

Climate stability in Mediterranean-type ecosystems: implications for the evolution and conservation of biodiversity

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ABSTRACT: Both short-term (interannual) and long-term (Quaternary) climate stability varies substantially in the four mediterranean-type ecosystems (MTEs) where fire is a normal and natural part of the selective regime (southwestern Australia, southwestern Cape, Mediterranean Basin and California). Short-term climate stability, measured as rainfall reliability, was highest in the southern hemisphere MTEs (especially southwestern Australia) and much lower in the northern hemisphere ones, especially California. There was a positive relationship between the frequency and importance of traits associated with post-fire population growth and rainfall reliability in the four MTEs, although fire regime effects also contributed to explaining patterns of trait incidence. A novel implication of this study is that the distinctive trait assemblages in the southern hemisphere MTEs may be a consequence not of their shared nutrient-poor soils, but of the similarly reliable rainfall regimes. Long-term (Quaternary) climate stability was highest in the southern hemisphere MTEs (especially the southwestern Cape) and much lower in the northern hemisphere ones. There was a strong positive relationship between long-term climate stability and regional-scale plant diversity in the four MTEs. This finding supports the hypothesis that climate stability during the Pleistocene promoted diversity through enhancing speciation rates and dampening extinction rates. The impacts of anticipated anthropogenic climate change are likely to be severe in MTEs, but especially in the southern hemisphere ones with their currently stable rainfall regimes. Conservation assessments need to identify and target the spatial components of corridors that will enable vulnerable species to migrate along environmental gradients in response to climate change.

1 INTRODUCTION

Mediterranean-type ecosystems (hereafter MTEs) have been cited as classic examples of convergence in ecosystem structure and functioning, owing to their shared summer-dry, winter-wet climates (Cody and Mooney 1978). Many divergences across regions have been observed and these are attributed to differences in soil nutrient status, intensity of summer drought and fire regimes (Cowling and Campbell 1980, Lamont et al. 1985, Keeley 1992). Others have stressed the importance of historical and phylogenetic effects in explaining differences (Herrera 1992, Verdú et al. 2003).

Interestingly, only very recently has the importance of short-term (inter-annual) and long-term (Quaternary) climate stability for convergence been identified in MTEs (Cowling et al. 2004). In this study, short-term climate stability was conceptualized as rainfall reliability, and quantified as

(i) the coefficient of variation (CV) of monthly rainfall, (ii) and the number, amount and intensity of rainfall events in the winter and summer seasons. Cowling et al. (2004) hypothesised that reliable rain falling in frequent events after summer-autumn fires in MTEs would select for plant traits that maximize population growth in the immediate post-fire period, such as strong serotiny (Lamont and Enright 2000), non-sprouting (Ojeda 1998) and fire-cued germination (Keeley and Bond 1997).

There is a growing literature that suggests areas of exceptionally high biodiversity and endemism are characterized by unusually stable climates both now as well as in the past (Fjelds  et al. 1997, Lovett et al. 2004). It has been suggested that long-term (i.e. throughout the Quaternary), relative climate stability would correlate with greater overall diversity owing to higher speciation rates and lower extinction rates than areas subjected to large environmental fluctuations (Dynesius and Jansson 2000.).

In this paper we review the literature on short- and long-term climate stability in MTEs and discuss the implications of stability for the evolution, convergence and conservation of plant biodiversity in MTEs. We consider only those MTEs where fire is regarded as a normal and natural component of the selection regime; on this basis, Chile has been excluded (Munoz and Fuentes 1989). Characteristics of the contemporary selective regimes usually invoked to explain convergence and divergence of plant traits among the four MTEs included in this study are shown in Table 1.

