Analyzing temporal trends in regional diversity: a biogeographic perspective

Kaustuv Roy

Abstract.—Evidence for species range shifts in response to climatic change is common in the Pleistocene and earlier fossil record. However, little work has been done to model how such shifts in species range limits would change compositions of species assemblages over different spatial scales. Here I present a simple model that explores the role of biogeography in constraining changes in the compositions of species assemblages under the null hypothesis of random range shifts. The model predicts that localities where most species are far away from the edges of their ranges (e.g., localities at the center of a biogeographic province) would show relatively stable diversity patterns even during episodes of climatic change. Only localities with many range endpoints (such as those near the edges of biogeographic provinces) would show large fluctuations in species composition (and richness) in response to changes in the ambient climatic conditions. I test the predictions of the model using (1) simulations and (2) the Pleistocene bivalve fauna of California. The simulations as well as the empirical data from the Pleistocene terraces are consistent with the model predictions. These results show that attempts to quantify temporal trends in local and regional diversity and assemblage compositions need to take biogeographic structure into account.

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"The continued activity of European ecologists, and to a somewhat smaller extent of American ecologists as well, in discussing the fundamental nature, structure, and classification of plant associations, and their apparently chronic inability to come to any general agreement on these matters, make it evident that the last word has not yet been said on the subject." Gleason (1926)

Introduction

How the richness and compositions of communities and regional species assemblages change over time has been the subject of debate in both community ecology and paleoecology. Many observations of species' geographic range shifts and changes in relative abundance over timescales ranging from ecological to paleoecological argue for an individualistic view of species behavior in response to climatic changes (e.g., Dayton 1989; Overpeck et al. 1991, 1992; Valentine and Jablonski 1993; Barry et al. 1995; Coope 1995; Taper et al. 1995; FAUNMAP Working Group 1996; Patzkowsky and Holland 1996, 1999; Parmesan 1996; Roy et al. 1996; Cannariato et

al. 1999; Sagarin et al. 1999). On the other hand, some paleontological studies have found that regional species assemblages may persist as stable entities over geological time even in the face of environmental change (Jackson et al. 1996; Pandolfi 1996; Alroy 1999; also see Brett et al. 1996). Some of these differences in empirical patterns clearly result from the differences in temporal and spatial scales of these studies (DiMichele 1994; Jackson et al. 1996; Miller 1997). However, a more pervasive problem is the lack of null expectations about how shifts in species range limits would change compositions of species assemblages over different spatial and temporal scales (Jackson et al. 1996). The lack of such models makes it difficult to compare results from different empirical studies, and to draw general conclusions about responses of communities and regional biotas to environmental change (Jackson et al. 1996). In this paper I discuss one approach to analyzing temporal changes in species distributions that generates a null expectation of change in regional diversity while taking into account the biogeographic structure of the fauna. I test the predictions of the model using simulations and

empirical data from the late Pleistocene fossil record of California. The model is spatially explicit, and applicable to the kinds of distributional data commonly available from the fossil record.

This paper is centered on how spatial distributions of species change over geological time and not on temporal trends in evolutionary turnover. In other words, this paper is about local extinctions and recolonizations and not about global extinctions and speciations. In fact, in using the Pleistocene data I ignore the few species that have become globally extinct since the late Pleistocene. Temporal trends in evolutionary turnover have been the central focus of the debate over coordinated stasis (sensu Brett et al. 1996), and previous studies have applied appropriate stochastic models to explore such evolutionary patterns (e.g., Baumiller 1996; Holland 1996). However, spatial patterns of local extinction and recolonization of species are certainly relevant for the hypothesis of coordinated stasis (in that it calls for tight ecological interactions between species), and hence the model discussed below could also be used to test some aspects of that hypothesis. That said, at present few pre-Pleistocene paleontological studies provide the empirical data on patterns of regional extinction necessary for addressing the issue (see Patzkowsky and Holland 1996 for an exception).

Testing Temporal Trends in Community Structure

A number of ecological models have explored patterns of community compositions and the maintenance of regional diversity using differing assumptions about the dynamics of both species interactions and changes in the physical environment (e.g., Chesson and Huntley 1989; Pease et al. 1989). However, applications of these ideas to paleontological data have been lacking largely because of the difficulties involved in estimating the relevant parameters from paleontological data. Instead, the focus in paleontological studies has been to test the observed temporal changes in the composition of species assemblages against a null expectation of change due to sampling alone. For example, Pandolfi (1996) tested empirical data from a set of Pleistocene coral species assemblages from Papua New Guinea against an expectation based on random resampling of regional diversity, using a method originally proposed by Connor and Simberloff (1978). Results showed that the observed number of species present at a given site through time was significantly larger than that expected from sampling alone, thereby suggesting that a stable regional metacommunity persisted over a period of about 95,000 years during the Pleistocene (also see Jackson et al. 1996). This conclusion is an important deviation from the general Pleistocene norm that argues for an individualistic behavior of species in response to climatic change resulting in the breakup and reassembly of species assemblages (see Roy et al. 1996 for a review). Given that the temporal and spatial scales of Pandolfi's (1996) study are comparable to that of many other Pleistocene ones, his results raise the issue of whether the long-term dynamics of coral reefs are inherently different from those of other noncolonial benthic marine invertebrates (and terrestrial organisms, for that matter), or whether the differences simply represent different dynamics of tropical versus temperate communities. Testing these alternatives requires that we evaluate the observed patterns in marine invertebrate species assemblages against appropriate null expectations of change (Jackson et al. 1996). A major problem in conducting such tests, however, involves the formulation of the null hypothesis itself, and there has been considerable debate in community ecology as to what constitutes a proper null hypothesis when compositions of species assemblages are compared (e.g., Connor and Simberloff 1978, 1979; Diamond and Gilpin 1982; Roughgarden 1984; various papers in Salt 1984). The model I present here argues that biogeography plays a primary role in determining the expected changes in regional diversity in response to changing climates.

