EVOLUTION AND BIOGEOGRAPHY OF *PINUS RADIATA*, WITH A PROPOSED REVISION OF ITS QUATERNARY HISTORY

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(Received for publication 8 December 1997; revision 20 March 2000)

ABSTRACT

The genus *Pinus* evolved about 100 million years ago, spreading from centres in eastern North America and western Europe throughout middle latitudes of the supercontinent Laurasia. Many early subsections of *Pinus* are recorded from fossil remains of this period, but it is not until the early Tertiary, when the genus was fragmented by changing global climates and continental tectonics into latitudinal refugia, that secondary centres of origin appeared. From one of these areas, now Mexico and Central America, the subsection *Oocarpae* is thought to have arisen. This subsection includes the California closed-cone pines, *P. radiata* D. Don, *P. muricata* D. Don, and *P. attenuata* Lemmon, which evolved 15–25 million years ago as they migrated northward to California from Central America. *Pinus radiata* appears to have occupied coastal or near-coastal habitats throughout its history in the California region.

A synthesis of recent evidence from microfossils in sediment cores, oxygen-isotope ratios in ice and sediment cores, and re-evaluation of available macro-fossils yields an improved characterisation of Quaternary climatic and vegetation changes in the California coast region. Over the last million years, California climates fluctuated quasi-cyclically, at long- (multi-millennial), medium- (century), and short- (decadal to annual) periodicities in patterns similar to those documented elsewhere in the world. Changing plant fossil assemblages in the California coast region reflect major and minor fluctuations, with *Quercus* and Compositae dominating floristic communities during warmest and driest periods, and Taxodiaceae/Cupressaceae/Taxaceae taxa dominating coldest periods. Pines, notably *P. radiata*, expanded in abundance and shifted locations along the coast during climates intermediate to these extremes. Such climates occurred during transitional periods of major and minor cycles, including onset and terminations of major glacial stages, extended interstadials, and shorter cool, mesic intervals within warmer climates.

This evidence is used to argue against a long-standing scenario that *P. radiata* was broadly distributed along the coast throughout the Pleistocene (10 ka – 2 Ma), and that the Holocene climatic optimum (warm, dry period 4–8 ka) triggered contraction into the present fragmented, relictual populations. Instead, it is proposed that the species has maintained a metapopulation strategy throughout its history in the California region, growing in distinct coastal populations that were subject to repeated events of colonisation, coalescence, and local extirpation in response to fluctuating climates. Population differences are thus likely to reflect frequent founder and bottleneck effects, and complex introgression.

Appropriate conservation and restoration approaches to *P. radiata* may be revised given this perspective. Rather than restricting views about native populations to the five extant locations, coastal sites beyond the current distribution might also be accepted as "neo-native". Areas where *P. radiata* has naturalised along the California coast during historic climate periods similar to the present include many sites known from the Quaternary fossil record. Rather than treating *P. radiata* in these areas as an undesired exotic, these and other locations could be considered appropriate places in which to encourage conservation populations of *P. radiata*. This would mimic the natural potential of *P. radiata* under the generally cooler climate of the late Holocene (relative to earlier millennia) to colonise and expand in abundance, which may be inhibited currently by human development.

Keywords: Quaternary; fossil history; paleoecology; biogeography; conservation; *Pinus radiata*,

ORIGINS OF *PINUS RADIATA*: CURRENT VIEWS

Taxonomy and Evolution

Over 40 systematic treatments have been published for *Pinus*, each based on slightly different interpretations of traits significant in pine evolution (Shaw 1914; Pilger 1926; Flous 1937; Campo-Duplan 1950; Duffield 1952; Gaussen 1960; de Ferre 1965; Mirov 1967; Little & Critchfield 1969; van der Burgh 1973; Klaus 1980; Farjon 1984; Price 1989; Farjon & Styles 1997; Price *et al.* 1998). Authors have classified *Pinus radiata* in several ways, suggesting various relationships of *P. radiata* to other species and groups (Table 1). Considering Little & Critchfield's (1969) system for comparison, *P. radiata* has been placed by different authors in each of the six subsections within Section *Pinus*. *Pinus radiata* has been allied with, for example, *P. contorta* Loudon, *P. taeda* L., *P. rigida* L., *P. sabiniana* L., *P. teocote* L., and *P. halepensis* Miller. This is a challenge when tracing the phylogeny of the species, since early fossils (usually not recognised as modern species) are assignable only to subsection levels. *Pinus radiata* is most often considered allied to the Mexican and Central American subsection *Oocarpae* (Little & Critchfield 1969), although the distinction of the California closed-cone pines within this heterogeneous group has been recognised by placement in a separate subsection *Attenuatae* (van der Burgh 1973; Price *et al.* 1998). I use the system of Price *et al.* (1998) for taxonomic reference.

Origin of *Pinus*

Prior to the last 20 years, pines were thought to have evolved in the late Paleozoic or early Mesozoic (older than 225 million years ago) in the "lost" circumpolar continent, Beringia, and to have migrated steadily southward over millions of years, evolving in temperate latitudes into the 100+ species that we now recognise as temperate (Chaney 1940; Mirov 1967). With increases in fossil discoveries, improved taxonomic identification and dating of fossils, and increased understanding about global paleoclimates and plate tectonics, a new hypothesis replaced the Beringial theory for pine origins (Miller 1976, 1982; Eguiluz 1985a; Axelrod 1986). The oldest known fossils confirmed as *Pinus* were found in middle-latitude deposits from the early to late Cretaceous (oldest dated at 130 Ma*) at many sites around the

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* Terminology used in this paper is: Ma = million years ago; ka = thousand years ago; kyr = thousand years; and kyr B.P. = uncalibrated thousand radiocarbon years before present, or 1950

TABLE 1–Examples of taxonomies that have placed *Pinus radiata* in different subgroups within the genus *Pinus*.

Pilger (1926)	Shaw (1914)	Duffield (1952)	Little & Critchfield (1969)	Van der Burgh (1973)	Perry (1991)	Price *et al.* (1998)
Sect. 11, *Taeda*	Subsection *Pinaster* Group XII, *Insignes*	Subsection *Pinaster* Group XIV	Subsection *Oocarpae*	Subsection *Attenuatae*	Subsection *Patula*	Subsection *Attenuatae*
attenuata	*attenuata*	*attenuata*	*attenuata*	*attenuata*	*attenuata*	*attenuata*
coulteri	*banksiana*	*greggii*	*greggii*	*greggii*	*greggii*	*muricata*
greggii	*clausa*	*muricata*	*muricata*	*muricata*	*muricata*	***radiata***
patula	*contorta*	*oocarpa*	*oocarpa*	*patula*	*patula*	var. *binata*
radiata	*greggii*	*patula*	*patula*	***radiata***	var. *patula*	var. *cedrosensis*
rigida	*halepensis*	*pringlei*	*pringlei*		var. *longepedunculata*	var. *radiata*
sabiniana	*muricata*	***radiata***	***radiata***		***radiata***	
serotina	*oocarpa*					
taeda	*patula*				Subsection *Oocarpa*	
	pinaster				*jaliscana*	
	pringlei				*oocarpa*	
	pungens				var. *oocarpa*	
	radiata				var. *microphylla*	
	rigida				var. *ochoterenai*	
	serotina				var. *trifoliata*	
	virginiana				*pringlei*	
					tecunumanii	

Northern Hemisphere. The climate of this zone at the time is inferred to have been equable and warmer than present, and probably on average wetter, with precipitation distributed year round. During the early Jurassic and the Cretaceous, the Northern Hemisphere continent Laurasia had already separated from the Southern Hemisphere Gondwanaland, but was only beginning to break apart into what would become North America and Eurasia.

These clues lead to the hypothesis that pines evolved in middle latitudes, in the region now eastern North America and western Europe (Miller 1976; Eguiluz 1985a), during the early-middle Mesozoic. The earliest *Pinus* fossils record much of the breadth of diversity found in the modern genus: both major subgenera and six subsections are represented. It is, thus, exceptional within *Pinus* that no early Tertiary fossils have been found that obviously relate to *Oocarpae/Attenuatae*, although their assumed ancestral lineages (related to *Ponderosae/Australes*) occur early. The serotinous cone habit and other specific fire adaptations are not known from early deposits in any of the lineages.

Pines went through a series of evolutionarily significant episodic shifts in the early Tertiary, from about 65 to 34 Ma (Miller 1978, 1982; Eguiluz 1985a; Axelrod 1986; Millar 1993, 1998a). Changes in tectonics and ocean circulation led to climate patterns very different from those that existed in the Mesozoic. Polar and equatorial regions became cooler and drier, while a broad zone at middle latitudes became tropical-like: from about 30°N to 70°N latitude, climates were warm/hot and humid (Prothero & Berggren 1992; Parrish 1999). During the Eocene, conifer fossils, including pines and other temperate-adapted species, were rare or absent in the temperate-latitude deposits they had previously occupied. They were replaced worldwide at these latitudes by diverse, rich, and regionally variable floras containing mostly hardwood elements and resembling present-day Malaysian and Amazonian forests (Wolfe 1975, 1978, 1985; Tiffney 1985). Pines retreated to refugia at high and low latitudes where climates were favourable, and to a few highland refugia at middle latitudes (Millar 1993, 1998a).

