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Selectivity during background extinction: Plio-Pleistocene scallops in California

J. Travis Smith and Kaustuv Roy

Abstract.—Most studies of extinction selectivity have focused on mass extinctions. Here we analyze the patterns of susceptibility to extinction during the late Pliocene and Pleistocene of California in the family Pectinidae. The Pectinidae declined in diversity from a high of 32 species in the late Pliocene to the current level of 11 species living in the California region, indicating that the composition of the living fauna has been shaped primarily by extinction in the last several million years. Extinction appears to have occurred in one large pulse, but because of uneven sampling we were unable to resolve the timing further and have analyzed the patterns of extinction treating the late Pliocene through middle Pleistocene as a single period of elevated extinction. Extinctions were not random with regard to taxonomic relationships. Species-level extinctions were higher in more speciose genera, but these genera were buffered against genus-level extinctions. This resulted in a disproportionately large number of monospecific genera in the living fauna. In addition, extinctions were not random with regard to body size, with large species preferentially surviving. This selectivity pattern is evident only when clade membership is taken into account; when analyzed across the entire family, no pattern of size selectivity was apparent. Our results suggest that (1) patterns of extinction selectivity at the genus level may be a poor proxy for species-level patterns, and (2) whole-fauna analyses may not uncover strong selectivity within lineages.

J. Travis Smith. Scripps Institution of Oceanography, University of California, San Diego, 9500 Gilman Drive, La Jolla, California 92093-0244. E-mail: j8smith@ucsd.edu
Kaustuv Roy. Section of Ecology, Behavior, and Evolution, Division of Biological Sciences, University of California, San Diego, 9500 Gilman Drive, La Jolla, California 92093-0116

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Introduction

Relative vulnerability of taxa to extinction has been the focus of studies in both paleontology and conservation biology (McKinney 1997). Although it has been argued that biased extinction is a common phenomenon both today and in the past (McKinney 1997), most of our existing knowledge of extinction selectivity in the fossil record comes from studies of mass extinctions. Selectivity during background extinctions still remains poorly studied (Jablonski 1991, 1994, 1995), thus making comparisons of past patterns with those from ongoing extinctions difficult. In addition, most analyses of extinctions in the fossil record have focused on higher taxonomic levels and considerable uncertainty exists about species-level trends (Jablonski 1995).

The past 2.5 Myr of earth history provides us with a rich record of extinctions and survival of species and lineages in the face of long-term climatic and environmental changes. Elevated levels of extinction during the late Pliocene and Pleistocene have been reported from the Caribbean (Stanley and Campbell 1981; Jackson et al. 1993; Johnson et al. 1995; Allmon et al. 1996; Roopnarine 1996, 2001; Anderson 2001; Todd et al. 2002), the Mediterranean (Raffi et al. 1985), New Zealand (Johnson and Curry 2001), and the northeastern Pacific (Stanley 1986). In the temperate northeastern Pacific, especially in California, species within the family Pectinidae show high levels of extinction during the Plio-Pleistocene and are the focus of this study. The California pectinids provide a useful system for analyzing patterns of species-level extinction; the group is well studied taxonomically (e.g., Grau 1959; Stump 1979; Moore 1984; Waller 1991, 1993; Smith 1991; Coan et al. 2000) and has an excellent Neogene fossil record due to the calcitic composition of the shells (Waller 1993). In this paper we use the fossil record of pectinids in California to test for patterns of selectivity during late Neogene extinctions.

Database

We compiled a database of stratigraphic occurrences and body sizes of Neogene pectin-

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ids from California. These data were collected through an extensive search of the primary literature and the collections at the Los Angeles County Museum of Natural History, San Diego Museum of Natural History, and the University of California Museum of Paleontology. The database consists of 72 species of Pectinidae and approximately 2650 occurrences, recorded by locality, as well as measurements for more than 700 individual specimens (see online supplemental material at http://dx.doi.org/10.1666/05078.s1). Of these, 32 species occurring during the late Pliocene and Pleistocene were used in this study to analyze extinction selectivity.