Table 1. Characteristics of contemporary selective regime – in addition to winter-wet, summer-dry climate – previously invoked as explanations for convergence and divergence of plant traits among the four mediterranean-climate ecosystems used in this study. Sources of information are given in Cowling et al. (2004)

	Fire interval ¹ (y)	Soil fertility	Summer drought
Mediterranean Basin	>50	Moderate	Moderate-high
California	30-90	High-moderate	High
Southwestern Cape	5-40	Low	Low
Southwestern Australia	3-20	Low	Moderate-low

2 SHORT-TERM CLIMATE STABILITY

2.1 *Patterns*

Cowling et al. (2004) assessed CV of monthly rainfall for four MTEs, namely California (22 sites), Andalusia in the southwestern Mediterranean Basin (40), the southwestern Cape (25) and southwestern Australia (26). There was no significant difference in mean annual rainfall averaged across all sites in the four regions. Californian sites experienced virtually no summer rain whereas about 25% of mean annual rain fell in the summer months in the other three regions, suggesting that summer drought is less intense there.

During the winter months, rainfall is significantly more reliable in southwestern Australia and the southwestern Cape than Andalusia and California (Fig. 1). A similar pattern holds for the summer months (Fig. 1).

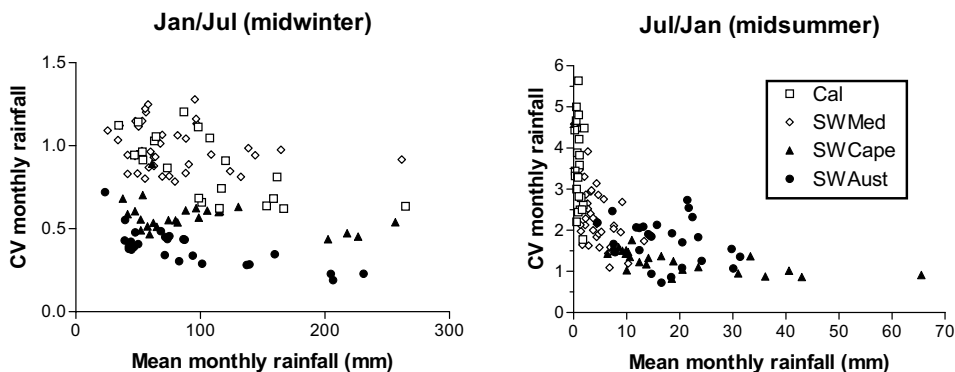


Figure 1. Relationship between the coefficient of variation (CV) of monthly rainfall and mean monthly rainfall in midwinter and midsummer for selected sites in four mediterranean-type ecosystems. The northern hemisphere winter is defined as October – March and the southern hemisphere as April – September. Cal = California, SWMed = southwestern Mediterranean Basin, SWCape = southwestern Cape, SWAust = southwestern Australia

Cowling et al. (2004) observed significant differences in the number of events (defined as any period \geq two consecutive days in which some rain was recorded) and the length and amount of rainfall per event during the winter months in the four MTEs (Fig. 2). Southwestern Australia sites experienced a significantly greater frequency of events, as well as a greater frequency of short events of low (≤ 10 mm) rainfall; patterns for the southwestern Cape were intermediate between Australia and the two northern hemisphere regions, which both received fewer, longer events in which large amounts of rain fell.

In summary, southwestern Australia's winter rainfall regime is characterized by many small rain events of low duration that are highly reliable from year to year. The regime in the southwestern Cape is only marginally different from that of Australia. The rainfall regimes of the two northern hemisphere MTEs are substantially different from the southern hemisphere ones, being characterized by fewer events of longer duration and more rainfall that are highly unreliable from year to year. The regime in California is less reliable than that of the southwestern Mediterranean Basin. Measured thus, climatic conditions in northern hemisphere MTEs are fundamentally less stable than in the southern hemisphere ones.

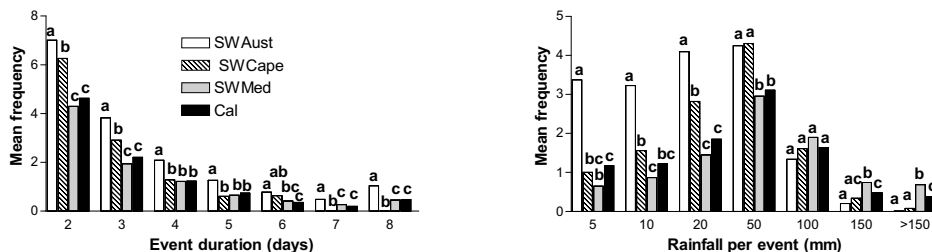


Figure 2. Mean frequency per year of event duration and rainfall per event in winter for selected localities in four mediterranean-climate ecosystems (MTEs). Shared letters above bars per event category indicate $P > 0.05$ (Dunn test). See Fig. 1 for explanation of MTE abbreviations.