This global displacement of pines into Eocene refugia appears to have been catalytic to evolution of primary modern pine diversity. Fragmentation, isolation, creation of new environments by tectonism, and variable local climates must have exerted intense selection pressures and opportunities for diversification in *Pinus* during the early Tertiary. Important secondary centres of origin were initiated for pines in southern latitudes (Mexico/Central America, Mediterranean, South-east Asia) and in polar regions (Eguiluz 1985a; Axelrod 1986; Millar 1993).

The end of the Eocene (ca. 34 Ma) was marked in middle latitudes by a relatively rapid change in global climates (Wolfe 1978; Prothero & Berggren 1992). In both Northern and Southern Hemispheres, climates shifted to zonal conditions more similar to present than any period in the Eocene or Cretaceous (Parrish 1987, 1999). During the "terminal Eocene event" (Wolfe 1978), temperatures declined throughout middle latitudes, and active mountain-building led to steep moisture gradients and development of large dry regions. In particular, the warm, moist, tropical climates, and the boreotropical flora, disappeared from middle latitudes—in some places within about a million years. Conifers, including pines, again became abundant in middle-latitude locations, presumably migrating from refugia in the far north and south, and expanding from the few middle-latitude highlands.

This dramatic climatic event marked the beginning (at a multi-millennial scale) of the modern period in the Northern Hemisphere. Tectonic events that eventually led to uplift of the major mountain ranges of the northern continents began in this period, and many important desert regions also had their origins during this time. During the periods that followed the Eocene, in particular the Miocene, pines appeared in areas and habitats where they now grow. Many of the lineages identifiable to extant species appear for the first time in deposits dating to the middle Tertiary. Pine fossils became dominant in many deposits, rendering possible interpretations of their habitats and migrations, and enabling preliminary reconstructions of evolutionary pathways for groups of species and species lineages.

Tertiary Origins of California Closed-cone Pines

Although many of the major groups of modern pines appear to have evolved within the primary temperate latitudinal distribution of *Pinus*, a few originated in secondary pine centres at high and low latitudes. On several grounds, subsection *Oocarpae/Attenuatae*, and *P. radiata* within it, appears to be relatively recently derived, with origins in Mexico/Central America. No Cretaceous or early Tertiary fossils have yet been found resembling subsection *Oocarpae/Attenuatae* (Table 2) (Millar 1993), and fossils with these affinities do not become abundant until the middle-late Tertiary. With one exception, all fossils with affinities to this subsection have come from deposits in south-western North America, suggesting that this region has been the area of evolutionary development of the group. The closed-cone (serotinous) habit, as well as an oblique (asymmetric) cone axis, have long been considered derived (recently evolved) traits in *Pinus* (Shaw 1914; Duffield 1952; Miller 1976; Little & Critchfield 1969; Eguiluz 1985a). An analysis of 10 subsections represented by living *Pinus* species in Mexico indicated that *Oocarpae* (as exemplified by *P. oocarpa*) was the most evolutionarily modified (Eguiluz 1985b). This was based on cone serotiny and also anatomical and growth traits of *Oocarpae*, such as multinodal branching, persistent cones, and epicormic sprouting as well as seed, resin-canal, and needle anatomy. Molecular evidence supports the recent origins of *P. radiata* and *Oocarpae/Attenuatae* relative to other subsections (Strauss & Doerksen 1991; Krupkin *et al.* 1996).

Tertiary macrofossils of *Oocarpae/Attenuatae* have not been found in Mexico/Central America to support this hypothesis, but this is not surprising as there are few exposed cone-bearing deposits of that age that have as yet been investigated. Subsection *Oocarpae* has been related to species now placed in subsection *Australes* (Pilger 1926; Shaw 1914; Duffield 1952; Miller 1976; Perry 1991; Strauss & Doerksen 1991; Millar 1993, 1998a; Krupkin *et al.* 1996). Evidence for the ancestral nature of *Australes* lineages is adduced from the age of the fossils and from morphological and molecular evidence. *Australes* taxa appear to have evolved in middle-latitude centres in low-latitude Gulf-coast and south-eastern United States where early fossils were recovered (Axelrod 1986). They may have migrated along the Gulf coast and southward into Mexican/Central American refugia during the early-middle Tertiary when higher latitudes were subject to warm-wet climates that were inhospitable for pines. Thus *Australes* may have provided germplasm to the nascent secondary pine centres in Central America which later gave rise to *Oocarpae/Attenuatae*.

Although the early ancestors of *Oocarpae/Attenuatae* remain unclear, most authors agree that the radiations that gave rise to many of the taxa commonly accepted within subsections

TABLE 2–Distribution of fossil pines with affinities to *Pinus radiata* populations from Tertiary and Quaternary deposits, listed in approximate order of age from old to young. Fossil locations are in California, unless otherwise indicated.

Identification	Affinity	Location	Current lat./long.	Age*	Reference
P. burtii	*Oocarpae*	Martha's Vineyard (Massachusetts)		Early Miocene (22 Ma)	Miller (1978)
Pinus sp.	*Oocarpae*	Mickey Wash (western Nevada)		Late Miocene	Schorn & Shelton (1991)
P. lawsoniana	*P. radiata* Cedros Is/ Guadalupe Is.	Santa Barbara	34° 25′N 119° 40′W	Middle/upper Miocene (15Ma)	Mason (1949) Axelrod (1967a)
P. celetomensis	*P. radiata*/ *P. attenuata* (*Oocarpae*)	Celetom Quarry (E. of Reno, Nevada)		~ Purple Mtn? (13Ma)	Axelrod (1986)
P. lawsoniana, *P. hazeni*	*P. radiata* Monterey/ Guadalupe Is.	Mt. Eden	33° 52′N 117° 01′W	Early Pliocene (7 Ma)	Axelrod (1967a)
P. lawsoniana	*P. radiata* Monterey	Mussel Rock (S. San Francisco)	37° 37′N 122° 30′W	Early Pliocene (5–6 Ma)	Axelrod (1967a)
P. diegensis	*P. radiata* Guadalupe Is.	Chula Vista (San Diego)	32° 40′N 117° 10′W	Pliocene	Axelrod & DeMere (1984)
P. lawsoniana	*P. radiata*	Merced Formation, San Francisco	37° 38′N 122°30′W	Lower-middle Pliocene	Axelrod (1967a)
P. radiata	Monterey	Drakes Bay (Pt. Reyes)	38° 10′N 122° 38′W	Late Pliocene (3.5 Ma)†	Axelrod (1980)
P. hazeni	*P. radiata*?	Pico Formation, (Ventura)	34° 17′N 119° 15′W	3 Ma	Dorf (1930) Axelrod (1986)
P. radiata		Spring Valley Lakes		Early Pleistocene (2 Ma)	Axelrod (1980)
P. radiata Guadalupe Is.		Veronica Springs (Sta Barbara)	34° 25′N 119°40′W	1.5–2 Ma	Axelrod (1980a)
P. radiata	Monterey/Año Nuevo	Santa Susana Mtns (San Fernando)	34° 18′N 118° 30′W	1.5–2 Ma	Axelrod & Cota (1993)

TABLE 2–Distribution of fossil pines (*cont.*)

Identification	Affinity	Location	Current lat./long.	Age*	Reference
P. radiata	Guadalupe Is.	Crystal Springs Reservoir (S. of San Mateo)	37° 30′N 122° 25′W	Early Pleistocene	Glen (1961) Axelrod (1967a)
P. radiata		Thornton Beach (San Francisco)	37° 37′N 122° 30′W	Early Pleistocene	Axelrod (1967a)
P. radiata	Guadalupe Is./ Monterey	Potrero Canyon (Pacific Palisades)	34° 01′N 118° 30′W	Early Pleistocene	Axelrod (1967a) Axelrod (1990)
P. radiata		Seacliff (w. of Ventura)	34° 20′N 119° 25′W	Early Pleistocene (1Ma)	Axelrod (1983)
P. radiata	Monterey	Costa Mesa	33° 38′N 117° 55′W	Early Pleistocene (1Ma)	Axelrod & Govean (1996)
P.radiata	Año Nuevo/ Cambria	Carpinteria	34° 24′N 119° 30′W	38–40 kyr B.P.	Chaney & Mason (1933), Axelrod (1986)
P. radiata	Guadalupe Is.	Millerton (Tomales Bay	38° 07′N 122° 50′W	29.05 kyr B.P.	Mason (1932, 1934)
P. radiata		Laguna Niguel (N. of San Clemente)	33° 30′N 117° 45′W	30 ka	Axelrod (1988)
P. radiata	Guadalupe Is.	Rancho La Brea	34° 10′N 118° 25′W	28–40 kyr B.P.	Axelrod (1967a)
P. radiata	Monterey	Point Sal (W. of Sta Maria)	34° 53′N 120° 40′W	28–40 kyr B.P.	Axelrod (1967a)
P. radiata	Guadalupe Is./ Monterey?	Little Sur	36° 15′N 122° E	Late Pleistocene/early Holocene (*ca.* 10 ka)	Langenheim & Durham (1963)
P. radiata?		Sta Rosa	38°28′N 122°40′W		Axelrod (1986)

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* Ma is million of years ago; ka is thousand years ago; kyr B.P. is uncalibrated thousand radiocarbon years before present (present = 1950), that is, dates are determined radiometrically.