Biogeography and Change in Community Composition

Most attempts to predict how species geographic ranges would shift in response to environmental change are based on the assump-

tion that each species can be characterized by the climatic conditions (temperature is the parameter generally used) that are present at the limits of its range, and any shifts in this climate envelope would lead to a corresponding change in the range of a species (e.g., Emanuel et al. 1985; France 1991; Westman and Malanson 1992; Malanson 1993; Parmesan 1996; Davis et al. 1998b). This is, of course, also the basic rationale used to reconstruct paleoclimates and paleoenvironments using transfer functions based on present-day distributions of species (e.g., Cronin et al. 1993; Ikeya and Cronin 1993; Dowsett et al. 1994; Markwick 1998). The climate-envelope approach assumes that species ranges are in equilibrium with present-day environmental conditions. This may be problematic given that in modern ecosystems many invasive species can thrive well outside their native ranges once they are transported to the new areas (Case and Taper 2000). However, because the actual ecological and evolutionary processes that determine species range limits are still poorly understood, the climate-envelope models provide a useful empirical approach. An important prediction of the climate-envelope models is that shifts in distributions of species would be detectable mainly at the edges of their geographic ranges (Davis et al. 1998b; Sutherst et al. 1995). This widely used assumption also makes ecological sense given that abundances of species tend to be low at the edges of their ranges and high near the center of their ranges (Brown 1995; Enquist et al. 1995).

In practical terms, the climate-envelope approach predicts that our ability to measure temporal changes in species associations at a given locality should be directly proportional to the number of species whose ranges end at or near that locality. Thus localities where most species are far away from the edges of their ranges (e.g., localities at the center of a biogeographic province) should appear to be temporally stable even in the face of significant range shifts that take place at the margins of the province. This pattern would prevail even if species were wholly individualistic in their behaviors and geographic ranges overlapped only because of shared environmental tolerances. Conversely, localities with many

range endpoints (such as those near the edges of biogeographic provinces) should show large fluctuations in species composition (and richness) given any change in the ambient climatic conditions. A very simple and hypothetical scenario illustrating this is shown in Figure 1. In general terms, therefore, the null expectation is that for a given change in the environment, there should be spatial variation in the amount of temporal change in community composition (or species richness) observed at the level of individual localities, and that this variation should be predictable as long as we know the distributions of species ranges at these localities. Of course, such variation would only become important when ranges are distributed nonrandomly in space, but that is a reasonable assumption for most shallow marine invertebrates (e.g., Valentine 1974) and is also predicted by theoretical models (e.g., Case and Taper 2000).

The scenario outlined above suggests that we need to know at least three parameters in order to predict how species compositions at a locality would change in response to climate change: (1) the number of species (N) that are at or close to their range limit at the locality of interest *before* the environment changes, (2) the number of species (S) in the region that actually change their range endpoints, and (3) the magnitude (R) by which the species ranges change. Of these parameters, N can be empirically estimated for both Recent and paleontological data. S and R for past events can never be known for certain and have to be estimated. How different values of these parameters would affect species diversity at a locality or in a region can be explored through simulations. Here I use a data set comprising range limits of Recent bivalves of the Californian province to explore how stochastic changes in S and R affect the species diversities at latitudes that differ in N. I then apply the model to study actual species range shifts preserved in the Pleistocene record of California.

Simulations and Application of the Model

The late Pleistocene molluscan fauna of California has been extensively studied and comparison with the Recent fauna has revealed
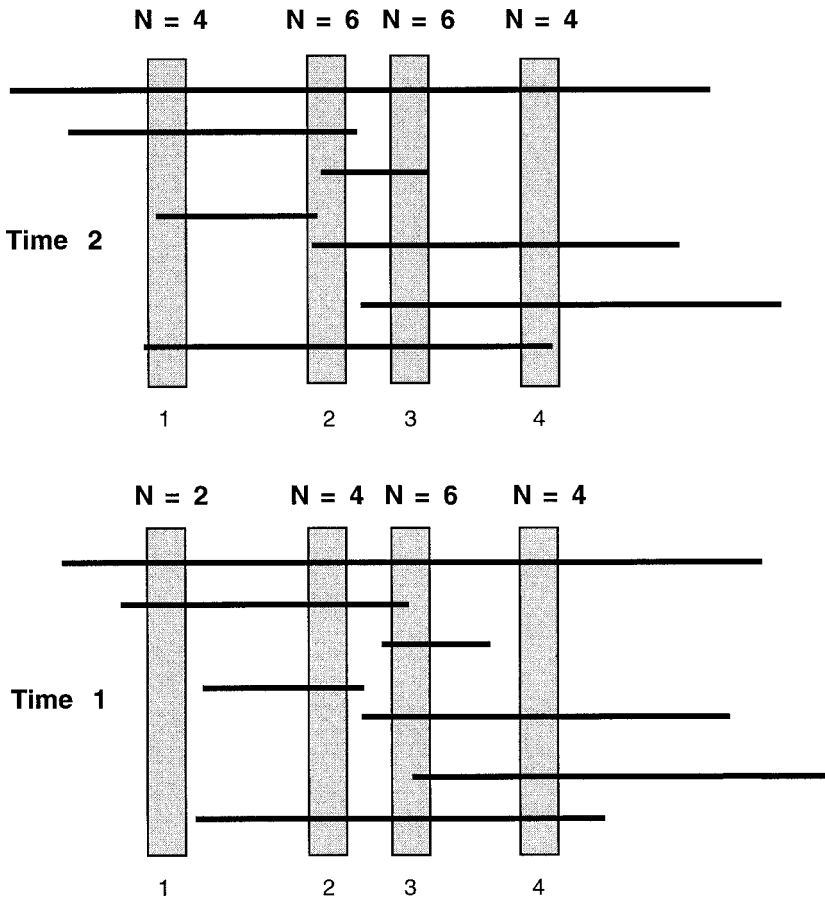
FIGURE 1. A simple hypothetical example of how the position of sampling localities relative to the geographic ranges of species can affect the estimation of changes in assemblage composition following range shifts. The vertical bars represent individual localities and the total ranges of the species are shown as horizontal lines. The ranges were randomly placed relative to the localities. At time 2 the ranges of all the species were changed by the same amount in the same direction. However, the diversity at different localities changed by different amounts; locality 1 shows a doubling of species diversity whereas localities 3 and 4 show no change. These differences are simply a function of the magnitude of the range shift and the position of the original ranges relative to a given locality. Clearly locality 1 gives us a very different picture of temporal change in community composition compared with, say, locality 3 or 4. The differences, however, do not reflect the biological processes underlying the species range shifts; they simply reflect how those changes are expressed spatially.

