

# The Paleoecology of Coral Reefs

John M. Pandolfi

**Abstract** Reefs are one of the oldest ecosystems in the world, and coral reefs have had a rich and varied history over hundreds of millions of years. The long-term history of living reef organisms provides an essential window in which to view a number of fundamental evolutionary and ecological processes over extended time frames not available to modern ecology over years or decades. Many of the constituents of modern reefs are calcifying organisms that leave a record of their presence in the fossil record. Thus, coral reef paleoecology has been undertaken on tropical ecosystems worldwide with applications in ecology, evolution, biogeography, extinction risk, conservation and management, and global change biology. Because many reef organisms secrete their calcareous skeletons at or near isotopic equilibrium with ambient seawater, they have also been used to reconstruct environmental conditions over long time frames. The examination of ecological and evolutionary change in the context of environmental variability provides an ideal framework for understanding coral reef paleoecology and placing the modern biodiversity crisis in an historical context.

**Keywords** Coral reefs • paleoecology • reef management • ecology • evolution • global change • biodiversity • evolutionary turnover • biogeography • conservation biology

## 1 Introduction

To those not familiar with the nuances of time and geology, mining the literature on the fossil record of extant groups of marine organisms can seem a daunting pursuit. In many cases, this has led to a reduced appreciation of the utility of placing modern empirical studies on the ecology of living

organisms into a historically informed context. As in all facets of life, ignoring the lessons of history is done at one's own peril. In this chapter, I briefly review the salient aspects of coral reef paleoecology that help to place modern studies into a historical framework. I mostly concentrate on the ecology of coral reefs of the Quaternary Period (over the past 1.8 million years – myr), but where it becomes useful some examples are drawn from reefs that lived during much older intervals.

### 1.1 What Is Paleoecology?

Paleoecology is the study of the distribution and abundance of organisms based on their remains from the fossil record. What constitutes a fossil has been much debated, but in general fossils are the remains of organisms and their activity that have been preserved within the sedimentary or rock record.

Predictive ecology is a central but elusive goal for experimental ecology on modern ecosystems, and this can hold even more so when confronting the vagaries of the fossil record. The fossil record has the advantage of recording the state of the ecosystem during repetitive time periods and thus under various combinations of environmental factors; however, processes must always be inferred from “natural experiments” where certain conditions have fortuitously been constant while a single or small number of factors vary. In this way, patterns derived from the fossil record can be used constructively for inferring potential processes acting over extended time periods.

### 1.2 A Brief History of Reefs

While the definition of just what is a “reef” has a long and tortuous history of debate in the scientific literature (Hatcher 1997), there is no dispute about the importance of the reef ecosystems of the coastlines, continental shelves, and ocean provinces of the tropical realm. Hatcher (1997) defines reefs

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J.M. Pandolfi (✉)  
ARC Centre of Excellence for Coral Reef Studies, Centre for Marine  
Science, School of Biological Sciences, University of Queensland,  
4072 St. Lucia, Queensland, 4072, Australia  
e-mail: j.pandolfi@uq.edu.au

as "...a marine limestone structure built by calcium-carbonate secreting organisms, which, with its associated water volumes supports a diverse community of predominantly tropical affinities, at a higher density of biomass than the surrounding ocean..." (p. S78). Reefs in their many forms are found throughout the fossil record and represent some of the earliest structure-forming ecosystems on Earth. Since the explosion of metazoans in the Cambrian around 540 million years ago (mya), many groups of organisms have formed "reef-like" features on the seafloor making reef communities difficult to singularly characterize (Wood 1999). *Coral* reefs are one of the oldest reef systems on Earth. Following the greatest extinction of all time, the Permo-Triassic event (251 mya), scleractinian corals, bivalve molluscs, and crustose coralline algae have dominated the construction of wave-resistant organic carbonate structures on the planet.

### 1.3 The Past, The Present, and The Future

All students of geology are indoctrinated with Hutton's famous principle that "the present is the key to the past," the "Law of Uniformitarianism." However, it has become increasingly clear over the past couple of decades that the past can also provide key insights into modern processes, especially in predicting future likely ecosystem states. Studies of the paleoecology of reefs have provided some interesting and useful data with which to place the modern biodiversity crisis in some perspective, identifying the degree to which reefs have been subject to the shifting baseline syndrome (Pauly 1995; Pandolfi and Jackson 2006), and continue to offer ecological insight into the potential future health of modern ecosystems in the light of predicted environmental change.