† A recent radiocarbon date shows this to be >40,000 yr B.P. (Axelrod 1988), although the strata from which it is recovered was inferred to be equivalent to Sonoma Tuff (3.5 Ma).

Oocarpae/Attenuatae took place in Mexico and Central America. Diversification and radiation of these taxa have been considered in two groups now thought to be distinct subsections (Axelrod 1967a, 1980a, 1986; Eguiluz 1985a; Millar 1986; Millar *et al.* 1988; Krupkin *et al.* 1996; Price *et al.* 1998): subsection *Attenuatae*, the California closed-cone pines (*P. radiata, P. muricata, P. attenuata*), and a heterogeneous Central American group (*Oocarpae*: *P. greggii, P. pringlei, P. patula, P. oocarpa* and *P. tecunumanii*, and related species of *Australes*). Genetic, phenetic, tectonic, floristic, and fossil evidence indicates that the California closed-cone pines are closely related to one another, originated in Mexico/ Central America, and are more distantly and inconsistently related to Central American taxa of *Oocarpae* and *Australes* than they are to one another (Duffield 1952; Critchfield 1967; Axelrod 1980a, 1986; Millar 1986; Millar *et al.* 1988; Strauss & Doerkson 1991; Hong, Hipkins & Strauss 1993; Hong, Krupkin & Strauss 1993; Strauss *et al.* 1993; Krupkin *et al.* 1996; Wu *et al.* 1999).

Axelrod (1967a, 1980a, 1983, 1986) postulated a phyletic scheme for the California closed-cone pines to explain their evolution from a *P. oocarpa*-like ancestor, and for their migration to California. Because fossils in mid-late Miocene appear indistinguishable from the modern species, diversification of the California closed-cone pines probably took place in the mid-Tertiary and before they arrived in present-day California (Table 2) (Axelrod 1980a; Millar *et al.* 1988a, b; Hong, Hipkins & Strauss 1993; Hong, Krupkin & Strauss 1993; Krupkin *et al.* 1996; Wu *et al.* 1999). Axelrod (1980a) postulated that a lineage reminiscent of *P. oocarpa*, growing in equable Mexican climates and having traits (especially cones) reminiscent of *P. oocarpa*, diverged into mesic-adapted *P. radiata* and *P. muricata*-complexes. Another group evolved into the montane, dry- and cool-adapted *P. attenuata*.

The California taxa would have migrated north into California and adjacent regions during periods that were climatically favourable in the early to middle Tertiary. Axelrod (1967a, 1980a) suggested that passive transport on the Pacific plate aided migration. Sideslip along the San Andreas fault began about 6–8 Ma (Karig & Jensky 1972) and Axelrod (1980a, b) reconstructed the cumulative displacement along the fault to place the current ranges of the California closed-cone pines originally along an area of the Sonora-Sinaloa-Jalisco coast. This would be close to extant species of *Oocarpae* and linked to related pines by way of Mexican mountain ranges. Subsequent development of the Sonoran desert would have isolated the Californian members from the Central American pines, whichever route they took north.

Recently Krupkin *et al.* (1996) undertook a molecular analysis of chloroplast diversity in section *Pinus* that called into question both the antiquity of *P. oocarpa* and the phylogenetic integrity of subsections *Oocarpae/Attenuatae*. Their analyses suggested that *Oocarpae* is polyphyletic and that the Californian closed-cone pines are closely related to one another but have origins distinct from the Central American species. They support the hypothesis that the Californian closed-cone pine group and the species of *Oocarpae* are recently evolved, but that the Californian group is unlikely to have evolved specifically from *P. oocarpa* or any other known extant or fossil Central American *Oocarpae* taxon. Rather, these groups appear to have diverged from a distant common ancestor. Approximate divergence times for the California closed-cone pines from an unknown Mexican progenitor are given as 21–22 Ma (Krupkin *et al.* 1996). Subsequent molecular work corroborated the joint and southern ancestry of the closed-cone pines (Wu *et al.* 1999).

Tertiary and Quaternary Dynamics of *Pinus radiata* in the California Region

Over the past 60 years, abundant Quaternary (about the last 2 million years) fossils allied to *P. radiata* have been recovered and described from California (Table 2). Most of the fossils positively identified are seed cones, many occur in moderate to large numbers, and all of the sites are either coastal or near-coastal. The fossil localities extend from Tomales Bay and Millerton (Pt. Reyes) in the north to the United States-Mexican (Baja California) border in the south (Fig. 1) (Axelrod 1988) and range in age from early to latest Pleistocene (2 Ma to 10 ka) (Table 2).

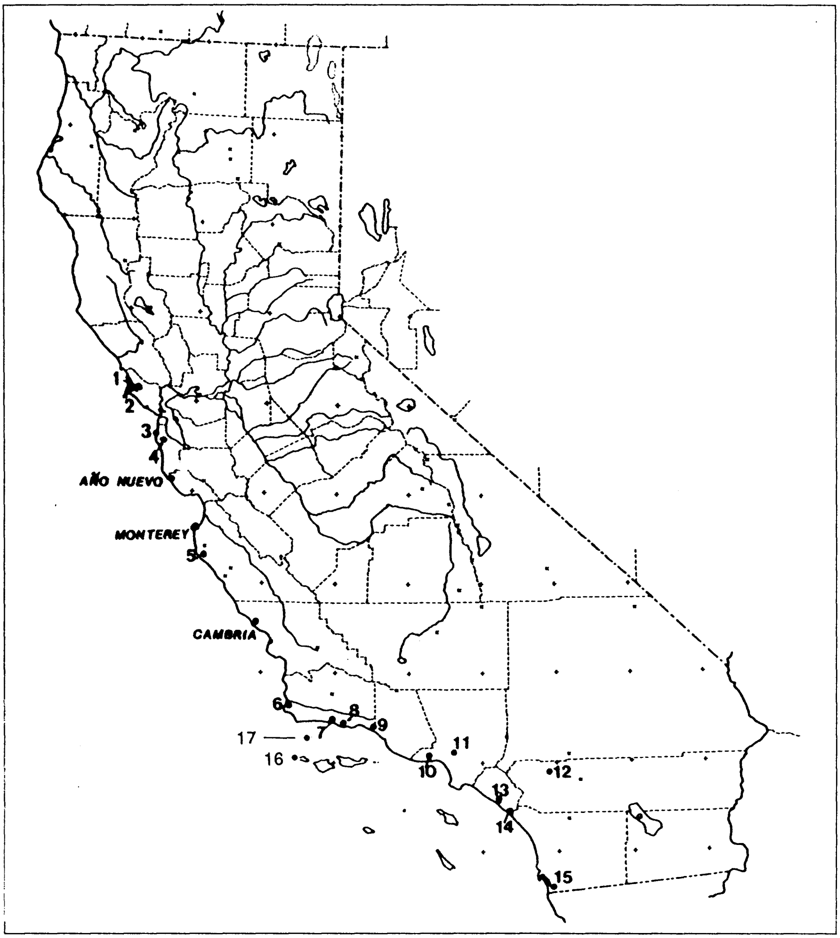


FIG. 1–Localities where fossil *Pinus radiata* cones have been recovered. 1, Tomales; 2, Drakes Bay; 3, Mussel Rock; 4, Spring Valley Lakes; 5, Little Sur; 6, Pt. Sal; 7, Veronica Springs; 8, Carpinteria; 9, Seacliff; 10, Potrero Canyon; 11, Rancho La Brea; 12, Mt Eden; 13, Laguna Niguel; 14, San Clemente; 15, Chula Vista; 16, San Miguel Island; 17, Drill site Hole 893, Santa Barbara Basin. (Modified from Axelrod 1988.)

Mason (1930, 1932, 1934) argued that the current disjunct locations of the maritime closed-cone pines (*P. muricata* and *P. radiata*) were indicative of their fragmented distribution since the middle Tertiary. On the basis of far fewer fossils than now recovered, and without the benefit of plate tectonic theory, he advanced a hypothesis that the closed-cone pines evolved on Tertiary islands, which he suggested were formerly abundant along the Californian coast. Following continental uplift, the islands became part of the mainland. The locations of current and extinct closed-cone pine populations indicated locations of Tertiary islands where Mason suggested that pines had evolved.