2.2 Implications for evolution of plant traits

Cowling et al. (2004) argued that climate stability, experienced as frequent and reliable rainfall events throughout the winter months (when germination and establishment occur), and occasional but relatively reliable rain in the summer months (when seedlings are vulnerable to drought-induced mortality), would favour traits that maximize post-fire population growth such as serotiny, non-sprouting and fire-cued germination. This hypothesis predicts that the rank order of MTEs in terms of short-term climate (rainfall regime) stability would correspond to the order of the frequency and importance of species in regional floras with the traits mentioned above.

There is support for this hypothesis (Fig. 3); however, two interesting anomalies emerged. Firstly, the southwestern Mediterranean Basin was ranked behind California (Table 2), despite having a more reliable rainfall regime. Secondly, the incidence of non-sprouting woody plants was higher in the southwestern Cape than southwestern Australia, despite the latter's highly reliable rainfall.

Clearly, factors in addition to rainfall reliability have also shaped patterns of trait representation in fire-prone MTEs. Foremost among these are historical fire regimes (Table 1). Thus, there is considerable doubt as to whether fire in the Mediterranean Basin was a significant factor prior to the establishment of a Neolithic culture there (Mesleard and Lepart 1989, Ojeda 2001). This being true would explain the lower incidence there than in California of traits promoting post-fire population growth, despite a more reliable rainfall regime than California, which experiences regular fire, albeit at longer intervals than the southern hemisphere regions (Table 1). Also, the relatively high incidence of resprouters in the southwestern Australian flora has been attributed to a more frequent fire regime there than in the Cape (Lamont et al. 1985, Bell 2001). Southwestern Australia's subdued and unbroken landscapes do not provide barriers to the spread of wildfires whereas the rugged and broken Cape landscapes would limit the spatial extent of any one fire event, resulting in a lower overall frequency of events in any given place.

Table 2. Rank scores for the frequency and importance of selected life history and reproductive traits of plants in regional floras from four mediterranean-climate regions. 1 = highest relative frequency. Med = Mediterranean, Calif = California, SW = southwestern, Aust = Australia. From Cowling et al. (2004).

	Med Basin	Calif	SW Cape	SW Aust
Woody plants only				
Serotiny	4	3	2	1
Non-sprouting	3.5	3.5	1	2
All plants				
Fire stimulated breaking of seed dormancy	4	2.5	2.5	1
Score	11.5	9	5.5	4

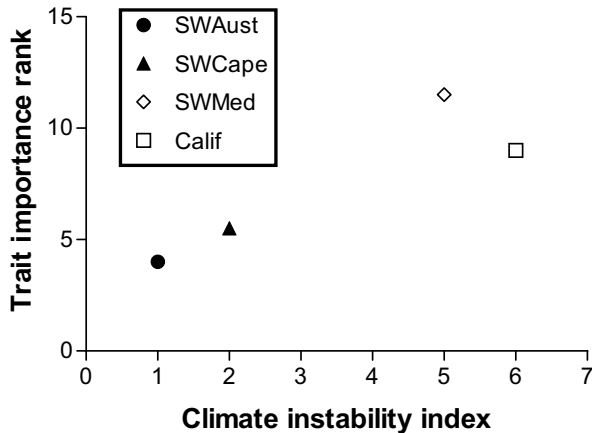


Figure 3. Relationship between trait importance (derived from an assessment of the frequency and importance of serotiny, non-sprouting (woody plants only) and fire-cued germination in regional floras from the four mediterranean-climate ecosystems (MTEs) and an index of short-term climate instability (derived from an assessment of the degree of significance among the four MTEs in measures of rainfall reliability). Original data from Cowling et al. (2004). See Fig. 1 for explanation of MTE abbreviations.