the presence of a number of species that have since shifted their geographic ranges outside that region (Valentine and Meade 1961; Valentine and Jablonski 1993; Roy et al. 1995, 1996). Although the presence of such extralimital species shows that compositions of assemblages at the scale of individual localities as well as at the provincial scale have changed over the last 125,000 years, the observed patterns have never been tested against a random model of change. Below I use the spatial distribution of these extralimital species to empirically test some of the general predictions of the biogeographic model described above.

For this study I use data for bivalve species because their present-day geographic ranges along the eastern Pacific are well documented (Jablonski and Valentine 1990; Roy et al. 1994, 1998, 2000) and they have an excellent fossil record in the Pleistocene of California (Valentine 1989).

The data for the late Pleistocene mollusks of California come from coastal terrace localities that sample well over 75% of the shallow-water molluscan species living along the eastern Pacific coast today (Valentine 1989). A large proportion of these terraces are interglacial and date to oxygen isotope stage 5e (~125

TABLE 1. Pleistocene localities used in the analysis.

Locality	Latitude (°N)	No. of species	Comments and primary references
San Nicolas I. (5e terraces only)	33.3	27	Well sampled and situated near the northern provincial margin; only island locality considered here (Vedder and Norris 1963; Lindberg and Lipps 1996)
Newport Bay	33.5	117	The best sampled late Pleistocene terrace in California; the 117 bivalve species are based on 38,765 specimens (Kanakoff and Emerson 1959)
Nestor Terrace, San Diego	33	30	Well sampled and described; a composite of several close and similar-age terrace localities (Kern 1977)
Mission Bay, San Diego	33	28	Well-sampled terrace (Kern et al. 1971)
Punta Banda	32.3	23	(Valentine 1957)
San Quintin Bay, Baja California	30	96	A rich terrace that remains undersampled; further sampling will certainly add to the species diversity (Jordan 1926)
Turtle Bay	27.5	28	Situated at the edges of present-day Californian and Surian provinces (Emerson 1980)

Ka); a subset of these localities that are well dated and sampled among all the Pleistocene localities is used here (Table 1). In this system, the ranges of individual species are arrayed along a linear and very narrow shelf along the coast, thus simplifying the analyses of geographic range shifts; the major changes are latitudinal, longitudinal changes can be ignored. It is also worth noting that estimates of changes in assemblage compositions in this system are based exclusively on species that are known to co-occur in the Pleistocene but whose ranges today are disjunct (Valentine and Jablonski 1993). Therefore, the patterns are robust to sampling and taphonomic biases, but the method provides only a minimum estimate of change (Roy et al. 1995).

I use the Pleistocene and Recent bivalve data to test the biogeographic predictions outlined above in two ways. First I use simulations, using Recent range limits and different values of the parameters S and R, to explore how extralimital species will be distributed at various latitudes within the province given random range shifts. In particular, I test the prediction that the number of species range endpoints at a locality is a good predictor of the changes in species diversity at that locality. Next applying the model to the fossil record, I compare the observed percentages of extralimital species at different Pleistocene lo-

calities that are situated at different distances from major biogeographic boundaries (Table 1). These data were collected from the published literature and museum collections and were taxonomically standardized. Provincial boundaries along the eastern Pacific are defined by clusters of species range endpoints (Fig. 2) (Valentine 1966; Roy et al. 1994), and hence under the current hypothesis localities close to these boundaries would be expected to show more fluctuations than those near the center of a province.