Axelrod (1967a, b, 1980a, b, 1983, 1986, 1988) developed an alternative and detailed hypothesis about the historical biogeography and evolution of the maritime closed-cone pines in California that has been widely accepted. Variability and trends in cone shape, associated flora, geological evaluations, and inferred climate provided the bases for his reconstructions. Accepting *P. oocarpa* as the ancestral taxon, Axelrod suggested that the evolutionary trajectory in *P. radiata* has been toward increasing cone length, umbo development, and asymmetry. This trend was interpreted as an adaptation to increasingly drier climates (Axelrod 1967a, 1980a, b), with retention of the ancestral small ovoid cone condition in areas having persistent cool temperate climates (Axelrod 1982; Axelrod & Cota 1993). The series of fossil *P. radiata* cones, arranged in a time sequence, support this model, with the oldest cones being smallest, and the youngest being largest (Axelrod 1980a, b, 1986). Of the extant *P. radiata* populations, the island populations, which have the smallest and most symmetric of cones, were considered most ancestral. Of the mainland populations, Monterey retained the most ancestral condition and Cambria was most recently evolved. Axelrod attributed the lack of clinal gradients in morphological traits to highly localised climates along the coast: Cambria has a strong Mediterranean climate, yet adjacent Monterey is cooler and moister than Año Nuevo. The Monterey micro-climate is due partly to the chilling effect of a deep offshore canyon that likely maintained a relatively cool equable climate over the Monterey peninsula for millennia (Axelrod 1982).

Axelrod (1980a, b) ascribed changes in distribution between the Tertiary/Early Pleistocene and current locations of *P. radiata* to recent changes in California/Baja California coastal climates. He interpreted the locations of fossil deposits, which extend far beyond the current distributions of the populations, to suggest that appropriate habitat was widely available and that *P. radiata* was broadly distributed along the Californian coast throughout the Pleistocene (10 ka–2 Ma) (Axelrod 1967a, 1980a, b, 1981). Axelrod viewed the Pleistocene as a singular climate period, whose expression along the coast was, relative to the last 10 kyr, persistently cool and mesic, with rainfall distributed year-around. In his view, the first significant climate change affecting population distribution was in the early Holocene. Increasing heat and aridity, culminating in the "Xerotherm" (*sensu* Axelrod 1981, the warm period lasting from 4 to 8 ka, commonly referred to as the "early Holocene warm period" or the "Holocene climatic optimum"), abruptly fragmented the continuous coastal forest band, leaving the small and disjunct populations of the present as relicts. The current distributions of *P. radiata* were considered limited to those few locations along the coast (and islands) where local topography and/or ocean currents maintained cooler conditions even during the Xerotherm (Axelrod 1982). Axelrod interpreted the large-coned variant at Cambria to be a post-glacial derivative, reflecting recent adaptations to the hot dry climates of the Xerotherm.

A NEW MODEL FOR QUATERNARY DYNAMICS OF *PINUS RADIATA*

I have assembled climatic, fossil, genetic, and floristic evidence to advance a new hypothesis for Quaternary dynamics of *P. radiata*. Significant new information on global and regional paleo- climatology has changed our understanding of Quaternary environments. Because much of this is valuable in interpreting evolutionary histories of species besides *P. radiata*, yet little is cited in forest-science literature, I will introduce key concepts here before presenting details relevant to *P. radiata*.

Quaternary Climates and Vegetation Response

Global climate dynamics

In recent years new methods in Quaternary sciences have clarified much about origins and mechanisms of forces that affect historic climates at long- (multi-millennial), medium- (century), and short-(annual to decadal) period fluctuations (for summaries *see* Cronin 1999). Isotropic and microfossil analyses of marine sediments and ice strata in deep cores provide valuable records of glacial-interglacial cycles throughout the Quaternary. Over 40 chemical and physical variables can be analysed from core sections, including CO_2, NO_x, Ca^{++}, cosmogenic isotopes, stable isotopes, and dust. Individually and combined, these provide enormous amounts of information about historic climates. Core sections can be radiometrically dated with high accuracy and precision, yielding continuous and high-resolution records for the past several million years.

Oxygen isotopes analysed from ice and sediment cores are especially useful as proxies for historic temperatures (Fig. 2a). A complex relationship exists in the relative incorporation of O^{16} and O^{18} into ice and ocean water depending on ambient atmospheric temperature. Records of oxygen-isotope ratios (called $\delta^{18}O$) taken from core sections act as high-resolution thermometers over long historic times. Cold periods are marked by low $\delta^{18}O$ values, whereas warm periods have high values. Standard curves have been developed that relate oxygen-isotope ratios to temperature. Oxygen-isotope curves are now widely used in Quaternary science as standard global climate reference. Glacial and interglacial stages are numbered and referred to as oxygen-isotope stages, or OIS (Fig. 2b). Cores have been taken from many places around the world, providing geographic resolution.

These ice-core records have refined what was previously thought to be only four major glacial periods into at least 11 major glacial advances during the last 900 kyr and many more before that (Fig. 2a). Major cycles of glacial and interglacial periods are now understood as resulting from earth's orbital movements relative to the sun, known as Milankovitch cycles (Imbrie *et al.* 1992), interacting with earth's internal physical systems (e.g., ocean and atmosphere circulation, position of the continents; Broecker *et al.* 1985). Combined effects produced a strong 100-kyr glacial-interglacial rhythm that began about 900 ka. Glacial periods averaged 90 kyr in length, while warm interglacials averaged about 10 kyr. The Holocene epoch is just the most recent warm period. Prior to 900 ka, a 41-kyr frequency dominated, with weaker glacial expansions but more rapid fluctuations between glacial and interglacial periods (Imbrie *et al.* 1992).

Ice core analyses also reveal many minor peaks and valleys indicating shorter-frequency oscillations in climate within the glacial/interglacial cycles referred to collectively as sub-Milankovitch climate variations. These are being analysed for their origin and mechanisms,

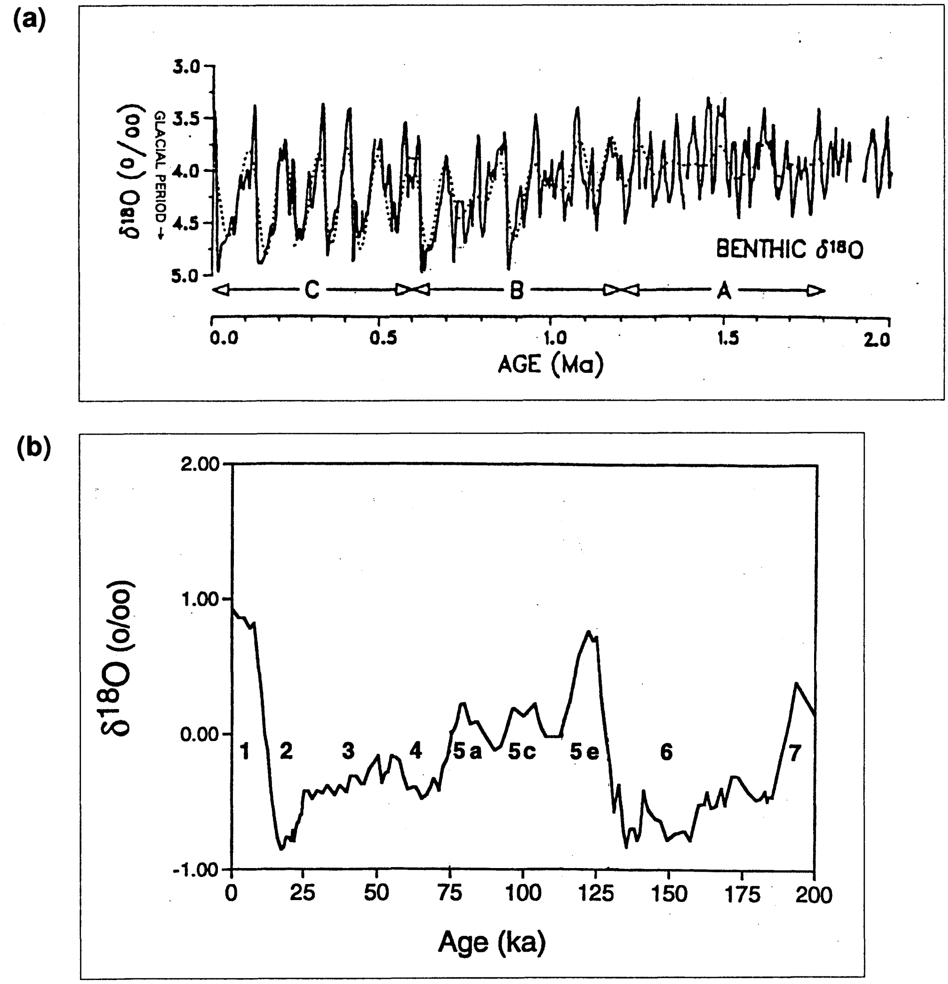


FIG. 2–(a) Benthic oxygen isotope curve ($\delta^{18}O$) from the Atlantic Ocean for the past 2 million years showing the lower intensity, shorter cycle (41-kyr) fluctuations of the first million years of the Quaternary and the 100-kyr cycle of the last million years (modified from Imbrie *et al.* 1992);

(b) Oxygen isotope curve for the last 200,000 years showing standard oxygen-isotope stages (OIS). Odd-numbered OIS stages are interglacials or interstadials, even numbered stages are glacial or pluvial stages.

whether they represent climate events or artifacts of the ice cores, whether they are global or local events, and how biota responded. Increasingly many of these are found to represent important mid- to short-frequency global climate events. For instance, 23 interstadial events (known as Dansgaard-Oeschger events), each lasting 2–3 kyr and with temperatures >5°C warmer than periods before and after, are recorded in oxygen-isotope records between 10 and 115 ka (Dansgaard *et al.* 1982). Transitions to these warm periods were abrupt, occurring within one to several decades. Similarly, rapid swings in oxygen isotopes record six to seven distinct cold periods known as Heinrich events regularly paced between 14 ka and 70 ka, each lasting 1–2 kyr and with rapid transitions (Heinrich 1988). The well-known glacial excursion known as the Younger Dryas (c. 11.5–12.5 ka), which followed the initial warming at the end of the last glacial period, now appears to be a Heinrich event. Significant changes in biotic conditions around the world correlate with many of these warm and cold phases (Dansgaard *et al.* 1993; Grimm *et al.* 1993; GRIP Members 1993; Clark *et al.* 1999).