Perhaps it is the low-nutrient soils of the southern hemisphere regions (Table 1) that explain their distinctive mix of traits (Cowling and Campbell 1980, Milewski 1983, Cowling and Witkowski 1994, Lamont 1995). Wisheu et al. (2000) suggest that the high incidence of non-sprouting shrubs in Cape fynbos and Australian kwongan, compared with vegetation in other MTEs, is a consequence of the highly infertile soils in which these vegetation types grow. They argue that under these conditions, the investment required to develop and maintain a below-ground storage organs is not worth the cost. Why then is the incidence of resprouters higher in southwestern Australia than the Cape where soils are equally infertile (Cowling and Witkowski 1994), and why are resprouters more frequent in the non-seasonal (and less reliable) (unpublished data) rainfall zone of the Cape (Ojeda 1998), despite these two regions having similarly infertile soils? Moreover, other selective forces being equal, infertile soils are likely to select for non-sprouting as a consequence of slow growth rates to maturity (Bond and Midgley 2003). We suggest that the importance of non-sprouters is maximized when fire frequencies are sufficiently long to enable reproductive maturation of genets, and where rainfall is reliable – conditions experienced only in the Cape MTE.

Phylogenetic and historical factors may profoundly influence the mix of traits in a region. Tropical or pre-mediterranean persistors, which are obligate resprouters (recruiting from short-lived, fleshy propagules in the inter-fire period) (Keeley 1977), are most abundant in Mediterranean Basin maquis, followed by Californian chaparral; their abundance in Cape fynbos is variable but generally lower than in chaparral, and they are virtually absent from Australian kwongan (Keeley 1992, Cowling and Witkowski 1994, Wisheu et al. 2000). These plants, which are generally much longer-lived than those associated with mediterranean lineages, require long fire-free intervals for seedling establishment (Keeley 1992). Their relative abundances are most likely a consequence of historical fire regimes: this would explain their dominance in the Chilean MTE (Wisheu et al. 2000), and the hierarchy of abundance described above for the four regions that we consider. The traits associated with these species are markedly different from the ones considered in this study, having evolved in tropical (pre-mediterranean) environments (Herrera 1992, Verdú et al. 2003). Clearly, their frequency in regional floras will significantly influence the relative importance of traits associated with mediterranean lineages, such as the ones that we considered.

Overall, patterns of rainfall reliability, in conjunction with fire regime, provide a novel explanation for the distribution of certain plant traits in fire-prone MTEs. Predictable winter rains, and reliable, albeit occasional rainfall during summer, may have comprised a substantial selective force for the evolution of traits that promote post-fire population growth. However, the role of fire regime, especially fire frequency, is of paramount importance in the evolution of traits. Nonetheless, one of the novel implications of this study is that the distinctive trait assemblages in the southern hemisphere regions may be a consequence not of their shared nutrient-poor soils (Milewski 1983, Cowling and Witkowski 1994), but of their similarly reliable rainfall regimes.

3 LONG-TERM CLIMATE STABILITY

Historical, region-specific factors, such as different degrees of climate stability, are likely to have had a profound effect on the diversities of MTEs, as a consequence of different speciation and extinction histories (Herrera 1992, Cowling et al. 1996). The difference in mean annual temperature between the last glacial maximum and the present was greatest in the northern hemisphere MTEs and markedly less in the southern hemisphere ones, especially the south-western Cape, as indicated by palaeodata (Axelrod 1975, Arroyo et al. 1994, Blondel and Aronson 1995, Dodson and Ramrath 2001, Linder 2003) and predictions from general circulation models (Weaver et al. 1998). Warmer and more stable Pleistocene climates are likely to have reduced extinction rates and enhanced diversification rates, especially of mediterranean lineages (Arroyo et al. 1994, Cowling et al. 1996, Dynesius and Jansson 2000), thereby influencing overall species diversities (Cowling et al. 1996). Therefore, it is reasonable to predict a close relationship between long-term climate stability and regional-scale diversity in MTEs.

