Quaternary palaeoecology and nature conservation: a general review with examples from the neotropics

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ABSTRACT

Palaeoecology, as an ecological discipline, is able to provide relevant inputs for conservation science and ecosystem management, especially for issues involving long-term processes, such as ecological succession, migration, adaptation, microevolution, and extinction. This use of palaeoecology has been noted for several decades, and it has become widely accepted, especially in the frame of ongoing and near-future global warming and its potential biotic consequences. Selected palaeoecological insights of interest for conservation include the following: 1) species respond in an individualistic manner to environmental changes that lead to changes in community composition, suggesting that future ecosystems would have no modern analogues; 2) in the short-term, acclimation is more likely a response of species that are expected to persist in the face of global warming, but the possibility of evolutionary change linked to the existence of pre-adapted genomes cannot be dismissed; 3) species unable to acclimate or adapt to new conditions should migrate or become extinct, which has been observed in past records; 4) current extinction estimates for the near-future should be revised in light of palaeoecological information, which shows that spatial reorganisations and persistence in suitable microrefugia have been more common than extinction during the Quaternary; 5) biotic responses to environmental changes do not necessarily follow the rules of equilibrium dynamics but depend on complex and non-linear processes that lead to unexpected “surprises”, which are favoured by the occurrence of thresholds and amplifying positive feedbacks; 6) threshold responses can cause the movement of ecosystems among several potentially stable states depending on their resilience, or the persistence of transient states; 7) species and their communities have responded to environmental changes in a heterogeneous fashion according to the local and regional features, which is crucial for present and future management policies; 8) the global warming that occurred at the end of the Younger Dryas cold reversal (ca 13.0 to 11.5 cal kyr BP) took place at similar rates and magnitudes compared to the global warming projected for the 21st century, thus becoming a powerful past analogue for prediction modelling; 9) environmental changes have acted upon ecosystems in an indirect way by modifying human behaviour and activities that, in turn, have had the potential of changing the environment and enhancing the disturbance effects by synergistic processes involving positive feedbacks; 10) the collapse of past civilisations under climate stress has been chiefly the result of inadequate management procedures and weaknesses in social organisation, which would be a warning for the present uncontrolled growth of human population, the consequent over-exploitation of natural resources, and the continuous increase of greenhouse gas emissions; 11) the impact of fire as a decisive ecological agent has increased since the rise of humans, especially during the last millennia, but anthropic fires were not dominant over natural fires until the 19th century; 12) fire has been an essential element in the development and ecological dynamics of many ecosystems, and it has significantly affected the worldwide biome distribution; 13) climate–fire–human synergies that amplify the effects of climate, or fire alone, have been important in the shaping of modern landscapes.
1. Introduction

This paper reviews the most significant literature available on the usefulness of palaeoecology in the field of nature conservation to extract the more relevant lessons from the past to improve present and future ecosystem management. This paper also provides several selected case studies from the Neotropical region to show how palaeorecords can address real conservation problems, with assessments and recommendations of immediate applicability. This review also attempts to be a service to the palaeoecological community to facilitate access to the more relevant knowledge and related literature on the subject. In addition, we hope that this contribution may enhance the interest of palaeoecologists on the importance of our disciplines for conservation, thereby promoting discussion and hopefully leading to the continuous improvement of our skills. Our approach is based on the broad concept of ecology, which is seen as a discipline embracing palaeoecology, neoecology and predictive ecology. Interaction between these disciplines is needed for a proper understanding of the biosphere and its functioning and to deal with its potential reactions to future environmental change (Rull, 2010a). As expressed in the title, the emphasis is on global warming and fire as environmental stressors; other subjects, such as eutrophication, acidification, pollution, and soil erosion, have been reviewed and discussed elsewhere (e.g., Smol, 2008; Pelejero et al., 2010; Albright et al., 2010). Emphasis will be placed on the Quaternary (i.e., the last 2.58 million years (Ma), as defined by Gibbard et al. (2010); however, references to former periods will be included when necessary.

The review begins with a discussion of the meaning of “long-term” in ecology to set a suitable temporal framework and to emphasise that neoecology and palaeoecology, despite methodological differences, share common objectives. The second part is a summary of the biotic responses documented so far to past climate changes, and their significance to ongoing and future global warming. Following these sections, a summary is provided of key developments in the applications of palaeoecology to conservation. This account is based mainly on review papers and aims to introduce the relevant concepts in a historical fashion and highlight the leading researchers and research groups in this field. The next section concerns potential past analogues for projected global warming, which could be used in forecast modelling. The anthropic factor is then introduced in the section about indirect impacts of climatic change. This section is devoted to the possibility of disentangling natural from human causes for past ecological changes and records those situations in which synergies between these two drivers have determined a priori unexpected ecological responses. Fire, which is among the more influential ecological disturbances of anthropic origin, is then discussed based on its occurrence patterns and incidence throughout Earth’s history, with an emphasis on its natural or human-induced nature since the last glacial period, when present-day ecosystems developed. Concerning examples of the usefulness of past records for conservation, we use our own work in the Neotropical region of northern South America, mainly in the Andean highlands, the Gran Sabana midlands, and the summits of the Guayanan tabular mountains, or tepuis. We provide past analogues for rapid and gradual climatic changes and fire, acting either separately or simultaneously, along with their ecological consequences. Finally, the main conclusions of this review are identified, and we highlight several conservation recommendations derived from these conclusions.

2. Ecology and palaeoecology: what is long-term?

Presently, it is widely acknowledged that short-term ecological studies are not enough for reliable predictions on the potential consequences of future environmental changes and human disturbance, and long-term surveys are increasingly recognised as a necessary tool for this purpose (e.g., Huntley, 1996; Jackson, 2001). However, there is no agreement on the meaning of short-term and long-term. For example, in a recent special issue of Trends in Ecology and Evolution entitled “Long-term ecological studies”, most papers deal with data extending to a couple of decades, and only one uses a palaeoecological approach (Willis et al., 2010a). There is no standard definition for long-term in ecology, but some explicit statements within papers on the subject consider a lower boundary between 20 and 50 years for long-term studies (Willis et al., 2007a).

For obvious reasons, the connection between palaeoecology and conservation science has many coincidences with the relationship between ecology and palaeoecology that, despite what their names may suggest, have progressed historically as separate disciplines. According to Rull (2010a), this unfortunate disjunction has been facilitated by the following: 1) the past–present dissociation characteristic of the human mind, 2) the diversity of fields of provenance for palaeoecologists, 3) the contrasting nature of the evidence and associated methodological differences, and 4) misunderstandings caused by the use of the prefix palaeo-. However, the principle of uniformitarianism emphasises that past, present and future are not discrete units, but rather a time continuum through which species and communities flow, change and evolve, and that ecology and palaeoecology are simply different approaches with a common objective, which is the ecological understanding of the biosphere. Ecology, in a broad sense, includes inferences about the past (palaeoecology), present studies (neoecology or contemporary ecology) and future projections (predictive ecology). Therefore, palaeoecology is essentially community ecology stretched backward through the fourth dimension of time (Schoonmaker and Foster, 1991), or it can also mean ecological studies that use the past as proxies (Rull, 2010a). In this context, long-term should have a single meaning.

The importance of temporal and spatial scales in ecology and palaeoecology has been emphasised by Delcourt and Delcourt (1988). More recently, Jackson (2001) has distinguished three time domains useful to deal with the ecology–palaeoecology continuity. These domains are as follows: real-time, which is the time frame usually considered in neoecology, which spans from weeks to decades and includes processes such as population dynamics, competition or predator–prey interactions; Q-time (where Q is for Quaternary), which ranges from centuries to millennia, encompasses processes such as succession, migration or extinction; and deep-time, which includes a wide range of
timescales typically over $10^5$ years and accounts for evolutionary trends and large-scale biogeographic reorganisations. The time length of the processes mentioned above depends on the organisms involved, mainly in relation to their generation times and the duration of their biological cycles. For example, ecological succession in plankton communities may elapse over a year or merely a season, whereas in a forest, it may take centuries or millennia to occur. Therefore, a multidecadal study would be able to capture actual long-term processes for the first case, but it is clearly insufficient in the second case. Therefore, it seems appropriate to refer to real-time phenomena as short-time ecological processes, and to use long-term for ecological processes occurring at Q-timescales (Rull and Vegas-Vilarrúbia, 2011). This will be the convention used in this paper. Therefore, real long-term ecological studies and, hence, conservation science need evidence from the past, that is, palaeoecological input.

### 3. Biotic responses to environmental change: past and future

Forecasts about the nature of future responses to climate change and other environmental disturbances require a deep knowledge of the past and present biotic responses to the same or similar ecological forcings. Palaeoecology has provided decisive evidence on the responses of organisms and their communities to past environmental shifts, mainly in relation to climate changes. Multi-proxy studies are especially well suited for this purpose because they furnish independent physical and/or chemical evidence of environmental change and avoid potential circular reasoning. Important aspects of the biotic responses to environmental shifts are the nature (individualistic or collective), the type (migration, extinction), the magnitude and extent (local, regional, global), the time lags with respect to the environmental shift, and the rates of change. Palaeorecords of these features can be used as past analogues to infer potential future responses of organisms and communities to the predicted future environmental changes. The records can also be used to disentangle natural from anthropic causes of ecological change. Hewitt and Nichols (2005) have synthesised the three more important types of biotic responses in the expression “adapt, move or die”, which equates to evolution, range shifts or extinction. However, there is a fourth possibility, which is persistence, despite environmental change, because of phenotypic plasticity in the less sensitive species (Davis et al., 2005). According to the palaeorecords, there are five main modes in which organisms and communities respond to climatic variations: growth or death, species migration, changes in community composition, evolutionary changes, and extinction (Overpeck et al., 2003). The nature of the response depends on the scale, considered in both space and time (see also Delcourt and Delcourt, 1988). The following section provides an updated summary of the main elements required for the evaluation of biotic responses to external factors based on the information provided by past records.

#### 3.1. Individualistic responses and non-analogue communities

The issue of the individualistic (at the species level) vs. collective (at a community level) biotic responses has been a long ecological debate between the Gleasonian and the Clementsian schools, which are defenders of the first and second option, respectively (Clements, 1916; Gleason, 1926). The classical works of Davis (1981) in North America and Huntley and Birks (1983) in Europe have shown that postglacial recolonisation of these continents by trees from temperate forests proceeded in an individual fashion, and, as a consequence, current forests are composed of species that arrived at different times from various southern glacial refugia (Schoonmaker and Foster, 1991). Furthermore, individual differences in response lags and migration rates complicated the picture. Another important consequence is that communities have not been constant through time, suggesting that they are loose and relatively ephemeral assemblages of species populations, as formerly proposed by Whittaker (1951). Further palaeoecological evidence has reinforced this view (Bennett, 1997, and literature therein). The projection of these results into the future allowed researchers to prognosticate that, by the end of this century, the occurrence of novel climates and biotic communities with no modern analogues will be common on the planet as a consequence of ongoing climate change (Williams and Jackson, 2007; Williams et al., 2007). Therefore, management procedures should adapt to these new combinations, with unknown community organisation, functional properties and ecosystem dynamics (Hobs et al., 2006; Willis et al., 2007b; Willis and Bhagwat, 2010). Current predictions of non-analogue or novel communities are based on ecological models parameterised from present-day observations that may fail to predict ecological responses to novel climates. These models should be validated against palaeoecological evidence to enhance their robustness and predictive accuracy (Williams and Jackson, 2007).

Key elements to be considered in the individualistic behaviour of species in relation to environmental change include particular differences in their sensitivity to relevant environmental factors, response lags and migration ability, and the availability of specific niche requirements (suitable substrates, pollinators, etc.). These factors would constitute a handicap for many organisms to track the projected climate change at similar rates. In principle, it could be assumed that organisms with short lifecycles (e.g., planktonic organisms) would respond faster than those with longer generation times, such as trees, which could take decades to centuries to respond (Davis, 1985). However, several recent palaeoecological records have depicted short or absent time lags between rapid environmental shifts and a varied array of organisms, including cladocera, chironomids and vascular plants (Ammann et al., 2000; Birks and Birks, 2008). Historical records have also shown relatively rapid migrational responses (1 to several m per year, depending on the species) of vegetation to the global warming experienced during the last century, especially in the form of altitudinal and latitudinal migrations (Walther et al., 2002; Parmesan and Yohe, 2003; Parmesan, 2005, 2006; Kelly and Goulden, 2008; Lenoir et al., 2008; and literature therein). Therefore, according to palaeoecological and historical records, the capacity of organisms to track the ongoing climate change at similar rates seems to be higher than previously expected.