Medium-frequency events such as these, once considered unique or unrelated, are now being interpreted as integrated expressions of internal earth systems (atmosphere, ocean circulation) interacting with orbital cycles. Many appear to be linked as expressions of a pervasive rhythm called Bond cycles (Bond *et al.* 1992, 1997). Importantly, counter to earlier assumptions, these oscillations seem to continue throughout interglacials, including the Holocene, affecting climates in similar periodicities, if somewhat dampened amplitude, as during glacial periods (Bond *et al.* 1999). Several long-reported climate periods of the last 2000 years are now considered expressions of Bond cycles. The so-called Medieval Climate Anomaly (c. AD 900–1340) and Little Ice Age (c. AD 1450–1880) are, respectively, century-long warm/dry and cold phases that exerted significant influence on development of modern ecosystems (Grove 1988; Hughes & Diaz 1994; Stine 1998; Bond *et al.* 1999).

At still higher frequency, decadal and annual climate events occur nested within longer-interval fluctuations. Quasi-decadal cycles, such as the North Pacific Decadal Oscillator (Mantua *et al.* 1997) and the North Atlantic Oscillation (Hurrell 1995) affect regional climates significantly and regularly. The short-cycle (2–7 years) pulses known as ENSO (El Niño/Southern Oscillation) have only recently become well characterised and their atmosphere/ocean-circulation mechanisms understood (Diaz & Markgraf 1992). These events have significant impacts in specific regions of the world—wet/warm in some, dry/cold in others. The ENSO pattern seems to have begun long ago (c. 6 Ma), likely triggered by closure of the Isthmus of Panama, which led to fundamental changes in ocean circulation and cascading effects on climate. An element of ENSO important for biota is its apparent cyclic clustering of extreme and frequent El Niño events. For instance, decades and even several-century-long cycles have occurred in the last 24 kyr with heightened El Niño activity (Sirocko *et al.* 1993, 1996, 1999).

Quaternary climate of the Pacific Southwest coast

Although early oxygen-isotope records derived from high-latitude and marine sediments, evidence is mounting that the basic patterns of long-period (glacial/interglacial), medium-period (e.g., Bond cycles, interstadials), and many short-period (e.g., decadal oscillations, ENSO) events are recorded in many locations worldwide. Dates of a particular event often are time-transgressive, that is, they vary among regions. For instance, the Younger Dryas, the Medieval Climatic Optimum, and Little Ice Age occurred at somewhat different times in Europe and North America (Rind *et al.* 1986; Grove 1988; Stine 1998).

For the California coast, a rapidly building literature documents correlations of marine and terrestrial biota with climates for the last 160 kyr and corroborates that this region experienced many of the oscillations documented elsewhere. The most valuable record is a highly resolved, marine sediment core from an ocean drilling project in the Santa Barbara Basin off south-central California, which yielded many climate proxies, including oxygen isotopes, chemical components, and marine and terrestrial fossils (Fig. 3). The oxygen-isotope curve resembles standard curves from high latitude polar and marine regions, and

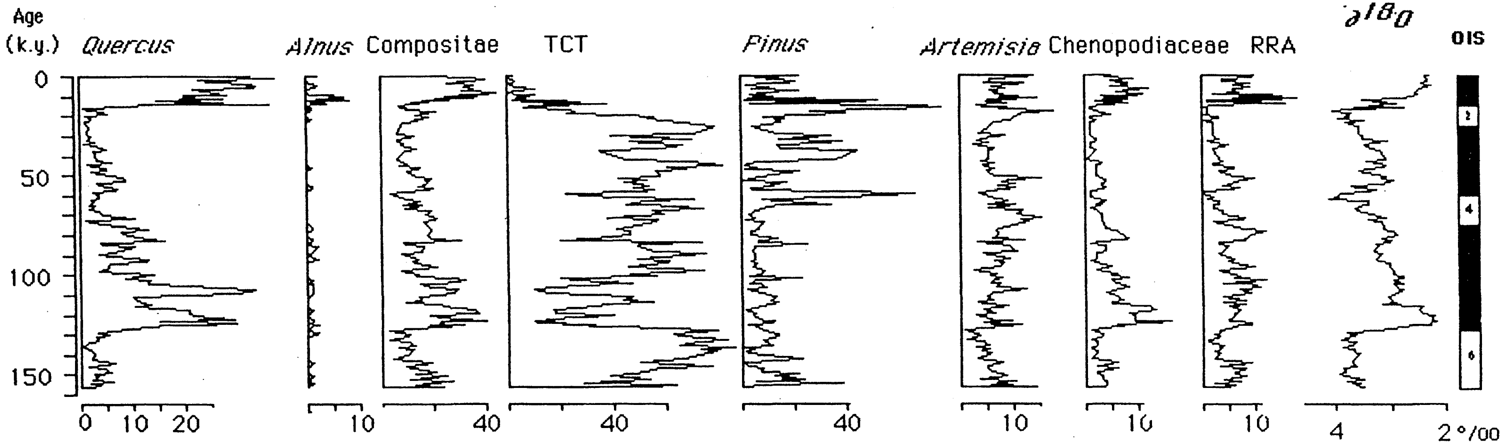


FIG. 3–Percentage relative abundance of selected pollen types (left eight curves) over the last 160 000 years from the Santa Barbara Basin, California, record corresponding to glacial/interglacial and interstadials (warm phases within glacial periods) of the Atlantic deep-sea oxygen-isotope ($\delta^{18}O$; OIS) curve (dark bars are odd-numbered stages, open bars are even-numbered stages). TCT = combined Taxodiaceae, Cupressaceae, and Taxaceae pollen taxa; RRA = combined Rosaceae, Rhamnaceae, and Anacardiaceae pollen taxa. (From Heusser 1995 .)

documents the current interglacial (OIS 1), the previous interglacial (Eemian, OIS 5), the most recent glacial (Wisconsin, OIS 2–4), and parts of the previous glacial (Illinoian, OIS 6) (Fig. 3). Frequencies and abundances of planktonic foraminifera (Kennett & Venz 1995) and terrestrial pollen (Heusser 1995) correspond to major oxygen-isotope phases, indicating abrupt biotic responses to rapid transitions between cold and warm periods of the late Quaternary.

Pollen from such marine cores has been documented to accurately reflect adjacent mainland vegetation in the same way that pollen cores from terrestrial basins represent regional vegetation (Heusser 1994, 1995). The Santa Barbara Basin core indicates that high oak (*Quercus*), Compositae, and Chenopodiaceae abundances on the coast corresponded to warm-hot (interglacial) periods, while conifers, primarily Taxodiaceae/Cupressaceae/Taxaceae (TCT) taxa, dominated during cold (glacial) periods (Fig. 3) (Heusser 1995, 1998). Heusser called these "end member" plant communities, representing climate extremes of the last 160 kyr, while other taxa were abundant during intermediate and transitional climates.

Pollen records from terrestrial sites in California record similar patterns. For instance, large shifts in dominance from *Quercus* and Compositae woodland and non-wooded types to conifer forests correspond to glacial/interglacial cycles at Clear Lake (northern California, inner coast range, 125 kyr record—Adam 1988; Adam & West 1983), at San Miguel Island (Channel Islands, 16 kyr record—West 1994; Erlandson *et al.* 1996), and at Owens Lake in the eastern Sierra Nevada (Litwin *et al.* 1997). Similar major shifts in cool-adapted *versus* warm-adapted vegetation corresponded to glacial/interglacial oscillations in long marine and terrestrial cores taken from Oregon and Washington (Heusser & Heusser 1990; Whitlock & Grigg 1999), the Queen Charlotte Islands, and mainland British Colombia (Heusser *et al.* 1980; Mathewes *et al.* 1993).

