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THE FATE OF CLADES IN A WORLD OF RECURRENT CLIMATIC CHANGE: Milankovitch Oscillations and Evolution

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Abstract Variations in Earth's orbit with periods of 10–100 thousand years (kyr) (Milankovitch oscillations) have led to recurrent and rapid climatic shifts throughout Earth's history. These cause changes in the geographical distributions of clades, which we term orbitally forced range dynamics (ORD). The magnitude of ORD varies geographically, e.g., with latitude. Climatic shifts cause extinction, splitting, and merging of gene pools and clades. They select among individuals and clades for traits enhancing the ability to survive in situ and to establish new populations. There is also nonadaptive sorting caused by the large geographical variation in ORD, as only gene pools that are in the right place when climate shifts survive. ORD lead to sorting at many levels of genealogic inclusiveness. Clades that have survived climatic shifts during at least one entire period of the longest significant Milankovitch oscillations (100 kyr), we name β -clades. The products of more recent cladogenesis are α -clades, which are always nested within a β -clade. We conclude that ORD may promote α -clade formation but curb rates of β -clade formation. In areas with little ORD, where gene pools persist without going extinct or merging, clade splits and divergence may accumulate leading to high rates of β -clade formation and β -anagenesis (evolutionary change persisting >100 kyr). High ORD should lead to low numbers of β -clades, β -clades with low levels of spatial genetic divergence, little geographical subdivision and large ranges, organisms with high vagility and low specialization, high proportions of β -clades formed by polyploidization, and little β -anagenesis. We predict global and interregional geographic patterns in these variables caused by differential ORD. Thus, ORD potentially explains a wide array of patterns, suggesting ORD as a fundamental factor in evolution. The vulnerability of biotas to many human activities should vary with the magnitude of ORD.

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INTRODUCTION

Research in recent decades has led to a major expansion in the knowledge of long-term climatic variability and of how organisms respond to such changes. The discovery that Earth's climate varies with variations in its orbit (Berger 1988, Hays et al. 1976, Imbrie et al. 1993b) revolutionized modeling of past climates (Wright et al. 1993). Owing to increased sampling of fossils and new dating techniques, it is now possible to document evolutionary responses and changes in the distribution of organisms in relation to climatic events (Bennett 1997). The combination of methods and ideas from genetics, systematics, and biogeography in the field of phylogeography (Avise et al. 1987, Avise 2000) has also made it possible to infer past changes in geographical distributions and levels of gene flow from patterns of genealogical relatedness among clades (Cruzan & Templeton 2000). All this new information has led to the realization that recurrent climatic changes affect evolution and cause biogeographical and macroecological patterns (Bennett 1997, Dynesius & Jansson 2000, Hewitt 1996).

BACKGROUND

Orbital Forcing of Climates

Beyond seasonal changes, the amplitude of climatic changes increases towards longer timescales but has marked peaks on the timescale of 10–100 thousand years (kyr) (Figure 1A). These climatic variations are caused by periodical changes in Earth's orbit, called Milankovitch oscillations, resulting from gravitational interactions with other planets in the Solar System, primarily Jupiter because of its size and Venus because of its proximity to Earth (Berger 1988, Berger & Loutre 1991). The tilt of Earth's axis varies with a 41-kyr period, the eccentricity of the orbit varies with a 100-kyr period, and the annual timing of minimum Earth-Sun distance varies with 19 and 23 kyr periods (Berger 1988). These orbital variations modify the spatial and temporal distribution of solar radiation received on Earth (Berger 1988, Imbrie et al. 1989). Combined with earthbound feedbacks from, e.g., atmospheric CO₂, global ice volume, and surface albedo, the variations in insolation produce large, rapid, nonlinear climatic changes (Berger 1988; Imbrie et al. 1989, 1993b) and stable conditions generally lasting only a few thousand years at a time (Imbrie et al. 1989, Webb & Bartlein 1992, Wright et al. 1993) (Figure 1B). In fact, the climate during the present 10-kyr-long interglacial period has been more stable than during glacial periods, which make up more than 90% of the Quaternary (Kukla 2000). Superimposed on orbital variation, there are millennial-scale climatic variations, which have been more pronounced during glacial periods (Dansgaard et al. 1993). Milankovitch oscillations have been a feature of Earth's entire history, as documented in rhythmic sedimentation patterns having the same periodicity as orbital variations (Olsen 1986, Zachos et al. 1997), although the amplitude and the relative importance of variation in different orbital

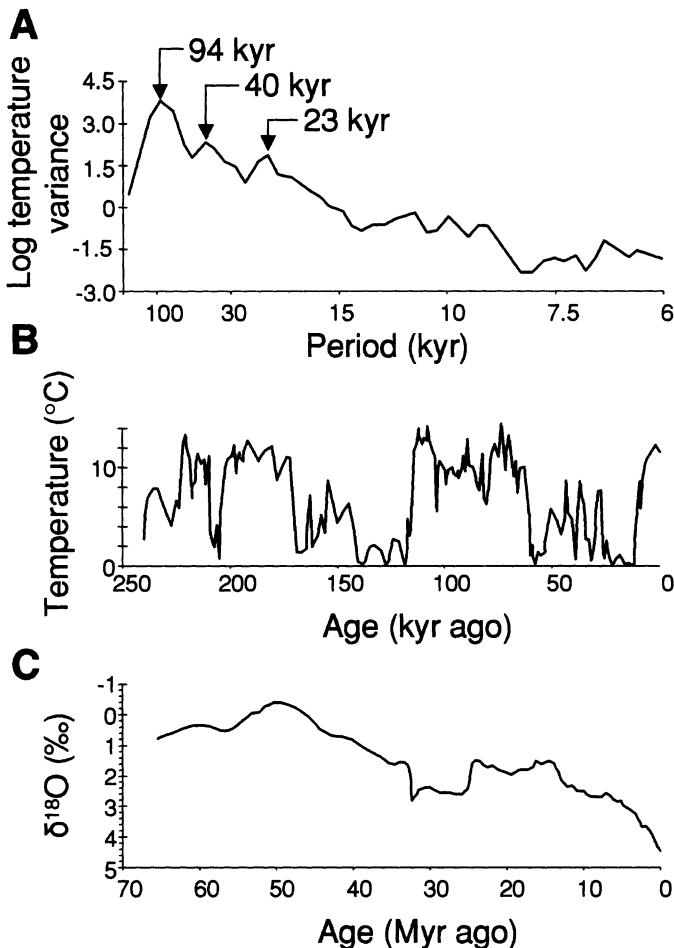


Figure 1 Climatic variability on different timescales. (A) The relative variance of climate is concentrated into peaks corresponding to variability in parameters of Earth's orbit. Data from the late Quaternary southern Indian Ocean. Adapted from Hays et al. (1976). (B) Sea-surface temperatures during the last 250 thousand years (kyr) at a site situated 50°N in the Atlantic, illustrating variability on Milankovitch timescales. Adapted from Imbrie et al. (1989). (C) Longer term variability in Earth's climate during the Cenozoic. Higher $\delta^{18}\text{O}$ -values indicate lower temperatures and larger global ice-volume. Myr = million years. Adapted from Zachos et al. (2001).

parameters have varied over time. For example, 100-kyr oscillations dominated during the past 800 kyr (Figure 1A), whereas 41-kyr oscillations dominated during the late Tertiary and the early Quaternary (Hooghiemstra & Sarmiento 1991, Imbrie et al. 1989, Webb & Bartlein 1992). Over millions of years, there are also long-term trends in Earth's climate caused largely by plate tectonics of oceanic and

atmospheric flows (Figure 1C), determining the mean climate over many Milankovitch oscillations.

Orbitally Forced Range Dynamics

Paleoecological studies show that the dominant responses to recurrent climatic shifts of species and other clades recognizable in the fossil record, have been changes in the size and location of their geographical distributions (Coope 1979, Cronin et al. 1996, Davis 1976, Graham et al. 1996, Huntley & Birks 1983, Roy et al. 1996). Such range fluctuations have occurred globally, although the magnitude of change has varied tremendously among regions (Bennett 1997). In a previous paper (Dynesius & Jansson 2000) we named changes in geographical distributions in response to Milankovitch climate oscillations “orbitally forced species’ range dynamics.” However, the term applies to clades at any level of genealogical inclusiveness, from single gene pools to phyla, and therefore should be more generally rephrased “orbitally forced range dynamics” (ORD). ORD entail advances and retreats of range limits and also movements and extinctions of genes, genotypes, and subclades in nonmarginal parts of the geographical ranges caused by the moving environmental gradients.

