúa, Caracas, pp. 95-196.

Huber, O., 1995. Vegetation, in: Berry, P.E., Holst, B.K. and Yatskiewych, Y. (eds.) Flora of the Venezuelan Guayana, vol. 1, Introduction, Missouri Botanical Garden Press, St. Louis, pp. 97-160.

Hughen, K.A., Eglington, T.I., Xu, L. and Makou, M., 2004. Abrupt tropical vegetation response to rapid climate changes. Science 304, 1955–1959.

Hughen, K. A., 2000. Synchronous radiocarbon and climate shifts during the last deglaciation. Science 290, 1951-1954.

Jansen, B., de Boer, E.J., Cleef, A.M., Hooghiemstra, H., Moscol-Olivera, M., Tonnejick, F.H., Verstraten, J.M., 2013. Reconstruction of late Holocene forest dynamics in northern Ecuador from biomarkers and pollen in soil cores. Palaegeogr. Palaeoclimatol. Palaeoecol. 386, 607-619.

Lea, D.W., Pack, D.K., Peterson, L.C. and Hughen, K.A., 2003. Synchroneity of tropical and high-latitude Atlantic temperatures over the last glacial termination. Science 301, 1361–1364.

Lear, C.H., Rosenthal, Y. and Slowey, N., 2002. Benthic foraminiferal Mg/Ca-paleothermometry, a revised core-top calibration. Geochim. Cosmochim. Acta 66, 3375–3387.

Martinez, N.C., Murray, W.R., Thunell, R.C., Peterson, L.C., Muller-Karger, F.E., Astor, Y. and Varela, R., 2007. Modern climate forcing of terrigenous deposition in the tropics (Cariaco Basin, Venezuela). Earth Planet. Sci. Lett. 264, 438–51.

McGregor, G.R. and Nieuwolt, S., 1998. Tropical climatology. J. Wiley and Sons, Chichester.

Monasterio, M., 1979. El páramo desértico en el antiandino de Venezuela, in: Salgado-Labouriau, M. L. (Ed.), El Medio Ambiente Páramo, IVIC Centro de Estudios Avanzados, Caracas, pp. 117-146.

Monasterio, M., 1980. Las formaciones vegetales de los páramos de Venezuela, in: Monasterio, M. (Ed.) Estudios ecológicos en los páramos andinos, Universidad de Los Andes, Mérida, pp. 93-158.

Montoya, E. and Rull, V., 2011. Gran Sabana fires (SE Venezuela), a paleoecological perspective. Quat. Sci. Rev. 30, 3430-3444.

Montoya, E., Rull, V., Stansell, N.D., Bird, B.W., Nogué, S., Vegas-Vilarrúbia, T., Abbott, M.B. and Díaz, W.A., 2011a. Vegetation changes in the neotropical Gran Sabana (Venezuela) around the Younger Dryas Chron. J. Quat. Sci. 26, 207-218.

Montoya, E., Rull, V., Stansell, N.D., Abbott, M.B., Nogué, S., Bird, B.W. and Díaz, W.A., 2011b. Forest-savanna-morichal dynamics in relation to fire and human occupation in the southern Gran Sabana (SE Venezuela) during the last millennia. Quat. Res. 76, 335-344.

Montoya, E., Rull, V. and Nogué, S., 2011c. Early human occupation and land use changes near the boundary of the Orinoco and the Amazon basins (SE

Venezuela), palynological evidence from El Paují record. Palaeogeogr. Palaeoclimatol. Palaeoecol. 310, 413-426.

Nogué, S., Rull, V. and Vegas-Vilarrúbia, T., 2009. Modeling biodiversity loss by global warming in Pantepui, northern South America, projected upward migration and potential habitat loss. Clim. Change 94, 77–85.

Ortiz, J.D. and O'Connell, S., 2004. Toward a non-linear grayscale calibration method for legacy photographic collections, in: Francus, E. (Ed.), Image Analysis, Sediments and Paleoenvironments. Springer, Dordrecht, pp. 125–141.

Pielou, E.C., 1969. An introduction to mathematical ecology. J. Wiley and Sons, New York.

Pipoly, J.J. and Ricketson, J.M., 2001. Mysinaceae, in: Berry, P.E., Yatskievych, K. and Holst, B.K. (Eds.), Flora of the Venezuelan Guayana, vol. 6, Liliaceae-Myrsinaceae, Missouri Botanical Garden Press, St. Louis, pp. 748-775.

