

The ecology of extinction: molluscan feeding and faunal turnover in the Caribbean Neogene

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Molluscan faunal turnover in the Plio–Pleistocene of the tropical western Atlantic has been attributed to drops in temperature or primary productivity, but these competing hypotheses have not been assessed ecologically. To test these alternatives, we compiled data on changing molluscan life habits and trophic composition over 12 million years derived from 463 newly made collections from the southwestern Caribbean. Shelf ecosystems have altered markedly in trophic structure since the Late Pliocene. Predatory gastropods and suspension-feeding bivalves declined significantly in abundance, but not in diversity, and reef-dwellers became common. By contrast, all other ecological life habits remained remarkably stable. Food-web changes strongly support the hypothesis that declining regional nutrient supply had an increasing impact on regional macroecology, culminating in a faunal turnover.

Keywords: faunal turnover; primary productivity; Caribbean; Neogene; macroecology

1. INTRODUCTION

Faunal turnover in the tropical western Atlantic about 1–2 million years ago (Myr ago) profoundly altered the gross taxonomic composition of benthic communities (Jackson & Budd 1996) and from this event the ‘modern Caribbean fauna’ emerged in organisms as taxonomically and ecologically distinct as molluscs (Robinson 1993; Jackson *et al.* 1999) and reef corals (Budd & Johnson 1999). A synchronous extinction peak occurring across taxa with such varying life habits and showing long-standing and very different regional diversity dynamics (Budd & Johnson 1999; Jackson & Johnson 2000) demands that an explanation ultimately be sought in climatic or oceanographic change. All previous analyses of the molluscan turnover (Stanley & Campbell 1981; Stanley 1986; Vermeij & Petuch 1986; Allmon *et al.* 1993; Jackson *et al.* 1993; Petuch 1995) have been based on numbers of taxa rather than on ecological groups. Therefore descriptions and explanations for this turnover are also devoid of ecology. Two current hypotheses, declining seawater temperature (Stanley & Campbell 1981; Stanley 1986; Petuch 1995) and primary productivity change (summarized in Allmon (2001)), have been invoked to explain general patterns of diversity change, but without considering whether taxa with widely differing ecologies vary in relative susceptibilities to extinction or speciation.

Across the tropical west Atlantic, environments changed markedly in the Late Pliocene but timing and rates of

change are still poorly constrained (Jackson & Budd 1996). Both temperature and productivity almost certainly declined considerably, but arguments for temperature change are still controversial (CLIMAP 1976; Beck *et al.* 1992; summarized with full citations in Allmon (2001)) and the signals for productivity change are indirect and regionally variable (Keigwin 1982; Allmon 2001). Considering just primary productivity change, we predict that a major decline should restructure benthic communities and result in a corresponding decline in heterotrophic animals dependent on phytoplankton, such as suspension-feeding molluscs (Birkeland 1987). The biomass of sessile epifauna falls massively with declining nutrient supply (Birkeland 1977), therefore we might also expect a decline in predators directly dependent on heterotrophs, were there to be an overall large drop in prey biomass. By contrast, reef-associated molluscs should greatly increase because reef development greatly increases with reduced nutrient supply (Highsmith 1980; Birkeland 1987). We tested these predictions for both the taxic diversity and abundance of molluscs partitioned by their life habits.

2. METHODS

(a) Database

Molluscs are ideal for examining the ecological and evolutionary responses of benthic ecosystems to faunal turnover because they are widely distributed, exhibit a wide variety of documented life habits and dominate all sampled fossil and Recent skeletonized benthic macrofaunas of the region. Our archived database of southwestern ‘Caribbean’ molluscs (gastropods, bivalves, scaphopods and cephalopods) consists of 463 newly made collections comprising 202 897 specimens. Our analysed dataset consists of 198 655 specimens of bivalves and benthic gastro-

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Table 1. Summary of analysed dataset with records assigned to the three time-intervals.