## 2 Constraints and Influences over Coral Reef Development

### 2.1 Local Controls

The growth of living coral reefs is intimately tied to environmental conditions. Local controls over reef growth include wave energy, water quality, turbidity, salinity, tidal regime, and light. In the Caribbean Sea, clearly defined zones that characterize both modern and Pleistocene assemblages could reliably be predicted based on their spatial distribution with respect to wave energy (Geister 1977). Early efforts to understand the relationship between coral growth and local environmental parameters were almost exclusively concentrated

on fossil sequences (Adey 1975, 1978; Geister 1977; Chappell 1980) and have been confirmed with more quantitative studies on both modern (Done 1982) and fossil (Pandolfi and Jackson 2001) taxa. Ecophenotypic plasticity in response to wave energy and light was long thought to be the main driver of differential reef growth but much earlier work focusing on environmental controls (Graus and Macintyre 1976, 1982; Connell 1978) turned out to have a largely genetic component (Knowlton et al. 1992), and the full implications for the fossil record have yet to be investigated (Pandolfi et al. 2002; Budd and Pandolfi 2004; Pandolfi and Budd 2008).

### 2.2 Regional and Global: Secular

Physical controls on reef building and decline, over geologic timescales, include variations in seawater chemistry and cyclic changes (at varying time scales) in sea level, sea-surface temperatures, and global levels of atmospheric CO<sub>2</sub>. These factors are necessarily interrelated. Regional and global variation in sea-surface temperatures (SST), CO<sub>2</sub>, and sea level have continued to exert substantial influences over coral reef growth during the Cenozoic, all the way through to the Holocene period (Montaggioni 2005). However, a long-term database on reef development throughout the past 540 million years (my) of the Phanerozoic Eon shows that, whereas long-term climate change is influential in the biotic composition of reefs, neither climate nor chemical changes in the sea are correlated with the waxing and waning of reefs (reviewed in Kiessling 2009).

### 2.3 Latitudinal Range Limits

A large number of factors can contribute to latitudinal variability in coral species composition and community structure: water temperature, aragonite saturation, light availability, currents and larval dispersal, competition between corals and other biota including macroalgae, reduced coral growth rates, and failure of coral reproduction or recruitment (summarized in Harriott and Banks 2002). Living reef-building corals are generally confined to the tropical oceans between 30°N and 30°S latitudes, and these limits often characterized reefs in the past (Copper 1994; Kiessling 2001). In the Silurian period (443–417 mya), tropical reefs closely matched the geographic distribution of their modern counterparts (Copper 1994). But over the broad swath of the Phanerozoic, there is no strict correlation between the geographic distribution of reef growth and tropical placement (Kiessling 2001, 2005).

## 2.4 Biotic Factors

Paleontologists have used ancient reefs as model ecosystems in the study of ecological succession, or the orderly changes in communities of a specific place over a period of time (Masse and Montaggioni 2001). For ecologists, one of the great limitations of assessing the frequency or validity of the processes of succession is that the complete successional sequence might take longer than the period of time over which most ecosystems are studied within ecological research programs. Since succession is by its very nature a process that occurs over time, it is not surprising that paleontologists have investigated the degree to which it can be understood from evidence in the fossil record.

Four major phases of succession in eight ancient reefs ranging in age from the Early Ordovician (488 mya) to the Late Cretaceous (65.5 mya) have been established: stabilization, colonization, diversification, and domination (Walker and Alberstadt 1975). The stabilization stage involves the initial colonization of the sea floor that results in the establishment of a firm substrate. The colonization stage is characterized by encrusters and frame builders, those organisms capable of colonizing a hard substrate and that begin to build three-dimensional structures above the sediment–water interface. Some authors consider the first two of these stages to be the same, equivalent to the pioneering stage of ecologists studying succession in living forest communities. The third stage in the succession of fossil reefs is referred to as the diversification stage, where maximum diversity of the reef community is developed. Diversity then decreases as a “domination” stage sets in whereby a single functional entity characterizes the reef community. As the communities ascend through the first three stages of succession, species diversity, degree of stratification and pattern diversity, niche specialization, and the complexity of food chains all increase. These successional sequences typically occur through significant intervals of time and are the result of the gradual alteration of the submarine substratum by individual species, and the elaboration of energy-flow pathways as the community proceeds through time. Shorter-term successional episodes have also been observed where occasional environmental perturbations destroy the pre-existing community. Here, subsequent community development involves a rapid biologically induced sequence of communities that culminate in the climax community that was established prior to the perturbation. Just as in the longer-term successional sequences, increases in major functional and structural attributes of the community accompany these shorter-term successional sequences.

There are, of course, a number of potential problems associated with the identification of succession in the fossil record. In Walker and Alberstadt's (1975) model, an increase in diversity may come about just as easily from an increase in the zonation of the reef (habitat heterogeneity) as to

intrinsic biological changes. In the domination phase, the accompanying decrease in diversity may reflect a community that caps a reef after it dies, as opposed to a decrease during the life of the reef. However, in the fossil record of the Quaternary period (the past 1.8 Myr), these difficulties can often be overcome through precise age dating and detailed understanding of the sea-level history of the reefs. Quaternary sequences of coral reefs are particularly well suited for understanding community development through time (Mesolella 1967; Geister 1977; Crame 1980).