The magnitude of climatic change varies geographically owing to variation in the amplitude of insolation change and to spatially varying effects of the earthbound feedbacks. For example, the 41- and 100-kyr oscillations cause larger temperature changes toward the poles (Imbrie et al. 1989, Wright et al. 1993), causing more ORD (Bennett 1997). For example, plant taxa in tropical rain forests persisted locally in large proportions of their ranges during the last glacial period (Flenley 1998). In contrast, tree taxa of the temperate deciduous forests of the Northern Hemisphere were often restricted to small refugia during the last glacial period and have since expanded up to many thousands of kilometers (Davis 1976, Huntley & Birks 1983). The latitudinal gradient in the 100-kyr oscillations is caused by earthbound feedbacks, whereas the 41-kyr orbital oscillations intrinsically lead to a latitudinal gradient in insolation change (Imbrie et al. 1989, 1993b; Wright et al. 1993). Therefore, we assume that a latitudinal gradient in ORD has been continuously present. Local to regional factors can buffer against regional climatic change. For example, tropical mountain cloud-forests have generally been considerably less climatically variable than the region to which they belong because local factors lead to persistent mist and cloud formation (Fjeldså 1995, Fjeldså et al. 1999). Oceanic islands are generally little affected by Milankovitch climate oscillations at least in tropical latitudes (Cronk 1997). Steep physical gradients reduce ORD because organisms only have to move short distances as temperature, moisture conditions, or water levels change (Brown 1995, Darlington 1943, Hewitt 1996, van der Hammen 1995). The prime examples are steep slopes, both on land and under water. Both local moderation of climate variability and steep gradients were probably important for the survival of tree species in the

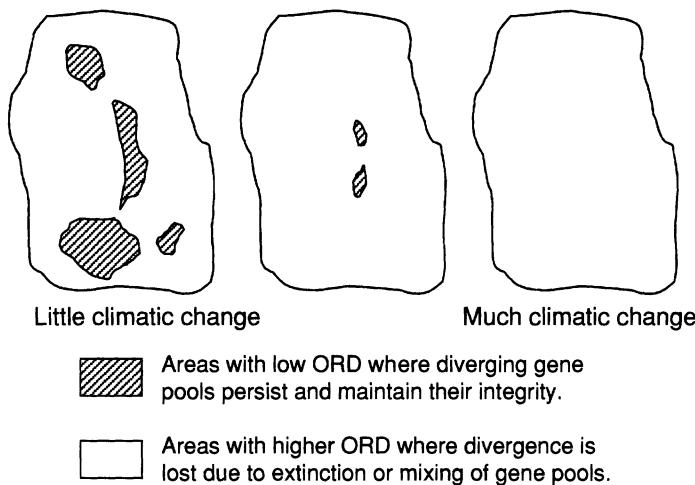


Figure 2 Schematic maps showing the total area occupied by a clade over an entire period of the longest significant Milankovitch oscillations (about 100 kyr). The level of orbitally forced range dynamics (ORD) of the constituent gene pools of the clade varies within this area. With increasing magnitudes of regional climatic change, smaller proportions of the total area maintain gene pools that both survive and remain separated over the entire time period.

mountains of southern Europe during glacial periods (Bennett et al. 1991). All else being equal, the lower the magnitude of climatic change, the larger the area continually inhabited by a clade (hatched areas of Figure 2). Those of the clade's gene pools that are in such areas will exhibit low levels of ORD.

ISSUES AND SCOPE

Concepts and Scale Dependence

A gene pool is the pool of genetic information carried by all individuals in a population. A gene pool and all its descendant gene pools constitute a clade (Williams 1992). Evolution is affected by sorting among genetic variants at any level of genealogic inclusiveness (Williams 1992). The evolutionary effects of climate change vary with genealogic inclusiveness and are thus spatially and temporally scale dependent. Individual gene pools occupying small areas are more likely to be strongly affected by climate shifts than more inclusive clades occupying larger areas. Therefore, we use a hierarchical approach, considering how orbitally forced climatic oscillations lead to sorting of genetic variation at different levels of genealogical inclusiveness. Sorting can be by natural selection, e.g., clade selection

sensu Williams (1992), or occur by chance, e.g., stochastic extinctions of populations that happen to be in the wrong place when climate shifts. We do not restrict clade selection to selection on emergent group properties because of the difficulties in determining which properties are emergent and at what level selection actually occurs. Ultimately, of course, any property of a clade can be ascribed to characters of individuals. If any process operating at a lower level, such as selection of genes within gene pools, results in differences in fitness among gene pools, it has produced the kind of fitness variation required for a higher level of selection (Williams 1992).

Evolutionary effects of orbitally forced climatic change are strongly temporally scale dependent. Most cladogenetic events (splitting of gene pools) do not contribute to long-term evolution, because gene pools merge or go extinct after relatively short time periods. To make a conceptual distinction, we name clades that at any point in time have survived and remained genetically separate for more than 100 kyr β -clades (Figure 3). These clades have been sorted by all climatic challenges during at least one entire period of the longest significant Milankovitch

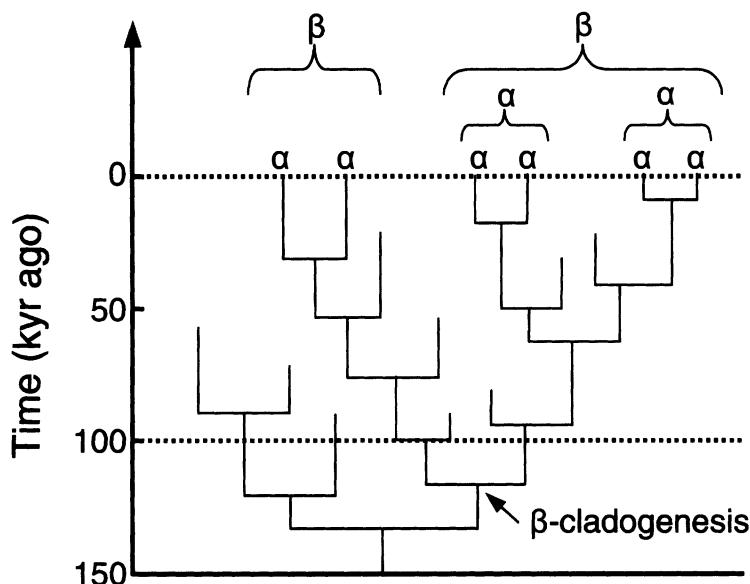


Figure 3 Conceptual distinction between recently produced clades and older ones that have been sorted during several climatic shifts. β indicates β -clades, i.e., clades older than 100 kyr at time zero. These clades have been sorted by all climatic challenges during at least one entire period of the longest significant Milankovitch oscillations. α indicates α -clades, i.e., clades produced by more recent cladogenesis. A single node, marked by an arrow, represents β -cladogenesis at time zero. All other nodes represent α -cladogenesis.

oscillations. A β -clade may or may not be reproductively isolated or morphologically distinguishable from its sister β -clade, and thus taxonomically recognized. The sister clades produced by more recent cladogenesis are α -clades, which are always nested within a β -clade (Figure 3). Of course, all β -clades started out as α -clades. In accordance with the naming of clades, we name all cladogenesis irrespective of the subsequent duration of the resulting clades α -cladogenesis. The subset of α -cladogenesis in which both sister clades survive and remain genetically separated at least 100 kyr becomes β -cladogenesis. Thus, a β -cladogenetic event must be at least 100-kyr old. The rate of α -cladogenesis equals the frequency of gene pool separation, whereas the rate of β -cladogenesis is also determined by later events. By analogy, we name any evolutionary change within a lineage over time α -anagenesis, and the change persisting more than 100 kyr β -anagenesis.

Orbitally Forced Range Dynamics as a Factor in Evolution

The primary role of recurrent orbitally forced climatic shifts is to put limits on how far evolutionary processes may go, rather than being a creative force in macro evolution. Orbitally forced climatic shifts can be seen as an overarching tier, interrupting evolutionary trends accumulating during the relatively short periods between climatic shifts, as gene pools mix or go extinct, or selective regimes change (Bennett 1990, 1997). Geographical variation in the magnitude of climatic shifts will cause variation in the degree to which evolutionary processes are interrupted. If the magnitude of ORD is low, cladogenesis and anagenesis, triggered by a wide range of processes, may continue, leading to an accumulation of β -clades and anagenetic change. In an influential paper, Hutchinson (1959) posed the question, "Why are there so many kinds of animals?" As pointed out by Blackburn & Gaston (1996), most models to explain large-scale, geographic patterns in numbers of taxa have, in the spirit of Hutchinson, considered high diversity, e.g., in the tropics, as the phenomenon. In contrast, we conclude that Milankovitch climatic oscillations curb rates of β -cladogenesis, leading to fewer taxa in a region than otherwise (Figure 4). Thus, Hutchinson's question might better be rephrased, "Why are there so few kinds of organisms in most parts of the world?" If the arguments presented here are correct, a world without orbitally forced climatic oscillations would have had biota with higher taxonomic diversity and more phenotypic disparity. This is in direct opposition to the idea that Milankovitch climate oscillations are primarily a factor raising diversity in the long term by fragmenting ranges, allowing divergence among isolated refugia owing to restricted gene flow (Clarke & Crame 1997; Haffer 1969, 1997; Valentine 1984; Vrba 1992). If this was shown to be generally true, our arguments would be undermined. However, molecular genetic data of rain forest faunas, for which the hypothesis was originally formulated (Haffer 1969), lend little support to the hypothesis that orbitally forced climatic changes favor speciation (Moritz et al. 2000). Instead, we argue that orbitally forced climatic shifts generally increase gene flow directly by

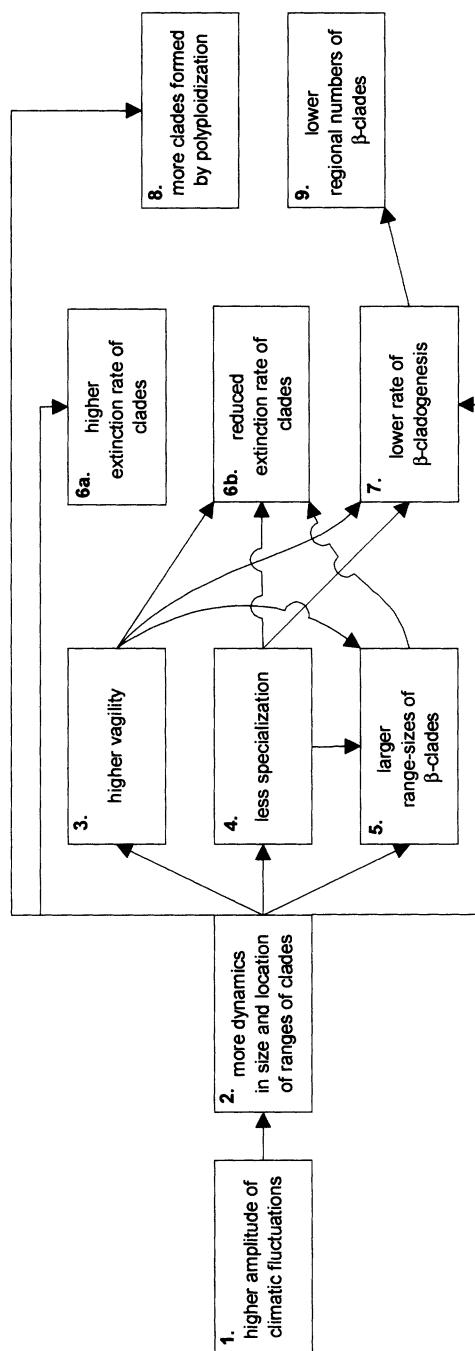


Figure 4 More ORD may lead to less specialization and more vagile organisms, clades with larger geographical ranges, lower rates of β -cladogenesis, more clades formed by polyploidization, and fewer β -clades.

reshuffling gene pools (Futuyma 1987), as well as indirectly by selecting for vagility and generalism. In areas where a clade is continuously present, gene pools may survive and maintain their genetic integrity, in allopatry or sympatry, over many climatic oscillations (García-Moreno & Fjeldså 2000). ORD reduces the extent of these areas and thus also curbs β -cladogenesis and β -anagenesis. For example, many European species have persisted and diverged genetically during both glacial and interglacial periods in the southern mountainous peninsulas, whereas northern expansions during interglacials were extinguished by each cold period (Bennett et al. 1991, Hewitt 1999). Good examples of radiations within stable areas are found in Lake Baikal, in the Cape flora, and among salamanders in Middle America (see below).