	classes and total	total	Late Miocene	Early Pliocene	Plio–Pleistocene to Recent
number of taxa	bivalves	262	146	190	191
	gastropods	520	282	356	350
	total	782	428	546	541
number of collections	bivalves	433	194	148	91
	gastropods	443	202	150	91
	total	463	218	154	91
number of occurrences	bivalves	7182	1811	2341	3030
	gastropods	11107	3700	4373	3034
	total	18289	5511	6714	6064
number of specimens	bivalves	107–558	25475	44017	38066
	gastropods	91097	33831	39550	17716
	total	198655	59306	83567	55782

pods, comprising 782 genera and subgenera and representing 18 289 taxon/collection occurrences (data summarized in table 1). Archived systematic and taxon/collection-occurrence data for bivalves and gastropods are available through the Neogene Marine Biota of Tropical America (NMITA) website, <http://nmita.geology.uiowa.edu> (Budd *et al.* 2001) and full stratigraphic, locality and collection information for fossil samples is at the Panama Paleontology Project (PPP) website, <http://www.fiu.edu/~collins/>. Fossil bulk and specimen samples have been newly collected by the PPP from the Late Middle Miocene (12 Myr ago) through to Pleistocene sediments of the Republic of Panama and Costa Rica (Coates 1999) and Recent samples dredged from near the Los Cochinos Archipelago (Honduras), the Cayos Misquitos, (Nicaragua) and the San Blas Islands (Panama) with station details available at <http://cayoagua.ucsd.edu/datasets>.

Our database has been created at the generic level because comprehensive systematic revisions are available for very few genera or families, and species diversity of unrevised taxa cannot be estimated accurately (Jackson *et al.* 1999; Todd 2001a). Further, species life habits of congeneric molluscs vary little and the value of genera as species proxies in regional biodiversity studies has already been demonstrated (Roy *et al.* 1996). Faunal lists were made using standardized collecting and counting protocols (Jackson *et al.* 1999), in which bivalves were counted using the ‘maximum number of individuals’ approach (Gilinsky & Bennington 1994). Dredged Recent faunas of the region consist overwhelmingly of dead shells (Best & Kidwell 2000). Collected as time-averaged faunas and at a similar spatial scale, we consider them to be directly comparable with the fossil assemblages. Our fossil collections contrast with those of previous analyses (Stanley & Campbell 1981; Vermeij & Petuch 1986; Petuch 1995) that lack sampling replication and protocols, or controls for variations in sedimentary environment, bathymetry or spatial heterogeneity, and are combined with inadequate stratigraphic dating (Allmon *et al.* 1993; Jackson & Budd 1996; Jackson *et al.* 1999), whereas we use integrated bio-, litho- and magnetostratigraphies (Coates 1999; McNeill *et al.* 2000).

(b) Molluscan taxonomy

Taxonomic compendia covering the whole of this time interval or region are lacking. Current faunal monographs and stan-

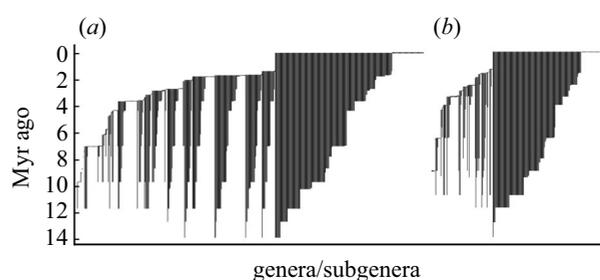


Figure 1. Stratigraphic ranges of (a) 520 benthic gastropod genera and subgenera and (b) 262 bivalve genera and subgenera sorted by their ages of last appearance. Taxon ranges were calculated from the midpoint of the age of the collection in which the taxon first occurred to the midpoint of the age of the collection in which the taxon last occurred.

ard taxonomic syntheses often use very different supraspecific concepts and nomenclature, even for some of the most abundant and widely occurring taxa (Todd 2001a). The difficulties inherent in accurate taxonomic compilation have, to our knowledge, previously gone unmentioned. To ensure consistency of taxonomic application and specimen identification we have developed our own consistent systematic framework for neotropical molluscs from the Recent back to the Middle Miocene. This follows available authoritative systematic revisions and is supported by taxonomic reference collections. Systematic lists and bivalve reference collection images are available at the NMITA website (J. A. Todd, in Budd & Foster 1996–2001). Our consistent system of open nomenclature allowed us to exclude from analysis those specimens that because of poor preservation, incompleteness, or juvenility, could not be reasonably identified to the appropriate generic or subgeneric level.