Fig. 4 shows a tight relationship between long-term climate stability and regional-scale diversity in the four MTEs. There is growing evidence that regions of high contemporary diversity are also regions that experienced unusual stability during the Pleistocene (Fjeldså et al. 1997, Dynesius and Jansson 2000, Lovett et al. 2004). Not only would such stability permit uninterrupted speciation, but it would also reduce extinction rates (Arroyo et al. 1994, Cowling et al. 1996, Dynesius and Jansson 2000, Lovett et al. 2004). We suggest that relative climate stability during the Pleistocene in southern-western Australia and the Cape has contributed to the high diversity recorded there. On the other hand, the two northern hemisphere regions experienced greater thermal extremes during the Pleistocene (Weaver et al. 1998) and marked changes in vegetation formations (Axelrod 1975, Blondel and Aronson 1995) that undoubtedly impacted negatively on the accumulation of species by reducing speciation and increasing extinction rates.

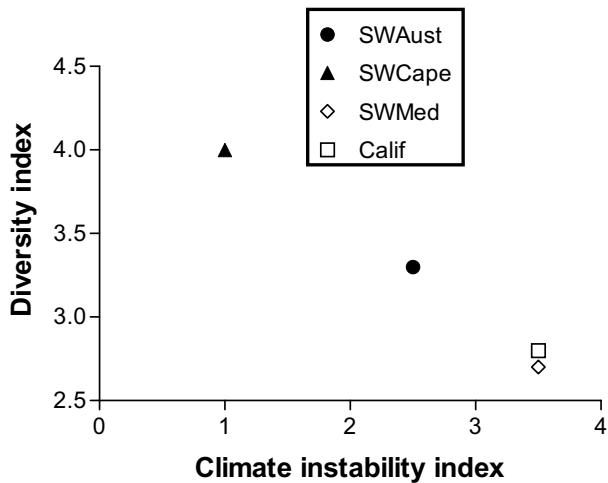


Figure 4. Relationship between an index of regional-scale plant diversity (derived from a statistical comparison of the intercepts of species-area curves presented in Cowling et al. (1996) and a Quaternary climate instability index (based on the difference in the mean annual air temperature between the last glacial maximum and the present, estimated from a recent general circulation model (Weaver et al. (1998).

4 IMPLICATIONS FOR BIODIVERSITY CONSERVATION

The patterns of climate stability reported here, and their consequences for plant trait evolution and regional diversity, have important implications for biodiversity conservation in MTEs. Owing to their location at the margin of temperate and subtropical synoptic systems, mediterranean-climate regions are especially vulnerable to anthropogenic climate change. Predictions from general circulation models suggest increasing temperatures and a change in the amount and reliability of winter rainfall (Westman and Malanson 1992, Pittock 1998, Tyson et al. 2002), which in turn, may alter the season and increase the frequency of fire (Bond and van Wilgen 1996). These climate changes are likely to have a negative impact on those species adapted to contemporary environments, especially non-sprouting ones that recruit all genets in the immediate post-fire period (Bond 1993). The implication is that the floras of the Cape and southwestern Australia, which harbour large numbers of species with these traits, are the most vulnerable, whereas the floras of the Mediterranean Basin and California, which include many pre-mediterranean persistors, may be more resilient to climate change (cf. Balmford 1996).

Using bioclimatic modelling to predict the extent of Cape fynbos under different climate change scenarios, Midgley et al. (2003) present a gloomy picture: most fynbos in the western, strongly winter rainfall region – where much of the Cape’s plant diversity is concentrated (Cowling et al. 1996) – disappears by 2050. Species-level bioclimatic models predict marked range shifts (including range elimination) by 2050 for Cape Proteaceae at present on the western lowlands. Many of the modelled species show potential to shift their ranges into adjacent regions (Fig. 5). This underscores the importance of identifying corridors that will enable the shift in ranges in response to climate change (Hannah et al. 2002). Such corridors have been identified by conservation assessments in the Cape (Rouget et al. 2003), and conservation actions are currently being implemented (Cowling et al. 2003). Similar approaches are required for other MTEs, especially southwestern Australia.

