

Interpreting Resilience through Long-Term Ecology: Potential Insights in Western Mediterranean Landscapes

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Abstract: Many studies on ecosystem resilience often lack sufficiently long time scales to determine potential cycles of landscape response. In this paper we review some examples on how palaeoecology has provided an important aid to modern ecology in understanding ecosystem resilience. We focus some of these ideas on two Holocene sites from Southern Spain (Zoñar and Gádor) where current plant diversity is very high. Both sites presented resilient pattern at centennial and millennial time scales with several stable phases. Vegetation in Zoñar proved to be very sensitive to environmental changes, especially moisture availability while forest in Gádor responded elastically to fire and drought to a threshold level when the forest recede to a more open landscape. We conclude that any serious attempt to understand ecosystem resilience should include the long-term perspective.

Keywords: Palaeoecology, landscape dynamics, biodiversity, Holocene, palynological methods, Iberian Peninsula.

INTRODUCTION

The ability of ecosystems to absorb disturbances, to be changed and then to re-organise and still have the same identity, retaining the same basic structure and ways of functioning (Resilience Alliance, 2009), is the definition of resilience and it is one of the key concepts of modern ecology (Holling, 1986). This notion is becoming of great relevance as international concern increases about global change and the cascade response it may provoke upon the biosphere.

Most of the studies dealing with the resilient response of ecosystems are made from the neontological perspective, which precludes the use of pre-instrumental time scales

(Arnan *et al.*, 2007; Elmqvist *et al.*, 2003; Ludwig *et al.*, 1997; Válega *et al.*, 2008). This implies that potential cycles defining the thresholds of a system may not ever be totally disclosed and researchers have to contend with results truncated by the short term approach (Redman and Kinzig, 2003). This is partially due to the lack of interdisciplinary projects aiming to the holistic conception of ecosystems dynamics and the difficulty of defining concepts such as stable ecosystem and equilibrium dynamics. Understandably, cross-discipline studies demand a greater investment, both in funding and human resources, and the definition of a new glossary accessible to several disciplines within natural sciences and beyond them when social scientists are involved.

The need to understand past environmental fluctuations to improve our knowledge on the current global change, biodiversity management and conservation has been widely acknowledged (e.g. Birks *et al.*, 2003; Oldfield, 2005; Tinner and Ammann, 2005; Dearing *et al.*, 2006). Assessing the impact of climate change on biodiversity is difficult because changes occur slowly and effects of climate change interact

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with other stress factors already imposed on the environment.

As the long-term approach is implicit to palaeoecological and archaeological methods, past landscape response to disturbance and resilient patterns can be revealed. These disciplines have already been proved useful in determining ecosystems dynamics under disturbance regimes, both human and naturally driven (e.g. Birks, 1996; Godwin, 1956; Carrión, 2002; Virah-Sawmy *et al.*, 2009; Willis *et al.*, 2005; Willis and Birks, 2006; amongst many others) but they are still much required in biodiversity hot-spots. In these regions there is an urgent need for estimating ecosystem functionality, response and resilience under disturbance. This might be the case of Mediterranean Iberia, whose great biodiversity represents ca. 83 per cent of the European flora (ten thousand out of the twelve thousand species identified in Europe) and fourteen percent of the plant species found here are endemic to the region (Rey Benayas *et al.*, 2002).

This article briefly reviews examples of palaeoecological research used to understand resilience patterns and it shows its potential with reference to the Iberian Peninsula.

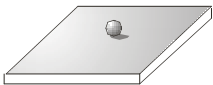
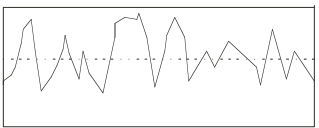
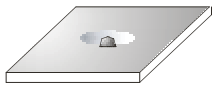
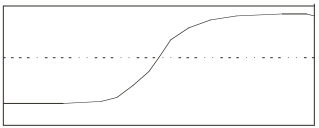
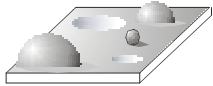
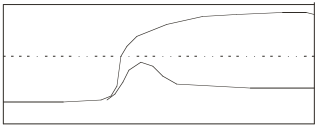
Connecting the terms of resilience and stability to those of long-term ecology demands a definition of how we understand these concepts. Hence we will explore different Nature models describing a variety of systems and we will define the main palynological working hypothesis, setting the frame in which our review is elaborated. Since the focus of this paper is mainly on vegetation dynamics reconstructed from fossil pollen records, we will interchangeably use the terms palaeoecology and palaeopalynology. We discuss possible interdisciplinary approaches to the investigation of

ecosystem resilience through the analyses of two records from southern Iberia.