The Simulations.—The simulations presented below are based on shifts (decreases) only in the northern range endpoints of species as would be expected under a scenario of climatic cooling. Consequently the Pleistocene data that are compared with these simulations are based solely on southern extralimital species, i.e., species whose northern range endpoint during the Pleistocene was north (outside) of its present range endpoint. Because the Pleistocene terraces considered here are all interglacial terraces from 125,000 years ago, the majority of the extralimital molluscan species in them are southern extralimitals (Roy et al. 1995). Of course, some of the northern species would have also extended their ranges south in response to the same climatic cooling, but traditionally these species would not be counted as extralimitals in the California
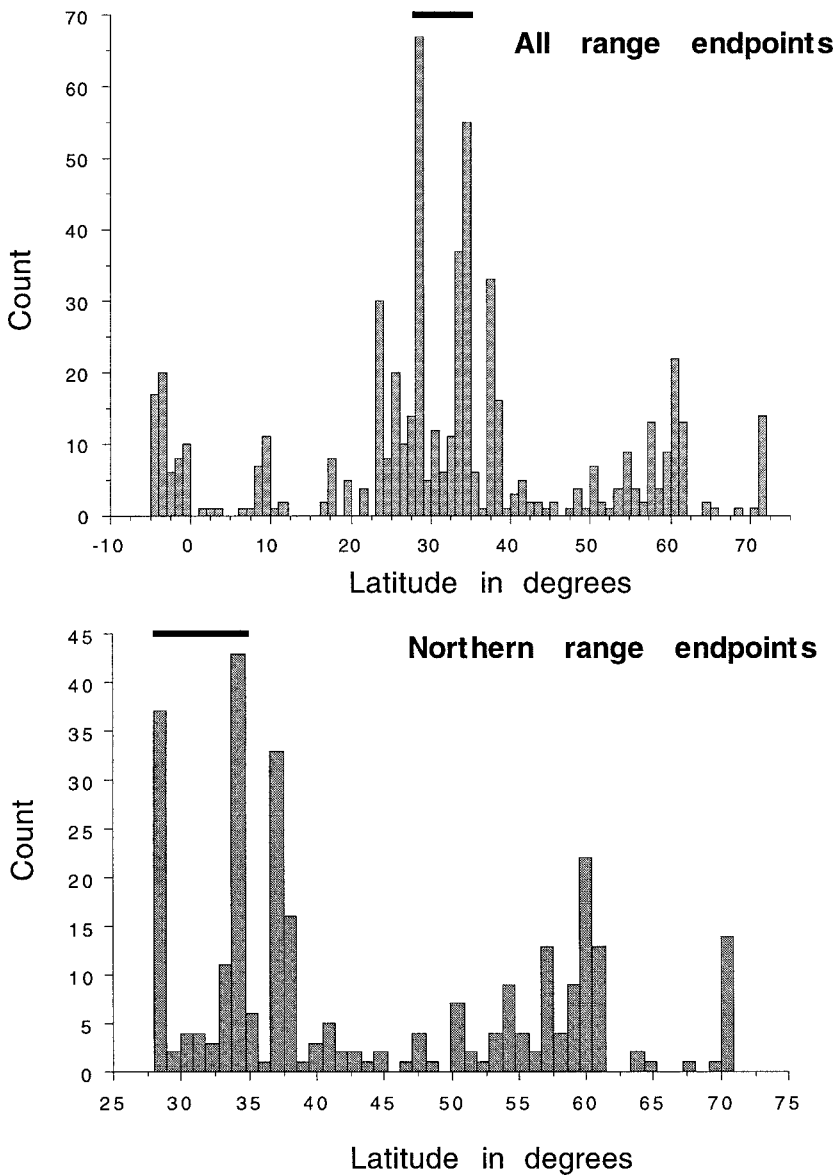
FIGURE 2. Latitudinal distribution of range endpoints of all shallow-water (<200 m) bivalve species living in the California province. The upper plot shows the distributions of both northern and southern range limits, and the lower plot shows only northern range endpoints. Only the southern range endpoints that lie north of 5°S are shown here; some species of California province bivalves extend south of that latitude. The black bars represent the extent of the California province. Note the clustering of range endpoints at 28°N and 34.5°N, the southern and northern limits of the Californian province, respectively. Also note that the northern range limits of many species living in the province fall well to the north of the provincial boundary. The simulations in this study used only the lower distribution (see text for details).

Pleistocene because, in this case, it is difficult to separate taphonomic effects from real range extensions (i.e., for these species, the Pleistocene range limits are not outside the modern range limits). Thus I have excluded the southern range endpoints from the simulations. Addition of southern range endpoints would increase the clustering near the province boundary (Fig. 2) and should make the spatial gradients of change seen in the simulations stronger. Finally, the presence of northern and southern extralimital species in the same ter-

race deposit may also partly reflect time-averaging rather than ecology (Roy et al. 1996). Thus the protocol used here is appropriate for the question and the predictions should be conservative.

True range limits of species are extremely difficult to estimate in the fossil record and the true range limits of the species living in California during the late Pleistocene can never be known for certain (Koch 1987; Russell and Lindberg 1988). Hence I used the present-day range limits of the species in the Californian province in the simulations. Although the present-day range limits of many species clearly are different from their Pleistocene limits, and many species that occurred in the late Pleistocene of California do not even live in the province today, the use of the present-day limits is still reasonable given that the general biogeographic structure along the eastern Pacific coast has not changed significantly since the late Pleistocene (see Addicott 1966; Valentine 1966). As my aim is to compare dynamics of localities with many range endpoints versus those with few, the stability of the biogeographic structure (i.e., presence of regions with clustering of species range endpoints) indicates that relative comparisons should still be possible at the level of the regional fauna. Implications of this assumption are further discussed below.

Each simulation started with the range limits of all the living bivalve species in the California province, and a specific proportion of species (S) was chosen using a random number generator. The northern range limit of each species in this subset was then changed (decreased) by a certain magnitude (R) to simulate range shifts under a scenario of climatic cooling. For some simulation runs a fixed value of R was assigned to all species, whereas for other simulations, R for each species was randomly chosen within certain limits (either between one and two degrees or between one and ten degrees). The values of R that I have used here are entirely arbitrary, because there are no quantitative data on how large a change in the latitudinal range of a bivalve species is to be expected in response to a given change in climate. However, judging from empirical evidence from the California Pleistocene

changes between one and ten degrees of latitude seem reasonable and should bracket the average levels of change for bivalves; larger latitudinal shifts are certainly documented but only involve a few species (see Valentine and Meade 1961; Roy et al. 1995). For each simulation the new range limits were then used to compute the number of extralimital species (i.e., the changes in diversity) at six different latitudes from one edge of the Californian province to the other. Each simulation was repeated 1000 times to compute the mean change in species diversity at a particular latitude and the 95% confidence limits of the mean. The program Resampling Stats and its random-number generator were used for all the simulations (http://www.resample.com/randgen.html).