#### 3.2. Migration and microrefugia

The more common biotic response to climate change during the Quaternary seems to have been migrational range shifts (Davis and Shaw, 2001; Seppä and Bennett, 2003). The better known examples of this are the postglacial recolonisations of northern temperate continents by tree forest species from southern refugia with a favourable climate, where they endured the last glaciation (Davis, 1981; Huntley and Birks, 1983). This led to estimated migration rates between 100 and 1000 m/year, which are unrealistic considering the known dispersal mechanisms of the species involved (Clark et al., 2003; MacLachlan et al., 2005). Alternatively, migration could have also proceeded from numerous, more or less widespread, microrefugia, or “small areas with local favourable environmental features, in which small populations can survive outside their main distribution area (the macrorefugium), protected from the unfavourable regional environmental conditions” (Rull, 2005c). The expansion of these widespread, small populations, favoured by postglacial warming, is more consistent with the relatively rapid continental colonisation rates under the current dispersal mechanisms of these tree species (Pearson, 2006). These microrefugia are...
difficult to identify with common palaeoecological methods because of their assumed small size and unknown distribution (Rull, 2010b), but intra-specific genetic patterns of the involved species provide evidence of their existence and suggestions for their geographical distribution (Willis and van Andel, 2004; Bhagat and Willis, 2008; Petit et al., 2008; Provan and Bennett, 2008). The idea of micro-refugia is not only interesting for migration rates and species’ genetic structure but also for biodiversity conservation purposes because hypothetical future microrefugia (natural or artificially created) could help to mitigate the extent of the projected biotic extinction resulting from climate change by providing suitable microhabitat conditions for threatened species (Rull, 2009c). According to Davis and Shaw (2001), past records show that range shifts and genetic adaptation proceeded together during the Quaternary climatic changes and could not be considered alternative biotic responses, but this topic will be analysed further in the next section. The potential of palaeoecology records, especially pollen, macrofossil and charcoal records, for the reconstruction of plant migration and invasion patterns in both space and time has been reviewed by Mitchell (2010), who emphasises the need for enhanced mapping of pollen and biomes on continental and global scales and more collaborative efforts among palaeoecology, community ecology and genetic studies to improve the testing of ecological hypotheses.

3.3. Acclimation and adaptation

Sensitivity is another key parameter to understand the reactions of organisms to environmental changes. In principle, the more sensitive species should be those with a narrow tolerance for the relevant environmental variables (stenotopic), or those living near the edge of their ranges. Eurytopic species, with a large phenotypic plasticity, should be less sensitive to changes, especially if they live far from their range boundaries. In every case, to produce a biotic response, a given environmental change should cross a threshold determined by the range of tolerance of the involved species. The process by which a species resists an environmental change because of its wide tolerance or phenotypic plasticity is called acclimation, whereas adaptation involves genetic (i.e., evolutionary) changes. There is the general a priori perception that the high rates of climate change predicted for the near-future will prevent genetic adaptation, but some authors think that the role of adaptation as a response to future climate change has been overlooked. According to these authors, populations may adapt to the new climates through the occurrence of pre-adapted individuals that can eventually increase their density (Davis and Shaw, 2001; Kelly et al., 2003). Indeed, species can adapt to new environments by either waiting for the appearance of novel, advantageous mutations or evolving immediately using alleles from the standing (pre-existing) genetic variation (Stapley et al., 2010). Therefore, the adaptation of populations to a different climate will depend on the level of climate-related genetic variability already contained in the population. Another source of adaptive genetic variation is admixture and the resulting gene flow between two divergent populations (Barrett and Schlatter, 2008). In the case of relatively contiguous populations, adaptation may be aided by migration (Jump and Peuhulas, 2005). These hypotheses, however, are difficult to confirm or reject with the traditional Quaternary palaeoecological methods (Seppä and Bennett, 2003) because of lower taxonomical resolution than required, and they have been evaluated in combination with molecular phylogenetic evidence (Willis et al., 2003).

Recent molecular phylogenetic studies have shown that Quaternary speciation has indeed occurred -for example, humans are only a 200,000-year-old Quaternary species (Tattersall and Schwartz, 2009)- and has been important in many biomes (e.g., Richardson et al., 2001; Lister, 2003; Rull, 2008; Valente et al., 2010); however, given the rapid rate at which the ongoing climate change is predicted to occur during this century, it is difficult to develop potential analogies. Hewitt and Nichols (2005) have reviewed this topic and concluded that there is no conclusive evidence supporting or denying genetic adaptation to changing climates in the recent past. Palaeoecological records since the Last Glacial Maximum (LGM) show that changes in distribution fuelled by climate changes have had important consequences for intra-specific genetic diversity (see also Hewitt, 2000, 2003; Lascaux et al., 2003; Magri, 2008). The key question is if genetic changes have persisted long enough to be fixed and, if so, if the standing genetic diversity has influenced species’ fitness.

According to Davis et al. (2005) and Lavergne et al. (2010), biotic responses to climate changes involve both ecological and evolutionary elements that cannot be disentangled. For example, responses, such as persistence, migration or extinction, are intimately linked to microevolutionary reorganisation that influences species’ sensitivity and adaptation ability (Davis et al., 2005). Microevolution also affects ecosystem assembly and functioning (Cavender-Bares et al., 2009); therefore, emergent properties, such as biodiversity or stability, affect not only the response to environmental changes but also future evolutionary trajectories. Therefore, the incorporation of eco-evolutionary feedbacks is needed for biodiversity forecasting, and for a better understanding of ecological dynamics in relation to anthropic environmental changes (Lavergne et al., 2010). Currently, models to properly forecast potential adaptation to environmental change are under development (Salamin et al., 2010). We should also note that the structure and survival of source populations and their genetic legacy may be endangered for many species, and the need for identifying and conserving glacial refuge areas should be emphasised (Hewitt and Nichols, 2005).

3.4. Extinction

Extinction occurs when all the other potential responses fail. Under changing environments, extinction of a species may result from an inability to migrate and to resist or adapt to changes, but it may also occur if the species’ habitat is lost or fragmented/reduced to the extent that populations lack the genetic variability to survive natural perturbations, such as extreme climatic events, epidemics, and fire (Overpeck et al., 2003). Additionally, because of the ecological interplay within the ecosystem, the extinction of certain key and/or dominant species may generate cascade effects affecting other related species (hosts, parasites, pollinators, etc.) in the form of the so-called secondary extinctions (e.g., Lafferty and Kuris, 2009). Biodiversity loss by increased extinction because of direct (habitat fragmentation, pollution, fire) or indirect (global warming) consequences of human activities is a common output of predictive models for the end of this century (e.g., Thomas et al., 2004; Peterson et al., 2005). Some believe that the ongoing and future human-induced global biodiversity reduction is comparable to one of the five major extinctions that have occurred in the geological history of Earth (Courtillot, 1999), and they term it the sixth extinction (Wake and Vrumba, 2008).

At a human time scale, the last significant extinction event occurred between 50,000 and 10,000 years ago, when most large mammals became extinct everywhere except Africa (Koch and Barnosky, 2006; Barnosky, 2009). Contrastingly, there is evidence for the extinction of one single plant species (Picea crichtfieldii, a spruce) in North America during the same period (Jackson and Weng, 1999). The competing causal mechanisms for mammal extinction were either climate change or human activities;
however, it is now widely accepted that the extinction was caused by the synergy of both, especially the coincidence of the Younger Dryas cooling (ca 13.5 to 11.5 kyr BP) and increased human hunting (Barnosky and Lindsey, 2010). This has been considered a potential analogy for the present and the near-future because of the coincidence of rapid climate change and increased human population and disturbance. In this sense, it is important to note that the failure to adjust to changing climates did not arise from the magnitude alone, but also from the rapid rates of change. Generally, a complicating factor to avoid extinction by biotic adjustment to environmental changes is that these have occurred at different rates and magnitudes and over different temporal and spatial scales, thus causing disequilibrium or dynamic equilibrium between the environment and the biotic communities (Overpeck et al., 2003).

A contrasting view is provided by Willis et al. (2010b), who has noted that, in the fossil record, global extinctions due solely to global warming are very rare (mammal extinctions are associated mainly to human action in this case), suggesting that extinction rates because of future climate change would have been overestimated (see also Pearson, 2006). This would be due in part to the coarse scale of the models used to estimate habitat loss, which fail to capture potential microclimatic features that could help species avoid extinction (Willis and Bhagwat, 2009; Sublette et al., 2011). Indeed, recent models using more detailed topographies have resulted in less catastrophic extinction predictions (e.g., Randin et al., 2009; Hole et al., 2009). According to Willis and Bhagwat (2009), the more likely responses of future ecosystems to climatic change will be, like in the past, rapid community turnovers, broad-scale migrations, threshold events and the formation of novel ecosystems. This would be valid for widely distributed species, but local extinction, which has been well documented by palaeoecology (e.g., Postigo-Mijarra et al., 2010; González-Sampérriz et al., 2010 and literature therein), can be fatal for endemic species.

3.5. Spatial heterogeneity

An important lesson from palaeoecological studies is that, like the physical changes, the biotic responses have not been homogeneous throughout the planet. Indeed, palaeoecological evidence has shown that, in northern temperate latitudes, the most important responses of biota to past change have been migrations, or changes in the spatial extent and location of species’ ranges, and extinctions by habitat loss. Adaptive responses have also been recorded, but mostly from persistent environmental shifts. Consequently, it was predicted that the main response to future climate change will consist of extinctions and individual range adjustments, whereas evolutionary change will be limited (Huntley, 2005). In the southern continents, human activities seem to have been decisive for current biotic patterns, and climate variability was considered at least as important as climate absolutes in governing biodiversity responses. Therefore, these two factors were considered to be the most significant for future biotic patterns. Based on the palaeoecological evidence, it was predicted that range adjustments to future climate change will be difficult or impossible in most cases because of the current, severe habitat fragmentation. Competition with introduced alien species will likely be another complicating factor for the survival of native species (Markgraf and McGlone, 2005).

In the tropics, available palaeoecological evidence supports the observation that species have been more resilient to climatic change, and extinction has been rare. The main response to environmental shifts seems to have been changes in community composition because of the individualistic behaviour of species. Therefore, it was prognosticated that, under future climatic change, species will expand or contract their ranges and determine the replacement of current communities by novel species combinations. As a result, emphasis for biodiversity conservation was not placed on the preservation of communities but on the maintenance of species’ ecological niches (Bush and Hooghiemstra, 2005). Concerning marine ecosystems, the observed responses to past environmental shifts have been varied, ranging from large biogeographical reorganisations to insignificant changes, even in the face of significant climate changes, such as the glacial—interglacial alternation, as in the case of corals (Roy and Pandolfi, 2005). Similarly, some past climatic events seem to have determined widespread extinctions, whereas others of similar intensity have not. The cause of these heterogeneous patterns remains unknown. According to the same authors, a possible synergistic relationship between climate change and the consequences of human activities, primarily in the form of habitat degradation and biodiversity loss, will be important for understanding future marine responses to climate change.

3.6. Transient and non-linear responses

Potential future biotic responses to global change are often approached by biome simulations, which implicitly assume biotic equilibrium responses. However, palaeoecological records have shown that this equilibrium between organisms and climate is rarely attained, and most of the time, the responding biota shows a transient response to environmental fluctuations characterised by extended time lags. This response, combined with the potential occurrence of unpredictable responses and the existence of positive biosphere-climate feedbacks that can magnify both environmental changes and biotic responses, severely constrains the possibility of anticipating future threats to biodiversity and ecosystem dynamics, even if future climatic changes are well known (Overpeck et al., 2003).

During the past decades, the concept of non-equilibrium ecology has emerged, emphasising the complexity and non-linearity of ecosystem dynamics that explains such behaviour (Holling, 1973; May, 1977). According to the non-equilibrium concept, rare events, management disturbances and resource exploitation have the potential to move the systems between multiple stable states. No large impacts are needed to promote dramatic shifts; even a tiny incremental change in conditions can trigger a catastrophic shift if a critical threshold is passed (Holling et al., 1995). Complex interactions, such as positive feedback, would account for this pathway (Suding and Hobbs, 2009). In this context, equilibrium would be a temporary artefact of observation, not an intrinsic system property (Wallington et al., 2005). There are some recent examples that illustrate how such changes occur suddenly (Scheffer and Carpenter, 2003 and literature therein).

Sudden and unexpected responses in the behaviour of environmental and ecological systems have been called surprises (Broecker, 1987; Overpeck, 1996). Concerning conservation, the more important surprises seem to be those linked to abrupt threshold-crossing changes manifested as “jumps” in the palaeoecological records. Given the complexity and non-linearity of nature, these jumps should be expected to occur in the future in a stochastic fashion, much as they have occurred in the past. Palaeoecology may be useful for predicting their occurrence, understanding their causes, and preventing their biotic consequences. The non-linear dynamics of the earth system and the existence of thresholds, which, if crossed, may determine abrupt and unexpected environmental and biotic changes, have also been highlighted by Bradley et al. (2003), who declared that the message from the palaeorecords is that change is normal and the unexpected can happen. According to these authors, abrupt responses to gradual forcing are common in past records at all time and space.
scales. They also provide some selected examples. The upper and lower bounds within which atmospheric CO₂ concentrations have varied over the past four glacial cycles seem to be thresholds for the global carbon cycle, which influences photosynthetic efficiency. The glacial/interglacial cycles are thought to be threshold responses to gradual insolation changes. Another threshold is the potential migration rate of organisms, which may determine their extinction if environmental change proceeds faster. Willis and Bhagwat (2010) provide selected palaeoecological examples of ecological thresholds. If these thresholds are crossed, the ecosystem switches from one stable state to another within a relatively short-time interval. Human impact is emphasised as a driver of these switches.