Beyond Milankovitch timescales, over millions of years, mean climates change (Figure 1C). These changes are potentially strong creative forces in macroevolution, in contrast to Milankovitch oscillations. Changes in mean climate are claimed to cause periods of increased speciation and species extinction, so-called turnover pulses (Vrba 1985, 1993). Turnover pulses may be produced in the following way: Changes in the long-term mean climate lead to a pulse in β -cladogenesis because regionally ephemeral habitats become persistent and because new habitats appear. Conversely, β -clade extinction rates should rise because persistent habitats may become regionally ephemeral or disappear. In addition, the change in mean climate adds to Milankovitch climate oscillations, increasing the challenges for organisms. On an even grander timescale, tropical climates have probably been continuously present, whereas arctic and boreal climates have only been present during some geological epochs. Therefore, it has been argued that tropical biotas have existed for longer periods, allowing more clades to accumulate (Fischer 1960).

Relation to Other Theories

Because Milankovitch climate oscillations are global in extent and have been working during Earth's entire history, their predicted consequences can be tested using many independent data sets. To do this, data on ORD with sufficient temporal resolution and spatial coverage are needed. As an alternative, levels of ORD might be inferred from climatic data. Because alternative explanations have been proposed to most of the patterns we predict, a catalogue of patterns confirming our individual predictions constitutes a weak test of our hypotheses. Stronger cases can be made if (a) several spatial patterns predicted by varying levels of ORD co-occur, (b) predictions that are unique to one hypothesis are tested, and (c) if hypotheses make contradictory predictions. We analyze the co-occurrence of patterns in three different contexts: latitudinal gradients, biota of the Cape Region of South Africa, and New World salamanders (see Co-Occurrence of Several Predicted Patterns, below).

To evaluate other hypotheses in relation to the role of ORD is beyond the scope of this paper, but some general comments are relevant. First, proper null models should be defined (e.g., Colwell & Lees 2000) to identify phenomena

in need of explanations. Second, some hypotheses are only correlative models, lacking mechanisms to generate predictions beyond the empirical correlation they describe. Third, because the factors behind many hypotheses covary spatially, it is necessary to identify situations in which they make opposing predictions. For example, most hypotheses of diversity patterns have been developed to explain the latitudinal gradient in taxonomic diversity, and consequently the proposed factors covary with latitude and make similar predictions along the gradient. The mechanisms most discussed recently are gradients in productivity (Wright 1983) and in the available area (Rosenzweig 1995). We consider ORD, productivity, and area as potentially complementary explanations. The question lies in their relative importance in different situations and whether they taken together suffice to explain observed patterns. The productivity hypothesis and our ORD hypothesis make opposite predictions in situations with low levels of ORD (hereafter “low ORD”) and low productivity. One such example is the extremely species-rich, low productive fynbos vegetation of the Cape region (Cowling & Pressey 2001), conforming to the predictions of ORD but not the productivity hypothesis. Furthermore, within the Cape Region, the climatically stable and low productive western parts support more species than the more productive, climatically variable areas to the east (Cowling & Lombard 2002).

Climate change affects the factors involved in the productivity and area hypotheses. Productivity as well as the extent of biological provinces and the range sizes of their taxa change with climate. This variation increases with the amplitude of climatic changes. For example, the temperate forest biome in Europe at the last glacial maximum about 21-kyr ago was only a small fraction of its early Holocene size about 12 kyr later.

We synthesize and review the evolutionary consequences of Milankovitch climate oscillations. First, we review relatively short-term processes at work within populations and gene pools during ORD. In the next section we explore higher-order consequences concerning clade sorting, rates of clade extinction, cladogenesis, and anagenesis. Then we deduce predictions about geographical patterns caused by spatial variation in ORD and review data to test them. We conclude by describing implications for conservation. The hypothesized consequences are summarized in Figures 4–6.

RESPONSES OF POPULATIONS TO ORBITALLY FORCED CLIMATIC CHANGE

ORD entail several different processes. Given that populations are locally adapted, changes in climate and associated biotic and abiotic factors should alter fitness optima of population phenotypes throughout the range of the clade (Davis & Shaw 2001). In response to this, local populations may either go extinct, adapt to the new conditions *in situ*, or individuals may disperse to and establish new populations in environments that have become suitable (Jackson & Overpeck 2000). Gene

flow may increase as individuals from previously separated populations come into contact and interbreed (Futuyma 1987). The type of response depends on the magnitude and rate of the climatic change, but traits and locations of the organisms are also important.

Consequences of Advancing Range Limits

SELECTION FOR VAGILITY When climate changes, range boundaries may advance. Marginal populations at range boundaries may become sources for new populations beyond the present range boundary. Phenotypes with high vagility (i.e., high dispersal ability and propensity) are more likely to found new populations and to initiate range advances. The descendants of the individuals arriving first preempt suitable habitats to the disadvantage of organisms arriving later (Hewitt 1999). This leads to selection for vagility, provided differences in vagility are heritable (Figure 4, *box 3*). Repeated founding events after long-distance dispersal would result in rapid directional selection for vagility (Cwynar & MacDonald 1987). Range advances are often achieved by long-distance dispersal. For example, the observed rapid advances in the beginning of the Holocene of north temperate tree taxa can only be explained this way (Cain et al. 2000, Clark et al. 1998, Skellam 1951). In such situations, selection for vagility should primarily affect traits associated with the tail of dispersal curves.

There are several examples in which advances of range limits are correlated with higher proportions of vagile phenotypes, although it has seldom been conclusively shown that the change is heritable. Lodgepole pine, *Pinus contorta*, has, into recent time, been advancing northwards from glacial refugia. Seed dispersability, measured as the size of the seed wing relative to seed mass, increases the more recently the population was founded ($r^2 = 0.77$, $P < 0.001$, $n = 14$) (Cwynar & MacDonald 1987). Two bush cricket species, *Conocephalus discolor* and *Metraptera roeselii*, have expanded their distributions in Britain over the past decades (Thomas et al. 2001). In both species the frequency of the most long-winged, dispersive form was higher in recently founded populations, which is argued to at least partly have a genetic basis. Assuming that virtually all long-distance movements are achieved by the longer-winged morphologies, their higher frequencies in populations founded less than 10 years ago represent about 4-fold and 14-fold increases in long-distance dispersal for *C. discolor* and *M. roeselii*, respectively (Thomas et al. 2001). Individuals of the butterfly *Pararge aegeria* subsp. *tircis* from populations established after recent range advances were heavier and had relatively more flight muscles compared with older populations, which should make them able to fly longer distances (Hill et al. 1999). The individuals were raised in a common laboratory environment, excluding environmental (except maternal) effects on the phenotype.

Selection against vagility owing to local adaptations, dispersal-related mortality, and (at least among flying insects) tradeoffs with reproductive investment are ubiquitous. Given this, can we expect to see persistent trends in vagility among

taxa from regions differing in ORD? The carabid beetle *Pterostichus melanarius* is dimorphic for wing length. In its native range in Europe the proportion of the long-winged form was low in old habitats (about 2%) but considerably higher (24%–45%) in new and unstable habitats (den Boer 1970). In its introduced North American range the proportion of the long-winged form increased from about 20% to 60% to 70% in successively more recently founded populations (Niemelä & Spence 1991). In one such recently established population, the proportions of long-winged individuals dropped from 61% to 43% over 5–6 years, suggesting that the long-term effect may be less conspicuous (Niemelä & Spence 1999). Cody & Overton (1996) reported that plants colonizing small islands along the coast of British Columbia evolved reduced seed dispersal distances within 10 years. In this case the fitness of dispersing seeds must be effectively zero because they are lost in the ocean. In continental settings selection against dispersal must be much less severe. Furthermore, less conspicuous range dynamics also occur at millennial and shorter timescales (Webb & Bartlein 1992), suggesting that traits enhancing vagility should be frequently favored in climatically variable areas.