In terms of species range shifts, these simulations are individualistic in the sense that each species is free to change its range within the specified limits. Even in the cases where each species was assigned the same value of R, the species were chosen at random and hence do not represent a tightly coevolved assemblage in the Clementsian sense. However, these simulations do not strictly mimic a Gleasonian individualistic response to climate change either, as both S and R were determined using a random-number generator. In a Gleasonian model S and R would not be random but would be determined by the climatic/physiological requirement of each species. In theory the model can be changed so that the responses of species (R in particular) follow some physiological rule, but that requires additional assumptions about how different species would respond to a particular environmental change. In any event, my aim here is not to simulate a strictly Gleasonian pattern but to explore how stochastic patterns of range shifts translate into the spatial patterns of change and to explore how such patterns compare with the ones documented in the fossil record. Finally, the simulation results are only used in a heuristic manner; statistical comparisons of the simulated trends with the Pleistocene patterns from the same region are not undertaken because such comparisons require that we know the true geographic ranges of species in the fossil record (see below).
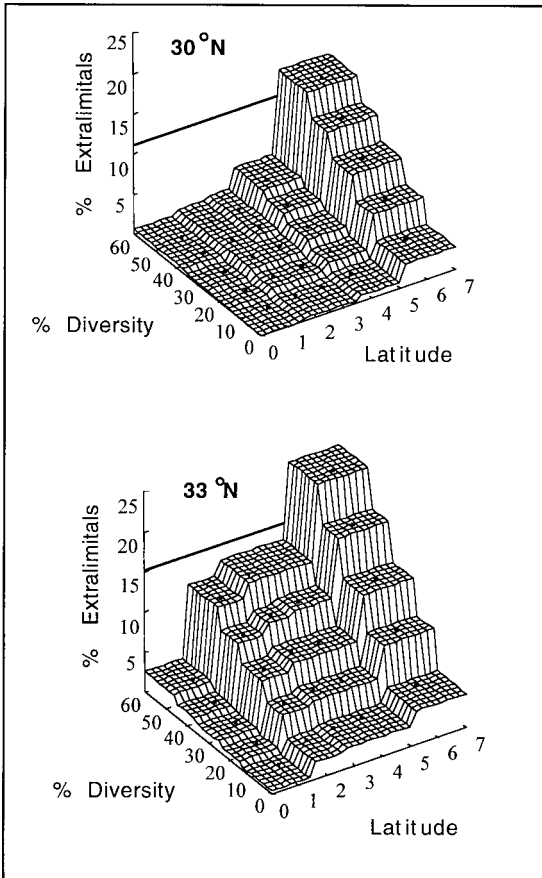
FIGURE 3. Results of the computer simulations showing the percent change in species composition expected at two different localities (near the middle and edge of the California province) as a function of the proportion of species shifting their ranges and the amount of latitudinal range shift experienced by each species. The expectations are mean changes based on 1000 iterations of each simulation run. In these simulations the species were chosen at random, but for each draw all species were assigned the same amount of latitudinal shift (see text for details). The simulations were run with 10% increments in the proportion of diversity sampled up to a maximum of 50% of total diversity. For each diversity level, latitudinal shifts were assigned in increments of one degree up to a maximum of six degrees of latitudinal shift. The dark line on each plot shows the maximum percentage of change observed at a Pleistocene terrace locality at that latitude.

Results

Simulations.—The results of the simulations support the major predictions of the model. The change in diversity (i.e., the number of extralimital species) at any given latitude increases with both the number of species whose ranges have shifted (S) and the magnitude of these range shifts (R) (Fig. 3). Sec-

ond, for simulations where the magnitude of the range shifts is small (i.e., one to two degrees), the number of species range endpoints at a latitude is an excellent predictor of the number of extralimitals at that latitude (Fig. 4). However, this relationship is much weaker in simulations where the magnitude of the range shifts is large (compare Fig. 4A and 4B). In the latter case, even latitudes with few initial range endpoints tend to accumulate appreciable numbers of extralimital species. Of course, this makes intuitive sense; the California province has a latitudinal extent of 6.5°, and range shifts of the magnitude shown in Figure 4B would have a cascading effect even on the latitudes near the center of the province, thereby reducing the latitudinal differences.