Polissar, P.J., Abbott, M.B., Wolfe, A.P., Bezada, M., Rull, V, and Bradley, R.S., 2006. Solar modulation of Little Ice Age climate in the tropical Andes. Proc. Natl. Acad. Sci. 103, 8937–8942.

Poveda, G., Waylen, P.R. and Pulwarty, R.S., 2006. Annual and inter-annual variability of the present climate in northern South America and southern Mesoamerica. Palaeogeogr. Palaeoclimatol. Palaeoecol. 234, 3–27.

Rada, F., García-Núñez, C. and Rangel, S., 2009. Low temperature resistance in saplings and ramets of *Polylepis sericea* in the Venezuelan Andes. Acta Oecol. 35, 610-613.

Rasmussen, S.O., Andersen, K.K., Svensson, A.M., Steffensen, J.P., Vinther, B.M., Clausen, H.B., Siggaard-Andersen, M.-L., Johnsem, S.J., Larsen, L.B., Dahl-Jensen, D., Bigler, M., Röthlisberger, R., Fischer, H., Goto-Azuma, K., Hansson, M.E. and Ruth, U., 2006. A new Greenland ice core chronology for the last glacial termination. J. Geophys. Res. 111, D06102, doi, 10.1029/2005JD006079.

Rull, V., 2006. A high mountain pollen-altitude calibration set for paleoclimatic use in the tropical Andes. Holocene 16, 105–117.

Rull, V., 2012. Community ecology, diversity and dynamics over time. Comm. Ecol. 13, 102-116.

Rull, V., 2014. Ecological palaeoecology: enhancing ecological scope and bridging the gap between ecology and evolution. Collect. Bot. 33, 65-73.

Rull, V. and Vegas-Vilarrúbia, T., 2006. Unexpected biodiversity loss under global warming in the neotropical Guayana Highlands, a preliminaryappraisal. Glob. Change Biol. 12, 1-9.

Rull, V. and Vegas-Vilarrúbia, T., 2011. What is long-term in ecology? Trends Ecol. Evol. 26, 3-4.

Rull, V., Abbott, M.B., Polissar, P.P., Wolfe, A.P., Bezada, M. and Bradley, R.S., 2005. 15,000-yr pollen record of vegetation change in the high altitude tropical Andes at Laguna Verde Alta, Venezuela. Quat. Res. 64, 308-317.

Rull, V., Abbott, M.B., Polissar, P.J., Wolfe, A.P., Bezada, M. and Bradley, R.S., 2010a. Paleoenvironmental trends in Venezuela during the last glacial cycle, in: Sánchez-Villagra, M., Aguilera, O.A. and Carlini, A.A. (Eds.), Urumaco and Venezuelan paleontology-the fossil record of the northern Neotropics, Indiana University Press, Indinana, pp. 52-83.

Rull, V., Stansell, N.D., Montoya, E., Bezada, M. and Abbott, M.B., 2010b. Palynological signal of the Younger Dryas in the tropical Venezuelan Andes. Quat. Sci. Rev. 29, 3045-3056.

Rull, V., Montoya, E., Nogué, S., Vegas-Vilarrúbia, T. and Safont, E., 2013. Ecological paleoecology in the neotropical Gran Sabana region, long-term records of vegetation dynamics as a basis for ecological hypothesis testing. Persp. Plant Ecol. Evol. Syst. 15, 338– 359.

Salgado-Labouriau, M.L., 1982. Pollen morphology of the Compositae of the northern Andes. Pollen Spores 24, 397-452.

Salgado-Labouriau, M.L. and Rinaldi, M., 1990. Palynology of Gramineae of the Venezuelan mountains. Grana 29, 119-128.

Seddon, A.W.R., 2012. Paleoecology, in: Gibson, D. (Ed.), Oxford Bibliographies Online, Ecology. Oxford University Press, Oxford.