Another non-linear dynamic feature common to past climate and environmental processes is hysteresis, or the irreversibility of changes once a given threshold has been crossed. Examples of this behaviour are the thermohaline circulation shutdown that occurred at the onset of the Younger Dryas cold event and the present-day increase in atmospheric CO₂ (Bradley et al., 2003).

3.7. Resilience

Resilience was formerly defined in ecological terms as the magnitude of disturbance that an ecosystem can experience before it shifts into a different stability domain (Holling, 1973), or, in other words, before crossing a threshold towards another stable state (Willis and Bhagwat, 2010). Ecological resilience was re-defined by Folke et al. (2004) as the capacity of an ecosystem to absorb disturbance and reorganise to retain the same function, structure, identity, and feedbacks. It is believed that the resilience of ecosystems is being constantly eroded by the ongoing environmental deterioration because of human activities, resulting in systems that are progressively more vulnerable to changes that could have previously been absorbed (Folke et al., 2004). Therefore, in conservation ecology, it is essential to know how, when and why a given ecosystem is approaching a critical resilience threshold to adopt more adequate policies (Scheffer et al., 2009). According to Rockström et al. (2009), humanity has already transgressed three of the nine known critical environmental thresholds, including the rates of climate change and biodiversity loss and the interference with the nitrogen cycle.

Palaeoecology provides illustrative examples of ecosystem resilience to environmental change at several temporal domains, occasionally followed by threshold responses, which are often, but not always, linked to climatic surprises and human impact (Carrón et al., 2001, 2010; Willis et al., 2007b; Willis and Bhagwat, 2010). A detailed analysis of these past records can be useful to identify the nature, extent and magnitude of external forcings needed to affect relevant ecosystem properties (i.e., biodiversity or composition) and improve conservation strategies. Of great interest is the potential for palaeoecological records to provide information about the combinations of biotic and abiotic processes that determine ecosystem resilience and the multiplicity of potential equilibrium states, which are two aspects considered critical for future biodiversity conservation (Willis et al., 2007b).

4. Palaeoecology and conservation: historical background

Several reviews have been published recently by eminent scholars on the usefulness of a palaeoecological approach for nature conservation, with emphasis on biodiversity issues (e.g., Lyman, 2006; MacDonald et al., 2008; Smol, 2008; Dietl and Flessa, 2009; Davies and Bunting, 2010; Willis et al., 2007a, 2010a, among others). These papers already provide an excellent summary of the findings on this subject. Here, we will only summarise them in a historical and conceptual fashion to provide a sound background for our own approach. The following historical review should not be considered a comprehensive account of all the papers and authors involved in the development of this field. Rather, it is an attempt to show how the main concepts have progressively emerged through time to conform to the present state of the art. Despite the relatively short-time elapsed, barely two decades, the evolution of ideas and proposals on this topic has been intense, likely because of the sound ecological background of the leading scholars involved.

The importance of palaeoecological knowledge for nature conservation began after 1960, when it was realised that many environments were seriously threatened by eutrophication, acidification, pollution and accelerated soil erosion (Oldfield, 2004). A couple of decades ago, the discussion about future global climatic and environmental changes, and their potential impact on Earth's life, determined the full establishment of palaeoecology as an important input for nature conservation (Delcourt and Delcourt, 1991). The International Geosphere–Biosphere Programme (IGBP) was created in 1986 by the International Council of Scientific Unions (ICSU) to study the interactions between biological, chemical and physical processes and interactions with human systems to develop and impart the understanding necessary to respond to global change (http://www.igbp.net). In 1991, PAGES (Past Global Changes) was launched as a core project of the IGBP to support research aimed at understanding the Earth's past environment to make predictions for the future (http://www.igbp-pages.org). Therefore, PAGES is responsible for palaeoecological knowledge in the context of global change. Despite this official appointment, the role of palaeoecology in conservation, and in ecological science in general, has often been underrated by many scholars and institutions, and palaeoecological results have traditionally had little impact on ecological thinking (McGlone, 1996). This has favoured the proliferation of reviews and opinion papers from palaeoecologists trying to convince the general ecological and conservation audience of the need for a palaeoecological approach (Rull, 2010a).

Although not properly acknowledged in many recent reviews and research papers on palaeoecology and conservation, the eminent palaeoecologist Margaret B. Davis pioneered this field and summarised the contribution of palaeoecological knowledge to nature conservation into five lessons related to biotic responses to environmental change as follows (Davis, 1989, 1991): 1) species respond individually to changing environments, which determines changes in community composition through time (Davis, 1981); 2) biotic responses have a time lag with respect to environmental shifts, where the magnitude depends on the duration of the life-cycle of the species involved; 3) disturbance regimes and climate changes are not independent, as is shown by the higher fire frequency in drier climates, for example (Davis, 1985); 4) some human activities, notably agriculture, can have more impact than climate change on shaping the landscape; and 5) presently, a variety of impacts are occurring that have not been seen in the palaeoecological records (warming, UV radiation increase, acid deposition), which may result in new species' assemblages. The first comprehensive account trying to relate palaeoecology and conservation was a special issue of Trends in Ecology and Evolution entitled “Biology and Palaeobiology of Global Climate Change”, coordinated by M.B. Davis. A general conclusion of this special issue was that predictions of the effects of climate change on biological systems required much more information on environmental physiology and its genetic control, at both organism and community levels (Davis, 1990). Shortly after, Hazel and Paul Delcourt, who greatly contributed to the view of palaeoecology as an ecological discipline, proposed that the mid-Holocene Hypsithermal Interval could be a partial analogue for global warming-induced biotic changes, which would be useful to anticipate the nature and
geographic patterns of biotic response to the initial 2 °C warming (Delcourt and Delcourt, 1991). After the analysis of several palaeoecological case studies, these authors have proposed that modern communities may disassemble and lose biodiversity by local or global extinction. Community reassembling is considered, but not in the same geographical areas and only after a lag of several millennia, depending on differential migration rates and the trajectories of species. Additionally, palaeoecological records may help to identify more vulnerable areas, which is useful information needed to select suitable sites for ecological preserves (Delcourt and Delcourt, 1991).

Coincidentally, another outstanding scientist who has led the field from the beginning, Brian Huntley, has published interesting reviews of palaeoecological case studies oriented to demonstrate its potential usefulness for biodiversity conservation (Huntley, 1990, 1991). According to this author, one of the main contributions is to provide long-term records that are able to elucidate if the present-day nature of communities, sites and landscapes are the result of either stability or change, including human disturbance. Like Davis (1989, 1991), Huntley (1990) emphasised the temporary nature of communities at a millennial time scale, mainly because of the individual character of the biotic response to environmental changes. The consequent differential migration rates of species (Huntley and Birks, 1983; Huntley and Webb, 1989; Huntley et al., 1989). Concerning conservation strategies, this author emphasised that strategies that rely upon the conservation of isolated sites in an otherwise inhospitable terrain will likely be unsuccessful. According to Huntley (1990), the main conservation concern should be the human pollution of the atmosphere, primarily in the form of global environmental change derived from increased amounts of CO2 and other greenhouse gases.

The Intergovernmental Panel on Climate Change (IPCC) was created in 1989 as a joint effort of the World Meteorological Organisation (WMO) and the United Nations Environmental Program (UNEP) to provide the governments of the world with balanced information and a clear scientific view of climate change (http://www.ipcc.ch). The first IPCC assessment report, published one year later, used palaeodata to show the millennial-scale relationship between atmospheric CO2 concentration and temperature over the last 160,000 years and noted that the projected warming for the 21st century would be 15–40 times faster than natural changes (Houghton et al., 1990). Concerning the potential biotic response to warming, the first IPCC report mentioned that palaeoecological studies were able to provide insights on potential future consequences, emphasising poleward migration and extinction (Tegart et al., 1990). The striking progress of palaeoclimatic and palaeoecological science experienced during the last two decades has produced high-quality historical records, with resolution and accuracy that make them comparable to actual measurements and, therefore, useful to validate explanatory and predictive models (Huntley, 1996; Rull, 2010a). Consequently, palaeodata are now recognised as a necessary component of climate change studies and its potential impacts, as described in the latest IPCC report (Parry et al., 2007; Solomon et al., 2007). The following is an account of the progress towards this realisation.

PAGES began by orienting the palaeo-research efforts towards three main points: 1) methodological homogenisation to make the records comparable; 2) focus on two temporal scales, namely the last two millennia (Stream I) and the two glacial cycles (Stream II); and 3) the disentangling of natural and anthropic causes of environmental change (Eddy, 1992). From a geographical perspective, the PAGES research was organised into three main Pole–Equator–Pole (PEP) terrestrial transects (i.e., the PANASH focus); the American continent (PEP-I), Asia–Oceania (PEP-II), and Europe–Africa (PEP-III). Other PAGES foci were as follows: the study of decade-to-century-scale climate variability (PAGES/CLivar intersection), the mechanisms and consequences of past climatic changes using ocean sediments (IMAGES), palaeoclimate and environmental variability in polar regions, and interactions between human activities, climate, and environmental processes (http://www.pages-igbp.org/science/formerfoci.html).

A few years after the creation of PAGES, Huntley (1996) noticed that, 30 years before, the understanding of mechanisms by which organisms and communities respond to a changing environment would have been only of academic interest, whereas today this knowledge is essential to nature conservation. During this time, palaeoecology (mainly pollen analysis and palaeolimnology) underwent significant developments in both methods and approaches in several major areas: chronological accuracy, which is derived from the application of new radiometric techniques; quantification and modelling of underlying patterns and processes, such as pollen dispersal or sedimentation rates; research design, including more precise targets and testable hypotheses; taxonomic accuracy, notably increasing the number of fossil taxa identified; spatial and temporal accuracy, by increasing the resolution or interpretations to meter-scale and yearly records; higher precision in the estimation of past environmental variables, such as temperature, precipitation, pH and salinity; the nature of training datasets and specific statistical methods; and the use of multi-proxy approaches that combine a variety of independent physico-chemical and biological indicators derived from more reliable reconstructions (Birks, 1996; Huntley, 1996). Despite these improvements and the potential contribution that palaeoecology would have made to nature conservation, the lack of synergy between conservation science and palaeoecology at that time was surprising (Birks, 1996). To illustrate the potential usefulness of palaeoecology in this context, Birks (1996), who has been instrumental in the development of modern palaeoecology, discussed using illustrative examples of how this discipline would be helpful for conservation assessments on the naturalness, fragility, and status of endangered species, and for supporting ecosystem restoration decisions. However, the lack of detailed autoecological information for most species of interest was still a handicap (Huntley, 1996).

Swetnam et al. (1999) defined “historical ecology” as a discipline embracing “data, techniques, and perspectives derived from palaeoecology, land-use history from archival and documentary research, and long-term ecological research from monitoring and experiments extending over decades”, and “time series from instrument-based observations of the environments”. According to these workers, historical ecology can inform conservation management by defining baseline conditions of vegetation communities, their range expansions and contractions through time, and by discriminating between natural and anthropic causes of environmental change. Historical ecology showed that the unpredictability of biotic responses to environmental change and the climate-organism non-equilibrium paradigm were key factors to consider. Therefore, the detection and explanation of historical trends and variability are essential for better nature management (Swetnam et al., 1999).

A review by Gorham et al. (2001) identified the following five major questions linked to conservation that palaeoecology can help to answer: What were the properties of communities, ecosystems, and landscapes prior to or following natural or human disturbances? What has been the pattern of recovery from disturbance, and was the prior state re-established? What is the nature and magnitude of natural variability and the frequency of unusually extreme conditions? Were communities and ecosystems relatively stable prior to disturbance, or were there significant trends or fluctuations in some of their properties? Do anthropic disturbances
have effects that are different in degree or kind from those of natural disturbances? These authors stress the wide range of spatial and temporal scales at which palaeoecological analyses are useful and the variety of environmental problems that it is able to address, emphasising freshwater acidification and biodiversity loss. Gorham et al. (2001) also discuss what they call the “surprise factor” in palaeoecology (see above). As a general conclusion, Gorham et al. (2001) stress the need for palaeoecological records to design more adequate environmental monitoring programs, and recommend the use of multi-proxy methodologies.