In Kenya, “obligatory succession” in the Pleistocene consisted of an early assemblage of sediment-tolerant corals (dominated by massive or doming corals) that was replaced by predominantly branching and platy/encrusting corals (Crame 1980). This kind of succession was mainly confined to the earliest portions of reef development on a bare substrate. Patterns through longer successional phases were varied, but under certain conditions massive or domed shape corals might replace the branching assemblages. However, clearly defined zones were rare – most temporal changes in reef species associations were random or unstructured.

## 2.5 Autecology of Reef Organisms

Autecological studies have also provided glimpses into biological processes occurring in the past. For example, Kaufman (1981) found galls on the branches of Pleistocene *Acropora* colonies indicating the antiquity of threespot damselfish (*Eupomacentrus planifrons*) territories on Caribbean coral reefs. While the presence of modern processes on past reefs should not be surprising, it is important for our predictive capacity of modern reefs to understand the temporal framework over which such processes have operated, how susceptible they might be to varying disturbance regimes and environmental change, and how their role in the maintenance of species diversity varied through time. The effects of some processes might be long-term or involve significant lag times, so their real significance might only be borne out through studies conducted over broad temporal scales.

The principal features of fossil coral reefs, like their modern relatives, lie in their ability to build three-dimensional structures above their surrounding substrate. While we are concentrating on “coral” reef paleoecology for this chapter, it is important to realize that reefs have not always been built by corals, and that corals have come and gone in their function as dominant frame builders throughout the geological record. In the Cretaceous Period (144–65 mya), rudist bivalves once formed lush and diverse reefs and may have even competitively displaced corals from their role as reef framework builders. However, others dispute this prominent

role and believe that rudists were confined to nonreefal, mobile sedimentary settings (Gili et al. 1995). Stromatolites have built wave-resistant structures through the entire Phanerozoic Eon (543 mya to present).

Within the corals themselves, there are vast amounts of untapped information on autecology that may help us uncover the nature of biodiversity crises in the sea. For example, Kiessling et al. (2005) found abundant massive colonies of *Haimesiastrea Conferta*, occurring in the Paleocene of the Lefipán Formation of Argentina. This coral made it through the Cretaceous-Tertiary mass extinction event, presumably as a result of a broad ecological niche and a wide geographic range. Further work on the characteristics of extinction-resistant reef taxa will aid in our ability to predict response of living coral reefs to environmental change.

Attention has been given to the analysis of growth rates of living corals from the colony level all the way down to the microstructural skeletal elements (Dullo 2005). Commonly, linear extension rates are compared, but other measures, including density and biomass, can be used when linear extension does not apply or is an inadequate descriptor of coral growth. Fossil coral growth rate studies are not as common, but have been undertaken on some Caribbean corals (Pandolfi et al. 2002; Dullo 2005; Johnson and Perez 2006). There is clearly more work needing completion to understand environmental controls over reef accretion and variation in coral growth rates over multiple environmental and anthropogenic regimes (Guzman et al. 2008).

### 3 Reef Paleoproductivity

Primary productivity in marine ecosystems is governed largely by nutrient availability and for coral reefs the balance between carbonate production and bioerosion may teeter on small changes in nutrient availability. This is because many of the organisms that compete with corals thrive better in high nutrient situations – those atypical of most oligotrophic coral reefs. However, small changes in nutrient availability have been implicated in the turn on and demise of coral reefs throughout the geological history of reefs (Hallock and Schlager 1986; Wood 1993). Paleoproductivity is a difficult parameter to measure in fossil sequences and its detection in fossil reefs has met with only limited success (Edinger and Risk 1996).

### 4 Biotic Interactions

Coral reefs are renowned for their biodiversity as well as the numerous vertical and horizontal links that characterize that

biodiversity. These processes include predation, competition, herbivory, and commensalism and can be traced back through the fossil record, providing important information on the evolutionary ecology of the reef ecosystem. Symbiosis is almost a defining characteristic of tropical reef communities. It almost certainly has been so for much of the geological history of the modern scleractinian reef-building corals (Stanley and Swart 1995; Muscatine et al. 2005). Despite the increased interest in corals as “holobionts,” we have very little evidence of nonalgal symbiosis (endolithic algae and fungi, Bacteria, Archaea, and viruses) (Wegley et al. 2007) in the fossil record of coral reef organisms. Commensalism is also an age-old occurrence in corals, with first evidence between Tabulate corals and endosymbiont trace fossils in the Ordovician Period (490–443 mya) (Tapanila 2004).