The relationship between range endpoints and extralimital species such as those in Figure 4 are of limited use for paleontological data because of the difficulties of reliably estimating the number of species range endpoints at a fossil locality. A more general prediction of the model that is better suited for paleontological data is that the changes near the edge of a biotic province should exceed changes near its center; past biotic provinces can be quantitatively defined and hence this prediction is testable using fossil data. Figure 5 shows that in simulations with smaller latitudinal shifts (i.e., one to two degrees), there is indeed a significant difference between latitudes near the province center and those near the edges. As expected, the relationship can be described by a second-order polynomial regression. However, as in the previous case, the pattern changes when the magnitudes of the range shifts are high (i.e., one to ten degrees). In the latter case, highest change is still observed near the northern edges of the province, but latitudes near the center also show appreciable changes in diversity due to the cascading effect of large range shifts to the north (Fig. 5). The predicted curvilinear trend is no longer significant, but there is a significant linear decline in the number of extraprovincials southward from the northern margin of the province. The difference between the trends in Figure 4 and Figure 5 is partially due to the position of a
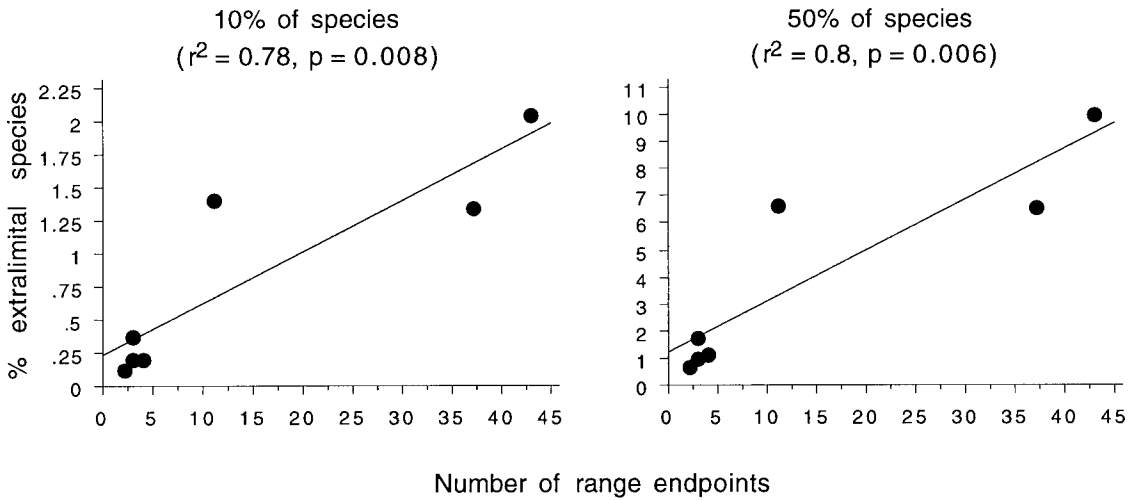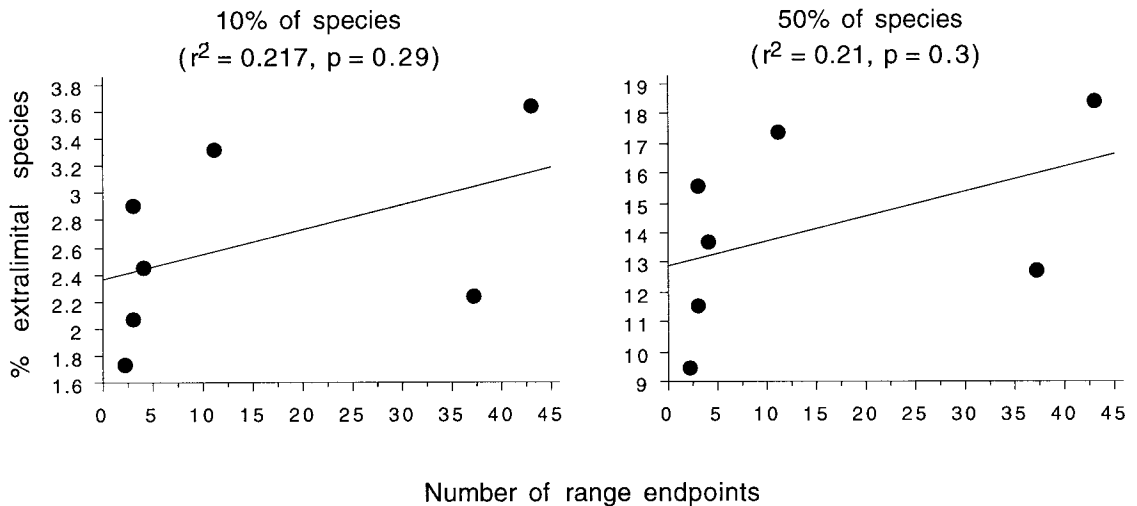
(A) 1-2⁰ latitudinal shifts

FIGURE 4. Results of computer simulations similar to those in Figure 3 showing that the number of range endpoints at a given latitude is a good predictor of the amount of change in diversity (expressed as % extralimital species) observed at that latitude. In these simulations, each randomly chosen species was randomly assigned a latitudinal shift of either 1–2° (A) or 1–10° (B). All the resulting points are means of 1000 iterations. For the California province the relationship between range endpoints and percent extralimital species is most significant when the magnitudes of range shifts do not exceed the latitudinal extent of the province (as in A).

locality within a province, which is only a rough approximation of the degree of clustering of range endpoints at the locality. Provincial boundaries are marked by clusters of range endpoints, but different boundaries are characterized by different levels of clus-