Seddon, A.W.R.; Mackay, A.W.; Baker, A.G.; Birks, H.J.B.; Breman, E.; Buck, C.E.; Ellis, E.C.; Froyd, C.A.; Gill, J.L.; Gillson, L.; Johnson, E.A.; Jones, V.J.; Juggins, S.; Macias-Fauria, M.; Mills, K.; Morris, J.L.; Nogués-Bravo, D.; Punyasena, S.W.; Roland, Th.P.; Tanentzap, A.J.; Willis, K.J.; Aberhan, M.; van Asperen, E.N.; Austin, W.E.N.; Battarbee, R.W.; Bhagwat, Sh.; Belanger, Ch.L.; Bennett, K.D.; Birks, H.H.; Bronk Ramsey, Ch.; Brooks, S.J.; de Bruyn, M.; Butler, P.G.; Chambers, F.M.; Clarke, S.J.; Davies, A.L.; Dearing, J.A.; Ezard, Th.H.G.; Feurdean, A.; Flower, R.J.; Gell, P.; Hausmann, S.; Hogan, E.J.; Hopkins, M.J.; Jeffers, E.S.; Korhola, A.A.; Marchant, R.; Kiefer, Th.; Lamentowicz, M.; Larocque-Tobler, I.; López-Merino, L.; Liow, L.H.; McGowan, S.; Miller, J.H.; Montoya Romo, E.; Morton, O.; Nogué, S.; Onoufriou, Ch.; Boush, L.P.; Rodriguez-Sanchez, F.; Rose, N.L.; Sayer, C.D.; Shaw, H.E.; Payne, R.; Simpson, G.; Sohar, K.; Whitehouse, N.J.; Williams, John W.; Witkowski, A. and McGlone, M., 2014. Looking forward through the past, identification of 50 priority research questions in palaeoecology. J. Ecol. 102, 256–267.

Skinner, L.C., Waelbroeck, C., Scrivner, A.E. & Fallon, S.J., 2014. Radiocarbon evidence for alternating northern and southern sources of ventilation of the deep Atlantic carbon pool during the last deglaciation. Proc. Natl. Acad. Sci. USA 111, 5840-5844.

Stansell, N.D., Abbott, M.B., Rull, V., Rodbell, D.T., Bezada, M. and Montoya, E., 2010. Abrupt Younger Dryas cooling in the northern tropics recorded in lake sediments from the Venezuelan Andes. Earth Planet. Sci. Lett. 293, 154-163.

Van der Hammen, T., Hooghiemstra, H., 1995. The El Abra stadial, a Younger Dryas equivalent in Colombia. Quat. Sci. Rev. 14, 841-851.

Van‘t Veer, R., Islebe, G., Hooghiemstra, H., 2000. Climatic change during the Younger Dryas chron in northern South America: a test of the evidence. Quat. Sci. Rev. 19, 1821-1835.

Van der Knaap, W.O., 2009. Estimating pollen diversity from pollen accumulation rates, a method to assess taxonomic richness in the landscape. Holocene 19, 159-163.

Vegas-Vilarrúbia, T., Rull, V., Montoya, E. and Safont, E., 2011. Quaternary paleoecology and nature conservation with an emphasis on global warming and fire, with examples from the Neotropics. Quat. Sci. Rev. 30, 2361-2388.

Velásquez, C.A. and Hooghiemstra, H., 2013. Pollen-based 17-kyr forest dynamics and climate change from the Western Cordillera of Colombia, no-analogue associations and temporarily lost biomes. Rev. Palaeobotany Palynol. 194, 38-49.

Wagner, E., 1979. Arqueología de los Andes venezolanos. Los páramos y la Tierra Fría, in: Salgado-Labouriau, M.L. (Ed.), El medio ambiente páramo. Centro de Estudios Avanzados, IVIC, Altos de Pipe.

Williams, J.W. and Jackson, S.T., 2007. Novel climates, no-analogue communities, and ecological surprises. Front. Ecol. Environ. 5, 475–482.

Williams, J.W., Jackson, S.T. and Kutzbach, J.E., 2007. Projected distributions of novel and disappearing climates by 2100 AD. Proc. Natil. Acad. Sci. USA 104, 5738–5742.

Willis, K.J. and Birks, H.J.B., 2006. What is natural? The need for a long-term perspective in biodiversity conservation. Science 314, 1261-1265.

Willis, K.J. and MacDonald, G.M., 2011. Long-term ecological records and their relevance to climate change predictions for a warmer world. Annu. Rev. Ecol. Evol. Syst. 42, 267-287.

Willis, K.J., Araújo, M.B., Bennett, K.D., Figueroa-Rangel, B. Froyd, C.A. and Myers, N., 2007. How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. Phil. Trans. R. Soc. B 362, 175-186.

Willis, K.J., Bailey, R.M., Bhagwat, S., Birks, H.J.B., 2010. Biodiversity baselines thresholds and resilience: testing predictions and assumptions using palaeoecological data. Trends Ecol. Evol. 25, 583–591.