ECOLOGICAL THEORY: RESILIENCE AND STABILITY UNDERSTOOD AS NATURE METAPHORS

There is a great variety of definitions for terms like resilience and stability in the ecological literature (e.g. Holling, 1986; McCann, 2000; Moore, 2005). This range of interpretations has led to different views on ecosystem functioning with subsequent policies for nature management based on those assumptions. These different views on nature have been described by Holling *et al.* (2002) as nature myths or metaphors. These models help us to understand the patterns and processes in different systems, being all of them only partially true. Nature flat (Table 1) describes a system in which there are few or no forces affecting stability, the processes that influence the position of the ball are totally random and there are no clear feedbacks from nature after disturbance. Nature balanced exists at or near equilibrium which can be static or dynamic. Hence if the system is disturbed it will return to an equilibrium through a negative feedback, thus this is the view of fixed carrying capacities for animals and humans, underpinning logistic growth. In Nature resilient we observe multistable states some of which become irreversible traps while others become natural alternating states that are experienced as part of the internal dynamics. This dynamics results from cycles organized by fundamentally discontinuous events and nonlinear processes. There are periods of exponential change, periods of growing stasis, periods of collapse and readjustment and periods of reorganization. Instabilities would organize the system as much as stabilities do.

Table 1. Nature metaphors defined by Holling *et al.* (2002). In Nature flat the ball's position is determined by random or stochastic factors so there is no feedback establishing stable states. Thus the ball can be moved in all directions stochastically amongst different statuses that are never the same. In Nature balanced, the ball is in a static or dynamic equilibrium so if the system is disturbed, and the ball gets out of the pocket, it will only go back to equilibrium through a negative feedback. In Nature resilient several stable states exist so the ball alternates through several states that are experienced as part of the internal dynamics. This is the case of the hyperbolic processes where the system's ascent is inevitably followed by a descent moved by internal dynamics. Alternatively the system will need an exogenous input to move back to a pocket, to the flat area or to start the hyperbolic process

	Stability	Processes	Depiction of myth	
			Metaphor	Trajectory
Nature flat	None	Stochastic		
Nature balanced	Globally stable	Negative feedback		
Nature resilient	Multiple stable states	Exogenous input and internal feedback		

It is important to recall that these metaphors are mutually complimentary and none of them is essentially right or wrong. They are rather incomplete perspectives of a spatial and time-hierarchical reality.

In the context of these metaphors our understanding of resilience not only refers to the ability of an ecosystem to recover after an impact, but also to the ability to learn from the disturbance, i.e. to reorganize in a way that buffers future disturbances. A resilient system is forgiving of external shocks (Holling *et al.*, 2002; Resilience Alliance, 2009) and as resilience declines the magnitude of a shock from which it cannot recover gets smaller and smaller.

A key question regarding ecosystem resilient response is to what extent the ecological baselines are recovered, or to what extent the system is stable. Ecological baselines in a system are arduous to define as the initial identity of it is always self-history dependent, i.e. community composition, ecosystem services, α and β diversity are conditioned by previous phases of the system. Thus assessing the status of a particular ecosystem requires the long-term ecology study of it and here is where palaeoecological studies might be used as a useful approach.

The stability concept refers to the tendency of a system to return to a position of equilibrium when disturbed, where equilibrium in a mechanical system is defined when the forces acting on it are in balance. This “balance”, when applied to ecosystems, usually refers to steady flows of energy and materials, rather than to a system whose components do not change (Ludwig *et al.*, 1997). Thus, in systems with multiple stable states, where the dynamics are organized by non-linear processes, there will be phases of constant change, readjustment or collapse and periods of reorganization (see Resilient Nature, Table 1), where both kind of periods define the system’s behaviour as much as the stable phases. These systems with several stable states have been often described from the control theory perspective, as system with hysteresis, where non-linear responses trigger abrupt changes from one stable state to the next (Janssen and Scheffer, 2004; Válega *et al.*, 2008).

Bearing this background in mind, and from the practical perspective, we will consider resilient behaviour if vegetation is able to recover a former state after disturbance, where functionality is somehow restored after a reorganization period. This functionality is focused on regaining important ecosystem characteristics; floristic composition, species richness and biomass (Carpenter *et al.*, 2001; Redman and Kinzig, 2003). When the disturbance crosses a certain threshold it may lead to an irreversible response such as species extinctions.

Our assumption on how to interpret resilience is as arguable as how to measure and characterize stability. This is one of the long-lasting debates in theoretical and applied ecology as it has been traditionally linked to increasing diversity (MacArthur, 1972; Huston, 1997; May, 1973). However, a growing number of studies in the last decade indicate that, if true, the positive correlation between diversity and stability does not necessarily imply a causal relationship between them (McCann, 2000; May and McLean, 2007). An experimental approach is needed to determine whether stability of an ecosystem is dependent

upon its diversity or whether these are correlated but merely coincidental events (Ives and Carpenter, 2007).