The taxonomy of Neogene and Recent Pectinidae is currently in a state of flux (Waller 1991, 1993). To maintain an internally consistent taxonomic structure for this study, we followed Moore (1984), Stump (1979), Smith (1991), Waller (1991, 1993, personal communication 1999), and Coan et al. (2000). Where opinions diverged, Waller's work took precedence over other publications, because Waller's (1991, 1993) analyses have been supported by independent genetic work using a variety of molecular markers (Matsumoto and Hayami 2000; Barucca et al. 2004).

The California region, as defined here, extends from Humboldt Bay, California, to Isla Cedros, Baja California Norte, Mexico. This includes the modern California Molluscan Province and part of the Oregonian Province (Valentine 1961; Addicott 1970; Bernard et al. 1991). We chose this region because of its excellent Neogene fossil record; the record for the rest of the Oregonian Province is too incomplete for the kinds of analyses presented here. A few of the Neogene basins of California have been the focus of sequence stratigraphic work (e.g., Blake 1991; Bowersox 2005) but the vast majority of named formations in this region represent lithostratigraphic units that are time transgressive (Blake 1991). Thus, correlating stratigraphic units across our entire study area remains problematic. In order to minimize such problems, we divided the late Neogene deposits of California into nine ''basins,'' or localized areas of deposition following the general outline of Weaver et al. (1944). From north to south these are Humboldt Basin, San Francisco Bay Area, San Joaquin Basin, Santa Maria Basin, Ventura Basin, Los Angeles Basin, Orange County, San Diego, and Isla Cedros. Wherever possible, we subdivided formations to get the best possible temporal resolution. The ages of individual localities within each ''basin'' were then determined by using the local stratigraphic framework. The ages of individual localities and the basis for such age assignments are given in Smith (2000; see online supplemental material for references).

Body size for each species was calculated as the geometric mean of length and height of the largest available fossil specimen (Stanley 1986; Jackson et al. 1996; Jablonski 1996, 1997). The only exception to this protocol is for ''*Flabellipecten*'' *diegensis*, a living species that is rare as a fossil. No adult fossil specimens of this species were observed in museum collections and none were measured for this study, hence we used the largest recent specimen for the size analyses. Trends in species diversity and extinction rates for the past 10 Myr were calculated from the stratigraphic range of each species computed from their occurrence data.

Timing and Magnitude of Extinctions

Pectinids in California suffered a high level of extinction during the late Neogene (Stanley 1986) (Fig. 1) although the timing of these extinctions remains poorly constrained (Addicott 1974, 1981; Stanley 1986). Our data show that over the past 2.5 Myr the diversity of pectinids in California has decreased from 32 species in the late Pliocene to 11 species in the Holocene, a 65% extinction at the species level (Fig. 1). In contrast, generic diversity declined from 14 to 10 genera, or roughly half the percentage decrease seen in species diversity. Moreover, all but one of the living pecten species in California originated before the Pleistocene. Thus the composition of the living pectinid fauna of California bears a strong legacy of the Plio-Pleistocene extinctions.

To constrain the timing of the extinction we analyzed the taxonomic diversity trends using 1-Myr intervals with the exception of the youngest time bin (0.5 to 0 Ma). Given our stratigraphic scheme, these intervals provided the best possible temporal resolution without