tering and the spatial change in range endpoints is not necessarily symmetrical around the center of the province (e.g., Fig. 2). Finally note that in all of the above analyses, the spatial autocorrelation present in the data would tend to reduce the spatial differences be-
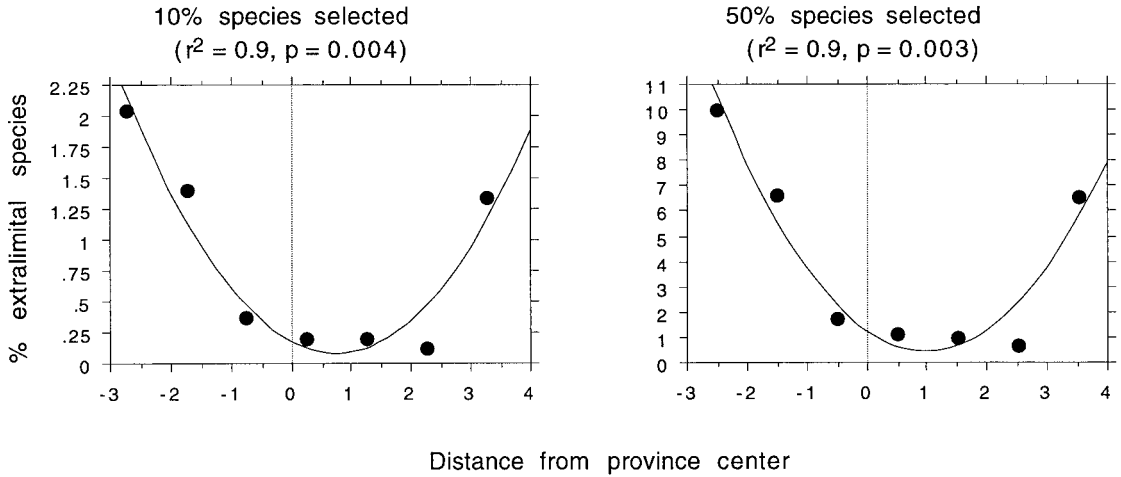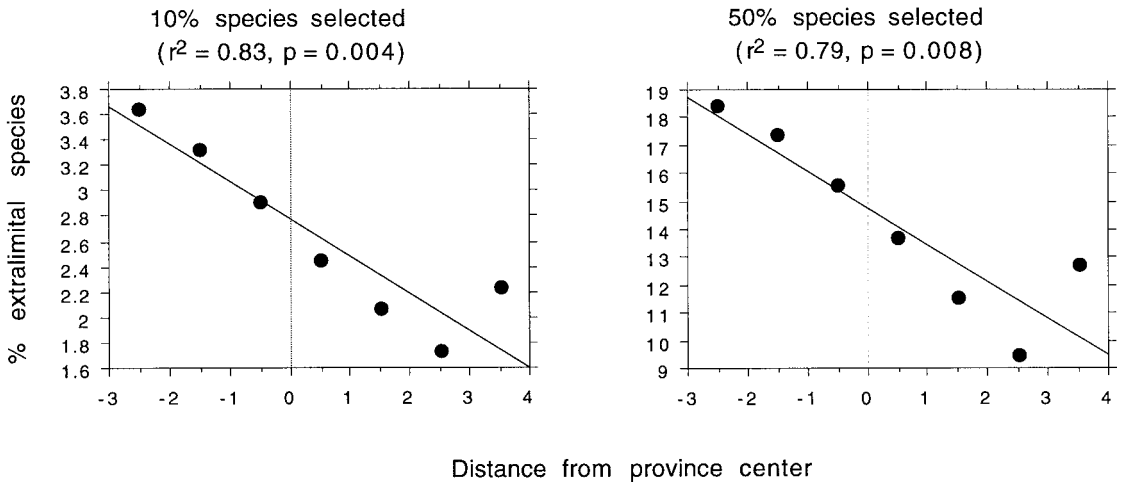
(A) 1-2⁰ latitudinal shifts

10% species selected
($r^2 = 0.9$, $p = 0.004$)

50% species selected
($r^2 = 0.9$, $p = 0.003$)

Distance from province center

(B) 1-10⁰ latitudinal shifts

10% species selected
($r^2 = 0.83$, $p = 0.004$)

50% species selected
($r^2 = 0.79$, $p = 0.008$)

Distance from province center

FIGURE 5. Same simulation results as in Figure 4, but in this case, testing the prediction that latitudes near the center of the province should have fewer extralimital species compared with those near the edges of the province. Again the relationship is strongest when magnitudes of range shifts do not exceed the length of the province (see text).

tween latitudes and hence these conclusions are conservative.

Pleistocene Changes.—The proportion of extralimital species found at individual Pleistocene terrace localities used in this study varied from 3% to 18%. These data fit the expectation that localities near the edges of the province should have a higher percentage of extralimital species compared with localities near the center of the province (Fig. 6). The

Pleistocene trend is also consistent with those seen in the simulations (Figs. 5, 6). Thus it is reasonable to infer that a large percentage of species in the California province shifted their range endpoints in response to the Pleistocene climatic changes. However, most of that dynamic cannot be captured by the record within the province because the range endpoints of many species were outside this region. For example, in the simulations roughly 40% of the
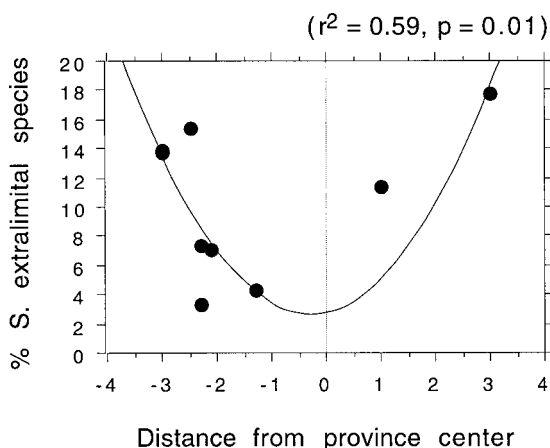
$(r^2 = 0.59, p = 0.01)$

FIGURE 6. Percentage of southern extralimital species found at various late Pleistocene (125 Ka) terrace localities in the Californian province as a function of their distance from the province center. The latitudinal extent of the California province during the late Pleistocene is taken as 28–34°N, following Addicott (1966) and Valentine (1966). These empirical data fit the prediction that localities near the center of a province should appear to be more stable temporally compared with those near its edges (see text).

species pool in combination with 6° latitudinal shifts is needed to approach the 11% extralimital species found in the late Pleistocene terrace at San Quintin (Fig. 3). These results are even more striking when we consider the fact, noted above, that the Pleistocene values provide minimum estimates of change at a given locality rather than the actual amount of change.

Of course, the general conclusions about the magnitudes of the changes as well as the spatial trends are dependent on how species range endpoints are distributed spatially. So the issue of how the use of Recent species ranges in the simulations (instead of Pleistocene ranges) affects our interpretation of the Pleistocene patterns needs to be addressed. The use of Recent ranges would be a serious problem if the clustering of species ranges at the biogeographic boundaries relative to the province center seen today was absent in the Pleistocene. In other words, if species ranges during the Pleistocene were distributed randomly within the province then the differences between localities at the center of the province versus those near its edges (where today ranges cluster) would not be expected. This scenario is unlikely given that the position of

the provincial boundaries during the Pleistocene have been long recognized using criteria very similar to those used for identifying modern provincial boundaries (Addicott 1966; Valentine 1966). Second, the fact that the Pleistocene data show spatial differences in the proportions of extralimital species that are consistent with the model predictions suggests that species ranges were not randomly distributed in space during the Pleistocene. However, it is true that the use of Recent ranges in the simulations does prevent a direct statistical comparison of the magnitudes of changes in the simulations with those empirically documented in the Pleistocene. Hence no such statistical comparisons were undertaken here.