ILUSTRATING RESILIENCE IN PALAEORECORDS: LINKING PALYNOLOGY TO THEORETICAL MODELS

The growing number of palaeoecologists researching on ecosystem’s functionality at different time scales has helped to develop our understanding of resilient patterns and long-term vegetation responses in various regions. These studies are mainly focused on vegetation reconstruction and have tried to overcome the traditional assumptions of palynology (Mazier *et al.*, 2006; Sugita, 2007b; Sugita, 2007a; Kunes *et al.*, 2008; Cañellas-Boltà *et al.*, 2009; Gosling *et al.*, 2009; Pelánková & Chytrý, 2009), frequently expressed as limitations (Sugita, 1994; Davis, 2000; Broström *et al.*, 2008; Bunting *et al.*, 2004; Gaillard *et al.*, 2008), where pollen productivity and the spatial pattern of pollen source is often unknown.

In the next lines we explain how some of these studies have defined very relevant ecosystem features at long-term scales. We have chosen some examples where the authors originally aimed to answer ecological questions in different ecosystems worldwide. These are just some of the very many palaeoenvironmental studies proposing that stochastic, complex, resilient responses over longer time scales defined much of the current ecosystem’s behaviour. As for the Iberian cases, we revisit two examples of late Holocene vegetation change, raising different issues regarding resilience and thresholds to illustrate the potential insight of palaeoecological studies in modern ecological questions in Mediterranean Iberia. We have chosen two palaeorecords in Southern Iberia as this is one of the largest European plant diversity hotspots (Blondel and Aronson, 1999) and it also presents a long-term human agency (Sánchez-Quirante, 1998).

Identifying Disturbance, Assessing Biodiversity and Testing Equilibrium Theory

The late Holocene record of Lake Erhai, in SW China (Dearing, 2008), is a good example of threshold response and disturbance recognition within the frame of a resilient nature. Dearing presents a three thousand multiproxy record where Monsoon intensity, forest cover, flood intensity and gullying are reconstructed using isotopic composition of speleothemes, fossil pollen contents, magnetic susceptibility and sand fraction. The palaeoenvironmental and documentary records from Erhai suggest different and complex associations through time between a number of human, climate and landscape processes. In order to reveal these relationships Dearing plots phase diagrams for the climatic disturbances (Monsoon and flooding) *versus* the landscape consequences (forest cover and soil erosion). While the direct analyses of the proxies suggest fairly smooth relationship between vegetation and disturbance, the phase diagrams showed a threshold response and alternative steady states at different periods during the last three thousand years. This resilient response would have been otherwise impossible to identify without the long-term perspective.

In a similar research carried out by Virah-Sawmy *et al.* (2009), resilience of an endangered sector of Madagascar's littoral forest is assessed using biodiversity changes and community fluctuations in a 6500 years multi-proxy record (fossil pollen, diatoms and charcoal). The authors found that marine transgressions, drought and agriculture activated abrupt, but differently intense, threshold responses which promoted new forest states, similar to those found today. This study highlights the need of palaeoecological research in order to test current stability of, presumably, well preserved environments.

Long-term ecology is also a valuable tool for the study of ecosystems traditionally discussed in the context of equilibrium and non-equilibrium theories (DeAngelis and Waterhouse, 1987) as savanna environments (Sankaran *et al.*, 2005 amongst many others). The coexistence of trees and grasses as a two-layer system in savannas has been explained using various mechanisms as main controls under the prism of equilibrium theoried. Time series analyses on the pollen and charcoal studied by Gillson (2004) on a 1500 years record from Tsavo National Park (South Kenya) suggested that state- and- transition dynamics and cyclic phases of tree

abundance of near 250–500 years shaped the savanna rather than a unique controlling factor. Thus savanna in that region is determined, at least locally, by non-equilibrium dynamics and fluctuation between tree and grass-dominated landscapes might be tuned by threshold rather than monotonic responses to disturbance. This is very relevant for rangeland ecologist as prediction of tree recruitment and bush encroachment would be potentially possible under stochastic and non-equilibrium models than under equilibrium theories.