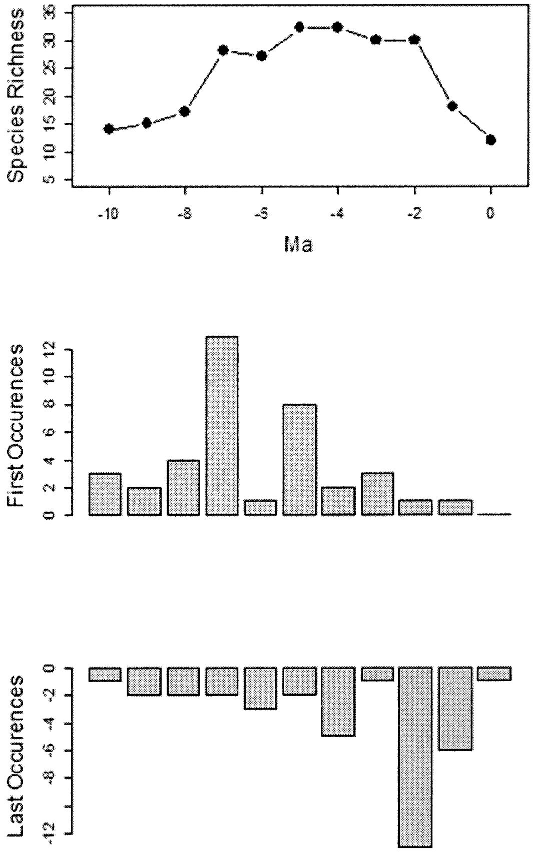

FIGURE 1. Extinction, origination, and diversity patterns. The upper plot shows the species richness in the California region over the past 10 Myr. The lower plots show the actual numbers of first and last occurrences in the region. The species diversity in the earliest time bin (10.5 to 9.5 Ma) includes species with first occurrences before 10.5 Ma that are not reflected in this plot.

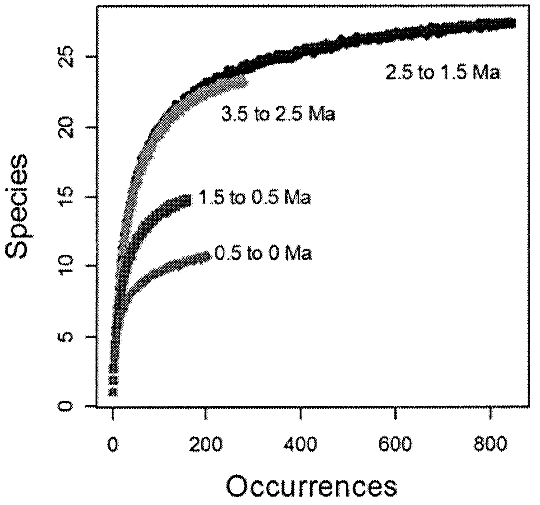

FIGURE 2. Sampling effort. The sampling effort for the four youngest time bins are shown. Number of occurrences is highest in the late Pliocene to early Pleistocene (2.5 to 1.5 Ma), but sampling is possibly most complete in the latest Pleistocene (0.5 to 0 Ma; see text).

introducing significant sampling error. Taken at face value, these analyses indicate that extinctions occurred in one main pulse during the latest Pliocene and earliest Pleistocene (2.5 to 1.5 Ma) with elevated extinction also occurring in the middle to late Pleistocene (1.5 to 0.5 Ma) (Fig. 1). However, sampling is poorest during the early to late Pleistocene (1.5 to 0.5 Ma, Fig. 2), which makes it difficult to separate sampling effects from true biological signals. Sampling effort based on occurrences is relatively low during the late Pleistocene (0.5 to 0 Ma, Fig. 2), but the shape of the sampling curve indicates that sampling completeness is high. In addition, 10 of the 11 living species have occurrences during this time interval. This indicates that the extinctions most likely occurred before 0.5 Ma. Resolving the timing of extinctions between the Plio-Pleistocene (2.5 to 1.5 Ma) and the early to middle Pleistocene (1.5 to 0.5 Ma) is difficult because of uneven sampling effort. The sampling curves (Fig. 2) indicate that the difference in diversity between the two time bins is real; however, there are approximately four times as many occurrences during the Plio-Pleistocene.

The temporal distribution of depositional environments poses another complicating factor. Middle to late Pleistocene deposits such as the Santa Barbara Formation, Lomita Marl, Timms Point Silt, Anchor Silt, and the San Pedro Formation represent deeper-water settings (Blake 1991), whereas others such as the upper terraces on San Nicholas Island and at Palos Verdes Peninsula represent the intertidal zone (Vedder and Norris 1963; Woodring et al. 1946; Lindberg and Lipps 1997). In contrast, the majority of the late Pliocene and earliest Pleistocene formations, such as the San Diego, Saugus, and portions of the Fernando Formations, represent shallow subtidal environments (Hertlein and Grant 1972; Groves 1991; Blake 1991). The lack of extensive shallow subtidal environments during the middle to late Pleistocene raises the possibility that instead of one Plio-Pleistocene extinction pulse, the entire period from the late Pliocene to middle

Pleistocene may have seen elevated extinction levels. Although it is still plausible that the California pectinids suffered one large extinction event, we prefer the more conservative interpretation that the late Pliocene to middle Pleistocene time in general was a period of elevated extinction for the California pectinids. The timing of these extinctions is correlated with known environmental changes including the onset of Pleistocene glaciation and the loss of several large shallow basins along the California margin, such as the San Joaquin Basin (Woodring et al. 1946; Addicott 1970; Bowersox 2005).