A synthesis of the results obtained by PAGES until 2003 was published in a book entitled “Palaeoclimate, Global Change and the Future” (Alverson et al., 2003). After analysing all the contributions of the PAGES book, Bradley et al. (2003) recommended the following policies: 1) reducing greenhouse gases to reduce global warming; 2) understanding, monitoring and possibly preventing changes in regional climate linked to thermohaline circulation; 3) sequestering fossil fuel carbon in terrestrial or oceanic reservoirs; 4) developing natural reserves to maintain biodiversity; 5) detecting and attributing global and regional change to natural or anthropic forcing; and 6) managing lake catchments, coastal zones and landcover to protect them for future generations. In the same PAGES book, Overpeck et al. (2003) analysed the response of the biosphere to the known past climate and environmental variability to extract information useful to predict potential future biotic reactions to ongoing global change. According to these authors, “assessments of future conditions without a strong palaeoenvironmental component will not be successful”, as “records of past climate and biosphere change are the only information we have on the nature and consequences of large environmental changes”. The resulting recommendations for future palaeoecological research were as follows: 1) improve the understanding of climate variability and biosphere responses and feedbacks; 2) emphasise high-resolution records that reveal the nature of interannual climate and biosphere change; 3) increase the number of investigations that examine the ecological consequences of future climatic change in light of past records; and 4) enhance the interaction among disciplines, such as palaeoenvironmental, ecological and land-use management, climate and climate modelling, and social science communities (Overpeck et al., 2003), Oldfield (2004) has provided similar recommendations and added the need for past analogues of the ongoing global warming, a better understanding of the role of solar variability, more information on hydrological variability, and a better understanding of Holocene eustatic sea-level changes.

As a result of this previous research and knowledge, the US National Research Council officially recognised the importance of palaeoecology for nature conservation and published a monograph entitled “The Geological Record of Ecological Dynamics: Understanding the Biotic Effects of Future Environmental Change”, which declared that “the understanding of the patterns, processes, and principles governing the participation of biological systems in environmental change — and understanding how those systems respond — is a scientific and societal priority of the highest rank” (NRC, 2005). In this sense, three initiatives were proposed: 1) to use the geological record as a laboratory to frame and test ecological theories at appropriate scales while encompassing a full range of earth conditions; 2) to study ecological responses to past climatic change to provide a more sound basis for forecasting the ecological consequences of future climate change and variability; and 3) to gain knowledge of the ecological legacies of societal activities to assess the ecological conditions and variability before human impacts and to gather the geohistorical records of how societal activities have affected present-day ecosystem dynamics. An important consequence of this official pronouncement was the commitment of the US National Ocean and Atmospheric Administration (NOAA), an organisation with a long tradition of involvement in research on palaeoclimate and management of marine fisheries, to take the lead not only in the management of global multi-proxy palaeoenvironmental databases and their forecasting potential but also in the incorporation of biotic responses to past climate changes as a proxy for future predictions (NRC, 2005), a task that is still one of NOAA’s primary mandates (http://www.ncdc.noaa.gov/palaeo/palaeo.html).

The importance of palaeoecology for conservation science experienced a promising increase, with regard to publications since 2007, coinciding with the publication of the fourth IPCC assessment, in which palaeoecology played a significant role (Parry et al., 2007; Solomon et al., 2007). The formerly limited use of historical evidence in biodiversity conservation has been attributed to the perception of insufficient resolution in both space and time, the lack of accessibility of palaeoecological records to non-specialists, and the lack of a positive attitude of many Quaternary scientists towards conservation issues (Willis et al., 2007a; Froyd and Willis, 2008). Since then, a number of palaeoecologists have devoted important efforts to make evident the direct usefulness of palaeoecology in conservation, not only from a theoretical perspective, as occurred previously, but also by providing examples and case studies and enumerating the areas in which the study of the past would be especially helpful. An interesting contribution, published almost at the same time as the fourth IPCC report, was made by Edwards et al. (2007), who explored the usefulness of palaeoecology to provide more robust estimates of temperature increase for this century. They concluded that modelling should benefit from the large amount of available palaeodata syntheses and palaeoclimatic reconstructions and that model simulations should focus on local rather than regional averages. The Oxford Long-Term Ecology Laboratory, headed by Katherine J. Willis, has made significant contributions to the utility of palaeoecology in conservation. This research team and several associated co-workers have shown that palaeoecology can significantly help conservation science, especially biodiversity conservation, in the following areas: 1) the identification of species at risk from extinction, 2) the setting of realistic goals and targets for conservation, 3) the identification of management tools for the maintenance or restoration of a given biological state, 4) the determination of baselines and natural ecosystem variability, 5) the understanding of ecological thresholds and resilience, 6) the assessment of climate change and conservation strategies, 7) the documentation of biological invasions, 8) the determination of rates and the nature of biotic response to climate change, 9) the management of novel ecosystems, and 10) the improvement of red lists and similar conservation tools (Willis et al., 2007a,b; 2010a; Froyd and Willis, 2008; Guillon et al., 2008; Willis and Bhagwat, 2010). The usefulness of palaeoecological knowledge for ecosystem restoration was emphasized by Jackson and Hobbs (2009). Additionally, Davies and Bunting (2010) identified 24 conservation questions, from the 100 posed by Sutherland et al. (2006), in which palaeoecology can make major contributions (Table 1). Concerning conservation strategies for protecting biodiversity, historical records can provide significant advice on the following: 1) managing novel ecosystems, as the emergence of unprecedented species’ combinations will likely be favoured by future climate change; 2) retaining ecological memory in the form of microrefugia; 3) conserving regions of high genetic diversity, as they may hold high evolutionary potential; and 4) developing resilience to threshold events (Willis et al., 2010b). Smol (2008) offered an excellent review and discussion, with many illustrative and convincing examples, on the contribution of palaeolimnological records to conservation aspects, such as acidification, eutrophication, metal and organic pollution, soil erosion,
species invasion, and ozone depletion, among others. Potential future ocean acidification has also been discussed recently, in the context of palaeoecological evidence, by Pelejero et al. (2010).

Conservation palaeobiology, a term coined by Flessa (2002), has been recently revived by Dietl and Flessa (2009). It has been defined as “a synthetic field of research that applies the theories and analytical tools of palaeontology to the solution of problems concerning the conservation of biodiversity” (Dietl and Flessa, 2010). This concept involves two different time scales: the “near-time”, which considers the last few million years, and the “deep-time”, which takes advantage of the entire history of life as a natural ecological and evolutionary laboratory. According to the same authors, the second approach sets the field apart from historical ecology, which is considered a sister discipline; such an approach is needed to deal with aspects like speciation, extinction or adaptation, which require a longer temporal perspective. The main palaeobiological contributions to conservation highlighted by Dietl and Flessa (2009, 2010) are the potential for defining baselines and natural variability, the identification of more vulnerable species to be protected, and the nature of biotic responses to climate change.

Much of the recent progress on the application of palaeoecology to conservation can be attributed to ongoing developments, such as higher chronological resolution, better models on atmosphere–biosphere system functioning, the incorporation of new chemical and biological proxies to reconstruct past species distributions and past climates, the availability of large geo-referenced databases with biogeographical and climatic data, and new approaches concerning fossil morphology and molecular DNA techniques (MacDonald et al., 2008). All of the previously mentioned authors recognise structural barriers to developing multidisciplinary teams and networks with ecologists and decision makers, but they emphasise the need for such collaboration for suitable nature conservation.

PAGES has progressively adapted its structure, objectives, programs and priorities according to new findings and the evolution of palaeoclimatology and palaeoecology outcomes. Currently, the PAGES research structure is organised around four foci and four Cross-Cutting Themes (CCT). Each focus covers a set of questions of prime importance to the global community. The CCT are more general in their scope and are of fundamental relevance to all foci and to palaeoscience in general (Fig. 1). Concerning

![Fig. 1. PAGES scientific structure: four thematic foci (coloured circles) are complemented by four circling Cross-Cutting Themes that are of relevance to all foci. Reproduced from http://www.pages-igbp.org/science/index.html.](http://www.pages-igbp.org/science/index.html)
5. Past analogues for future global change

Often, it is argued that the global change predicted for this century is unprecedented, mainly because of the high prognosticated rates at which it will occur. However, palaeoecologists continue to look for past analogues, for which high-resolution records are essential. The latter estimates predict, for this century, a likely increase in average temperatures between 2 and 4 °C, a sea level rise of around 1 m and an increase in atmospheric CO2 concentration of about 1000 ppmv, which is 2.5 times the present concentration (Solomon et al., 2007; Meinsenhausen et al., 2009). The better candidates for past analogues of such fast trends are changes associated with “abrupt” or “rapid” climate shifts, typically occurring at a centennial scale or below (Broecker, 2000). Willis et al. (2010a) provide several examples of palaeoecological records showing similar rates of change for temperature, sea level and atmospheric CO2.

The more recent of these events was the rapid warming that occurred during the transition between the Younger Dryas (YD) cold event and the Holocene, just before 11.5 kyr BP, when Greenland air temperatures increased more than 10 °C in about 60 years (Steffensen et al., 2008). According to Jackson and Overpeck (2000), an average increase of 5 °C in 50 years occurred at the end of the YD. Taken as a whole, the warming at the end of the YD proceeded at a rate of around 4 °C/century, which matches with the higher IPCC warming scenarios for the 21st century (Fig. 2). Vegetation responses to this rapid warming have been recorded palynologically in many regions of Europe and North America and include the following (Willis et al., 2010a): rapid expansion of local populations, large-scale species range shifts, community turnover, and formation of novel community assemblages (Williams and Jackson, 2007; Birks and Birks, 2008; Birks and Willis, 2008). There is no evidence of large-scale extinction in plants; only local or regional extinctions have been documented (Postigo-Mijarra et al., 2010), which contrasts with the conspicuous and well-documented mammal extinctions (see above). Especially noteworthy are the high-resolution studies around the YD performed in North Europe, which allowed detailed studies of the biotic response to warming. This made the long term temporal scales of palaeoecological results compatible with the fine temporal scales of modern observations (Birks and Birks, 2008; Bakke et al., 2009). The response of the different organisms studied, including both plants (pollen, macrofossils, mosses, diatoms) and animals (Chironomidae, Cladocera, Coleoptera, Trichoptera, Oribatidae), to warming showed clear differences in lags, rates and magnitudes (Birks and Ammann, 2000; Birks et al., 2000) that were likely due to different spatial scales, life-history temporal scales, sensitivities and ecological behaviours (Birks and Birks, 2008). The YD—Holocene transition seems to be an excellent past analogue for the predicted 21st century warming (Cole, 2009) because it occurred at very similar magnitudes and rates and acted on the same species that exist today.

Other potential past analogues are linked to the 1500-year Bond cycles, which occurred during both glacial and interglacial periods (Bond et al., 1997). These cycles were manifested as either abrupt warmings or coolings within glacial or interglacial conditions, respectively, and have been proposed as models to evaluate the possible consequences of the ongoing greenhouse gas buildup (Broecker, 2000). These cycles have been broadly identified, correlated and named, and the vegetation response to these cycles has been studied using pollen analysis (e.g., Tzedakis et al., 2004; Fletcher et al., 2010); however, suitable candidates for global warming analogues have not been proposed.

Some have also proposed the warming recorded at the Palaeocene—Eocene transition as another past analogue (McInerney and Wing, 2011). This warming trend initiated around 59 Ma and culminated with the Early Eocene Climatic Optimum, between 53 and 51 Ma (Zachos et al., 2008). Within this relatively gradual trend, a sudden acceleration occurred around 55 Ma, known as the Palaeocene—Eocene Thermal Maximum (PETM), during which the temperature increased more than 5 °C in less than 10,000 years (Zachos et al., 2001). During that time, the Earth was a “greenhouse Earth” (i.e., free from ice caps, even in the poles); average temperatures were between 8 °C and 12 °C higher than today, and the atmospheric CO2 concentration was around 1000 ppmv or higher (Zachos et al., 2008). Apparently, such a scenario could be similar to...
the scenario predicted under near-future global warming. However, the PETM occurred at rates 100 times lower than the 21st century predictions, and they took place during a gradual warming over approximately 10 million years. This is a very different situation from today’s "icehouse Earth", which is characterised by the glacial–interglacial alternation. Additionally, very few, if any, of the extant species, and probably few genera, existed by that time (Rull, 2008, and literature therein), which prevents the possibility of applying the niche stability assumption. Therefore, the PETM seems less powerful than the YD as a past analogue for the global warming prognosticated for this century.

A past analogue for the predicted sea level increase has been proposed by Virah-Sawmy et al. (2009), using a ~3 m rise that occurred in the Indian Ocean 2500–3000 years ago, based on fossil corals and higher beaches along the coasts of Madagascar (Camoin et al., 2004). At that time, these coasts were dominated by a highly biodiverse littoral forest, which was suddenly replaced by a heathland in less than 50 years. This heathland remained for thousands of years until the sea level fell again, and the littoral forest was re-established with a different composition than the former forest (Virah-Sawmy et al., 2009). This dramatic replacement of the littoral forest by the heathland has been interpreted in terms of a threshold response of the forest, determined by changes in salinity and aridity linked to the higher sea level (Willis et al., 2010b).

6. Indirect impacts of climate changes: human disturbances and human–climate synergies

We still know little about the probable impact of climate changes on the trajectory of human history, and we are even more uncertain of the environmental impact that human responses to those climate changes have had. In response to climate changes, human societies make adjustments to maintain their modes of life, or they try to lessen the magnitude of the derived impacts, thereby favouring the emergence of new environmental changes and problems with which future generations will have to cope.