THRESHOLD RESPONSE TO ARIDITY AND STABILITY CYCLES AT MILLENNIAL TIME-SCALES

Despite the considerable amount of palaeoenvironmental sequences in the Iberian Peninsula (Martinez Atienza, 1999; Red Paleodiversitas, 2009) virtually none have been used by ecologists, biodiversity managers and National Park authorities in order to assess the vegetation response to disturbance. However as new protected areas are planned in the Iberian Peninsula, and the existing ones may need to be updated, palaeoecological methods would help managing

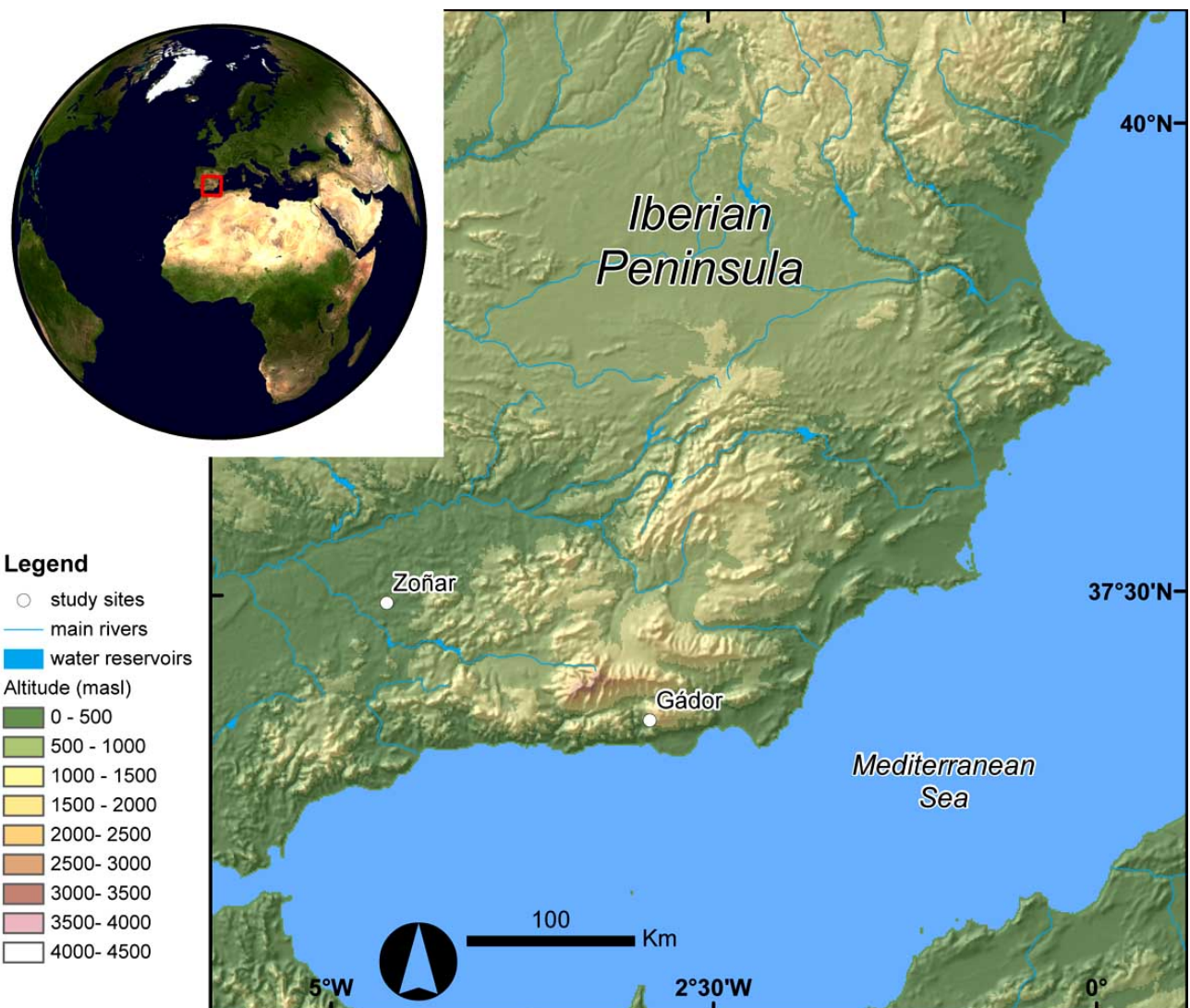


Fig. (1). Location map for the Iberian Peninsula sites mentioned in this paper.