SELECTION FOR LOW SPECIALIZATION Organisms differ in the width of their environmental tolerance, habitat and resource specialization, and in how dependent they are on specific species (Futuyma & Moreno 1988). Less specialized, more tolerant individuals are more likely to find suitable habitats, establish in new areas, and survive while moving through heterogeneous environments. Thus, range advances should select for low specialization and wide tolerance (Figure 4, *box 4*). This conclusion is supported by a spatially explicit patch-occupancy model (Bowers & Harris 1994). In the model a broad-niched generalist species was able to track environmental changes better than a specialist species. In constant or slowly changing environments the specialist species was favored owing to better competitive abilities, but with moderate or rapid environmental change, the generalist species was able to limit the ability of the specialist to survive and/or track the shifting environment. An empirical example of selection for generalism is the northward advance of the butterfly *Aricia agestis* in Britain (Thomas et al. 2001). Northern populations formerly laid their eggs mostly on *Helianthemum chamaecistus*, but recent range expansions have been accomplished primarily by utilizing *Geranium* and *Erodium* growing in habitats that formerly were probably too cool. This has enabled the butterfly to bridge gaps greater than 14 km in the fragmented distribution of the original host plant. This would have been extremely unlikely without these stepping-stones. In a field choice experiment wild females from recently founded populations preferred to lay eggs on *Geranium molle*, the most widespread host plant used during the range advance, even though they naturally used other host plants at these localities. Butterflies retained their differences in host plant preference when reared in a common laboratory environment, strongly suggesting a genetic contribution to host plant choice (Thomas et al. 2001).

Improved environmental conditions at existing range boundaries are likely to initiate range advances without any evolutionary change. Once the advance is

initiated, individuals that advance most rapidly are likely to be favored. Advancing range fronts become characterized by dispersive generalists or by specialists on habitats common in the colonized area (Thomas et al. 2001).

INTERBREEDING DURING RANGE ADVANCES Individuals from previously separated populations of sexual organisms may come into contact and interbreed during range advances. This may result in hybrid speciation (e.g., polyploidization; see below) or various degrees of introgression between differentiated gene pools or clades. Introgression may be counteracted by the formation of hybrid zones (Hewitt 1975, 2001; Remington 1968). The postglacial northward advance of European white oaks, *Quercus robur* and *Q. petrea*, and silver fir, *Abies alba*, involved introgression. The white oaks spread from three refugial regions with distinctive chloroplast DNA types and mixed in central and northern Europe. The geographic pattern of chloroplast DNA types is independent of the taxon boundary, implying both intraspecific and interspecific introgression (Comes & Kadereit 1998). Silver fir appears to have survived in five refugial regions and advanced northwards from three of these. The entire French refugial gene pool appears to have merged with the north Italian gene pool. The north Italian and the Balkan refugial gene pools have mixed in two extensive areas in central Europe, but also retain their genetic integrity in the refugia and over large expansion areas (Konnert & Bergmann 1995).

Responses to Climatic Change in Other Situations

The same processes as those at work during advances of range limits are active in other parts of the range where climate changes. However, populations in other situations are more likely to go extinct without leaving offspring during climatic change. Organisms may fail to establish new populations, either because they cannot move fast enough, because they encounter barriers (Ashworth 1996, Brown 1995), or because the preferred habitat becomes rare or temporarily disappears regionally. Establishment in new areas with suitable habitat may also be impeded by competition from individuals of the same clade already present before the change. Survival *in situ* is hampered by competition with immigrants better adapted to the new environment at that site. Again, all this may lead to selection for high vagility and low specialization (Figure 4, boxes 3 and 4). Low specialization is selected for because it is less likely that the niche of such individuals will disappear completely in an area (Jackson & Overpeck 2000, McGlone 1996). Moreover, less specialized organisms do not need to disperse as rapidly to track their habitat. If peripheral populations go extinct, range limits retreat.

MACROEVOLUTIONARY CONSEQUENCES

The immediate responses of populations to climate change add up to a number of evolutionary consequences on longer timescales and/or for more inclusive clades, including clade sorting as well as long-term cladogenesis and anagenesis.

Clade Sorting

The probability of long-term survival varies among clades depending on characters of organisms, e.g., degree of specialization and vagility. Generalism and high vagility promote high population densities and wide distributions. All these factors are positively correlated with low extinction rates at the level of species or higher taxonomical rank (McKinney 1997). There is also nonadaptive sorting caused by the large geographic variation in ORD. Clades that are in the right place, i.e., in areas demanding the least distributional change, have higher probability of surviving climatic shifts and should thus have higher fitness over long timescales. Oceanic islands have high proportions of paleoendemics, which have disappeared from continents, probably because stable climates and poverty of competitors and exploiters have allowed island clades to persist longer (Cronk 1997). For most taxa of European forest trees, only clades that persisted during both glacial and interglacial times in southern and southeastern Europe have living European representatives (Bennett et al. 1991). The northern populations of most taxa went extinct *in situ* during the glacials. In the beginning of interglacials northern Europe was colonized from southeastern and southern refugia (Bennett et al. 1991).

The relationship between extinction rates and magnitude of ORD should differ between α - and β -clades. For α -clades, represented by terminal branches in a cladogram, the risk of going extinct should increase with higher ORD. However, β -clades, which have been sorted by several previous climatic shifts, include at least one gene pool with traits that enabled survival, and/or occupy an area requiring little movement (Figure 2). Such gene pools are more likely to survive similar climatic shifts in the future, making the β -clades to which they belong less extinction prone (Figure 4, *box 6b*). Thus, climatic shifts act as extinction filters (Balmford 1996), pruning phylogenetic trees from extinction-prone clades. The filtering will be stronger, reducing extinction rates of β -clades more, the higher the magnitude of ORD. Thus, for β -clades the positive relationship between their extinction rate and ORD should be less steep than for α -clades, or even negative, depending on the effectiveness of filtering at climatic shifts in reducing subsequent extinctions. Evidence from fossils of marine taxa (species and higher taxonomic ranks) indicate that tropical taxa (low ORD) are on average geologically more short-lived and have higher extinction rates than taxa at higher latitudes (high ORD) (Flessa & Jablonski 1996). This suggests a negative relationship between ORD and extinction rate of β -clades.

Another aspect of clade sorting by climatic changes is the effect on the size and composition of regional assemblages of clades. For example, Europe is poor in temperate-forest tree taxa compared with eastern Asia and eastern North America, because Europe has lost more taxa owing to late-Tertiary and Quaternary climatic oscillations (Latham & Ricklefs 1993). Clades including vagile, generalist individuals are selected for when groups of clades respond to climatic shifts. An empirical example is the 46 nonmigratory butterfly species that reach their northern limit in the United Kingdom. If temperature is limiting, these species should

have benefited from climate warming during the past 30 years, but intensification of agriculture has led to 70% losses of seminatural habitats since 1940 (Warren et al. 2001). A higher proportion of the species that are mobile (45%) and/or habitat generalists (50%) expanded their ranges, compared with sedentary (8%) and habitat-specialist species (7%; habitat specificity and low mobility were highly correlated among species). Low mobility and/or high habitat specialization restrict species in fragmented habitats and slow down advances across patchy landscapes (Warren et al. 2001). Another example is the colonization of Scandinavia by alpine carabid beetles during the last deglaciation. Alpine environments generally select against wings in insects (Sømme 1989), but alpine specialist species of Scandinavia are instead better flyers than generalist species that occur in both alpine and lowland areas. Probably only the good flyers among the alpine specialists were able to colonize from glacial alpine refugia during the rapid postglacial warming, whereas flightless habitat generalists have been able to disperse slowly through nonalpine habitats (Nilsson et al. 1993). In the alpine flora of New Zealand the deglaciated regions have primarily been colonized by generalist species or species capable of long-distance dispersal (McGlone et al. 2001). The probability that a clade will colonize a new suitable area should generally decrease with distance. Grytnes et al. (1999) proposed this as an explanation for the strong latitudinal diversity gradient in Scandinavian plants, having their presumed glacial refugia mainly in southern Europe. The time since appearance of a new habitat may also effect how many species have colonized. In New Zealand the postglacial sea-level rise converted a number of freshwater lakes into marine fjords ~9–17 kyr ago. There is a strong positive correlation between fjord age and local species richness of marine epifaunal invertebrates of the subtidal zone (Smith 2001).

Cladogenesis

We argue that ORD may raise the rate of α -cladogenesis but curb β -cladogenesis (Figure 5). There is a wide range of mechanisms, abiotic as well as biotic, that could lead to separation of gene pools in sexual organisms. The separation occurs when gene flow is reduced or prevented by barriers to dispersal (allopatrically), distance (parapatrically), disruptive selection (sexual or ecological) within a locality (sympatrically), or abrupt speciation (e.g., polyploidization). If ORD is low, gene pools are more likely to survive and remain separated (Figure 5). Moreover, organisms may specialize and evolve reduced dispersal abilities without going extinct. This leads to decreasing gene flow, further favoring the integrity of gene pools and leading to radiation of β -clades.

The importance of isolate formation in controlling speciation rates has been emphasized, assuming, explicitly or implicitly, that speciation rates are limited by the rate of α -cladogenesis. However, gene pool separation (α -cladogenesis) leads to β -cladogenesis only if the gene pools survive and maintain their integrity. This fact has been accounted for in some speciation models, which argue that speciation is most likely at intermediate levels of disturbance. At low frequency