(c) Taxic turnover

To confirm that our current database reveals the regional taxic turnover previously derived from smaller datasets (Jackson *et al.* 1999; Jackson & Johnson 2000), we examined the stratigraphic ranges of the 782 benthic gastropod and bivalve genera and subgenera (figure 1). We analysed gastropods and bivalves both together and separately using first and last occurrences. Taxon ranges were calculated from the midpoint of the age of the collection in which a taxon first occurred to the midpoint of the age

Table 2. Turnover data for one-million-year duration stratigraphic bins; (a) bivalves, (b) gastropods.

age (Myr ago)	number of collections	number of (taxa)	first occurrences	last occurrences	per taxon origination	per taxon extinction
<i>(a)</i>						
Recent	55	169	34	—	0.201	—
1–0	0	135	0	0	0.000	0.000
2–1	36	157	13	22	0.083	0.140
3–2	22	163	18	19	0.110	0.117
4–3	91	172	30	27	0.174	0.157
5–4	35	151	21	9	0.139	0.060
6–5	3	130	0	0	0.000	0.000
7–6	102	138	28	8	0.203	0.058
8–7	14	111	5	1	0.045	0.009
9–8	8	106	13	0	0.123	0.000
10–9	32	98	28	5	0.286	0.051
11–10	16	70	11	0	0.157	0.000
12–11	12	60	32	1	0.533	0.017
<i>(b)</i>						
Recent	55	223	46	—	0.206	—
1–0	0	177	0	0	0.000	0.000
2–1	36	304	54	127	0.178	0.418
3–2	23	302	31	52	0.103	0.172
4–3	91	328	69	57	0.210	0.174
5–4	38	274	38	15	0.139	0.055
6–5	5	240	2	4	0.008	0.017
7–6	105	270	77	32	0.285	0.119
8–7	17	195	13	2	0.067	0.010
9–8	7	186	15	4	0.081	0.022
10–9	32	175	65	4	0.371	0.023
11–10	15	110	24	0	0.218	0.000
12–11	13	86	56	0	0.651	0.000

of the collection in which the taxon last occurred. The pattern of taxic turnover was described by counting the number of first and last occurrences of taxa within a set of stratigraphic bins with one-million-year durations. Total range-through taxic richness (Johnson & McCormick 1999) for a stratigraphic bin was calculated by counting the number of taxa that first occur prior to the end of the bin and that last occur after the start of the bin (table 2). Sampling intensity through the studied time-interval is uneven due to variation in outcrops of fossiliferous strata. Therefore, we tested the robustness of our patterns to this bias in two ways: by using a permutation test for all gastropods and all bivalves as previously undertaken (Jackson & Johnson (2000); for methods, Johnson & McCormick (1999)) and by rerunning this test on just the common bivalves and common gastropods. To identify common taxa we applied a quartile approach as suggested by Gaston (1994). A taxon was considered common if it fell within the top abundance quartile in at least one stratigraphic bin. All common taxa were included in the 'common-only' split of the dataset, therefore a taxon was included in all stratigraphic bins even if it was only abundant in a subset of the bins. For one-million-year-duration stratigraphic bins, the common-only dataset included 280 genera and subgenera and 195 985 specimens. This represents a 64% decrease in the total number of genera, but only a 1.3% decline in numbers of specimens. Clearly, most taxa are characterized by very low abundance (see Jackson *et al.* 1999; Jackson & Johnson 2000).

(d) Feeding and life habits

As benthic molluscs display a wide range of feeding and life habits, we tested whether the large differences in relative extinction levels across classes reflected a strong ecological component to the turnover. The main categories for analyses were ecological groupings that we examined for changes in taxic diversity and abundance. First we assigned feeding and life-habit information to all bivalve and benthic gastropod taxa in the dataset. This information, a bibliography and a discussion of life-habit assignments is available at the NMITA website (Todd 2001b). Then we examined how the representation of these categories changed through time as shown by: (i) the numbers of specimens and (ii) the numbers of taxa within each time interval. For each, we considered both raw numbers and abundance measured as a percentage of all other life habits recorded. Gastropods and bivalves were analysed separately because of their very different ecologies.