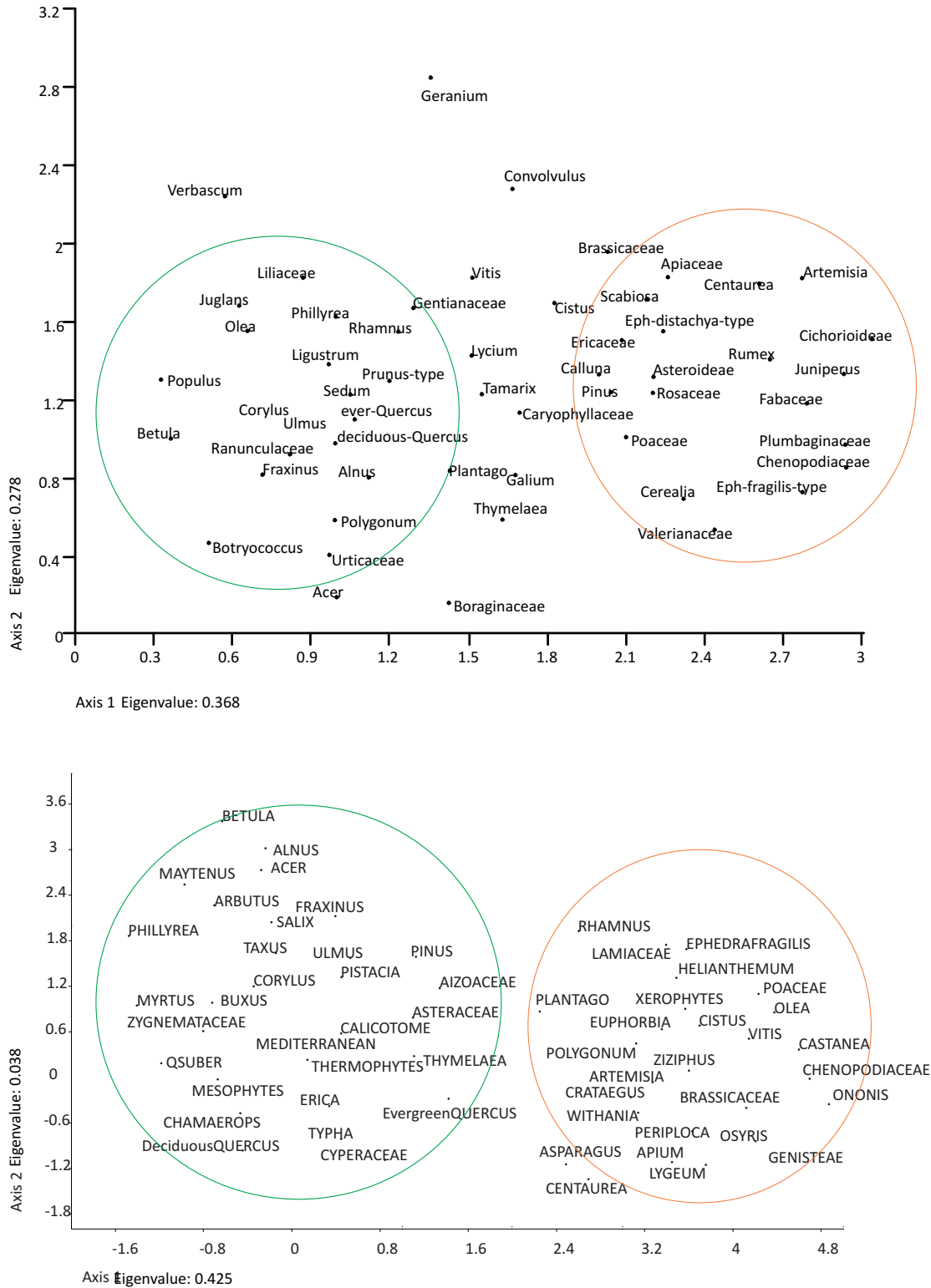


Fig. (3). DCA plots for Zoñar (top) and Gádor (bottom) pollen assemblages. The orange circle in Zoñar includes taxa indicating aridity or landscape opening while in Gádor it includes besides indicator of human activity. Green circles include in both cases most of the trees (see text for interpretation).

Axis 1 while those indicating landscape openness (and relatively drier conditions as *Juniperus*) presented higher values in the same axis. We interpret axis 1 therefore as an

openness index, where higher values would indicate declining forest cover, while the opposite is expected when the axis 1 values are lower. When the samples factor scores

are plotted in the pollen diagram (Fig. 2) we observe that open landscape phases often concurred with low lake levels, indicating a relatively rapid vegetation response to hydrological changes. This is particularly true during the humid phase in the Iberian Roman Humid Period (IRHP) between 2.6 and 1.6 cal Kyr BP, where tree cover rapidly increased at the onset of the humid phase and decreased during a dry pulse during that phase (ca. 2.1-1.8 cal Kyr BP). Zoñar's vegetation proved to be very responsive to drier conditions, with an immediate response to changing moisture availability. These fluctuations did not end collapsing the system though, as forest cover re-expanded after 1.8 cal Kyr BP forced by environmental drivers.

For investigating Zoñar's stability we estimated pollen diversity over time using rarefaction analyses. The pollen sample richness can give a measure of floristic richness, which indeed provides an indication of the landscape's plant diversity. Consequently, the number of pollen types in a sample provides the simplest measure of taxonomic richness. However, this approach is not exempt of problems as the number of pollen types in fossil samples depends on the sample size and pollen counts in a set of fossil samples are rarely of the same size (Odgaard, 1999; Odgaard, 2001). Thus, if the counting effort is not similar, comparison of richness among different samples will not be valid. One solution would be to use indices that are not dependent on the sample size or standardizing the sample size by any method (Hurlbert, 1971; Heck *et al.*, 1975). Currently the most used method to estimate fossil records' pollen diversity is rarefaction analysis. This standardizes sample size and does not consider abundances of different pollen types (Birks and Line, 1992; Foote, 1992).