Extinction Selectivity

Taxonomic Effects.—Traits that determine extinction susceptibility of species are not randomly distributed between lineages and higher taxa (McKinney 1997). For example, the distribution of rare species (i.e., those that are more extinction prone) may not be independent of the size of the taxonomic group; for plants and some arthropod groups the number of rare species scales positively with the size of the higher taxon (Schwartz and Simberloff 2001; Webb and Pitman 2002; Lozano and Schwartz 2005; Ulrich 2005) whereas the opposite is true for birds and mammals (Purvis and Gittleman 2000; Purvis et al. 2000). Thus clade membership can play an important role in determining the likelihood of survivorship of a given species. There is also increasing empirical evidence that extinction intensities are often not randomly distributed among higher taxa and that the pattern holds for both human-mediated extinctions as well as those in the geological past (Jablonski and Flessa 1986; McKinney 1995, 1997; Bennett and Owens 1997; Nee and May 1997; Purvis et al. 2000; Lockwood et al. 2002). Such nonrandom extinctions can have important ecological and evolutionary consequences, including the potential for homogenizing the surviving biota (McKinney 1997; McKinney and Lockwood 1999; Lockwood et al. 2000).

Within the family Pectinidae, genera differ substantially with respect to traits such as body size and life habits (e.g., *Crassadoma* is large and lives cemented to hard substrates whereas *Leptopecten* is small and lives bysally attached to either substrate or other organisms such as kelp), so we tested for taxonomic selectivity at the genus level. The Plio-Pleistocene extinctions significantly changed the distributions of species within genera (Fig. 3). For the living pectens, 90% (9 out of 10) of the genera are represented by just a single species, but during the late Pliocene, only 50% (7 out of 14) of the genera were monospecific. This is consistent with the observation that an ''extinction fauna'' may often be made up of an inordinately high number of species-poor lineages (Purvis et al. 2000).

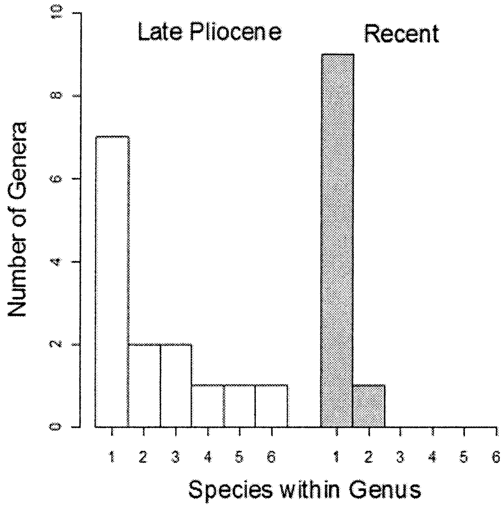

FIGURE 3. Distribution of species within genera. There is a significant change in the distribution of species from the late Pliocene to the Recent (Mann-Whitney *U*-test, $p < 0.05$).

To test statistically for taxonomic selectivity, we used a resampling algorithm to test if the number of surviving genera was significantly higher than would be expected under random extinction. We randomly drew 11 species without replacement from the total species pool (32 species) to generate an expected distribution of the number of surviving genera (Fig. 4). The observed number of surviving genera (ten) was significantly higher than would be expected if the extinctions were random with respect to genus membership ($p = 0.03$ based on 1000 iterations).

The level of extinction was not the same across all 14 genera and suggests that extinction risk of species was correlated with the species richness of the genus. To test this di-

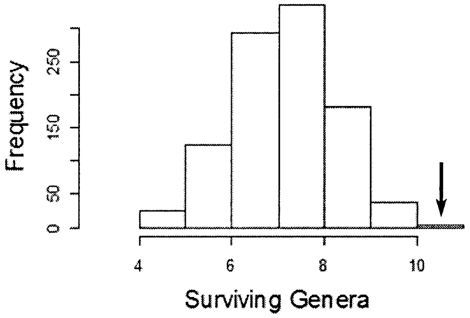

FIGURE 4. Resampling analyses. The distribution of surviving genera generated by using the resampling algorithm described in the text. The arrow indicates the observed number of surviving genera (ten), which is significantly more than is expected ($p = 0.03$, based on 1000 iterations).