Even when satisfactory records of climate change and high-resolution archaeological data exist for a given region, appropriate and sufficient palaeoenvironmental and/or palaeoecological information is missing, such as ecosystem recovery after depopulation or stresses on food resources after sedimentary settlement. This information is needed to allow for credible assertions on the causal links between human responses to climate and the derived environmental affectation. To establish such causal links, it is necessary first to show that climate impacts on human activities have indeed occurred and subsequently to show that these changes in human activities have prompted environmental and ecological modifications on a cause–effect basis.

Human responses to change may alter feedbacks between climate, ecological, and social systems, producing a complex web of multidirectional connections in time and space (Constanza et al., 2007). Ensuring sustainable future responses to the current global warming may partly depend on our understanding of this past web and how to adapt to future surprises. However, several questions become apparent: What is the time span needed by humans to become aware of an ongoing climate change and respond with an anticipatory behaviour? What kind of information do we need from the past to link the effect of past human responses to predictable human responses to current climate change? Are there really useful past analogues? In this section, we will examine some published palaeoecological, palaeoclimatic and anthropological studies to show how, and to what temporal and spatial extent, human responses to gradual and abrupt climate changes have affected the environment and ecosystems, and we contribute this information to the ecological debate and conservation management.

6.1. Gradual changes

The climate has changed over millennia, and these changes are likely to affect ecosystems and the physical environment, which often respond at the centennial to millennial scale and encompass long-term processes like succession, migration, extinction and landscape changes. However, gradual climate changes can trigger prompt shifts in ecosystems to an alternative state because of a loss of resilience (Scheffer et al., 2001). Drastic shifts in climate can also occur within a century or less (Dansgaard et al., 2003), triggering responses from the terrestrial biosphere and the physical environment in less than 200 years (Allen et al., 2000).

The ability of humans to recognise and respond to climate change is related to the limitation of the human scale and depends upon the culturally conditioned canons of perception and comprehension of the populations involved. Human societies are able to respond to climatic signals if they are within the scope of their perceptual time span. Within weeks to decades, rapid climate changes can be inferred from perceived or measurable modifications in direct climatic proxies (Hassan, 2009). Short-term environmental responses (such as resource shortages or habitat loss) are visible within the time frame of one to three human generations and prompt adjustments to maintain survival or social stability; however, long-term responses escape human awareness and cannot be taken into account. In fact, the long-term consequences of any decision to cope with climatic crises are commonly not within the lifetime of a person or a couple of generations (Hassan, 2009). The indirect effects of climate changes deal with the ways people respond to those changes and have received little attention, both in policy deliberations and scientific research with regard to current and past climate changes.

The climate varies gradually on millennial and centennial scales. Such changes are less likely to raise people’s awareness, and distant memories of how climate was before tend to fade gradually. However, practices that ensure survival in the face of gradual climate changes are slowly adopted, and cultural changes appear that can profoundly affect the environment (Hassan, 2009). An example might be the climate-driven origin of agriculture proposed by many authors (e.g., Reed, 1977; Richerson et al., 2001; Hassan, 2009; Turner et al., 2010a). This activity probably occurred as ecosystems responded to the drastic climate shift during the Pleistocene–Holocene transition, together with processes operating from within human social systems (Piperno et al., 2007). Richerson et al. (2001) hypothesised that, besides the decisive fact that the humans of the Last Interglacial were neither cognitively nor culturally able to develop agricultural subsistence, agriculture could not have easily evolved in the Pleistocene because of the harsh climatic conditions that prevailed. Instead, the beginning of plant-intensive, resource-use strategies would have started only after the gradual amelioration of climate took place during the Pleistocene–Holocene boundary. In fact, the oldest traces of agriculture date between 11,000 and 9000 cal. BP (Willcox, 2005; Piperno and Dillehay, 2008; Crawford, 2009). The associated changes from an ecological and environmental context would have created new selective pressures on hunter-gatherer human populations and their subsistence, leading to innovative and ultimately successful strategies that included exploitation of plant resources. For example, Piperno et al. (2007) illustrate this process for the Neotropics, showing that, during the late-glacial period (14,000–10,000 BP), three lake beds of the Central Balsas (Mexico) were dry and covered by open, cool adapted vegetation, with Zea mays as a constituent element. Strong shifts in climate and
vegetation associated with the last phases of tropical deglaciation took place as the Pleistocene was ending. Temperature and precipitation rose and the lakes filled up, becoming active human foci near water sources and allowing Z. mays to be cultivated at the lake edges, starting between 10,000 and 5000 BP.

During the Holocene climate conditions allowed the evolution of agriculture more or less simultaneously in vast areas with relatively warm, wet climates in the Near East, along with access to irrigation (Willcox, 2005). The transition from the barest beginnings of wild plant cultivation during the Neolithic to almost full dependence on domesticated foodstuffs occurred at a millennial scale (Liu et al., 2007; Piperno et al., 2007; Jones and Liu, 2009). The gradual climate change taking place was probably imperceptible to people, and the acquisition of a new innovation or technology happened only after several generations. At each point in time, lifestyle changes most likely seemed a result of traditions unrelated to the gradual warming trend. In contrast to these parts of the planet, intermittent and unpredictable droughts occurred in Southeast Amazonia. Droughts, together with environmental constraints on agriculture intensification and reliance on wild sources of protein, led to the perpetuation of nomadism and hindered cultural development (Meggers, 2007).

Human occupation and utilization of plant and animal resources have led to widespread landscape changes all over the world during the last 10,000 years. Land use and landcover changed because of water withdrawal; agriculture was most likely the primary way in which humans affected water regimes; irrigation and deforestation for agriculture have redistributed global evapotranspiration and altered the regional climate; the use of fertiliser led to nutrient runoff and promoted eutrophication in aquatic ecosystems around the world. These changes have driven a decline in ecosystem services other than agriculture, such as fisheries and flood regulation (Gordon et al., 2008). Environmental impacts derived from the post-Neolithic expansion of agriculture have been extremely important. Over the long-term, these impacts are probably as important as those generated by the industrial revolution. In fact, Ruddiman (2003) pushed back the start of the Anthropocene era by thousands of years based on a wide array of archaeological, cultural and geological evidence. The term “Anthropocene” was originally coined to denote the fact that current human activity was indeed changing the Earth on a scale comparable with some of the major events of the ancient past (Crutzen and Steffen, 2003). The defenders of the early Anthropocene hypothesis (Ruddiman, 2003; 2007; Ruddiman and Ellis, 2009) proposed that the start of forest clearance by humans reversed a naturally decreasing CO₂ trend 7000 years ago and promoted a new increase in CO₂ values, whereas early rice irrigation and livestock tending had a similar effect on the methane trend beginning 5000 years ago. In pre-industrial times, the annual rates of carbon release may have been more than 10 times lower, as populations were much smaller and technology was much more primitive than today, but the cumulative emissions could still have been extremely large because of the extended time interval over which they operated. The associated atmospheric warming was estimated to be 0.8–2 °C, on average. According to the authors, this would have been large enough to have stopped the glaciation of north-eastern Canada forecasted by two different climatic models.

If the hypotheses of climate-driven agriculture and early human-induced warming can be demonstrated, it could be assumed that the early human-induced global warming was an indirect effect of the onset of agriculture activities, giving rise to a positive feedback mechanism with important environmental consequences. The effects of these climate changes on the environment could have never been properly anticipated by humans because of the slow and gradual pace of both phenomena. Additionally, many of the effects are cumulative, which implies that they only achieved global significance by the widespread nature of their effects or because of their cumulative magnitude (Turner et al., 1990). In terms of conservation purposes, this means that the large-scale effects of slow environmental changes and the associated human responses are difficult to foresee and impossible to manage unless appropriate long-term records are available and considered when testing hind- and fore-cast model projections. The application of Quaternary palaeocology to conservation policies and actions could provide the necessary time perspective to anticipate impacts, such as succession, migration, extinction, and landscape changes, in a more realistic way. Time scales in conservation studies are typically limited to relatively short-time intervals and commonly ignore the magnitude of human responses and the dynamics of long-term processes with high environmental impact.

6.2. Abrupt changes

The palaeoclimatic record details how some climate changes were vast and in many cases occurred abruptly (Broecker, 2000; Alley et al., 2003). Rapid climate changes have often had profound effects on biological populations by imposing stronger selection and distance from environments to which they are adapted (Davis and Shaw, 2001).

The US National Research Council (NRC) study ‘Abrupt climate change (ACC): inevitable surprises’ defines ACC from two different points of view:

“technically, an abrupt climate change occurs when the climate system is forced to cross some threshold, triggering a transition to a new state at a rate determined by the climate system itself and faster than the cause. The cause may be chaotic and thus undetectably small (NRC, 2002, p. 14)”;

“from the point of view of societal and ecological impacts and adaptations, abrupt climate change can be viewed as a significant change in climate relative to the accustomed or background climate experienced by the economic or ecological system being subject to the change, having sufficient impacts to make adaptation difficult (NRC, 2002, p. 121)”.

Note that “abrupt” does not necessarily mean “severe”. The first definition highlights a fast transition to a new state and the apparent irrelevance of the cause, rather than the magnitude of the change. The second definition contrasts the abruptness of the change and its effects with the capacity of human and ecological systems to adapt and overcome the negative impacts over time or undergo remedial actions. This capacity depends more on ecological and social features, such as stability, resilience, vulnerability, flexibility and scale, than on the severity of the climatic disturbance (Hassan, 2009). The level of global climate variability and climate change that is tolerable varies enormously depending upon the geographic region and the society or ecosystem. The effect of ACC may be temporary, and the systems may recover if the environmental perturbation has not been too large (Alley et al., 2003).

ACC has had profound impacts on ecosystems (Davis and Shaw, 2001) and civilisations worldwide and is still the subject of much research by Quaternarists. Contrary to non-abrupt climate changes, ACC can be perceived and measured by humans because they take place in the frame of years or decades. Therefore, people are likely to recall and compare extreme events and deviations from “normal conditions” that they have experienced in their lifetimes, or those reported by previous generations (usually no more than three). Such awareness allows for adaptation or mitigation responses to the new conditions (Hassan, 2009; Turner et al., 2010b). Although ACC has been blamed on the collapse of complex civilisations (de Menocal, 2001; Weiss and Bradley, 2001), it has been proposed
that mismanagement of natural resources and the vulnerability of social organisations have played a key role in these outcomes (Hassan, 2009). One example is the Classic Maya Collapse (AD 750–830), which coincided with the most severe and prolonged drought of the last millennium. It happened at or near the time when other South and Mesoamerican cultures experienced declines, apparently also as a result of severe droughts. For example, the irrigation-dependent Moche civilisation in Perú suffered destruction and famines during the 6th century; the city of Tiahuanaco (México) was abandoned between AD 750 and 800; and the Tiwanaku civilisation, in the central Andes, collapsed around AD 1000 (Hodell et al., 2004, 2001; Weiss and Bradley, 2001). Droughts associated with the Maya Collapse occurred in a context of unsustainable use of resources, shifts in organisational and economic strategies and population movements, which likely hastened the civilization’s demise (Hassan, 2009).

Worldwide comparisons of the impact of different climate change events on past civilisations indicate that climate has been a driving force in some instances, and has played a significant role in others. In societies where environmental impacts of climate changes are not visible, climate shifts may be perceived simply as background noise (Catto and Catto, 2004). It is only recently that Quaternarists have looked at historical data to search for analogies with the present-day situation, where human emissions of greenhouse gases, combined with profound impacts on landscape and ecosystems, are leading to unprecedented transformations in the earth’s climate and creating new forms of vulnerability to rapid onset disasters and long-term environmental change (Anthes et al., 2006; Parry et al., 2007; WBGU, 2008). An increasing number of observational evidence indicates that climate change is already having effects on biological populations (Walther et al., 2002), such as changes in the extension of vegetative periods (Peñuelas and Filella, 2001) and the upward migrations of plants and animals (Peñuelas et al., 2002; Parmesan and Yohe, 2003), and on the environment, such as more frequent and severe hurricanes (Anthes et al., 2006) and greater fire risk (Flannigan et al., 2000).

Awareness of climate change triggers two types of human response, namely adaptation (involving actions aimed at preserving those systems of interest) and mitigation (actions to lessen the rate and magnitude of the change) (Turner et al., 2010b). Most mitigation efforts address the environmental change itself to prevent or mitigate climatic disturbances (Smithers and Smith, 1997). These efforts include seeking a reduction in CO2 emissions, encouraging the use of non-carbon or carbon-neutral energy sources, and the promotion of carbon sinks through land-use and habitat management. In poor and vulnerable populations of the world, climate-induced displacement may be the most likely mitigation response because of aridity, sea level rise, melting glaciers, coastal subsidence and erosion, which threaten roughly 600 million people (Johnson and Krishnamurthy, 2010). The German Advisory Council (WBGU, 2008) identified the following five regional "hotspots", where significant climate-induced displacement and conflict are expected to occur, most of them being the result of flooding, windstorms and rising sea levels: the Caribbean and the Gulf of Mexico; North Africa, especially the Nile Delta; South Asia, especially the Ganges— Brahmaputra Basin; Eastern China; and the Sahel zone. In this regard, paleoecological records have already shown how coasts dominated by a biodiverse littoral forest can be quickly replaced by a heathland in less than 50 years (Camoin et al., 2004).