The analysis of rarefaction allows the estimation of palynological richness [E(Tn)] that would be obtained if the counts of the different samples had the same size. In addition, it is one of the simplest methods to calculate the diversity of the fossil record (Seppä, 1997; Birks and Line, 1992) (see more on additional material). The diversity curve for Zoñar (Fig. 2) shows that abrupt richness changes are not linearly linked to the major hydrological fluctuations. Thus, as available moisture increased from 3 to 2.6 cal Kyr BP, pollen richness initially increased, followed by a rapid decline until ca. 2.1 cal Kyr BP, when a new rise in richness corresponds to a rapid fluctuation towards drier conditions. This pattern is observed in successive hydrological changes; every abrupt change in the lake level is linked to a change in pollen richness. Regardless the direction of the hydrological variation, biodiversity seems very sensitive as changes in the moisture availability may lead to the expansion of new taxa, or to those that were outcompeted during the preceding hydrological conditions, as it may provoke the loss of some other taxa. Hence a climatic change would have initially provoked a diversity increment linked to the appearance of pioneering species that would have been outcompeted by others if climate conditions remain constant.

Linear correlation was calculated between the charcoal area and the most relevant taxa, including the richness curve. Charcoal area is a measure of fire activity estimated from charcoal particles smaller than 150 microns (Higuera *et al.*, 2008; Tinner and Hu, 2003; Brunelle *et al.*, 2005; Whitlock *et al.*, 2003). No significant relationship was found, however

fire activity generally increased during the dry periods without appearing to promote variations in the plant richness. Fire activity could have not reached a critical threshold to radically change diversity, or could have acted preserving the existing diversity being this formed by fire prone taxa (*Pistacia*, Ericaceae, or Chenopodiaceae).

In the context of the nature metaphors defined at the beginning, Zoñar's landscape between ca. 3.3 cal Kyr BP and 740 BP could correspond to a resilient Nature where several multiple stable states can be identified. Every perturbation promotes an alteration in the system's diversity and landscape structure but it ultimately leads to a new state which will remain until a new threshold is crossed, triggering the change.

The Gádor Record

The site of Gádor lies at high altitude (ca. 2000 m.a.s.l.) surrounded by arid and semi-arid depressions near Sierra Nevada, in southern Spain (Fig. 1). This is currently a treeless area that had a much more forested past during the Mid-Holocene, as deduced from a six thousand years pollen and charcoal record (Carrión *et al.*, 2003) (Fig. 2). It is also an area where human activities have been evident since the Neolithic (7.4-5.7 cal Kyr BP) and where fire has had a determining role in shaping vegetation at millennial time scales (Carrión *et al.*, 2007; Sánchez-Quirante, 1998).

Similarly to Zoñar, we would need to understand how sensitive vegetation has been over time to disturbance and to what extent there is a resilient pattern in the vegetation response.

DCA was performed on the 192 samples forming the Gádor pollen record, between ca. 6.8 and 1.1 cal Kyr BP. We found that axis 1 (Fig. 3) plots with higher values taxa either linked to human activities such as *Castanea*, *Olea* and *Plantago* or to drier climatic conditions, as *Ephedra* and Chenopodiaceae. Lower values in axis 1 correspond to either arboreal taxa (*Pinus*, deciduous *Quercus*) or Mediterranean shrubs (*Pistacia*, *Chamaerops*). We therefore interpret axis 1 as a human activity-degradation gradient, where samples with higher values would point to increasing human agency.

Rarefaction analyses were carried out on the Gádor data obtaining a curve of pollen richness variation presented in Fig. (2).

Interestingly, the DCA plot for the Gádor record samples, which have been joined with a line in Fig. (4), show a linear trend where every of the four group of samples presents a different composition from the next and the previous groups in axis 1 and 2. Despite different sample number (23 in Zoñar versus 97 in Gádor), this is relevant as Zoñar samples showed similar pollen compositions with very little variation, while Gádor presents four main phases with different compositions, where there is no return to any previous landscape composition. This might be related to the fact that the Gádor record presents a clearer trend towards landscape opening at millennial scales. This tendency does not seem to revert to more forested landscapes at any particular time. Response to environmental change in Gádor has probably been as fast as in Zoñar but likely more linear than in the latter. Comparison between the two sites should