Shorter periodicity climate cycles are also recorded in the Santa Barbara Basin and other cores taken in California and the Pacific region. Oxygen-isotopes from benthic foraminifera populations in the Santa Barbara Basin document the Younger Dryas glacial excursion at the end of the Pleistocene and 16 Dansgaard/Oeschger interstadials (Behl & Kennet 1996; Hendy & Kennett 1999; Sirocko *et al.* 1999). The latter events each lasted a few centuries and record warming of up to 5°C within a few decades (Hendy & Kennett 1999). Pacific marine cores off northern California similarly document the Younger Dryas and abrupt climate events of less than 1500 years associated with rapid changes in biotic abundances (Mix *et al.* 1999). The Younger Dryas has also been inferred from rapid changes in vegetation types in several pollen records from coastal sites of the Pacific Northwest (Mathewes & Heusser 1981; Mathewes *et al.* 1993; Whitlock & Grigg 1999) and possibly in the Clear Lake record (Adam 1988; Adam & West 1983). Short-term (100–200 yr) interstadials with rapid transitions are recorded in the western Great Basin (Benson 1999). Changes in radiolarian distributions reveal that California El Niño events, with durations from annual to clusters of 200 years, began 5.5 million years ago and have characterised the southern California coast throughout at least the late Quaternary (Casey *et al.* 1989; Sirocko *et al.* 1999). Vegetation shifts and climate reconstructions from Clear Lake and associated marshes record warmer interstadials OIS 3 and OIS 5 (Adam & West 1983). El Niño periods appear to have been characterised by warmer, wetter winters than short-term averages. Century-long variations in coastal California vegetation, inferred from pollen records in marine Santa Barbara cores, reveal that significant changes in vegetation abundances correlate with these high-frequency

ENSO-like events (Fig. 4) (Heusser & Sirocko 1997; Heusser 1998; Sirocko *et al.* 1999). Although cycles of vegetation change persist through the Santa Barbara record, amplitude and abundances indicate differences in the strength of ENSO events between glacial and interglacial periods.

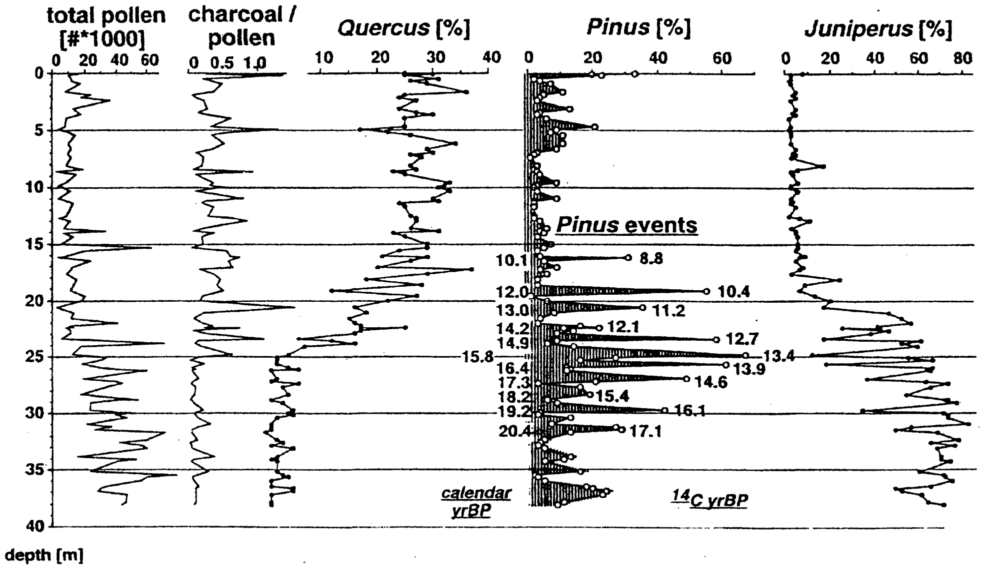


FIG. 4—Percentage relative abundance of *Quercus*, *Pinus*, and *Juniperus* pollen, charcoal/total pollen ratio, and total pollen grains recovered from a 24 000-year record of the Ocean Drilling Project (ODP) at Santa Barbara Basin, California. Large-scale patterns show *Juniperus* abundance persistent during the late glacial and dropping off at the termination of the Pleistocene, *Pinus* peaking in abundance at the termination of the last glacial period, and *Quercus* rising in abundance in the Holocene. Higher frequency pine events, lasting less than 200 years, correlate to El Niño/Southern Oscillation (ENSO-like) climate pulses. *Calendar yr BP* is thousand years before present; ^{14}*C yr BP* is uncalibrated thousand radiocarbon years before present. (From Heusser and Sirocko 1997.)

Holocene records from the Pacific coast also generally correspond to global patterns. The Santa Barbara Basin core indicates early Holocene warming with two peaks in the early/middle Holocene, about 8–6 ka (Kennett & Venz 1995). Records from inner coast range sites (Clear Lake and associated marshes) suggest a warm dry period from 7 to 3.2 kyr B.P. (Adam & West 1983). A climate model built from a composite of 59 sites ranging from northern California (Cape Mendocino) to the Aleutians indicated high temperatures and low precipitation peaking 8 ka (Heusser *et al.* 1980). A composite of 13 fossil pollen records from the inner coast ranges of northern California indicates a Holocene climatic optimum from 8.5 to 3.8 kyr B.P. (West 1990, 1993). These records also provide evidence for greater seasonality and stronger Mediterranean climates (lower precipitation and higher temperature extremes) at sites in the inner north coastal ranges during the early-mid Holocene than at present (West 1993). Pacific Northwest coastal sites record early Holocene peaks earlier than in California, with temperatures rising abruptly 10 kyr B.P., peaking about 8 kyr B.P., and dropping rapidly at 7.5 kyr B.P. (Mathewes & Heusser 1981).

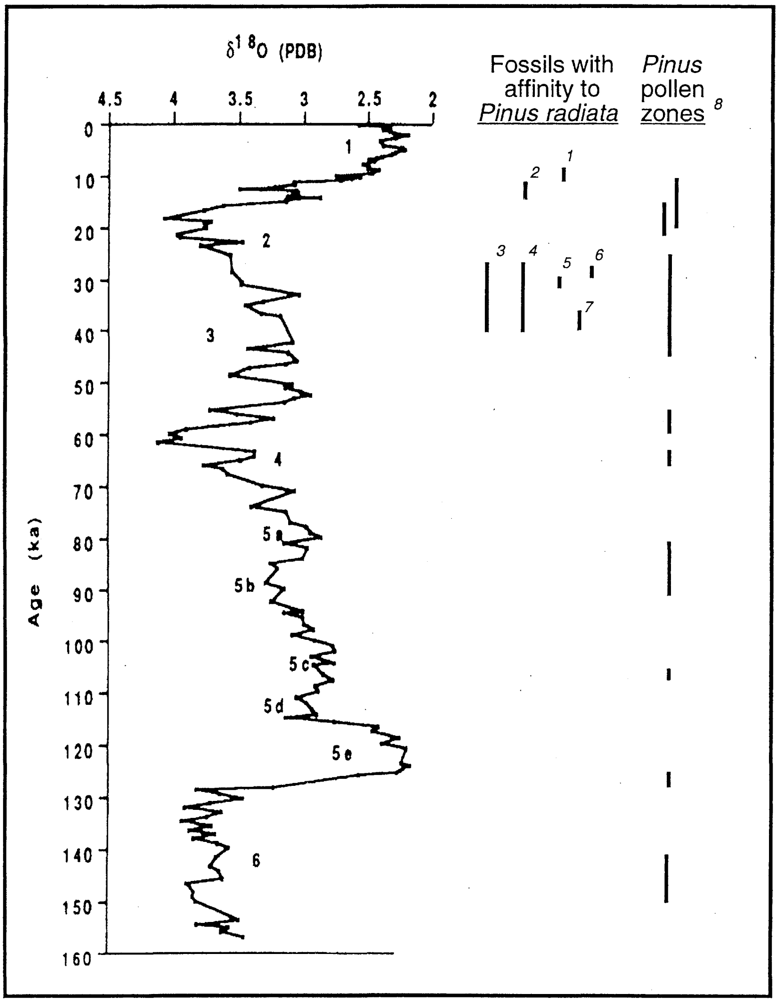
Other Holocene records from western California document short-term (multi-century) climate events that may relate to Bond cycles. One pollen record from the northern California coast indicates a warm dry period ending about 2.5 kyr B.P. (Heusser 1960). Analysis of fish scales from Clear Lake (northern California inner coast ranges) documents a warm period peaking between 4.0 and 2.8 kyr B.P. (Casteel *et al.* 1977; Casteel & Beaver 1978). Pollen from a marsh sediment core on Santa Rosa Island indicates a time of aridity from 5200 to 3250 yr B.P. (Cole & Liu 1994), which is corroborated by marine fossil radiolarian distributions from the Santa Barbara Basin that show a dry period at this time, with the exception of a cool period from 3800 to 3600 yr B.P. (Pisias 1978). Generally cool periods during the middle/late Holocene are evident in a pollen record from the northern California inner coast ranges after c. 3800–2300 yr B.P. (West 1993) and at Newport Bay, Orange County, California, at 3800, 2300, and 560 yr B.P. (Davis 1992). Pollen records from Santa Rosa Island indicate a period of precipitation increasing after 3250 yr B.P. that may correspond to the Newport Bay cool periods (Cole & Liu 1994), although a recent record from Los Penasquitos Lagoon (near Santa Barbara) indicates cooler and wetter climate developed there after 2.5 kyr B.P. (Cole & Wahl in press).