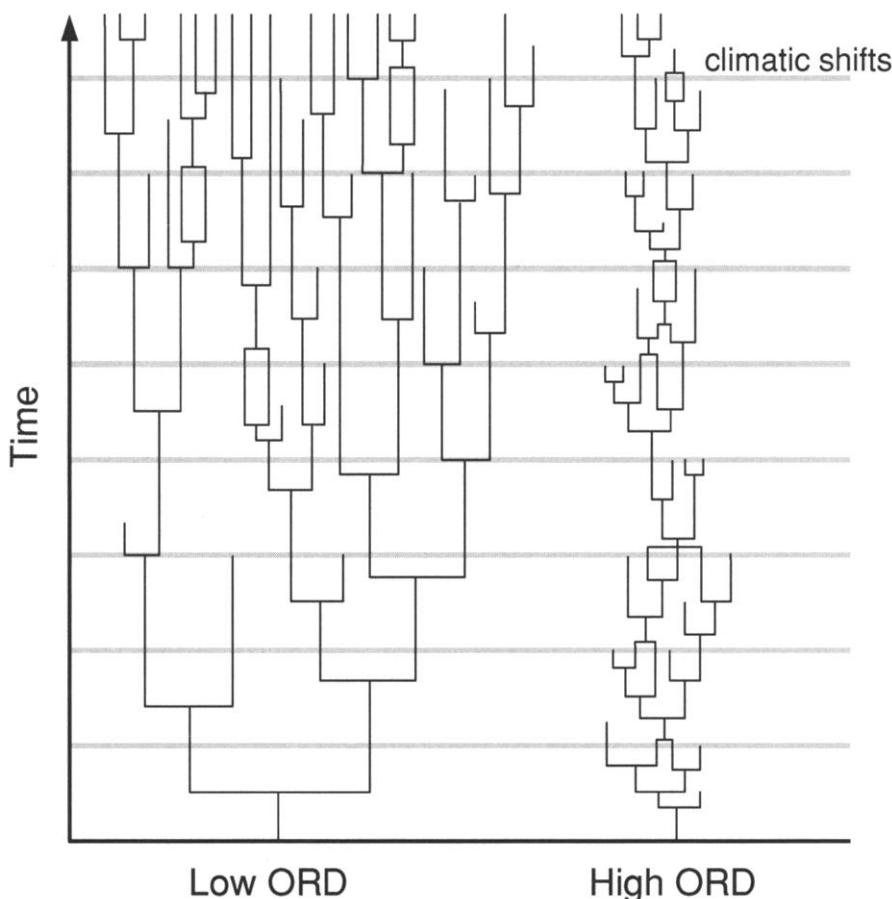


Figure 5 Cladograms depicting the evolution of lineages through several climatic shifts in regions with low and high ORD, respectively. Lineages may split (cladogenesis), merge (mixing of gene pools), or terminate (extinction). In situations with low ORD, α -clades persist longer, leading to deep-branched trees and accumulation of lineages. At high ORD, α -clades are more likely to go extinct or merge, keeping the number of β -clades low, even if α -cladogenesis may be more frequent. In this example, the probability of splitting and merging is more than twice as high whereas the persistence of lineages is less than half, at high compared to low ORD. Cladogenesis through hybrid speciation, e.g., polyploidization, is excluded from the cladogram.

or intensity of disturbance few isolates are formed, whereas at high levels isolates do not persist long enough to allow speciation (Allmon et al. 1998, Stanley 1986). We argue that the general relationship between rates of β -cladogenesis and ORD are monotonically negative under realistic conditions. In other words, even though ORD favor some factors leading to α -cladogenesis, the rise in rates of extinction of

α -clades (Bennett et al. 1991; Cronin 1985, 1987; Hewitt 1996) and of merging of α -clades through interbreeding (Cope 1994, Futuyma 1987, Glazier 1987) will be stronger. Moreover, these processes will also negatively affect cladogenesis not caused by ORD. Thus, the net effect of ORD will be to curb β -cladogenesis (Figure 5). We see two main reasons for this. First, there is much α -cladogenesis that is not caused by climatic change. Second, ORD indirectly disfavor all processes leading to α -cladogenesis (except polyploidization) because ORD select for characters enhancing gene flow (generalism and high vagility).

The magnitude of orbitally forced climatic change determines what proportion of a clade's gene pools remain unaffected by extinction and gene-pool merging. Such persistent gene pools will be primarily in areas continuously occupied by the clade (Figure 2). This concept of areas with persistent gene pools is more restrictive than that of glacial refugia (Bennett et al. 1991, Haffer 1997, Hewitt 1996) in being not only a place for clade survival, but a place where gene pools are not disrupted by climatic shifts. Regions with a large area with persistent gene pools should have high rates of β -cladogenesis and β -anagenesis.

POSITIVE EFFECTS OF ORD ON α -CLADOGENESIS ORD should favor gene pool splitting in three principal ways: (a) by creating physically separated (allopatric) gene pools, (b) by favoring expansion into new areas where parapatric divergence can start, and (c) by causing a paucity of specialized organisms, leaving resources underexploited and thereby making ecological divergence in sympatry more frequent (Schluter 2000). Parapatric divergence occurred in the marine gastropod *Acanthinucella spirata* as it expanded northward along the Californian coast following the last glacial maximum. The recently established populations form a clade morphologically distinct from populations in refugial areas, fossil as well as recent (Hellberg et al. 2001). At high latitudes suddenly appearing freshwater habitats following glacial retreat have led to bursts of cladogenesis and phenotypic evolution in colonizing fishes by providing environments with few competitors (Schluter 2000). Pairs of such divergent, closely related fish clades usually divide resources in the same way, one being a pelagic zooplanktivore, and the other a benthic prey consumer. Postglacial ecological cladogenesis has been repeated in many freshwater bodies and for several fish taxa in northern areas. Such evolution of similar clade pairs repeated in several waterbodies is virtually nonexistent at lower latitudes (Schluter 1996).

GENERALISM AND VAGILITY REDUCE BOTH α - AND β -CLADOGENESIS Indirectly, ORD reduces the probability of cladogenesis by selecting for generalism and vagility (Figure 4, *box 7*), thereby raising gene flow. For example, niche extension to a new host plant type by an herbivorous insect clade is more likely to lead to a new isolated gene pool, the narrower the host-plant use in the clade. If host plant specialization is low, gene flow between the individuals utilizing the new host plant and those using other host plants is more likely, preventing α -cladogenesis. Moreover, contact between two geographically separated but closely related clades is

more likely to lead to gene flow between them if the organisms have broad niches. This leads to lower β -cladogenesis. Empirically, the frequency of β -cladogenesis is lower in generalist than specialist clades (Chown 1997, Kauffman 1978, Stanley 1979, Vrba 1989).

High vagility enhances gene flow, making cladogenesis less probable (Chown 1997, Mayr 1963). High frequency and long distance of dispersal decrease the probability of both parapatric (Gavrilets et al. 2000b) and sympatric (Kawata 2002) cladogenesis according to model simulations. Empirically, there is a general negative correlation between the geographical genetic structure among populations and the vagility of organisms (Bohonak 1999). In marine taxa, high fecundity and highly vagile larvae are associated with low speciation rates in the fossil record (Chown 1997, Jablonski 1986). The same pattern is found among land plants (Chown 1997). On small islands, only vagile taxa are unable to radiate (Terborgh 1992). In Hawaiian crickets the low vagility and high specialization compared with their continental relatives have led to a tremendous radiation resulting in a unique concentration of species (Otte 1989). In regions with a large area with persistent gene pools (Figure 2), organisms that for some reason (e.g., low vagility or patchy habitats) have low levels of intraclade gene flow may radiate extensively while others do not. Thus, the latter type of organisms, with little innate tendency for cladogenesis, should exhibit less spatial patterning in relation to ORD. For example, the latitudinal diversity gradient is much less pronounced or is absent in generally vagile groups such as protozoa, microalgae, meiofauna, and bryophytes (Churchill et al. 1995, Hillebrand & Azovsky 2001).

ORD AND REPRODUCTIVE BARRIERS Reproductive barriers make clades resistant to merging with other clades, thus increasing clade persistence. Reproductive barriers may evolve gradually over many generations (allopatrically, parapatrically, or sympatrically) or form abruptly, e.g., by polyploidization (Mayr 1963). In this section, we discuss gradual formation of reproductive barriers; abrupt formation by polyploidization is treated in “Polyploidy,” below. It has been argued that the short stable periods during Milankovitch oscillations (Figure 1B) are generally not long enough for reproductive barriers to evolve before isolation is lost (Coope 1995, Futuyma 1987, Glazier 1987). It is believed that evolving reproductive isolation takes tens of thousands to millions of years in most cases (Avise et al. 1998, Coyne & Orr 1997, Mayr 1963), but it can occur much faster if divergent selection leads to reinforcement of mating barriers (Hendry et al. 2000, Higbie et al. 2000). In a review of extensive data on genetic distances and degrees of reproductive isolation (derived from crossing experiments) among species pairs of *Drosophila* fruit flies, Coyne & Orr (1989, 1997) concluded that evolving reproductive isolation takes about 0.2 million years (Myr) for taxa that currently are sympatric and about 2.7 Myr for allopatric taxa. Using molecular data and phylogenetic relationships among and within about 300 vertebrate species, Avise and coworkers (Avise et al. 1998, Avise 2000) estimated the average speciation duration to be ~1–3 Myr. McCune & Lovejoy (1998) concluded that the time for speciation ranged between

0.8 and 2.3 Myr for sister species of fish of putative allopatric origin and up to 0.5 Myr for fish species pairs assumed to have originated in the same lake. Eight pairs of marine clades that became separated by the Isthmus of Panama approximately 3 Myr ago have all evolved some degree of reproductive isolation, ranging from incomplete prezygotic to complete pre- and postzygotic isolation (Lessios 1998).

To conclude, although evolving reproductive barriers can be rapid if divergence affects mate choice, and seem to be rapid in radiations of freshwater fish in situations with much ecological opportunity, most estimates indicate that evolving reproductive barriers normally takes far longer than the stable parts of Milankovitch oscillations. Thus, the probability of evolving reproductive barriers should decrease with increasing magnitude of ORD, although the formation of hybrid zones may to some extent protect the genetic integrity of clades when partial reproductive barriers have evolved (Hewitt 1975, 2001; Remington 1968).

EXAMPLES OF ORD REDUCING β -CLADOGENESIS There are many examples indicating a monotonically negative effect of ORD on β -cladogenesis. Even within the low-ORD tropics, β -cladogenesis is higher in areas with the lowest levels of ORD, such as mountains with steep gradients and locally stabilized climate. In tropical South American and African birds and in tropical African plants low climatic amplitude, inferred from the occurrence of paleoendemic species that are extinct elsewhere, is well correlated with the occurrence of recently formed species with restricted ranges (neoendemics) (Fjeldså 1994, 1995; Fjeldså & Lovett 1997). These hotspots of paleo- and neoendemic congruence are found in montane forests, e.g., in specific parts of the tropical Andes, whereas the lowland rainforests are dominated by old, widespread species. The endemism hotspots are in places with peaks in climatic stability, caused by local, orographic moderation of regional climate (Fjeldså 1995; Fjeldså et al. 1997, 1999). The correlation between current climatic stability and peaks in paleo- and neoendemic congruence indicates that local moderation of climatic extremes persisted through the shifting climates of the Quaternary, permitting gene pools to survive and maintain their integrity.