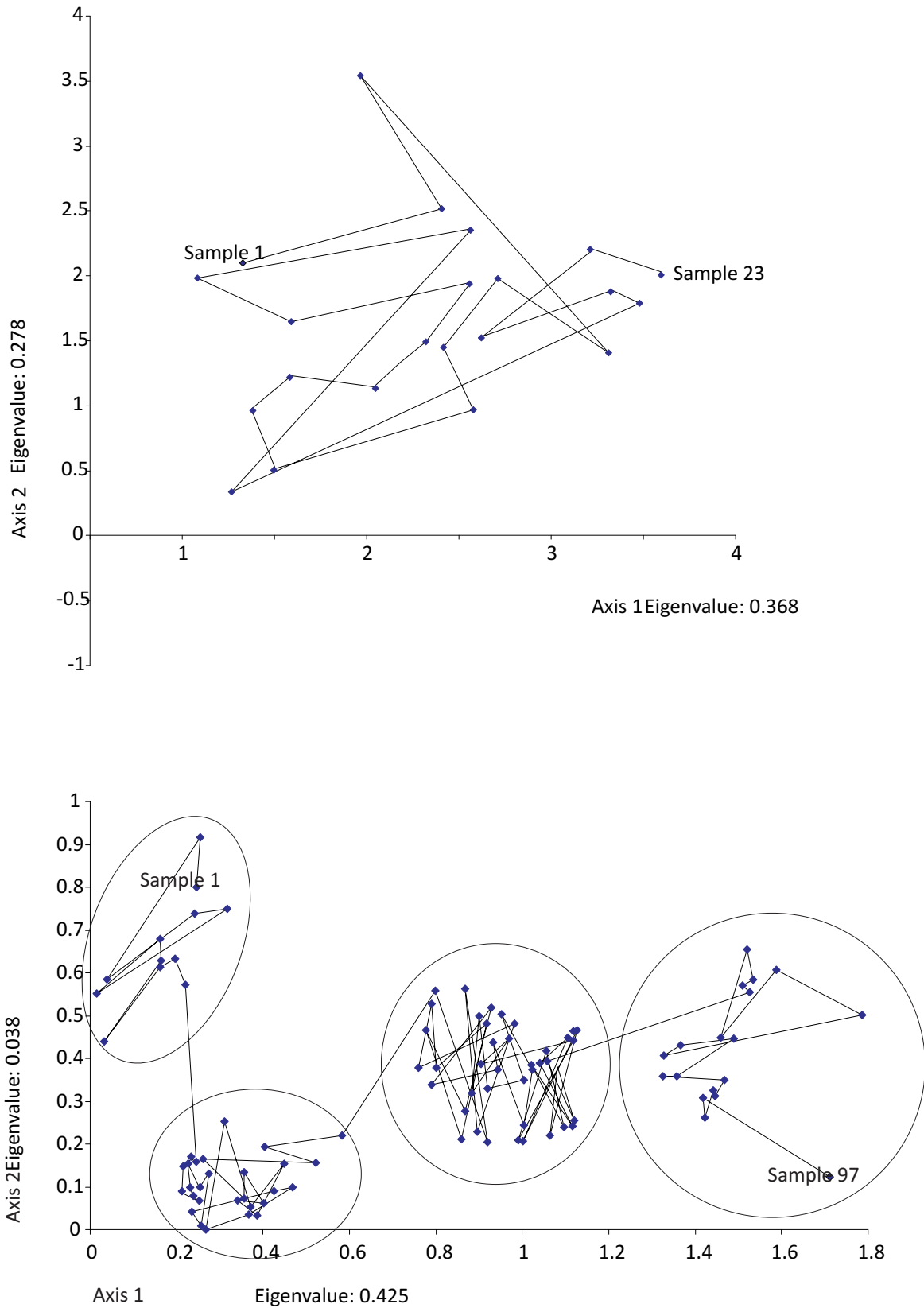


Fig. (4). DCA plots for Zoñar (top) and Gádor (bottom) pollen samples. The samples have been joined with a line and the oldest and youngest samples appear indicated with a circle and square respectively (see text for interpretation).

be taken though with care as Gádor records ca. five thousand years and Zoñar near two thousand.

Interestingly *Pinus* and evergreen *Quercus* in Gádor experienced several phases of expansion and contraction

within the declining forest trend. Successive, abrupt pine and evergreen oak forest expansion and reduction were very likely induced by increasing dry conditions between 4.6 and 2 cal Kyr BP as arid pulses from 4.2 cal Kyr BP have been widely described in Southern Spain (Martín-Puertas, 2008, Carrión *et al.*, 2007, Carrión *et al.*, in press). Drier conditions would have probably triggered intense fire activity as illustrated by increasing xerophyte and charcoal abundance (Fig. 2). Human agency cannot be disregarded as the taxa associated with human pressure (e.g. Sordiaraceae) increased from that time (ca. 4.8 cal Kyr BP), however we lack in this case any other subrogate environmental evidence to our pollen diagram in order to provide more definitive evidence of human activity.