Quaternary fossil evidence for ***Pinus radiata*** *and climate correlations*

Direct and indirect evidence exists for *P. radiata* in the Quaternary. Macrofossil remains, mostly seed cones with undeniable affinity to *P. radiata*, have been recovered in abundance from many sites along the California coast (Table 2 and Fig. 1), mostly at locations beyond and between their present native populations. Excluding the Tertiary floras, these fossils fall primarily into three time periods (Table 2 and Fig. 5): (1) early Pleistocene, 1.0–2.0 Ma (poorly dated; no OIS number); (2) late Pleistocene, 28–40 ka (OIS 3); and (3) Pleistocene/Holocene transition, 10–13 ka. The early Pleistocene fossils derive from the period when glacial/interglacial cycles were weaker and fluctuated more rapidly (Fig. 2a). Without improved resolution on their dates, little can be said about the climate under which they grew except that temperature peaks would not have been as extreme as in the late Quaternary, yet significant climate changes occurred more rapidly.

Pinus radiata cones dated 28–40 ka (Table 2) centre in interstadial OIS 3, which contains several Dansgaard-Oeschger events. Macrofossils attributed to *P. radiata* from the mainland central California site at Little Sur (Langenheim & Durham 1963), tentatively dated at 10 ka, indicate another period of pine presence. This period is also represented by pine pollen and macro-fossils in Daisy Cave on San Miguel Island (Channel Islands), identified from associated macrofossils as *P. muricata* (West 1994), a common extant and fossil associate of *P. radiata*. Pine was abundant and dominant from 13 ka to 11 ka, when it abruptly disappeared from this site and was replaced by oak and shrubs.

Indirect fossil evidence for the locations and dates of *P. radiata* occurrence on the California coast comes from pine pollen in California coastal deposits identified to genus, and from pollen and macrofossils of related pine species. Arguably *P. radiata* and *P. muricata* could have been the only or dominant pine species contributing to southern coastal (including marine) sediment samples. Analysis of contemporary pollen shows that despite the prolific production and dissemination of pine pollen in general, high pine values are found in deposits only where pines are the dominant local arboreal species (Adam & West 1983; Heusser 1994). This led in part, for example, to Cole & Liu (1994) excluding any other



1 Little Sur (Langenheim & Durham 1963)
2 San Miguel Island (Erlandson *et al.* 1996)
3 Pt Sal (Axelrod 1967a)
4 Rancho La Brea (Axelrod 1967a)
5 Tomales Bay (Mason 1932, 1934)
6 Laguna Niguel (Axelrod 1988)
7 Carpenteria (Chaney & Mason 1933; Axelrod 1986)
8 Oil Drilling Project Hole 898, Santa Barbara Basin (Heusser 1995; Heusser & Sirocko 1997)

FIG. 5–Dates and locations of late Quaternary pine fossils allied to *Pinus radiata*, plotted against the Kennet & Venz (1995) Santa Barbara Basin oxygen-isotope curve ($\delta^{18}O$). Fossils indicated as having affinity to *P. radiata* are macrofossil remains except the site at San Miguel Island, which combines pollen and macrofossil evidence. *Pinus* pollen abundances are from the Santa Barbara Basin (Heusser 1995) and include combined pollen zones and pollen spikes in the last 160 kyr. Not shown are *P. radiata* macrofossil sites from the early Pleistocene (*see* Table 2).

source than very local *P. muricata* and *P. torreyana* as potential contributors to fossil pine pollen deposits on Santa Rosa Island, and to West (1994) and Erlandson *et al.* (1996) assuming that pollen found on San Miguel Island was *P. muricata*. To the extent that the closed-cone pines were the primary pines in the coastal strip through the Pleistocene (Axelrod 1988), *P. muricata* and *P. radiata* would be primary contributors. Other candidates near the coast are *P. ponderosa*, *P. coulteri*, *P. lambertiana*, *P. attenuata*, and *P. monophylla*, which grow inland and in patchy southern California distributions today and have been inferred to be present in these regions during the Quaternary, although there is no direct evidence for their presence in coastal macrofossil deposits (Axelrod 1986).

The long-term perspective of the southern California coast shows three dominant arboreal vegetation modes for the last 160 kyr (Fig 3.) (Heusser 1995, 1998). In addition to the climate end members—oaks *versus* juniper—pine is a significant component, peaking in abundance at the termination of glacial maxima and during interstadials of the Wisconsin (termination of OIS 4 and 2, interstadial OIS 3, early OIS 6, and interstadial within OIS 6). A similar pattern for oak, pine, and TCT occurred at Clear Lake, in the inner coast range of northern California (Adam 1988). Pine dominance on San Miguel Island also peaks during transitional climates (West 1994; Erlandson *et al.* 1996).

Within this pattern, shorter interval pine events corresponded to minor interstadials of the Wisconsin (Fig. 3 and 4), and to apparent high-frequency ENSO periods (Fig. 4) (Heusser & Sirocko 1997; Heusser 1998; Sirocko *et al.* 1999). Pine spikes correlated with clusters of ENSO-like climatic events generally lasted less than 200 years and occurred about every 1000 years (e.g., at 10.1, 12.0, 13.0, 14.9, 15.8, 16.4, 17.3, and 19.2 ka) (Fig. 4). Peaks in pine pollen frequency corresponded to low values for oak and juniper, suggesting pine expansion in cool mesic periods within otherwise warming climates. Peaks in charcoal abundance correlated with pine events of the last 24 kyr (Heusser & Sirocko 1997).

Genetic evidence

Pinus radiata has been the subject of much genetic work, of which the following is but a cursory summary. The five native populations of *P. radiata* are distinct genetically, although different traits show varying degrees of resemblance. Differences in cone size and shape distinguish all five populations (Forde 1964; Linhart 1978; Axelrod 1980a, 1988; Burdon, Bannister & Low 1992; Burdon, Firth, Low & Miller 1997); as do some morphological traits (Fielding 1961; Burdon, Bannister & Low 1992; Burdon, Firth, Low & Miller 1997). Larger cone size with thicker umbos has been interpreted as a protection against squirrel predation on the mainland (Linhart 1978; Burdon, Bannister & Low 1992) and, especially at Cambria, against summer drought (Axelrod 1980a). In a study of chloroplast DNA diversity, no differences were found among populations, although markers distinguished the three Californian closed-cone pine species (Hong, Hipkins & Strauss 1993; Hong, Krupkin & Strauss 1993). The five *P. radiata* populations are interfertile (Brown 1966; Critchfield 1967; W.J.Libby unpubl. data). In terpenes (Bannister *et al.* 1962; Bannister & McDonald 1983; Burdon, Zabkiewicz & Low 1992; Burdon, Broekhuizen & Zabkiewicz 1997), immunological traits (Murphy 1981), isozymes (Plessas & Strauss 1986; Millar *et al.* 1988; Moran *et al.* 1988), RAPD DNA markers (Wu *et al.* 1999; three mainland populations), mitochondrial DNA (Strauss *et al.* 1993, but not chloroplast DNA; Hong, Krupkin & Strauss 1993), quantitative traits (Burdon, Bannister & Low 1992; Burdon, Firth, Low & Miller 1997), susceptibility to western gall rust (Kinloch & Libby 1997), and resistance to *Phytophthora cinnamomi* (Butcher & Stukely 1997) the five populations were differentiated from one another, with the mainland populations more closely related to one another and the island populations more distinct. Levels of biochemical genetic distance among the mainland populations compare to those among populations of the other California closed-cone pines (Millar *et al.* 1988; Moran *et al.* 1988). Genetic distances among the mainland *P. radiata* populations generally increased with distance; however, the most closely related pairs are ambiguous and not always related to geographic proximities. Considering all lines of evidence, the island populations are distinct both from each other and from the mainland populations, while different traits reveal various patterns of similarity among mainland populations.

New Hypothesis for Quaternary Evolution and Biogeography in *Pinus Radiata*

Accepting Axelrod's history that ancestral *P. radiata* migrated from Mexico/Central America northward into the California coastal region by the mid-late Miocene and evolved into the modern taxon by the late Tertiary, fossil evidence suggests that *P. radiata* occupied the coastal and outer-coast range region and did not extend far inland (Table 2). Early Pliocene fossils of *P. radiata* occurred in three coastal/outer coastal mountain locations: northern California in the vicinity of San Francisco / Pt Reyes, southern California at Mt Eden, and near the United States / Baja California border at Chula Vista. This suggests that *P. radiata* had spread at least as far north as Pt Reyes by this time. When the species next appeared in the macrofossil record, in Late Pliocene beds, two general regions were represented (Table 2), one again near San Francisco / Pt Reyes and one near Santa Barbara. Early Pleistocene fossils of *P. radiata* are from the same two regions. The *P. radiata* fossils from OIS 3, the interstadial of 28–40 ka, were recovered from three regions: Pt. Reyes, Santa Barbara, and Los Angeles. The most recent Quaternary fossil location (10 ka) is at Little Sur. None of the five extant locations has a *P. radiata* fossil record, although Quaternary fossil deposits occur in the vicinities of these areas.