Dependent on the way mitigation actions are performed, they can generate unintended environmental and ecological consequences (Paterson et al., 2008). Adaptation can result in purposeful responses or spontaneous adaptations to shifts in environmental conditions, which can differ from policy. Smithers and Smith (1997) identified three dimensions to accommodate human adaptation to climate changes: the force of change, the properties of the system that may influence its sensitivity, and the type of adaptation that is undertaken. More concretely, per capita income, inequality in the distribution of income, universal health care coverage and high access to information have been regarded as important determinants of adaptive capacity (Alberini et al., 2006).

Current approaches to ecosystem conservation still rely on the classic view of predictable and stable point equilibria of ecosystems (Wallington et al., 2005), and habitat management in most systems traditionally assumes linear succession-like trajectories (Schoon, 1999). Over the past several years, conservation and restoration biologists and managers have become aware that the potential for sudden shifts in ecosystem states is alarming, indicating that a system can be less resilient than expected (Suding and Hobbs, 2009). Non-equilibrium ecology may explain such behaviour. If disturbances can cause systems to shift between multiple stable states, it is reasonable to assume that indirect human impacts of climate change that are derived from adaptation or mitigation can widen the range of already vulnerable habitats, where threshold dynamics can occur and shift communities into new states that are difficult to reverse. Human activities to cope with climate change can incorporate new threshold triggers by converting transient events into persistent disturbances, by introducing chronic stress and starting new disturbances, or eliminating important disturbance patterns. The abrupt character of current climate change may accelerate these processes. The timely recognition of such situations is crucial to ecosystem management and conservation policies (Wallington et al., 2005). In this regard, threshold models in restoration and conservation that are being developed as a response to this shift in ecological thinking are central to cope with human response to climate change (Suding and Hobbs, 2009). These authors consider that current utilisation of threshold models in habitat management still lacks rigorous testing and underlying assumptions, and they suggest a framework for incorporating threshold models that effectively helps decision making and management on relatively short-time scales in human impacted systems.

There is increasing awareness of the need to assess the indirect effects of climate change derived from adaptation and mitigation actions: as people adapt to climate change across multiple scales, ranging from local to national and international, a wide range of new risks to ecosystems and biodiversity will emerge. Nonetheless, the effects of current climate change have not been pronounced enough to have prompted significant mitigation or adaptation efforts (Turner et al., 2010b).

Long-term ecological knowledge needs long-term biodiversity baselines and palaeoecological data, which are crucial for testing predictions about ecosystem thresholds and resilience (Dietl and Flessa, 2010; Willis et al., 2010a; Rull and Vegas-Vilarrubia, 2011). Some messages have been derived from these initiatives (Wallington et al., 2005; Suding and Hobbs, 2009) that are important for palaeoecology because the temporal dynamics of ecosystems have a number of implications for conservation management before considering the indirect human impacts to climate change:

- Ecosystems are complex and dynamic, and gradual or sudden changes in composition and structure can be expected over time. By understanding the history of a place to be preserved, we may improve our understanding, conservation actions and prediction of future responses, as it forms part of the essential context within which to evaluate current trends and probable future outcomes of any conflict, adaptation or mitigation actions.
- Rates of change can be highly variable and are essential information that managers need to maintain over the system they
are watching. The kind of managerial response to slow or fast changes as part of mitigation action may be very different and may determine the success of a given conservation strategy.

- Natural disturbance is an integral part of ecosystems with human assets and livelihoods and are important to consider. Natural disturbances plus anthropic initiatives may precipitate threshold dynamics of the ecosystem to be preserved. Adaptation strategies should take this synergy into account when trying to accommodate the new climate or climate derived situation.
- History of landscape use and human disturbance legacies may be important elements in shaping the current composition and structure of a particular ecosystem in such a way that the links between biotic assemblages and abiotic settings are not straightforward, thereby complicating the development of conservation actions.

7. Past fire records

Fire is a natural and/or anthropic element present in all vegetated lands. The main drivers of fire are the following: 1) the environment, mainly temperature, precipitation and the balance of atmospheric gas concentrations; 2) the flammability of fuels, mainly vegetation; 3) the existence of ignition sources; and 4) human activities (Flannigan et al., 2009; Whitlock et al., 2010). Understanding the complex mechanisms involved in fire ecology is not an easy task because internal and external variables act in a complex and non-linear fashion, resulting in synergies and positive feedbacks that lead to unexpected results (Bowman et al., 2009; Krawchuk et al., 2009). For example, vegetation flammability increases in dry climates because of a decrease in internal water content and the common occurrence and increased concentration of flammable metabolites, which may lead to fire events of unexpected virulence. This is the case of the so-called pyrophilous fire regimes or fires of regional character (Scott, 2000). For the purposes of the present review, the focus will be on the Quaternary, especially the last glacial cycle, when modern ecosystems were shaped with the help of anthropic fires.

The YD reversal has already been discussed as an example of rapid climatic change between 13 and 11.5 cal ky BP and as a potential historical model for present and future climatic shifts. The YD reversal also provides examples of increased fire incidence and their natural or anthropic nature. For example, Marlon et al. (2009) have reviewed the patterns of fire incidence and biomass burning during the YD in North America and have shown an increasing trend at both the onset and the end of this interval, with the last one being the more intense. The authors favoured a climatic origin for both, although they did not neglect other direct (deliberate or accidental burning) and indirect causes linked to the arrival and dispersion of human populations after crossing the Bering passage, such as the increase in flammable vegetation cover because of the decrease of herbivores, attributable to the well-documented megafaunal extinction prior to the YD. According to Marlon et al. (2009), the main climatic drivers of YD fires would have been the increase in average temperatures recorded since the onset of the Bølling-Allerød interstadial, which began approximately 14.7 cal kyr BP, just before the YD, and the abrupt warming

![Fig. 3. Estimated atmospheric oxygen levels over the last 600 Ma; adapted from Berner and Canfield (1989), and Scott (2000).](image)
at the YD/Holocene transition, which has been considered a past analogue for ongoing global warming. This climatic hypothesis has also been supported by other studies worldwide (e.g., Haberle and Ledru, 2001; van der Hammen and Van Geel, 2008). Moreover, Daniau et al. (2010) observed that, during the last glaciation, fire regimes varied synchronously with millennial-scale climate changes associated with Dansgaard–Oeschger (D/O) events, which are part of the above-discussed 1500-year Bond cyclic. According to the same authors, fire incidence increased during D/O warmings and decreased during rapid coolings, thus supporting the climatic hypothesis. The defenders of this hypothesis argue that, globally, climate has been the major control on fire regimes, even during the last two millennia, despite the dramatic increase in human population and the associated disturbances resulting from land use. They also argue that anthropic fires became more important after AD 1870 (Marlon et al., 2008). This contrasts with the proposal that, in the tropics, historical fire incidence has been regulated mainly by human activities and climate–human synergisms (Power et al., 2008). For example, ENSO variability coupled with human migrations and settlement shifts have been proposed as the main drivers for neotropical fire regimes since the mid-Holocene (Meggers, 1954; Uhl, 1998); However, now, and likely in the near-future, anthropic fires dominate the scene (Cochrane and Barber, 2009). Fires of human origin have also been proposed as important in the Neotropics during the Lateglacial, including the YD interval, and the Holocene (Bush et al., 2007; Rull, 2009b). As noted above, at a global scale, human fires would have been responsible for the earlier increase in atmospheric CO2 concentration and the onset of the Anthropocene in the early Holocene (Ruddiman, 2003, 2007).

The importance of Quaternary charcoal records as proxies for past fires and the associated changes in vegetation composition, diversity or local extinctions has been widely recognised (Whitlock and Larsen, 2001). These palaeorecords can be used not only to observe how past fires have disturbed the vegetation but also as modelling inputs to derive realistic scenarios of future fire–climate–vegetation–human relationships for management purposes. Whitlock et al. (2010) show the complexity of understanding fire behaviour at different levels and the need to incorporate long-term studies to obtain a more accurate view of fire events as a part of Earth-system dynamics. According to these authors, the following important points should be considered in the study of past fires: 1) fire regimes operate at different spatial and temporal scales, with distinct drivers at each scale; 2) climate–fire, fuel–fire, and human–fire relationships also act at different scales; 3) there is a huge impact from human practices where climate and fuel are not limiting factors, such as occurs in extreme conditions like deserts (no fuel) or rainforests (no favourable climate for ignition); and 4) the “fire regime” concept should be revised. The current definition of fire regime only considers short-term studies that are unable to capture the full range of fire variability in many ecosystems. Whitlock et al. (2010) have introduced the “super-fire regime” concept to better address the characteristic nature of fire within a biome by taking into account all the forcing factors involved, including humans at the appropriate temporal scales. This concept, with an important palaeoecological component, is more powerful to anticipate future variability within a given biome because it considers long-term ecosystem behaviour and humans as part of ecosystems and “climate changers” (Whitlock et al., 2010).

As an effort to manage the available information on fire palaeorecords, the Global Palaeofire Working Group (GPWG) was established to follow the rules of the IGCP Fast Track Initiative on Fire (http://www.gpwg.org). The open-access Global Charcoal Database (http://www.ncdc.noaa.gov/paleo/impd/gcd.html), created in 2003, gathers the available fire palaeorecords since the LGM. Using this database, Power et al. (2008) have observed that fire activity has varied globally and continuously since the LGM in response to long-term changes in global climate and short-term regional changes in climate, vegetation, and human land use. Fire frequency has been continuously increasing since the LGM until the present, with a significant increase in spatial heterogeneity beginning around 12 cal ky BP. The hope is that this database will contribute to a better understanding of fire patterns at global, regional and local scales to optimise conservation practices.

8. Neotropical examples

The Neotropics is a key region from a conservation perspective because of its amazing biodiversity and endemism patterns and the occurrence of extensive rainforests, some of which are in nearly pristine states; the Neotropics contain several conservation hotspots (Myers, 2001; Huber and Foster, 2003). This region is less well known than the northern temperate areas from a palaeoecological point of view, but several studies are available showing its suitability to provide case studies with conservation significance and highlighting the need for further studies (e.g., Bush, 1995, 2002; Bush and Silman, 2007; Mayle et al., 2007; Figueroa-Rangel et al., 2010; McKey et al., 2010). The examples provided here have been selected from our own research in northern South America.

8.1. The YD cooling–warming shift in the northern Andes: biotic responses

As stated above, the rapid warming initiated at the end of the YD is a potential analogy for the predicted future global warming, and its study may help forecast near-future biotic responses and facilitate the adoption of conservation policies. The occurrence of the YD cooling in the Neotropical region has been debated for decades. Several palaeoecological records favoured its existence, whereas others did not (Hansen, 1995; van der Hammen and Hooghiemstra, 1995; Rull et al., 2010a). Some records reported a cooling around the YD dates, but the dating was not good enough to provide the necessary bracketing for accurate correlations (van’t Veer et al., 2000; Mahaney et al., 2008). The first clear record was obtained in the Cariaco Basin (Fig. 4), where both palaeoclimatic reconstruction and dating supported a cool and dry event coinciding with the YD (Haug et al., 2001; Lea et al., 2003). On the continent, the first undisputed YD equivalent has been found recently in the sediments of a high-altitude Andean lagoon (Los Anteojos) after a multi-proxy study. Sedimentological and geochemical indicators documented a sudden cooling and a glacier advance initiated at 12.85 cal ky BP, with a maximum of around 3 °C below present average temperatures at 12.65 cal ky BP, followed by a rapid warming initiated at 12.3 cal ky BP, which ended near the YD–Holocene boundary. As in Cariaco, the Anteojos cooling was also characterised by dry climates (Stansell et al., 2010).

The response of vegetation to the cooling was heterogeneous, where the more sensitive taxa were Podocarpus (a genus of trees living at the upper altitudinal forest levels), Polylepis sericea (a tree that forms almost monospecific stands above the upper forest line, or UFL, within the “páramo” open vegetation), Huperzia (a genus of ferns typical of humid “páramos”), and Isoëtes (an aquatic pteridophyte growing submerged in shallow waters, including lake shores) (Fig. 5). Other taxa that responded to the cooling were the families Asteraceae and Poaceae, but the homogeneous pollen morphology of their genera and species prevented the necessary taxonomic resolution to analyse their detailed responses to climate shifts. However, these families characterise the open “páramo” vegetation in the northern Andes and increased during the cooling, which indicates an increase in this vegetation type. All the sensitive
genera and species mentioned reacted to the Anteojos cooling by decreasing their percentages, but the most sensitive taxa were \textit{Polylepis} and \textit{Isoëtes}, with pollen and spores that disappeared from the sediments during the maximum cooling and did not re-appear until the onset of the warming that initiated at 12.3 cal BP. This was interpreted as a downslope migration of the sensitive taxa and a decrease in lake levels because of cool and dry climates (Rull et al., 2010b).