Rather than analyzing the driving factor for the change, we focused our interpretation on the almost three thousand years of resilient response of pines and evergreen oaks. While deciduous oak basically collapsed during the drier phases, both *Pinus* and evergreen *Quercus* responded elastically to a certain threshold that allowed them to spread between ca. 2 and 1.7 cal Kyr BP. The accumulated effect of disturbance at millennial scales, concurrent with increasing pastoral activities (indicated by the abundance of Sordiaraceae, *Riccia*, *Polygonum aviculare* and thorny scrub) would have crossed the resilient threshold ca. 1.7 cal Kyr. BP, promoting then an eventual landscape opening.

The pollen diversity curve shows an interesting pattern as the maximum richness is found when the tree cover shrinks, as drought and human action intensifies. This could be partially due to pollen identification issues as several species are included under every tree pollen type while different genus of herbs can be classified and consequently the richness would increase when open landscapes appear. Alternatively, this pattern would agree with intermediate disturbance hypothesis (Grime, 1973) by which local species diversity tends to be maximal at an intermediate level of disturbance. If either drought or human pressure would become too intense only the most stress-resistant pollen species would have remained, which is probably not the case for most trees. Nevertheless, this hypothesis entails a number of assumptions (as vegetation patched in clusters) that we cannot infer from pollen records alone.

Gádor record evidences several stable phases but within a more obvious linear trend towards arid conditions and therefore a more arid-prone vegetation. The three thousand years fluctuating response of pines and oaks probably conditioned the surrounding plant assemblage response and it is worth wondering whether the system's functionality would have been maintained after every disturbance, or whether it adapted to new conditions with a progressive diversity enhancement.

Gádor mid-Holocene record would represent a bi-stable system with a more or less forested landscape that responds linearly to aridity. This would correspond with the balanced Nature metaphor, where only an external negative feedback could revert to a more forest landscape. We are aware though, that downscaling to a narrower time frame in the sequence, we would probably find a similar pattern to the one in Zoñar, with less variability in pollen composition from sample to sample. This highlights the need to compare

similar time scales in order to withdraw regional conclusions about resilient patterns.

CONCLUSIONS AND FUTURE PERSPECTIVES

This paper outlines some of the ecological questions regarding ecosystem resilience and stability where palaeo-ecological studies would be most helpful. Through the exposition of Holling's Nature metaphors to understand ecosystem dynamics we have defined a theoretical frame in which resilient systems present several stable states that result from cycles organized by discontinuous events and nonlinear processes.

Within that frame we have provided some examples from different regions of the world where long-term ecology has been proved very useful defining biodiversity patterns, threshold response to disturbance and to test equilibrium theories.

Biodiversity changes and multivariate analyses have been used in two late Holocene Southern Iberian sites (Zoñar and Gádor) in order to define ecosystem functioning and resilient responses at long-term time scales. We found that:

- Zoñar lake vegetation does not present an obvious linear trend for the time period analyzed (between ca 3.3 Kyr BP and 700 BP).
- Zoñar shows a resilient pattern as disturbance promotes an alteration in the system's diversity and landscape structure but it ultimately leads to a new state which will remain until a new threshold is crossed.
- Alternative dry and wet spells in Zoñar provoked a very active response from vegetation which responded very rapidly to the environmental change recovering soon afterwards.
- The Gádor record also shows several stable phases but these are less evident than the more obvious linear trend towards arid conditions that started at ca. 6 Kyr BP and conditioned a more arid-prone, open vegetation.
- Gádor presented an important pine and evergreen oak forest elasticity to the long term joint action of increasing aridity and fire activity for more than three millennia.
- The plant diversity curve in the Gádor record increases when the landscape is open agreeing with the intermediate disturbance hypothesis by which local species diversity tends to be maximal at an intermediate level of disturbance.

Plant diversity trends in both sites seem to correspond to changes in disturbance although in the case of Zoñar these are not directional as drought sometimes provoked rising diversity values and other it reduced the plant richness. Conversely in Gádor, intermediate disturbance levels seemed to be linked to increasing diversity although more studies on pollen taphonomy, deposition and calibration are needed.

Palaeoecological studies aiming to understand resilience in the long-term are far from common and collaborative research will undoubtedly boost the results as several different proxies can be produced and more questions can be answered. It is also essential to determine more precisely the

time interval in which the vegetation response is expected as it sets the landscape's resilience ability. Stronger chronologies are therefore needed, combined with higher resolution reconstructions for particular time periods.

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SUPPLEMENTARY MATERIAL

Supplementary material is available on the publishers Web site along with the published article.

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