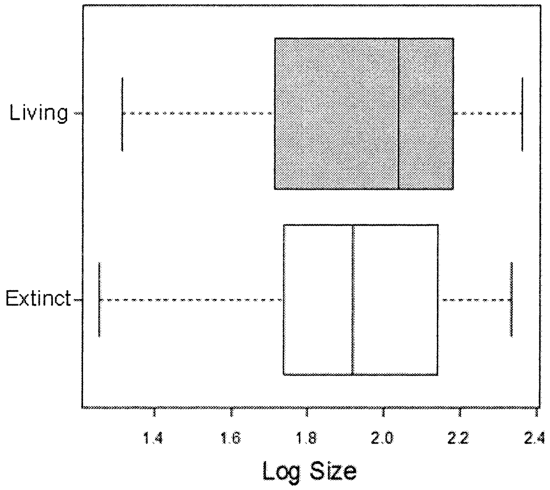

FIGURE 5. Body-size distributions for the extinct and living species. The line in the center of each box represents the median value. These size distributions are not significantly different (t-test, $p = 0.91$).

rectly, we compared the levels of extinction in small genera (one or two species during the late Pliocene) with those in larger genera (more than two species). Species-level extinction in the larger genera was significantly higher than would be expected from random extinctions (G-test, d.f. $= 1$, $p = 0.055$).

Size Selectivity.—Body size correlates with many ecological and life-history traits that can influence the extinction vulnerability of species (Peters 1983; Gaston and Blackburn 1996; Jablonski 1996). Hence considerable attention has been focused on body size and its relationship to extinction risk (Pimm et al. 1988; Gaston and Blackburn 1995, 1996; Jablonski and Raup 1995). Living species of birds and mammals that are at risk of extinction from anthropogenic factors often show significant size selectivity (Leck 1979; Pimm et al. 1988; Gaston and Blackburn 1995; Bennett and Owens 1997; Owens and Bennett 2000; Cardillo and Bromham 2001; Johnson et al. 2002). Similar patterns of size-related extinction have also been documented in some marine fish (Dulvy and Reynolds 2002). In marine invertebrates the pattern appears to be more complex. Selective extinction of larger species has been observed in tropical American corbulids (Anderson 2001) and several genera of venerids (Roopnarine 1996). Within corals in the same region however, larger species have preferentially survived (Johnson et al. 1995). In other cases, there is little evidence for size selectivity during large extinction events except for the late Pleistocene extinction of the vertebrate megafauna (Jablonski and Raup 1995; Jablonski 1996; McKinney 1997; Alroy 2001; Lockwood 2005).

For our data, when all species were analyzed together there was no significant difference between the size frequency distributions of extinct and surviving species (Fig. 5). This would suggest that extinction was not selective with respect to body size. However, such an analysis ignores phylogenetic affinities of species and could have missed selectivity within lineages. This is particularly important given the high heritability of body size (Jablonski 1987), the overlap in size among pectinid genera, and the observation that most extinctions are within species-rich genera. In fact, it has been shown that incorporating information about phylogenetic relationships even at a very coarse level in analyses of body-size distributions can provide insights often missed by non-phylogenetic approaches (Purvis et al. 2003). Because a well-resolved phylogeny of all the pectinid taxa used here is currently unavailable we tested for the presence of size-selective extinctions within individual genera to remove the effect of taxonomic membership (our approach is similar to previous studies such as Stearns 1983, 1984). Because within-lineage selectivity can be tested only for polytypic genera, sample size is sub-

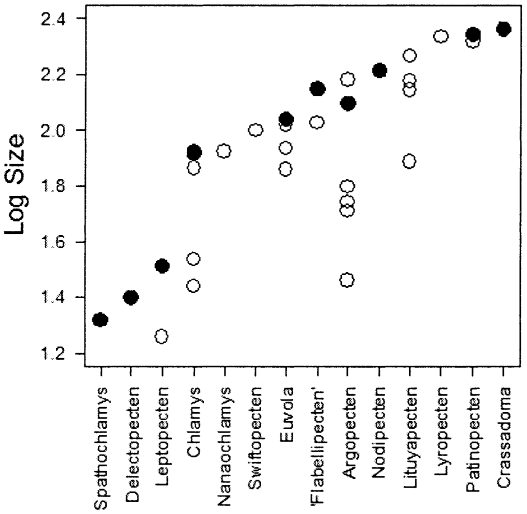

FIGURE 6. Body size within genera. Body sizes plotted for species within each genus. Solid circles indicate living (surviving) species and open circles represent extinct species. This figure includes the single-species genera that are not included in the within-genera analysis described in the text.