Discussion

Simulations using the range limits of living bivalves of the Californian province support the hypothesis that biogeography can have an important influence on how local or regional species assemblages would change over time. In general, species range shifts in response to changing climates are most readily observable at localities that are marked by clusters of species range endpoints. Conversely, localities or regions with few range endpoints would be relatively stable in the face of climatic change simply because the shifts in the ranges of the constituent species would not be detectable away from the edges of their ranges. This is particularly true when the magnitudes of range shifts are small relative to the range of a species. However, the simulation results also suggest that a much more complex spatial trend may result when the magnitudes of species range shifts are large and such shifts involve a large proportion of the species pool (e.g., Fig. 5A,B).

Because true range limits of species are impossible to measure in the fossil record (Russell and Lindberg 1988), a more generalized prediction of the above model that can be tested using paleontological data is that localities near the edges of biotic provinces should show more evidence of range fluctuations in response to a given climatic change compared with localities near the center of the province. The spatial distribution of extralimital bivalve

species in the late Pleistocene marine terraces of California supports this prediction; localities near the center of the province have a lower proportion of extralimital species compared with those near its edges.

The above results have a number of implications about how we should interpret empirical data on temporal trends in species diversities and compositions of regional faunas. The simulations show that at most localities the percentage of species for which we can even *expect* to see range fluctuation (irrespective of whether their range limits actually shifted or not) is quite small. This is simply because for most localities the range endpoints of a large number of species present would tend to fall well outside that locality or region. For example, given the biogeographic structure of the California province bivalves, the detection of 10–15% southern extralimital species in Pleistocene terraces near the center of this province would suggest that a large proportion of the species present in the province may have shifted their range limits in response to the Pleistocene climatic fluctuations (Fig. 3).

An important biological implication of these results is that in systems such as the California province, where species range limits tend to be spatially clustered, temporal stability of species assemblages at many localities, even during changing climates, may be the norm simply as a consequence of the biogeographic structure. However, such stability of species diversity at a given locality could occur even when the species constituting that assemblage may be responding individualistically to climatic change. This discordance between the behavior of the local assemblages and that of individual species is particularly important in that it argues against drawing conclusions about how individual species respond to climate change based simply on the diversity trajectories of a few closely spaced localities, particularly those that are away from the edges of provinces. Thus attempts to test the alternatives of Clementsian versus Gleasonian dynamics in response to environmental change should be restricted to localities that are close to the range limits of many species.

Modeling Species Response to Climate Change.—Miller (1997) argued that some (or much) of the debate in paleoecology about stability versus dynamism of species assemblages may simply be a consequence of different scales of analyses as well as different methodologies. Although Miller's (1997) comment was mainly about the distinction between Pleistocene and pre-Pleistocene (mostly Paleozoic) studies, I suspect the same is also becoming true for the Pleistocene. Differences of spatial and temporal scales of various studies aside (these are easier issues to resolve), we need to explore alternative ways of modeling how species assemblages would respond to changes in the ambient environment. In fact, the choice of an appropriate model remains one of the biggest challenges in testing temporal trends in the compositions of species assemblages. Although it is useful to generate expectations of change based simply on a random sampling of the species pools, (e.g., Connor and Simberloff 1978, 1979; Pandolfi 1996), biological relevance of the assumptions underlying such an approach has been questioned (e.g., Diamond and Gilpin 1982; Roughgarden 1984; also see Salt 1984). In particular, the model of Connor and Simberloff (1978) (used by Pandolfi [1996] in the Pleistocene context) assumes that all taxa have equal dispersal and persistence abilities (Connor and Simberloff 1978), and hence, presumably similar responses to climatic change. Connor and Simberloff (1978: p. 231) themselves acknowledged that this assumption is biologically not very meaningful (also see Roughgarden 1984), and the results presented above show that it is particularly problematic for the Californian mollusks given eastern Pacific biogeography. This assumption is further violated by the fact that the species showing range shifts in response to climate change may not be a random ecological subset of all the species present in the region (see Roy et al. 1995 for an example from the California Pleistocene). Moreover, the conceptual model shown in Figure 1 and supported by the simulations presented above suggests that at most localities the percentage of species for which we can even expect to see range fluctuation (irrespective of whether their ranges actually

shifted or not) would be quite small. This is simply because the range endpoints of a large proportion of species present at a locality or in a region often can fall well outside the locality or region, in areas where the fossil record may be nonexistent or poorly sampled (Fig. 3). Thus for such assemblages (e.g., the Pleistocene of California) the Connor and Simberloff (1978) null model (or any other unbiased random model that uses the total species pool to compute expectations of change) may be particularly prone to Type II error (also see Colwell and Winkler 1984 and Roughgarden 1984 for cautions about using total species pools).

The simple model presented here shows that biogeographic structure plays an important role in determining how compositions of local species assemblages would change in response to climatic fluctuations. Although I have empirically tested the model in a system where the major changes are only in one dimension (i.e., along latitude), it should also be applicable to shifts in longitudinal ranges of species and potentially even to changes in bathymetric distributions. In addition, factors such as the role of dispersal or complex ecological interactions between species, as well as metapopulation dynamics, may be important in determining how species respond to climatic change (e.g., Peters 1992; Malanson 1993; Walter and Patterson 1994; Lawton 1995; Jackson et al. 1996; Davis et al. 1998a,b). Incorporating these parameters into this type of biogeographic model remains a challenge.

Acknowledgments

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