In Indo-Pacific shallow-water corals, the frequent sea-level changes during the Quaternary repeatedly laid the continental shelves dry, so that any particular area was available for coral growth for on average 3.2 kyr at a time. These frequent large-scale distributional changes probably prevented β -cladogenesis, and most of the coral species have little geographical genetic subdivision (Potts 1983). During the Great American Biotic Interchange, a number of North American mammalian taxa entering South America diversified extensively, whereas South American taxa entering North America exhibited very little β -cladogenesis (Marshall et al. 1982). Our interpretation of this is that clades entering a region with low ORD (South America) radiate, whereas clades entering a region with high ORD (North America) produce few β -clades. In addition, the initial cladogenesis in the south-heading clades had already taken place in tropical North America prior to the interchange

(Webb 1991), the part of the continent that had lowest ORD during the Pliocene and Quaternary. A parallel to this is found among pelagic foraminiferans in the early Tertiary, during which acquisition of algal symbionts is associated with radiations. However, one symbiotic clade, originating at high latitudes, remained a low-diversity taxon for almost two Myr. As the clade then expanded into low latitudes, it gave rise to several β -clades (Quillévéré et al. 2001). In some situations, however, ORD may favor β -cladogenesis by allowing clades to colonize otherwise inaccessible refugial areas. For example, flightless grasshoppers of the genus *Melanoplus* have speciated in the Rocky Mountains during the high-ORD Pleistocene (Knowles 2000). Cool climates during glacial periods made it possible for populations to colonize mountaintops inaccessible during interglacial periods. Populations then diverged among mountaintops (Knowles 2001). Merging of gene pools during subsequent climatic shifts may have been prevented by rapid evolution of reproductive barriers by sexual selection (Knowles 2000). However, it is unknown what the rate of β -cladogenesis would have been in this sedentary clade under low ORD.

Anagenesis

Anagenesis is phenotypic evolutionary change within a lineage over time, irrespective of whether changes evolve gradually or are punctuated. As long as there are stable differences in selection among gene pools and gene flow is not excessive, gene pools can develop any degree of difference in any number of characters. The geographic variation among gene pools in different parts of extant species' ranges (Endler 1986) shows that such differences are ubiquitous. The level of genetic differentiation among gene pools depends on the rate of divergence among gene pools, and for how long the gene pools survive and remain isolated.

All aspects of ORD affecting cladogenesis may also affect anagenesis. ORD may drive anagenetic change by recurrently providing new biotic and abiotic environments favoring α -anagenesis. Clades that expanded into new areas during the Holocene have adapted to local environmental conditions (Davis & Shaw 2001, Hellberg et al. 2001). High ORD may lead to habitats poor in specialized clades setting the stage for adaptive radiations into vacant niches, causing surges of α -anagenesis (Schluter 2000). The rate of differentiation can be very rapid under strong selection, e.g., following expansions into new areas (Bell 1988, Schluter 2000). However, ORD also curb anagenesis by favoring vagile and generalized organisms, thereby promoting gene flow and slowing down divergence. In addition, oscillating climates are likely to produce oscillating selection pressures, thereby counteracting β -anagenesis. ORD also curb β -anagenesis by making it more likely that diverging gene pools accumulating anagenetic change go extinct or merge with other gene pools before evolving reproductive barriers (see above). Analogous arguments have been used for differentiation in metapopulations on short timescales. Rapid turnover of populations means that local populations are ephemeral and are likely to go extinct before they have diverged much (Gavrilets

et al. 2000a, Lande 1992, Slatkin 1977). However, when ranges expand by the successive founding of new populations, differentiation among populations in a metapopulation might be favored if the propagules come from only one source population (Harrison & Hastings 1996). In contrast, if the propagules for a new population come from many source populations, range expansion would lead to mixing and thus reduced differentiation among populations (Harrison & Hastings 1996).

NORMALIZING CLADE SORTING ORD may curb β -anagenesis by imposing long-term normalizing sorting. The gene pools most likely to survive climatic shifts are either inhabitants of locally persistent as opposed to ephemeral habitats (Bell 1988, Williams 1992) or clades that survive by habitat tracking, thereby always experiencing environmental conditions to which they are sufficiently adapted (Eldredge 1989). The survivors are likely to be the ancestral forms because the habitats producing new forms periodically disappear from the region. Because diverging lineages have lower probability of survival, cladograms will look more like a raceme than a tree (Figure 6). On a broad scale, such as in the fossil record, this will look like long-term anagenetical stasis. Clades branch off during each stable period, but these diverging branches are aborted at subsequent climatic shifts, leaving primarily the ancestral forms. The more a clade has diverged from the ancestral form and acquired adaptations to the local environment, the more likely it will be disfavored by climatic change. Therefore, although sometimes there will be more α -anagenesis in regions with high ORD, β -anagenesis will be lower. If ORD is low, normalizing clade selection will be less strong, making new locally adapted gene pools almost as likely to survive as the ancestral form (Figure 6). The idea of more β -anagenesis in regions with low ORD parallels Sheldon's (1996) hypothesis of continuous phyletic evolution and much anagenetic change in stable environments, whereas stasis is hypothesized to prevail in unstable environments.

Marine three-spined sticklebacks, *Gasterosteus* spp., have from the Miocene onward repeatedly invaded freshwater drainages, where extensive phenotypic differentiation has taken place (Bell 1988). Divergent clades within lakes are generally maintained despite gene flow between them (Taylor 1999). The freshwater forms soon go extinct, as the lakes they inhabit disappear (Bell 1988). Most extant forms inhabit lakes formed since the last glacial period (Bell 1988). McCune (1987) reports similar selective extinctions of lacustrine Mesozoic Semionotid fishes and persistence of their fluvial relatives. In the African Lake Turkana basin several mollusc populations diverged morphologically during Pleistocene periods of isolation owing to water-level regressions, but these divergent forms disappeared and were replaced with molluscs of ancestral morphology during subsequent transgressions (Williamson 1981). Despite New Zealand's cold, highly seasonal climates during most of the Quaternary there are no tree species adapted to those conditions because those conditions disappeared during brief, highly oceanic and warm periods (McGlone et al. 2001). High-latitude insects show almost no morphological

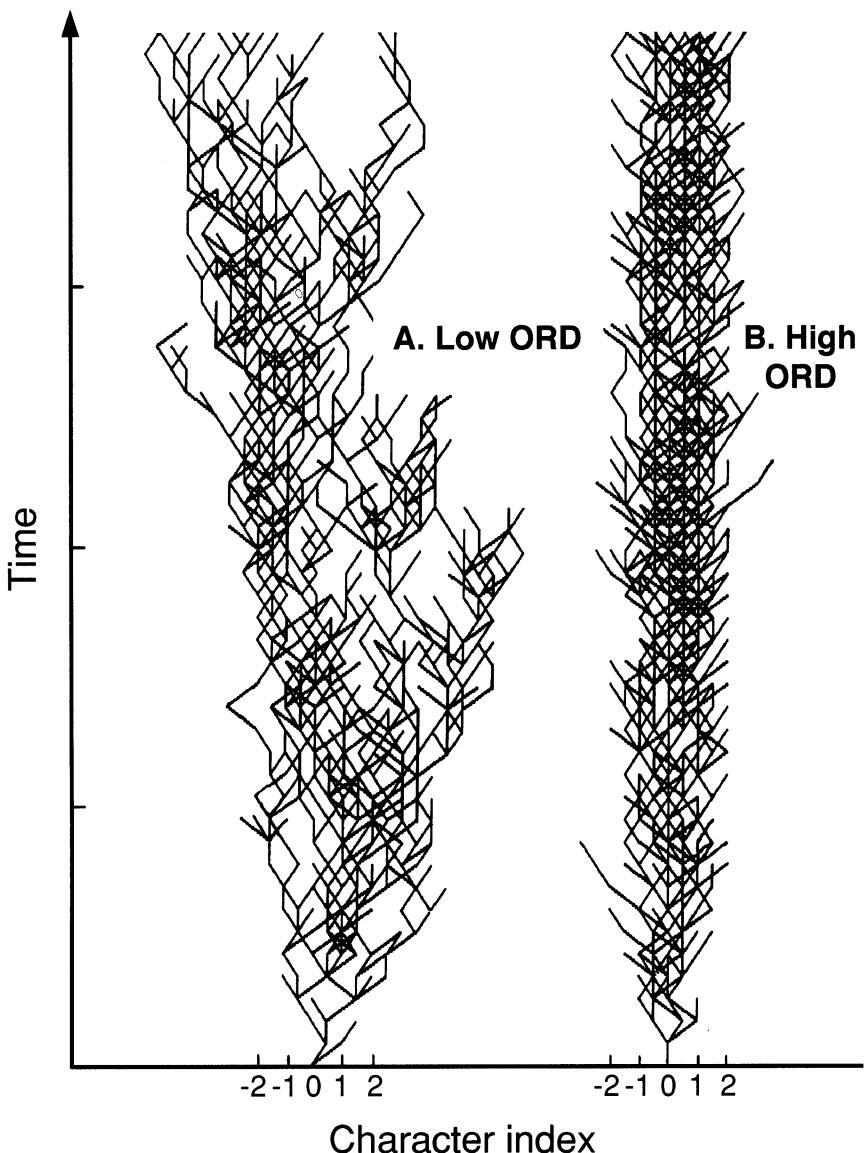


Figure 6 Normalizing clade sorting suppresses anagenetic change in lineages experiencing high ORD. The sorting becomes stabilizing as the gene pools most likely to survive inhabit persistent (as opposed to ephemeral) habitats, or are capable of moving sufficiently fast to track their preferred habitat. *A* (low ORD) shows a completely random phylogeny, whereas *B* (high ORD) shows random changes opposed by normalizing clade selection. At each time step, each lineage (gene pool) may change its character index. In *A*, the number of descendants is the same irrespective of character index, whereas in *B*, the number of descendant lineages is a decreasing function of character indices deviating from zero (simulating normalizing clade selection). Modified from Williams (1992). Used by permission from Oxford University Press, Inc.

change in the abundant Palearctic and Nearctic fossil record during the high-ORD Quaternary (Coope 1995) in spite of having short and often nonoverlapping generations, characters generally considered to promote evolutionary change.