The biogeographic evidence combined with paleo-climatic record is consistent with a hypothesis that *P. radiata* grew in disjunct coastal, near-coastal, and presumably some island locations throughout the late Tertiary and Quaternary. The changing patterns of *P. radiata* fossil locations over time, patchy nature of occurrences at any one time, distinctness of fossil locations from current distribution, correlations with climate fluctuations, and patterns of its genetic variation all suggest that *P. radiata* has long maintained a dynamic metapopulation structure (cf. Gilpin & Hanski 1991; Hanski & Gilpin 1997). That is, *P. radiata* may never have been widely distributed in continuous populations along the California coast, but rather occupied disjunct locations, expanding and contracting in response to shifts in climate and climate-influenced changes in fire-regimes. Population expansions, contractions, extirpations, and colonisations of new locations of varying sizes would lead to a dynamic mosaic of populations over time. The localised climate along the Californian coast, combined with a generally linear habitat and local environmental heterogeneity, would enforce a restricted distribution in limited suitable habitats, further promoting metapopulations dynamics.

The Quaternary climate of the California coast is likely to have been and remain a key factor influencing metapopulation dynamics of *P. radiata*. There is evidence that coastal pines, including *P. radiata*, respond to some documented climate cycles by population expansions, contractions, extirpations, and colonisations (Fig. 3, 4, 5; Table 2). At the general level, coastal pines appear most conspicuously in climate phases intermediate between extremes, occurring in high frequency neither at the coldest parts of the glacial periods when juniper dominated, nor during warmest parts of interglacials, when oak dominated.

Where we have continuous palynological information (the last 160 kyr), pines appear to have been most abundant within warm phases of glacial periods. They peaked in abundance, or expanded and colonised, during interstadials (e.g., OIS 3 and OIS 5) and during rather brief phases at the terminations of glacial maxima (e.g., transitions of OIS 2 to 1, 4 to 3, and 6 to 5). Within these, shorter-term pulses of pine events also corresponded to warm and wet El Niño phases (Fig. 5; Heusser & Sirocko 1997; Sirocko *et al.* 1999). When climate shifted to warmer periods (e.g., interglacials OIS 1, 5), pines decreased in abundance (Adam 1988; Heusser & Sirocko 1997; Heusser 1995, 1998) or disappeared locally (Erlandson *et al.* 1996; Heusser & Sirocko 1997) to be replaced by oaks. Similarly, during the cold phases of glacial cycles, pines decreased in frequency and locally disappeared, to be replaced by juniper. That the early Holocene warm period ("Xerotherm") was not the trigger for population fragmentation is indicated by several lines of evidence that coastal pines were abruptly extirpated at local areas several thousand years prior to the early Holocene. Although it is likely that hot, dry conditions of the early Holocene exerted additional pressure on *P. radiata*, pollen evidence suggests that a major shift in abundance occurred in the late Pleistocene. There is no evidence for significant change during the period reported for the Xerotherm.

This fossil evidence suggests that *P. radiata* favours (i.e., populations expand/colonise) conditions intermediate to long-term extremes. Heusser & Sirocko (1997), stressing that at least the last glacial termination was approximately synchronous with an extreme wet event throughout the Pacific Southwest, developed an argument that increases in pine frequency during these periods were related to wet winters, moderate temperatures, and strong seasonality. Abundance of charcoal coinciding with the pine events (Fig. 4) suggested that fire is associated with these climate periods, as has been seen elsewhere where winter precipitation allows accumulation of fuels (i.e., high productivity) and warm dry summers increase the potential for fires (Skinner 1996). Heightened wildfire frequencies correlate with these climate patterns in both the recent (Swetnam & Betancourt 1990) and 500-year records (Skinner 1996). Fire is important to *P. radiata*, as a serotinous-coned fire-adapted species (Linhart 1978). Climatic optima during interglacials appear to be too hot and dry for *P. radiata* expansion, with fuel conditions too sparse for fire to play a significant role. Glacial maxima are likely too cold and wet, without the seasonality and summer warmth to foster high productivity, fuel build-up, or frequent wildfires. During generally unfavourable climate periods, *P. radiata* would contract to sites where local conditions remained hospitable.

This suggests that the cyclic nature of climate is a macro-mechanism driving metapopulation dynamics in *P. radiata*. Periodic favourable intervals for pine growth and expansion relate to climate and its effect on increasing wildfire. In addition to the direct role of fire in stimulating pine expansion, historic fire periods may play a key landscape role on the Californian coast by affecting availability and quality of habitat. In other Quaternary ecosystems, fire has been implicated as a catalyst for reorganisation of vegetation during periods of rapid climate change (e.g., Whitlock 1992; Wigand *et al.* 1995; Millspaugh *et al.* 2000). Periods of increased fire frequency and expansion of pine coincide and peak in interstadial and glacial-termination times. *Pinus radiata* would occupy different sets of locations and varying total area as climate shifts between favourable and unfavourable periods, and alters the suitability of habitat at particular locations over time. The shifting mosaic structure suggested here for *P. radiata* over the last 2 million years or more would favor genetic drift in local population evolution more than has been implied previously. If this is so, fewer obvious adaptive trends in *P. radiata* populations may occur than in continuously distributed species. Differences between the proposed and previous schemes for *P. radiata* are summarised in Table 3.

Conservation and Restoration Implications

Although *P. radiata* is widely planted outside its range, the native populations have long been the focus of conservation concern (Jones & Stokes Associates Inc. 1994; Faber 1997; Libby 1997). From goat predation on Guadalupe Island to urbanisation, genetic contamination, fire suppression, and insect and pathogen epidemics—including, most critically, pitch canker—in the mainland populations, the species has been perceived as increasingly vulnerable. Current conservation efforts focus on maintaining and restoring the extant *in-situ* populations under the tacit assumptions that *P. radiata* is a relict species, and that the five populations occupy the only native habitat.

If elements of the evolutionary model suggested here have validity, conservation and restoration approaches for *P. radiata* may well consider a different approach (Millar 1998b). That is, if *P. radiata* has long existed in small disjunct populations and these have repeatedly changed in location over the Californian coast in response to fluctuating Quaternary climates (i.e., a metapopulation model), then sites beyond *P. radiata*'s current distribution might be considered suitable habitat for conservation. These, I suggest, may be thought of as "neo-native". *Pinus radiata* has readily naturalised in many California coastal locations, including locations documented by the fossil record as recently occupied by the species and under similar climates. Many of these areas are within the present range of its long-time tree associates, *P. muricata* and cypresses (*Cupressus spp.*), as well as many shrubs and herbs. *Pinus radiata* thrives in many of these locations. Concern for *P. radiata* "displacing" other native species in these areas seems minor since these are historically native sites; they are plant communities within which *P. radiata* has existed in the recent past, and associated controlling factors (insects/pathogens) are likely still present. If the presence of *P. radiata* in these communities causes shifts in native plant diversities, these may reasonably be considered natural dynamics under conditions where *P. radiata* is present.

A related conservation implication pertains to dispersal of *P. radiata* populations. Cooling climates of the late Holocene (relative to the early-mid) and trends of pollen abundance (e.g., Fig. 4, 5) suggest that *P. radiata* might naturally extend in abundance and location along the Californian coast, colonising new coastal sites and diminishing at others. Urban development and other human land-use activities at present may inhibit effective natural dispersal of the species. On the other hand, intentional and incidental planting in specific appropriate former habitat far beyond the current five populations may be viewed as assisting *P. radiata* to do what it might if natural migration conditions pertained.

None of this should be interpreted as licence or recommendation for allowing *P. radiata* to diminish at its present three mainland or two island locations. Nor does it mean the species shouldn't be considered an undesired exotic at certain inappropriate naturalised sites.

TABLE 3–Comparison of traditional Quaternary biogeographic scenario for *Pinus radiata* with that proposed in this paper.

Condition	Traditional scenario	This paper
Quaternary distribution	Widespread throughout Quaternary; fragmented in Holocene	Metapopulation: shifting populations, discontinuous and changing throughout Quaternary
Cause for fragmentation/ metapopulation shifts	"Xerotherm"	Oscillating climates cause periodic times when habitat favorable; suitable habitat shift in space
Times when populations fragmented or shifted	One episode "Xerotherm" (7–4 ka)	Repeated through Quaternary, e.g., termination of glacial maxima interglacials (12–10 ka; 130–125 ka) and to interstadials (65ka); termination of interstadials to glacial maxima (26–23 ka) and interglacials to glacial maxima (75–73 ka)
Favourable climate	Glacial (cool, wet)	Intermediate between climate extremes, i.e., interstadials and glacial/ interglacial transitions
Climate causing fragmentation	Hot, dry ("Xerotherm")	Shifts from favourable climates to cold wet (glacial maxima) and to warm dry (interglacial)
Primary causative agent for changes	Recent climate change	Quaternary climate oscillations and fire effects

Conservation of the native populations must surely remain a first priority. However, details of Quaternary climatology and biogeography provide challenging new perspectives on how we might develop conservation and restoration goals for the species.

ACKNOWLEDGMENTS

I thank Colin Burrows, Rowland Burdon, Ken Cole, William Libby, Matt McGlone, Howard Schorn, Nathan C. Skinner, Robert Westfall, and Wallace Woolfenden for reviewing various drafts of this manuscript.

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