Gastropods were categorized by diet through literature reviews for living taxa and by assuming taxonomic uniformitarianism for extinct taxa. Seven trophic categories were delimited: (i) predatory carnivores and scavengers; (ii) browsing carnivores (on sedentary, typically clonal animals; includes ectoparasitic habit); (iii) herbivorous omnivores; (iv) deposit feeders and detritivores; (v) microherbivores on rock, rubble or coral substrates; (vi) herbivores on plant or algal substrates and (vii) suspension feeders.

Three bivalve life-habit categories were analysed, with the

individual life habits listed in parentheses: (i) spatial relationship to substrate (reclining, epifaunal, semi-infaunal, infaunal siphonate, infaunal asiphonate, nestling on or within hard substrate, nestling within burrows, boring in hard substrate); (ii) presence and nature of attachment (unattached, bysally attached, cemented), and (iii) degree of mobility (swimming, actively mobile, sedentary, immobile). Five trophic categories were delimited: (i) suspension feeding, (ii) surface, (iii) subsurface and, (iv) chemosymbiotic deposit feeding and, (v) microcarnivory. For Recent specimens, these data were obtained from literature reviews and for fossils they were assigned through skeletal functional morphology and assumption of taxonomic uniformitarianism. For bivalves, we analysed the data by treating separately each of the twenty habits comprising the four categories. Preliminary analyses using guilds, identified by combining habits across the three categories, produced weaker and less easily dissected patterns than those obtained from individual life-habits and categories, due in part to the large number of combinations present (54).

(e) *Stratigraphic binning and bathymetry*

Collections were assigned to three time-intervals: Miocene (12–5.3 Myr ago); Pliocene (5.3–2.3 Myr ago); and Plio-Pleistocene transition to Recent (2.3–0 Myr ago), based on non-overlapping end-point age estimates given in Jackson *et al.* (1999). Coarse time-blocks served to maximize the macroecological signal by ensuring that a large number of individuals and a wide diversity of shelf environments and water depths were represented in each interval (78% were from less than 100 m). Palaeobathymetries were independently established using benthic forams (L. S. Collins, in Jackson *et al.* 1999).

(f) *Approach*

We examined whether differences existed across time-intervals in the relative abundance of molluscs with differing ecologies, by comparing numbers of genera and subgenera assigned to each life-habit category with the numbers of specimens of those taxa. To assess whether our ecological patterns relating to taxic diversity were unduly affected by differential sampling intensity across time-intervals, we again compared the patterns obtained from studying: (i) all the fauna (all bivalves, all gastropods), and (ii) just the common fauna (common bivalves, common gastropods). The results were very similar; the sampling of rare molluscs did not affect overall patterns. We suspected that some of the differences between Recent and fossil life-habit patterns might be the result of taphonomic filtering, particularly the removal of thin and fragile bivalves from the fossil record. This suggestion is in concordance with the doubling of the bivalve : gastropod ratio in the Plio–Pleistocene to Recent stratigraphic bin (table 1). To test this we removed the Recent collections from the third time-interval and reanalysed the ‘all’ and ‘common’ data subsets. The patterns remained unaltered, so any taphonomic bias shown by fossil faunas seems to have had little discernible effect on ecological patterns. All of these analyses were repeated just for the 361 ‘shallow’ water (less than 100 m) collections to ascertain whether patterns varied with water depth. The *G*-test for association was used (with random subsamples of 500 specimens per stratigraphic bin) to test for the association between: (i) number of specimens, and (ii) numbers of taxa within the examined trophic groups with time.