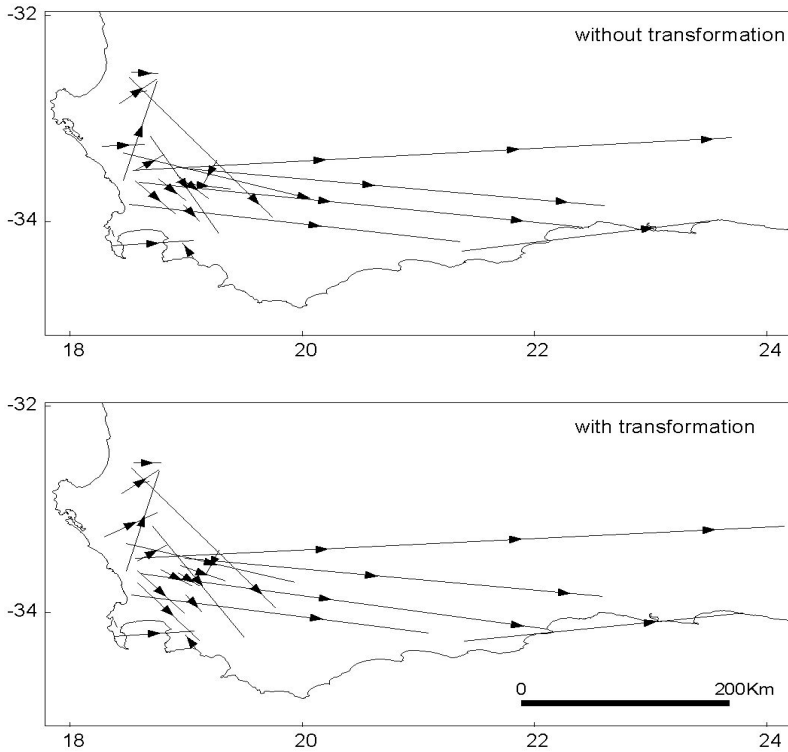


Figure 5. Modelled range shift of Cape Proteaceae in response to anthropogenic climate change, with and without taking patterns of transformation into consideration. These range shifts are required for species to retain their optimum bioclimatic range. Arrows join the geographic centroids of the current and future (~ 2050) ranges of modeled species, without (upper panel) and with (lower panel) the effects of land transformation. From Midgley et al. (2003).

5 CONCLUSIONS

We draw the following conclusions from our study.

(1) Short-term climate stability, measured as rainfall reliability, was not uniform across the four fire-prone MTEs assessed here. Stability was highest in the southern hemisphere MTEs (especially southwestern Australia) and much lower in the northern hemisphere ones, especially California.

(2) There was a positive relationship between the frequency and importance of traits associated with post-fire population growth and rainfall reliability in the four MTEs. However, the high incidence of woody resprouters in southwestern Australia and the ranking of the southwestern Mediterranean Basin behind California, despite the former region's higher rainfall reliability, are anomalous. We suspect that fire regime differences are responsible for these patterns. Nonetheless, one of the novel implications of this study is that the distinctive trait assemblages in the southern hemisphere MTEs may be a consequence not of their shared nutrient-poor soils, but of the similarly reliable rainfall regimes.

(3) Long-term (Quaternary) climate stability was highest in the southern hemisphere MTEs (especially the southwestern Cape) and much lower in the northern hemisphere ones. There was a strong positive relationship between long-term climate stability and regional-scale plant diversity in

the four MTEs. This finding supports the hypothesis that climate stability during the Pleistocene promoted diversity through enhancing speciation rates and dampening extinction rates.

(4) The impacts of anticipated anthropogenic climate change are likely to be severe in MTEs, but especially in the southern hemisphere ones with their currently stable rainfall regimes. Both of these MTEs, but especially the southwestern Cape, have many species that are entirely dependent on seeds for population maintenance and growth. These species are especially vulnerable to climate change.

(5) Conservation assessments need to identify and target the spatial components of corridors that will enable vulnerable species to migrate along environmental gradients in response to climate change.

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