Among the trees from the upper forest levels recorded through palynological analysis (including other well known indicators of this vegetation type, such as \textit{Alnus}, \textit{Hedyosmum} and \textit{Weinmannia}), only \textit{Podocarpus} has reacted to the YD climate shifts. This indicates that the taxonomic composition of these forests changed because of the different individual requirements of each taxon. It is also notable that sensitive taxa showed immediate responses to both the cooling and the subsequent warming, without any time lag at the resolution of the study, which is decadal to centennial (Fig. 6). This indicates that these taxa not only are the more sensitive but also react quickly to climate shifts, even the rapid ones. Consequently, they would be useful to monitor the biotic responses to ongoing warming to prognosticate the expected biotic changes in the near-future. It is known that high-altitude biomes are highly sensitive to climate changes and are therefore preferred environments for global change studies (Ives, 1999). Also, the Andean forests are known to be among the more biodiverse ecosystems on the planet, holding outstanding hotspots for conservation (Myers, 1999).
Therefore, the information obtained in the Anteojos case study on the biotic responses of high-altitude ecosystems to rapid warming should be considered for management purposes.

8.2. Fire, climate change, and savanna expansion in the Gran Sabana (Guayana region)

The Gran Sabana (GS) is a vast region of approximately 18,000 km² located in SE Venezuela, between the Orinoco and the Amazon Basins. The GS is a huge island of savannas within the normally forested Guayana landscape. These savannas form large extensions of treeless grasslands and are intermingled in some places with forests and shrublands, developing typical forest-savanna mosaics (Huber, 1994a). The GS is the homeland of the Pemón indigenous group, from the Carib-speaking family. It has been postulated that this culture reached the GS relatively recently, or approximately 300 years ago (Thomas, 1982; Colson, 1985), but some archaeological evidence may suggest an earlier human occupation beginning in the early Holocene (Gassón, 2002). A definitive assessment on the age of human settlements in the GS is

![Fig. 5. Summary percentage pollen diagram for the Lateglacial, as recorded in the Lake Anteojos sediments (northern Andes). The Anteojos cold reversal (grey band), equivalent to the YD, was defined according to independent sedimentary and geochemical proxies. The left column is the summary of all pollen taxa subdivided into three categories representing forest trees and páramo shrubs and herbs. The more sensitive pollen taxa are depicted individually. Algae remains include Pediastrum, Botryococcus, Debarya, Spirogyra and Zygnema (Rull et al., 2010b); Redrawn from Stansell et al. (2010).](image)

![Fig. 6. Correlations of the Pollen Index (PI) and the Polylepis curves with selected physico-chemical palaeoclimatic proxies measured in the same core and referential palaeoclimatic reconstructions containing the YD event (Cariaco and GISP). The PI was calculated as the ratio between sensitive taxa: (Podocarpus + Polylepis + Huperzia)/(Asteraceae + Poaceae). Gray bands represent the stadials based on the GISP isotopic curve. The glacier advance defined by Stansell et al. (2010) in the Anteojos core is indicated by a box around the MS and Ti curves. Note the parallelism among the curves of physico-chemical proxies for climate change, and the PI, and especially, the rapid response of Polylepis to environmental shifts; Redrawn from Rull et al. (2010b).](image)
not yet possible. Fire is an important component of the Pemon culture. They use it every day to burn great expanses of savannas and occasionally forests (Fig. 7). However, the high fire incidence of between 5000 and 10,000 observed fires per year (Huber, 1995; Leal, 2010) contrasts with the nearly inexistent agriculture or magic (Kingsbury, 2001; Rodriguez, 2004, 2007).

Caroni River Basin that includes the control of energy (EDELCA) has developed a conservation program for the protection areas, such as national parks, biosphere reserves and world heritage sites (Huber, 1995, http://whc.unesco.org/en/list/701). Despite this, only about 13% of fires lighted by the Pemon are controlled and extinguished (Sletto, 2008; Bilbao et al., 2010). This low success is due to the large extension of the GS, the high number of daily fires compared to the available prevention and extinction resources, and the unpredictability of fire locations (Rodriguez, 2007; Bilbao et al., 2010). There is a vivid debate between EDELCA and several local ecologists, on one hand, and the Pemon and their defenders, on the other, about fire dynamics in the GS. The first defend the current protection rules and the ecological knowledge, whereas the second argue in favour of the indigenous traditional practices, in which fire is an essential element (Rull, 2009a). A subjacent question in this debate concerns the origin of the GS savannas, given their isolated nature among the extensive Guayana and Amazon rainforests, in a climate more favourable for forest formations. It has been postulated that the open vegetation type of the GS may be due either to the action of anthropic fires or to palaeoclimatic and edaphic factors (Fölster, 1986; Fölster and Dezzeo, 1994; Huber, 2006).

Palaeoecological records can help to address these problems by providing additional tools for conservation purposes. The proposal of the climatic hypothesis predated the palaeoecological study of the region and was based on palaeoclimatic and biogeographic assumptions. According to this hypothesis, the GS is a relic of the former extension of savannas that dominated the Neotropics during the LGM because of the prevalence of drier climates (Eden, 1974). Recent palaeoecological studies have documented the replacement of either forests or shrublands by savannas during the Lateglacial and the early Holocene, thus bringing into question the climatic proposal. In the Mapauri locality, a mountain cloud forest dominated the landscape until approximately 10.2 cal ky BP, when it was replaced by a treeless savanna (Rull, 2007a) (Fig. 8). In the Lake Chonita catchment, the Lateglacial was characterised by a shrubland with no modern analogues, which persisted during the entire YD and was substituted with a treeless savanna in the YD–Holocene transition (Montoya et al., 2011) (Fig. 9). In both cases, the treeless savannas persist until today. These biotic shifts coincided with the late YD–early Holocene global warming (Kaufman et al., 2004; Kaplan and Wolfe, 2006) and were locally characterised by a decrease in the hydrological balance. In the case of Lake Chonita, the disappearance of the shrubland coincided with a charcoal peak, indicating a sudden increase of fire incidence (Montoya et al., 2011). In Mapauri, local forests appeared slightly after the vegetation replacement, when the savannas were already established, but regional forests were already increasing during the vegetation replacement (Rull, 2009b). Therefore, a synergistic effect between climate and fire seems to have been the driver of the establishment of present-day savannas in these areas. The origin of these fires (natural or anthropic) is still unknown, but their temporal patterns and intensity are very similar to recent records of anthropic fires. In addition, it has been proposed that the consistent occurrence of high charcoal concentrations is a strong indicator of human presence, even in the absence of other obvious evidence of land use (as is the case of the GS) (Bush et al., 2007). Therefore, a Lateglacial to early Holocene establishment of human populations using fire cannot be dismissed, though more clear evidence is still needed (Montoya et al., 2011).

![Fig. 7. Savanna fires in the Gran Sabana near Stanta Elena de Uairén (Photo: V. Rull).](image)
The GS forests and shrublands did not recover, resulting in a clearance that remains today. This is true even in the absence of further increases in fire intensity, as is shown in the palaeoecological record of Laguna Encantada covering the last 7500 years (Montoya et al., 2009). According to present-day ecological studies, the burning of GS forests triggered an irreversible degradational sequence leading to the establishment of savannas, and forest recovery was prevented by edaphic impoverishment, both in nutrients and water retention capacity (Fölster, 1986, 1992; Fölster and Dezzeo, 1994). This low forest resilience is supported by the Urué record, through the palaeoecological reconstruction of a secondary succession after a fire event that eradicated the forest from the site. The detailed record of the last millennium showed a degradational sequence from the original forests to open secondary forests of different composition, followed by shrublands, fern communities and, finally, treeless savanna, in the absence of further local fires (Rull, 1999). There were also increases in the moisture balance in the last centuries that were not followed by forest recovery, except for the establishment of "morichales" or palm stands dominated by Mauritia flexuosa (Fig. 10), which is a typical element of the present-day GS gallery forests (Rull, 1998). The same sequence has been observed in other GS lakes during the last two millennia (Rull, 1992). In all cases, the Mauritia arrival and expansion coincided with a remarkable charcoal increase, which likely represents the establishment of modern GS inhabitants with common burning practices (Montoya, 2011) (Figs. 11 and 12).

In summary, fire and its synergies with climate are largely responsible for the present-day GS landscape. Palaeoecological reconstructions reveal a progressive forest clearance and savanna expansion since the YD, mainly because of the low resilience of GS...
forests, which were unable to recover after fire, even under favourable climatic conditions. Forest clearance has accelerated during the last two millennia because of an intensification of human-driven fire incidence. Therefore, it could be predicted that savanna expansion at the expense of forest and shrub formations will continue in the GS if the current fire management continues. Fire extinction practices are not a solution because of their above-mentioned low efficiency. Forest conservation should focus on preventive rather than corrective policies; however, the deep rooting of fire practices in the Pemón culture is a handicap. At present, there is a multidisciplinary initiative to improve communication among the different actors involved in the GS conservation (Bilbao et al., 2010). However, it largely relies on the Pemón knowledge of fire and the a priori correctness of their practices for landscape management. Palaeoecological knowledge presented here should be considered for a more objective approach.

8.3. Biotic responses to environmental change in the Guayana Highlands’ undisturbed ecosystems

The Guayana Highlands (GH) are an assemblage of more or less flat summits of the quartzite/sandstone table mountains, locally called “tepuis”, located in the neotropical Guayana region of northern South America (Figs. 13 and 14). From a biogeographic point of view, the GH summits above 1500 m (which are the highest) constitute a biogeographic province called Pantepui (Huber, 1987, 1994b). The tepui summits can reach extensions up to about 1000 km² and altitudes up to 3000 m, and they contain amazing levels of diversity and endemism, as manifested in the approximately 2500 known species of vascular plants, of which almost 30% are Pantepui endemics and around 25% are local endemics or restricted to one single mountain (Berry et al., 1995; Berry and Riina, 2005). The Pantepui biomes have lasted in an almost-pristine state of conservation because of their remoteness and inaccessibility and, probably more importantly, the lack of natural resources to exploit (Huber, 1995). This makes them unique environments to record natural climatic variability and the corresponding ecosystem responses (Rull, 2007b, 2010c). The GH have

Fig. 13. View of the Tirepón-tepui and its densely forested slopes, close to the Eruoda-tepui, in the Chimantá massif (Photo: V. Rull).

Fig. 12. Fires affecting a morichal community near Santa Elena de Uairén. Note that *Mauritia flexuosa* palms are not burnt because of the rapidity in which fire propagates through herbs (Photo: V. Rull).

Fig. 11. Summary percentage pollen diagram and charcoal concentration for the last millennia recorded from Lake Chonita sediments (Gran Sabana). Note the coincidence between the sudden appearance and increase of *Mauritia* pollen and the onset of fire incidence, interpreted as the establishment of the present-day indigenous culture. Modified from Montoya (2011).

Fig. 14. General view of the Ilú-Tramen tepuian massif (Photo: V. Rull).
been free from direct human disturbances, such as mining for gold and diamonds, logging and burning, shifting cultivation, population pressure, and tourism, which are common in the surrounding lowlands and midlands (Huber, 1995). However, one of the main concerns for Pantepui biota is the potential effect of the ongoing global warming if the IPCC predictions for this century are accurate (Rull and Vegas-Vilarrúbia, 2006). Recent studies suggest that, under this scenario, a drastic reduction in the available habitat for summit taxa because of warming-driven upward migration would result in the extinction by habitat loss of around 80% of the Pantepui species (Rull et al., 2009, Nogué et al., 2009a).

Palaeoecological records may help to evaluate the reliability and the eventual impact of such estimates by comparing them with the natural upward migration rates since the LGM. Based on two sequences from the lowlands and midlands around the Guayana Highlands, it has been estimated that natural rates of temperature increase since the LGM have been approximately 0.025 °C/century, which corresponds to upward shifts of around 5 m/century (Bush et al., 2004; Rull, 2007a). The estimated rates for the projected global warming of the 21st century in northern South America are 3 °C/century (Solomon et al., 2007), which is equivalent to an upward migration of approximately 500 m/century (Rull and Vegas-Vilarrúbia, 2006; Nogué et al., 2008a). Therefore, global warming rates would be 100 times the natural rates for Pantepui species. Unfortunately, the lack of autoecological studies for the Pantepui taxa prevent an inference of their potential response to this warming acceleration, but similar rates have been measured for recent upward migrations forced by the ongoing global warming in other mountain regions (e.g., Kelly and Goulden, 2008; Lenoir et al., 2008). To test the ability of Pantepui species to migrate at similar rates in response to global warming, a comparison of the present-day situation with historical botanical records is needed (Rull et al., 2009).