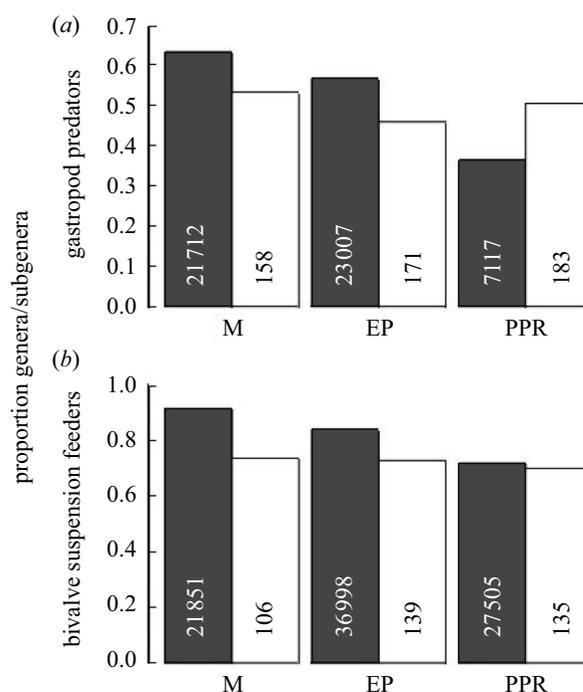


Figure 2. Temporal declines in abundance (shaded bar in each of three groups) relative to static taxic diversities (white bars) for two molluscan trophic groups, (a) predatory-carnivorous gastropods and (b) suspension-feeding bivalves. Bars show the proportion of each life habit as a percentage of (a) all gastropods and (b) all bivalves, within three time-intervals: M, Miocene (12–5.3 Myr ago); EP, Early Pliocene (5.3–2.3 Myr ago) and PPR, Plio–Pleistocene–Recent (2.3–0 Myr ago). The numbers within the bars for each time interval indicate total numbers of specimens (shaded) and genera plus subgenera (white) for the respective trophic groups. Decreases in numbers of specimens in (a) and (b) are highly significant (*G*-test for association based on numbers of taxa and random subsamples of 500 specimens per stratigraphic bin; $G = 242$; $p < 0.001$; and $G = 390$; $p < 0.001$ respectively), but changes in numbers of taxa are not significant; $G = 3.74$; $p = 0.15$ and $G = 0.65$; $p = 0.72$ respectively).

3. RESULTS

Stratigraphic range plots for gastropods and bivalves (figure 1) and calculations of turnover per million year (table 2) appear to show a period of heightened extinction between 2–1 Myr ago, but of markedly different intensities between these classes. At this time, proportionately three times more gastropods (42%) than bivalves (14%) recorded within, or ranging through, the preceding one-million-year interval (3–2 Myr ago) made their last appearance. The permutation test undertaken on these data confirms that the extinction peaks between 2–1 Myr ago were significant, particularly those of gastropods, and reveals a minor drawn-out increase in origination rate for both classes from 5–2 Myr ago, verifying the pattern shown by Jackson & Johnson (2000, fig. 2) using a smaller dataset. Overall, gastropods were much more volatile than bivalves, despite common gastropods being more eurytopic than common bivalves (Jackson *et al.* 1999).

Comparisons of numbers of specimens versus taxa within trophic and life-habit categories revealed strong and consistent changes in trophic structure but not in

bivalve life habits for all categories analysed. As the shallow-water collections showed very similar patterns to those shown by the whole dataset, we discuss only the latter here. Predatory gastropods suffered a massive decline in abundance from 63% (Miocene) to 36% (Late Pliocene–Recent) of all gastropods (figure 2a). This represents a relative decline in abundance of 43%, with three-quarters of this drop occurring between the Early Pliocene and Recent. In striking contrast, there was no corresponding change in diversity (from 53% to 50% of taxa) over 12 Myr ago from the Miocene to Recent. Indeed, recorded diversity slightly increases from the Pliocene to Recent. The drop in abundance seems to reflect a more general decline in predatory organisms and predation intensities in the Caribbean after isthmian uplift (Vermeij 1993), but it may also indicate an increase in non-gastropod predators at the expense of gastropods in some more widely occurring environments post-turnover; further study is required.

Suspension feeding is by far the dominant trophic mode within our bivalve dataset. However, the percentage of suspension feeders falls from 92% to 72% from the Miocene to Plio–Pleistocene–Recent (figure 2b), a relative drop in abundance of one-fifth, with 60% of this drop occurring between the Early Pliocene and Recent. Again, taxic diversity shows no significant decline over the Miocene to Recent interval (74% to 70%). With the decline in filter feeders there is a concomitant increase in all types of deposit feeders and microcarnivores. Abundant deposit feeders of all types (infaunal, epifaunal and chemoautotrophic; see Todd (2001b)) may characterize some shelf facies, particularly sea grass meadows. These are poorly represented in our current dataset; this under-representation emphasizes that the decline in suspension feeding was not habitat specific. Nor is it class specific. Infaunal suspension-feeding gastropods decline from 20% to 11% of gastropod specimens. This largely reflects a sharp regional decline in turrnellid abundance and taxic diversity; turrnellid shell beds are widespread and conspicuous in shallow shelf deposits in the southern Caribbean Miocene (e.g. Gatun Formation; Coates (1999)), are rarer in the Pliocene and today are confined to very localized upwelling pockets in the Recent southern Caribbean (Petuch 1976). Recent turrnellid shell beds typically occur in cool, nutrient-rich waters subject to upwelling (Allmon 1988). By contrast, epifaunally cemented or embedded, suspension-feeding gastropods ('worm snails') markedly increase in abundance from the Early Pliocene to Recent. This is reflected in the proportion of epifaunal to infaunal dwellers (figure 3) and indicates a post-turnover increase in rubble and shell debris (Vermetidae) and sponge substrates (Siliquariidae: *Tenagodus*) on the seafloor. In our Plio–Pleistocene samples the first abundant, reef-dwelling cypraeids (*Luria*, *Macrocypraea* and *Proadusta*) appear and these typify Caribbean reefs and rocky substrates to the present day (Lorenz & Hubert 2000).