EVOLUTIONARY INNOVATIONS One aspect of anagenesis is the appearance of evolutionary innovations, i.e., new traits which in hindsight have proved to have significant long-term repercussions. More innovations and new higher taxa have appeared first in the tropics. In post-Paleozoic marine invertebrates first appearances of orders increase dramatically toward lower latitudes, suggesting higher rates of origination of new body plans close to the equator (Jablonski 1993). Angiosperm plants first appeared close to the equator and were absent from high latitudes well after the flora at low latitudes had diversified (Crane & Lidgard 1989). Thus, all the many derived traits defining this clade arose at low latitudes, as did the traits of the later-appearing huge angiosperm clade eudicotyledons (Crane & Lidgard 1989). Genera and families in late Cretaceous and Tertiary floras of North America consistently appeared later at high latitudes, as did taxa of North American dinoflagellates from the Cretaceous (Spicer et al. 1987). However, there are more β -clades to produce innovations in the diverse low-ORD areas. This means that, on the basis of the cited studies, we cannot say if ORD reduce β -anagenesis by limiting β -clade richness, by reducing the amount of anagenesis per β -clade, or both.

BIOGEOGRAPHICAL PATTERNS

Numbers of Clades and Spatial Genetic Divergence

Regions with high ORD should have fewer β -clades (Figure 4, *box 9*), owing to lower rates of β -cladogenesis. The sorting of clades during climatic shifts makes clades less extinction prone (Figure 4, *box 6b*). However, it is unlikely that high-ORD regions should accumulate more β -clades than a low-ORD region as a result of low extinction rates, because extinction rates are diversity dependent (Rosenzweig 1995). If numbers of clades increase, population densities and/or clade range sizes decrease, both factors that raise extinction rates. Rising local diversity also increases competition among organisms of different clades, leading to selection to become more specialized (Rosenzweig 1995) and making clades more extinction prone. Rising diversity will increase extinction rates in regions with low ORD as well, but numbers of clades will be sustained by high rates of β -cladogenesis. Thus, we predict that numbers of β -clades should be highest in regions with little orbitally forced climatic change and with steep environmental gradients. Numbers of species is a good proxy to test the prediction about β -clades, as there are plenty of data, but also because species are reasonably close to the tips of the phylogenetic tree but seldom so close as to merely represent α -cladogenesis. Higher taxa, representing branching events further away from the tips are less likely to have originated within the region and under similar geographical variation in ORD as during recent oscillations. There are several examples of extreme numbers

of species in areas with low ORD, e.g., salamanders in Middle America, the Cape Floristic Region in South Africa, and the fauna of Lake Baikal (see below). Species diversity of South American birds peaks in the humid montane forests along the eastern slopes of the Andes (Rahbek & Graves 2001), where there is low ORD (Fjeldså 1995; Fjeldså et al. 1997, 1999). More generally, species numbers of mammals, birds, reptiles, amphibians, and vascular plants in different geopolitical units on the world's continents (differences in area controlled for) decrease with increasing amplitude of Milankovitch climate oscillations, measured as the estimated change in mean annual temperatures between the present and the last glacial maximum (R. Jansson, submitted).

There should be less spatial genetic divergence and less geographical genetic subdivisions within β -clades in regions with high ORD, all else being similar. The reasons are that higher proportions of the range should on average be recently colonized and that the β -clade has been subject to more extinction and merging of gene pools during climatic shifts. Such large-scale spatial genetic divergence is studied in the field of phylogeography (Avise 2000). The general pattern emerging from this field conforms to the prediction. Within β -clades, such as species, the genetic divergence among gene pools is deeper for clades that have experienced low ORD. In areas with high ORD, such as arctic and boreal regions, there is little genetic divergence among gene pools (Hewitt 2000, 2001), representing much α - but little β -anagenesis. In the climatically less variable southern Europe and southeastern United States, intraspecific genetic divergence is often high, and species are finely geographically subdivided genetically (Hewitt 2000, 2001). In southern Europe gene pools were able to survive and maintain their integrity in the mountains, where suitable habitats could be found continuously by small range changes (Hewitt 1996, 1999). For example, the Iberian endemic lizard, *Lacerta schreiberi*, has maintained separations between relatively closely situated inland and west coast gene pools since the Pliocene (Paulo et al. 2001). Divergence in mitochondrial DNA among phylogroups within fish species from Pleistocene glaciated areas in the Northern Hemisphere is much lower than within species from nonglaciated areas (Bernatchez & Wilson 1998, Billington & Hebert 1991). This pattern of less divergence in glaciated areas is even more evident within species with ranges spanning both glaciated and nonglaciated areas (Bernatchez & Wilson 1998). Gene pools within Neotropical bird species are genetically more deeply divided and more finely structured than temperate ones (Brawn et al. 1996). For example, in two Panamanian bird species genetic distances between two populations only 50 km apart exceed those found on a continental scale for many temperate species (Brawn et al. 1996).

LAKE BAIKAL In freshwater systems that have persisted for long geological periods, such as Lake Baikal, nonvagile clades have evolved. Such clades typically form radiating species flocks, whereas vagile clades do not (Cohen & Johnston 1987). Despite the high-latitude position of Lake Baikal, the lake was not covered by glacial ice-sheets during the Quaternary (Kashiwaya et al. 2001), enabling clades to

persist locally. The pelagic and deep benthic habitats harbor species flocks of both ancient, endemic clades and recently immigrated clades presently undergoing radiation, whereas widespread species primarily occur along the shorelines (Mashiko 2000, Sherbakov 1999, Sideleva 2000). One of the strongest radiations has been among amphipod crustaceans, and the lake contains 20% of the world's freshwater species of this group (Martens & Schön 1999). Spatial genetic divergence within species is also deep. The shallow-water, benthic crustacean *Eulimnogammarus cyaneus* has diverged for ~60 kyr on either side of the lake outlet, having a maximum depth of only 4 m (Mashiko 2000). The high numbers of β -clades and narrow endemics in Lake Baikal contrast sharply with other large but recently glaciated or geologically young boreal lakes that have few and widespread β -clades.

Geographic Range Sizes

ORD should also increase geographic distributions of β -clades (Figure 4, *box 5*). First, clades with wide distributions are more likely to survive climatic shifts (Bennett 1997, Brown 1995). In the fossil record taxa with large range sizes are generally less extinction prone (McKinney 1997). Second, generalist organisms are likely to find habitats over large geographic areas. Third, clades consisting of vagile generalists attain larger ranges through effective colonization of areas with suitable habitats and by effectively maintaining marginal sink populations. In addition, high gene flow prevents cladogenesis, and thus subdivision of ranges. In many taxa, e.g., gastropods (Jablonski 1985, Stanley 1979), vascular plants (McGlone et al. 2001), and mosses (van Zanten & Pócs 1981), species with effective dispersal range more widely.

Regions with low ORD have higher proportions of range-restricted clades. The smaller the geographic range size of a clade, the more likely it is endemic to a specific area. Numbers of endemic species of mammals, birds, reptiles, amphibians, and vascular plants per geopolitical unit (differences in area controlled for) increase with decreasing amplitude of Milankovitch climate oscillations, measured as the estimated change in mean annual temperatures between the present and the last glacial maximum (R. Jansson, submitted). In sub-Saharan Africa range-restricted vascular plant species are concentrated into specific areas likely to have been buffered against Quaternary climatic oscillations (Linder 2001), leading to low ORD. Likewise, in the Australian flora all centers of range-restricted species are near-coastal, probably because variation in the extent of the central desert during the Quaternary limited the function of inland refugia for range-restricted species (Crisp et al. 2001).

Polyploidy

Abrupt formation of reproductive barriers mostly takes place as polyploidization, but also by diploid hybridization. Polyploidization accounts for about 2%–4% of the speciation events leading to extant species in flowering plants and about 7% in ferns (Otto & Whitton 2000). ORD favor the formation, establishment, and

persistence of polyploid clades in at least four ways (Figure 4, *box 8*). First, large climatic oscillations lead to few clades being specialized to contemporary environments. This spurs ecological speciation by means not only of gradual divergence (Schluter 2000) but also polyploid establishment. Hybrid polyploids may rapidly provide reproductively isolated gene pools with new genetic combinations better adapted to new, suddenly appearing climates, habitats, or resources (Brochmann & Elven 1992; Stebbins 1971, 1984). Consequently, polyploids are more frequently found in human-made habitats or those most modified by recent climatic change (Hodgson 1987, Stebbins 1971). Second, during periods of large and rapid climatic change, a new hybrid clade can establish by expanding its distribution and thereby avoid competitive exclusion by its parental clades. Third, ORD make previously separated clades more likely to encounter each other and hybridize to form a new polyploid clade in a “secondary contact” (Stebbins 1971, 1984). Human introductions may play the same role. Several new allopolyploid plant species arose in the twentieth century, in each case involving an introduced taxon (Ramsey & Schemske 1998). Fourth, apomixis is generally associated with polyploidy, and facilitates dispersal and establishment, as one individual is sufficient for establishment and reproduction, and in plants no pollinator vector is needed to reproduce and spread in the colonized area. Consequently, apomorphic representatives of clades more often range into previously glaciated areas (Bierzychudek 1985). For example, outbreeding diploids of the fern genus *Asplenium* in Europe are largely restricted to southern refugia, whereas their selfing polyploid descendants dominate the high-ORD parts of the continent (Vogel et al. 1999). Good colonizing ability of apomicts should lead to wide distributions, and there are many examples of temperate/arctic clades of plants in which diploids have small distributions and polyploids wide (Stebbins 1971). There are several well-supported examples of polyploid cladogenesis in high-ORD regions during the last great climatic shift in the early Holocene (Dufresne & Hebert 1997, Franzke & Hurka 2000, Nilsson & Jorde 1998).