The available palaeoecological information for the tepui summits refers mainly to the Holocene. Most records proceed from the Chimantá tepuian massif, except for two from the Guaiquinima massif. In the Chimantá massif, three tepuis (Acopán, Amurí and Toronó) showed an outstanding vegetation constancy over the last 6000 years, with only minor local reorganisations between Stegolepis meadows and Bonnetia gallery forests, which is likely due to lateral migration of water currents along the extensive alluvial plains (Rull, 2005a). In the Eruoda-tepui, of the same massif, vegetation constancy was also the norm during the Holocene (Nogué et al., 2009b) (Fig. 15). However, a gentle vegetation shift at approximately 100–200 m elevation has been linked to an upward displacement of the altitudinal ecotone between the Stegolepis meadows and the Chimantaea shrublands in the Churí-tepui, approximately 2.5 cal ky BP (Rull, 2004a,b,c) (Fig. 16). The Guaiquinima records showed successive replacements of three vegetation types – Stegolepis meadows, Archytaea gallery forests and...
upland forests—during the last 8 cal ky BP, which were attributed to moisture changes, probably of regional extent (Rull, 2005b). Based on these tepuian records, palaeoecological and palaeoclimatic correlations have been elusive, and the norm seems to be an extended biotic constancy spiked with local ecological rearrangements or a spatial heterogeneity in the responses to minor temperature and moisture changes experienced during the Holocene (Rull, 2010c). Another factor to be considered is the sensitivity of the studied sites to climatic changes and variations. For example, the Churi site, the only one in which an altitudinal ecological shift has been recorded, is in a key ecotone. Other Chimantá localities, notably Acopán, Amuri and Toronó, are near the middle of the altitudinal range, where a small climatic oscillation is not enough to determine a significant vegetation change. The observed spatial heterogeneity of vegetation responses to Holocene climatic changes in the tepuian summits prevents any generalisation and complicates forecasts relating to global warming. On the one hand, local moisture changes seem to have been the decisive factor for biotic change, except for Churi, where a slight temperature shift seems to have played a role in vegetation replacement. This complicates the predictions of future responses of Pantepui biota to global warming and suggests that forecasting based only on temperature changes may overestimate the magnitude of projected extinctions by habitat loss. In addition, the potential existence of microsites with suitable environmental conditions for the persistence of the potentially threatened species would relax environmental stresses and favour the survival of a number of theoretically endangered species. Indeed, the potential occurrence of glacial and late-glacial microrefugia was first proposed for the tepuian summits (Rull et al., 1988; Rull, 2009c).

In summary, modelling based on present-day biogeographical patterns, physiography and an average IPCC scenario for the 21st century suggest catastrophic extinctions by habitat loss in the Pantepui vascular flora, which involves the extinction of a significant number of endemic species; however, palaeoecological records provide a more optimistic view, suggesting the possibility of survival for a number of species because of their ecological tolerance and/or ability to thrive in microrefugia. In the first case, only ex situ conservation strategies (botanical gardens, seed and germplasm banks, etc.) would be able to guarantee species’ conservation, whereas in the second, in situ practices would contribute to biodiversity preservation (Rull et al., 2009). The hope is that modelling and palaeoecological results will progressively have better agreement, when models will be properly parameterised and calibrated based on palaeoecological knowledge and use lower grid sizes to account for local topographical and microclimatic features (Willis and Bhagwat, 2009; Sublette et al., 2011).

9. Conclusions

Palaeoecological knowledge provides valuable clues to understand biotic responses to natural and human disturbances, as well as the synergies between them, and is a necessary input for nature conservation because it furnishes essential tools to anticipate potential biological consequences of ongoing global change, thereby contributing to better conservation policies. From the above literature review on the subject, the following lessons have been highlighted:

- The significance of palaeoecological studies for nature conservation issues could be considered a manifestation of the importance of past records for the elucidation of long-term ecological processes, which are difficult to resolve with only neoecological surveys that only cover several decades. Indeed, processes such as ecological succession, secular migration, extinction, adaptation, and microevolution may take centuries or even millennia to occur, depending on the duration of the lifecycle of the involved species. Therefore, predictions about potential biological consequences of near-future environmental changes rely on an appropriate knowledge of biotic responses to past, secular to millennial, environmental changes, which are only available from palaeoecological records.
- The available palaeoecological knowledge shows that potential biotic responses to environmental changes transcend the framework of neoecological studies. For example, the old ecological debate about individual or collective responses to environmental disturbances has been recently resolved in favour of the first option in the context of palaeoecological records. An interesting consequence is the possibility of new unknown species combinations with no modern analogues resulting from future environmental shifts. Past records have already shown similar situations and provided useful analogues for hypothesis testing about potential future scenarios.
- Acclimation and/or adaptation, with the first relying on phenotypic plasticity and the second involving genetic changes of potential evolutionary significance, have been proposed as two possible reactions to future global warming and as alternatives to extinction by habitat loss. Genetic adaptation seems to be an unlikely option given the short temporal frame involved. However, palaeoecological and molecular phylogenetic studies would support the possibility of rapid evolutionary changes resulting from the existence of pre-adapted genomes that would eventually be successful under the new predicted climatic conditions.
- In the context of the palaeoecological data available so far, the response of organisms and communities to future global warming is not expected to be homogeneous but rather highly dependent on local and regional environmental conditions. This highlights the importance of conducting micro- and mesoscale surveys that consider local particularities for conservation planning.
- Current predictions of species extinction by habitat loss would overestimate these risks and should be revised because they rarely consider the possibility of survival within small local...
Throughout history, humans have not always been aware of the environmental changes, such as the Pleistocene glaciations, and contribute to an understanding of the present-day genetic structure of species and their populations. To properly revise the existing extinction forecasts, models using spatial grids as small as possible are recommended to capture local topographical and micrometric conditions as potential future microrefugia. From this perspective, and accounting for the palaeoecological background, some authors propose that spatial reorganisations without extinction will be the dominant biotic response to the near-future global changes.

- Predictions about future biotic responses to future changes commonly rely on an implicitly assumed equilibrium between organisms, their communities, and the environment. However, palaeoecological records show that biotic reactions would be much more complex because of the non-linearity of the ecological processes involved, which would lead to unexpected biotic responses through enhanced feedback. The more common mechanism for the occurrence of these "surprises" is the existence of inherent biotic thresholds that, once surpassed, may lead to different potential stable states of the affected ecosystems. Environmental changes need not be necessarily abrupt to produce threshold responses; even subtle and gradual shifts may determine ecological surprises. It is also possible that ecosystems never attain equilibrium, and transient states perpetuate because of the recurrent action of environmental change.

- The resilience of an ecosystem, or its capacity to absorb disturbances with no significant changes, is a critical feature in the biotic response to environmental reorganisations. Past records provide examples of the type and magnitude of external drivers needed to modify significant ecosystem properties and determine threshold responses. One of the main lessons from this is that ecosystems may express their resilience when confronted with environmental shifts by attaining several possible equilibrium states, as manifested in changes in biodiversity and/or composition, without losing their ecological functions. Palaeoecological reconstructions also show that such ecological changes are often irreversible (hysteresis).

- Palaeoecology is able to provide past analogues for projected global warming and the corresponding biotic responses, which is of high relevance for delineating successful conservation policies. The global warming recorded at the end of the Younger Dryas (ca 13.0 to 11.5 kyr BP) emerges as one of the more powerful of these analogues because both magnitude and rate of change parallel those predicted for the present century. We should also note that the main biotic response to this palaeoclimatological event seems to have consisted of ecological reorganisations and changes in community composition because of differential species migration patterns and rates. So far, it has not been possible to associate large-scale extinctions to the YD climatic reversal. High-resolution studies of the YD would be decisive, not only to improve our knowledge on biotic responses of present-day species to climate shifts but also because it would provide the necessary link between palaeoecology and modern observations.

- Throughout history, humans have not always been aware of ongoing climate changes. Gradual shifts have occurred imperceptibly but have promoted profound and irreversible cultural changes, whereas abrupt changes have prompted adaptation or mitigation responses. In both cases, new environmental changes and problems have emerged. A suitable collaboration between palaeoecology and anthropology may furnish the necessary information to establish causal links, not only on the influence of climate changes in human activities but also on how the resulting changes in human practices may in turn affect the environment and ecological function. This, together with a sound knowledge of where and how sensitive ecosystems develop, would greatly improve forecasting and anticipation skills when confronted with current climate change.

- Mismangement of natural resources combined with vulnerable social organisation seem to have played a key role in precipitating the collapse of complex past civilisations under climatic stress. Present drawbacks, such as the exponential growth of human population under a globalised economy based on market rules and consumerism, promote social injustice and cause the overexploitation of natural resources, the uncontrolled increase of greenhouse gas emissions, and other environmental damages. Using historical examples as analogues would illustrate the structural weaknesses of modern societies, leading to the inability to appropriately cope with current and future climate change. The non-linearity of ecological processes would be an additional handicap to successfully adapt to or mitigate these unprecedented transformations of Earth’s climate. Indeed, negative synergisms would cause the appearance of new threshold triggers, promoting chronic stresses, which may result in the appearance of new disturbances and the elimination of others. The timely recognition of such situations is crucial for ecosystem management and conservation policies.

- The correct assumptions of threshold conservation models will strongly rely on knowledge about key indicator parameters and their spatial and temporal patterns of change. Ecological monitoring and surveys spanning weeks to decades are able to provide relevant indicator variables and threshold patterns. However, as noted above, many ecological processes occur over timescales that exceed the so-called long-term observational ecological datasets. Real long-term ecological knowledge needs long-term biodiversity baselines and palaeoecological data, which are crucial for testing predictions about ecosystems thresholds and resilience. Palaeoecological records may help answer key questions about the threshold dynamics of ecosystems, such as the following: What is the capacity for rebuilding an ecosystem? Have there been several stable states over time? What is the biotic capacity of a given ecosystem to cope with disturbance triggers? Are there particularly resilient species? Which situations have increased the vulnerability of a system in the past, favouring a change of state? Can transient states be recognised? Where and when are thresholds more frequent?

- One of the main drivers of ecological change introduced by humans has been fire incidence, through increases in both frequency and intensity. The occurrence of wildfires has been extensively documented through the history of the biosphere before humans and has been related to the flammability of vegetation, which is dependent on the O2 atmospheric concentration, climate, internal water content and the accumulation of flammable compounds. Fire has been considered an important factor for the distribution of vegetation because, in the absence of burning, forests would double their present global cover at the expense of open vegetation dominated by grasses. Fire incidence has increased and coincided with the rise of human populations and their geographical dispersal, especially from approximately 20,000 years ago. Fire events recorded during the last glaciation seem to have been synchronous with millennial-scale warmings associated with D/O events, thus...
suggesting that climate shifts have favoured their occurrence. The same is true for the YD, when an increase in fire incidence has been documented, especially during the YD—Holocene global warming. Since that time, the causes of fires documented in the palaeoecological records — either natural or anthropic — are difficult to ascertain, but there is a general consensus that human activities have been the main drivers of fire during the last millennia, especially since the 19th century. Another important element to consider is the occurrence and suitability of the available fuel (mostly vegetation). Synergistic effects among climate, human activities and fuel characteristics have also been considered decisive factors because of the occurrence of positive feedbacks.

- The neotropical case studies presented here emphasise the importance of concentrating efforts on the YD shift and the associated biotic responses as an analogue for ongoing global warming, the potential role of fire in the development of present-day neotropical landscapes, the spatial heterogeneity of biotic responses to climate changes, and the need for revising current habitat loss estimates as a consequence of global warming predicted for the 21st century. Another interesting consequence for conservation is that palaeoecology may provide decisive clues for choosing more appropriate sites and more sensitive organisms and communities to study biotic responses to both natural and anthropic disturbances. For example, high-altitude Andean environments would be a preferred target because of the occurrence of conspicuous vertical migrations in response to climatic shifts, which are easily recognisable in palaeoecological records. Also, the detection of sensitive taxa, such as Podocarpus, Polyplepis, Huperzia or Isoëtes, which are widely distributed in the northern Andes, provide suitable indicators for monitoring and modelling the biotic consequences of climate shifts, possibly at a regional level.

- The Gran Sabana and the Guayana highlands provide examples of contrasting situations. Indeed, despite a low population density, anthropic fires are the major driver of present-day landscapes in the Gran Sabana, whereas the tepui summits are a unique example of pristine ecosystems in which natural environmental changes have been the main force for ecological change. Concerning indicator taxa, in the context of the palaeoecological results, M. flexuosa would be considered a good proxy for the establishment of present-day indigenous culture in the Gran Sabana, and taxa, such as Chimantaea and Stegolepis, emerge as keystone species in the understanding of the responses of tepuian vegetation to climatic shifts. These two examples also reveal the suitability of ecotones as preferred palaeoecological targets to provide key information on biotic responses to environmental change of natural and/or anthropic origin.

The historical review carried out in this paper provides evidence that, despite its relatively recent inception in the conservation arena, palaeoecology is becoming an important and necessary discipline needed to properly understand subjacent ecological processes useful for management purposes. However, the lack of synergy between palaeoecologists, neoeocologists, anthropologists and conservation scientists is still a handicap. We hope that this paper may contribute and improve the situation by showing the variety of aspects in which palaeoecology can be utilised for conservation and by showing that palaeoecological input, beyond a theoretical proposal, should be based on sound knowledge, including real case studies and specific propositions and recommendations with straightforward applicability.

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