Massive cross-habitat and cross-shelf declines in abundance of carnivorous gastropods and suspension-feeding bivalves and gastropods provide by far the strongest regional support for the proximate role of productivity decline in the molluscan turnover. Patterns are entirely consistent with a transition from heterotrophic and nutri-

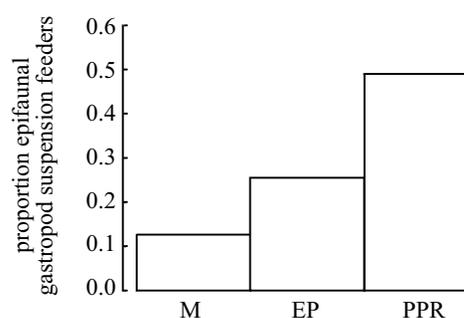


Figure 3. Temporal increase in ratio of epifaunal to infaunal suspension-feeding gastropods within three time-intervals: M, Miocene ($n = 7316$); EP, Early Pliocene ($n = 3589$); and PPR, Plio–Pleistocene–Recent ($n = 4488$).

ent-rich to more phototrophic and nutrient-poor ecosystems (Birkeland 1987) and significantly amplify more circumstantial evidence provided by size trends in two bivalve families (Roopnarine 1996; Anderson 2001) and carbon isotope data (Teranes *et al.* 1996). The post-turnover regional appearance of extensive reefs and their characteristic molluscs followed a long-term cross-Caribbean increase in carbonate-associated benthic foraminifers (Collins *et al.* 1996), diversification of reef corals and development of shallow sea grass communities. All are contingent upon the declining primary productivity and increased water temperatures predicted to arise from oceanographic changes, consequent upon closure of the Central American seaway (Collins *et al.* 1996). Further north, in Florida, a range of evidence: carbon and oxygen isotope data sediments and macrofauna, indicates the loss of nutrient-rich, upwelling water after the Plio–Pleistocene faunal turnover (Allmon 2001), but there the record is restricted to condensed shallow shelf deposits.

4. DISCUSSION

The Plio–Pleistocene molluscan turnover was pervasive across the shelf and led to such profoundly different community compositions that pooled regional data provides clear macroecological signals implicating primary productivity decline. Analyses of abundance data revealed striking changes in the proportions of different trophic groups over time that were undetectable by simply counting numbers of taxa comprising these groups. Remarkably, considering the magnitude of faunal turnover, changes in bivalve life habits are much weaker and not readily interpretable. These changes may represent the waxing and waning of particular bivalve clades or responses to sporadic lithofacies occurrences, rather than a consistent ecological response. Moreover, as higher taxa, gastropods and bivalves responded differently to changing oceanographic conditions, as revealed by patterns of changing taxonomic abundance and specimen richness. However, their faunal dynamics are more similar to each other than either is to that of reef corals, which show a pronounced and extended period of originations from 8–5 Myr ago (Budd & Johnson 1999; Johnson 2001). All three higher groups show asynchronous turnover, with originations preceding extinctions, suggesting that regionally there was an extended period of gradual escal-

ation of ecological reorganization (Jackson & Johnson 2000). Changes in Caribbean ecosystems post-isthmian uplift relative to those in the East Pacific have been so profound that the Caribbean and East Pacific today represent distinct macroecological realms (Jackson & D'Croz 1997).

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