Co-Occurrence of Several Predicted Patterns

We have deduced a number of evolutionary effects of ORD. From these effects we predict several geographic patterns caused by differential ORD. High ORD should lead to low numbers of β -clades; β -clades with low levels of intraclade genetic divergence, coarse geographical subdivision, and large ranges; organisms with high vagility and low specialization; high proportions of β -clades formed by polyploidization; and little β -cladogenesis and β -anagenesis. Thus, ORD parsimoniously explain a wide array of patterns, suggesting it is a fundamental factor in evolution. Below, we provide three good cases for the importance of ORD in which data concerning several of the predicted patterns are available.

LATITUDINAL GRADIENTS The prime gradient in ORD is the latitudinal gradient (see “Orbitally Forced Range Dynamics,” above). In a previous paper (Dynesius

& Jansson 2000) we explored the consequences of ORD along the latitudinal gradient. All nine patterns we predict along gradients in magnitude of ORD are found along the latitudinal gradient: (a) A latitudinal gradient in numbers of species has been recorded for most taxonomic groups (Rosenzweig 1995), within species. (b) Spatial genetic divergence increases and (c) geographical subdivision becomes finer towards lower latitudes (Bernatchez & Wilson 1998; Brawn et al. 1996; Hewitt 2000, 2001). (d) Vagility increases with latitude in a wide range of taxa. Diaspore size decreases, and vagility thus increases, with latitude in seed plants (Lord et al. 1997), lichens (Lawrey 1980), and polypore fungi (Ryvarden 1993). (e) Tropical organisms are often more specialized than high-latitude ones in, e.g., pollination systems (Johnson & Steiner 2000) and habitat requirements (Pagel et al. 1991). In high-latitude areas serpentine specialists are few and mostly represented by α -clades. The serpentine plants of the formerly glaciated Scandinavia are mainly ecotypes or subspecies of widespread, nonserpentine species (Rune 1953) and probably of postglacial origin. In contrast, in the tropics there are often many species or higher taxa specialized to serpentine soils (Whittaker 1954). (f) The geographical range sizes of taxa generally increase toward higher latitudes (Lawton 1994), a relationship called Rapoport's rule (Stevens 1989). (g) The proportion of polyploids increases with latitude in all taxa studied (Kuta & Przywara 1997, Rosenzweig 1995, Ward et al. 1994). However, in northwestern North America there is an inverted latitudinal gradient. The highest proportion of polyploid plant species is in formerly glaciated areas (higher ORD) to the south of the permanently ice-free northern Alaska (lower ORD), where diploids as well as range-restricted taxa are more frequent (Stebbins 1971, 1984). (h) Rates of β -cladogenesis increase toward lower latitudes, e.g., in New World mammals (Marshall et al. 1982), pelagic foraminiferans with algal symbionts (Quillévéré et al. 2001), and salamanders (García-Paris et al. 2000). (i) A latitudinal gradient with more β -anagenesis in the tropics has been recorded for a wide array of taxa (Crane & Lidgard 1989, Jablonski 1993, Spicer et al. 1987).

THE CAPE OF SOUTH AFRICA In the Cape Floristic Region (CFR) of South Africa, the Quaternary climate has been comparatively stable, with low ORD (Meadows & Sugden 1993). Many clades have radiated here since the Miocene (Richardson et al. 2001). Most notable is the massive diversification of many vascular plant lineages, which has led to an extremely species-rich flora (Cowling & Pressey 2001). Bryophyte endemism is exceptionally high, with the ranges of more than 40% of the hepatic species confined to southern Africa (Schofield 1992). Most vascular plants in the CFR occur in the low-productive Mediterranean shrublands called fynbos, and have narrow habitat specializations, highly specific pollinators (Bond 1995, Johnson & Steiner 2000), and small geographical ranges (Cowling et al. 1998, Goldblatt 1997). Diversification has been concentrated in lineages with certain traits. Diversifying lineages of woody plants are fire-killed (i.e., nonsprouting) shrubs with poorly dispersed seeds, small and weakly persistent seed banks, and insect-pollinated flowers (Cowling & Pressey 2001, Goldblatt 1997). These

traits lead to restricted gene flow and rapid turnover of nonoverlapping generations, favoring genetic divergence among gene pools on a relatively small spatial scale. Specialist pollinators have driven β -cladogenesis in several lineages, especially in the large geophyte flora (Johnson 1996). The diversifying clades have disintegrated into many range-restricted species (Wisheu et al. 2000).

Polyplody is considered to be infrequent in the Cape flora, although no comprehensive study has been done (Goldblatt 1978). Species-rich fynbos taxa such as *Erica*, *Aspalathus*, and Proteaceae have no recorded polyploid species (Goldblatt 1978). The CFR also has high proportions of range-restricted species of butterflies, fish, and amphibians, primarily in the fynbos (Rebelo 1992). On the Cape Peninsula local endemism of invertebrates is extremely high (Cowling et al. 1996, Picker & Samways 1996). The accumulation of nonvagile, specialized species with small ranges would not have been possible under high ORD. Thus, this is a good example of low ORD as a prerequisite for long-term accumulation of products of other evolutionary processes.

Plant diversification has been strongest within the western part of the fynbos biome (Cowling & Lombard 2002), which has had the least variable climatic conditions and lowest ORD (Cowling et al. 1999, Meadows & Sugden 1993). The western fynbos has more than twice as many species as the eastern part (Cowling & Lombard 2002, Cowling et al. 1992). Within the Cape flora the strong diversification and the associated characteristics of species are not confined to the fynbos but are equally pronounced in the adjacent succulent karoo biome, that also experienced low ORD during the Quaternary (Cowling et al. 1999). The succulent karoo is drier and less affected by fire than fynbos and has a different flora (Cowling et al. 1998). Thus, the strong diversification cannot be explained solely by ecological idiosyncrasies of the fynbos. To conclude, the Cape flora exhibits six character states that we predict for the β -clades of a region with low ORD: high regional richness of β -clades with small range sizes, organisms with high specialization, low vagility, high rates of β -cladogenesis, and few polyploids.

The only other area with Mediterranean climate with a density of plant species similar to the CFR is southwestern Australia. Here, shrublands and woodlands persisted through the last glacial maximum (Dodson 2001). This is in sharp contrast to the equal-sized Mediterranean region in southeastern Australia, which has only a tenth as many species. Here, the vegetation was much more disrupted during the last glacial period, and the current vegetation formations were assembled from refugial areas (Dodson 2001). Again, low ORD begets diversity.

NEOTROPICAL SALAMANDERS Salamanders (order Caudata) initially diversified in northern temperate areas. Late in the history of the clade a tiny twig (the supergenus *Bolitoglossa* of the family Plethodontidae, lungless salamanders) entered and established in the mountains of tropical Middle America, an area with low ORD. This resulted in an extensive diversification, and the supergenus now contains more than 40% of the world's salamander species (García-Paris et al. 2000).

Strong differentiation is also evident within species over distances of a few kilometers, such as in *Bolitoglossa pesrubra* (García-Paris et al. 2000). García-Paris and coworkers (2000) state, "... there is long-term stability and geographic integrity of the distribution of haplotype clades and clusters of populations identified by protein variants; the phylogeographic units do not intermix or even overlap The combination of low vagility, high philopatry, ... and nonmigratory life history ..." establishes the foundation for local differentiation and regional genetic fragmentation." Ecological specialization is higher, expressed by narrow altitudinal ranges of species, than in another salamander hotspot, the southern Appalachians (García-Paris et al. 2000). Once again we have the syndrome of low ORD, a remarkable radiation of clades, small range sizes, narrow specialization, and low vagility.

ASPECTS FOR CONSERVATION

The global warming of the past century has resulted in poleward and upward shifts of species distributions across a wide range of taxonomic groups and regions (Walther et al. 2002). Extant β -clades have experienced many climatic shifts, implying that they may have the potential to survive human-induced climatic changes as well. However, global temperatures have been warmer than today's for less than 5% of the past three Myr (Webb & Bartlein 1992). Future warming may extinguish habitats regionally, e.g., cloud forests on mountaintops (Pounds et al. 1999). Most species survived previous climatic shifts by tracking their habitats through space, which is becoming increasingly difficult because of human habitat transformation and fragmentation (Coope 1995). Furthermore, the insular habitats produced by human-made fragmentation select against vagility if the matrix is hostile. Thus, large human efforts will be needed to allow species to track their preferred environments in response to the projected rapid global warming.

If, as we argue, differences in ORD lead to differences in traits of organisms and clades among regions, conservation strategies may not be interchangeable. Regions with a history of low ORD are often hotspots of β -clades with small geographical ranges, harboring organisms with high specialization and low vagility. These traits render them vulnerable to both climatic change and habitat destruction, and therefore these regions should be of high priority for conservation. For example, of 25 areas identified globally as hotspots of endemism and threat of extinction (Myers et al. 2000), most have experienced low ORD, being situated in the tropics (17 areas), on oceanic islands (5), and/or in mountainous regions (10). Conversely, β -clades that have experienced high ORD should be more resilient to many human disturbances (Balmford 1996, Coope 1995, Mönkkönen & Welsh 1994). As humans make habitat tracking increasingly difficult, areas where global climatic change is buffered against and/or where steep environmental gradients reduce the need for migration, become more important for clade survival. Thus, characters related to low ORD, i.e., high climatic stability (Fjeldså et al. 1997) or steep environmental gradients, could be used to identify both regional and global priority areas for conservation.

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