stantially reduced ($n = 25$, 7 extant and 18 extinct). Despite the reduced sample size a striking pattern emerges. The larger species preferentially survived within each polytypic genus (Fig. 6). In seven out of seven cases, the surviving species is larger than the median size for the genus. Assuming a probability of $p = 0.5$ for a surviving species to be larger than the median size for the genus, the binomial probability of all seven being larger than the median size is $p = 0.0469$. Thus, significantly more large species survived than expected if the extinctions were random. Moreover, the assumed probability of $p = 0.5$ in this argument is a conservative estimate because six of the seven surviving species were the largest member of their respective genera (the two largest in the genus *Chlamys*). Thus for California pectinids, body size significantly affects extinction susceptibility within individual genera but not across all genera.

Discussion

The late Neogene extinction of scallops in California was nonrandom with respect to taxonomy. Extinction risk was higher for species in species-rich genera, but genera with more species were less susceptible to extinction. The substantial increase in the proportion of monotypic genera following extinction suggests that species richness can provide a buffer against the extinction of genera. In this respect our results differ from those of many other studies where species richness did not provide a similar advantage to genera (see Jablonski 1995 for a review). This difference could reflect the fact that most studies of extinction selectivity in the fossil record have focused on mass extinction events. Patterns of selectivity during background times (i.e., extinctions of lesser magnitude) remain understudied. Alternatively, different clades or lineages may show different patterns of selectivity irrespective of the magnitude of extinction. These alternative hypotheses need to be tested by comparing taxonomic selectivities across extinctions that differ in intensity but involve the same clade(s). Johnson et al. (1995) did analyze selectivity patterns across differing levels of extinction, but they did not account for clade membership.

For pectinids in California, the Plio-Pleistocene extinction was also nonrandom with respect to body size, but the pattern was evident only within genera. No size selectivity emerged when all genera were analyzed together, so the result of our whole faunal analysis is consistent with that of other studies such as the K/T extinction of bivalves (Jablonski and Raup 1995; Lockwood 2005) and differs from studies of bivalves in the Caribbean during the same time period in that this study found selectivity against larger species (Roopnarine 1996; Anderson 2001). However, the strong lineage-level selectivity in our study suggests that the results from whole faunas may not reflect patterns within lineages. Body size is highly heritable and there may be a strong phylogenetic component to size selectivity during extinction events that could be obscured in analyses that do not take clade membership into account. The size selectivity patterns observed here are also very different from those in extinctions driven by anthropogenic activities where species-level extinction has been quantified within a phylogenetic framework. For birds and mammals small-bodied species appear to be more resilient to extinction (Gaston and Blackburn 1995; Bennett and Owens 1997; Cardillo and Bromham 2001; Johnson et al. 2002; but see Owens and Bennett 2000), a pattern exactly opposite of that found in this study. The ecological underpinnings of these differences remain poorly studied but fundamental life-history differences such as the scaling of fecundity and body size (positive in marine mollusks but negative in endothermic vertebrates) are potentially important here (Jablonski 1996; Roy et al. 2002).

In summary, the Plio-Pleistocene extinction of pectinids in California shows strong taxonomic and size selectivity. The patterns of extinction selectivity documented here stand in contrast to those from many earlier studies of extinction selectivity in the fossil record. However, very few of those studies have focused on background extinctions or have analyzed patterns within lineages at the species level. Our results demonstrate that patterns of extinction selectivity at the generic level may be a poor proxy for species-level patterns, at least during background extinctions. Whole-fauna analyses could also miss significant selectivity within individual lineages. Finally, these results underscore the importance of history in shaping the composition of living faunas and the differential recovery of taxa from extinction events. The pectinids in California have not rebounded from the Plio-Pleistocene extinctions and those events remain one of the major determinants of the present diversity patterns within this group.

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