The origins of herbivory and history of grazing in marine fishes was derived from analyses of functional morphospace (Bellwood 2003). The Cenozoic witnessed the appearance and proliferation of herbivory and grazing by marine fishes – opening the door for radical modification of benthic marine communities.

Competition among Pleistocene corals from the *Montastraea* “*annularis*” species group resulted in competitive release when one of the species went extinct (Pandolfi et al. 2002). *Montastraea nancyi* (Pandolfi 2007), with an organ-pipe growth form, dominated leeward shallow water habitats from the Caribbean Sea. It became extinct sometime between 82 and 3 ka (thousand years ago) (Pandolfi et al. 2001); in modern reefs, columnar *M. annularis* s.s. is dominant over other species in the complex in shallow water, whereas it was subordinate to *M. nancyi* prior to the latter’s demise. Ecological release resulted in the dominance of *M. annularis* and a decrease in the diameter of its columns – toward the ecology and morphology of its extinct counterpart.

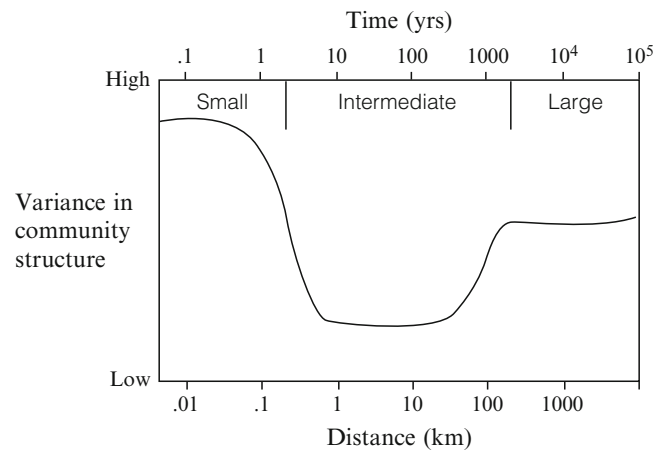
Detecting the influences of density dependence on processes in the marine realm is very difficult in the fossil record, first and foremost because population size is never really known. However, there are still clear instances of shifts in dominance of reef frame builders in the geologic past. One of the classic instances involved the alternation in dominance between the scleractinian corals and the rudist bivalves in the Cretaceous Period. Some workers believe that corals and rudist bivalves were locked in a competitive battle for dominance on Cretaceous reefs (Kauffman and Johnson 1988), but other authors refute that claim and interpret distributional trends on the basis of differential response to environmental change (Ross and Skelton 1993). Regardless, post-Cretaceous reefs were again dominated by the scleractinian corals, as the rudists never recovered from the Cretaceous–Tertiary (K–T) extinction event.



## 5 Paleo Community Ecology

Much of our knowledge about the long-term ecological dynamics of modern corals comes from studies of their counterparts in the Quaternary fossil record, that is the past two million years of Earth history. One of the most important questions in ecology is: how are species, and hence biodiversity, maintained in ecological communities? This question has always been elusive, at least in part because so much of ecology is confined to studies of living species at limited temporal scales. Recent studies of the paleoecology of corals use the recent past history (hundreds to hundreds of thousands of years) of living species to investigate ecological dynamics over meaningful time periods, to “re-run the tape” (Savage et al. 2000) for community assembly. Contrary to many shorter-term studies, which have evoked relative chaos in the community structure of living corals, persistence appears to characterize Pleistocene reef corals from both the Indo-Pacific (Pandolfi 1996, 1999) and the Caribbean (Pandolfi and Jackson 2006). Evidence for stability in coral community composition over broad time scales has also been found in both the older Pleistocene development of the Great Barrier Reef (Webster and Davies 2003) and the Caribbean (Klaus and Budd 2003), and the younger Holocene deposits of Belize and Panamá (Aronson and Precht 1997; Aronson et al. 2004). These results challenge conventional ecological views of coral reefs (derived mainly from studies at restricted spatial and temporal scales) as mainly disturbance-influenced ecosystems that contain species that are ephemeral in space and time (summarized in Karlson 2002). In fact, temporal persistence in community structure has been detected in a number of ecosystems throughout many intervals of geological time (DiMichele et al. 2004). Studies conducted on small spatial and temporal scales show the greatest degrees of variability in coral composition and those completed at the largest scales within biogeographic provinces show intermediate variance (Pandolfi 2002). However, studies conducted at intermediate spatial and temporal scales show high degrees of order in coral composition (Fig. 1) (Pandolfi 2002).

In the study of Pleistocene coral assemblages from the Huon Peninsula in Papua New Guinea (Pandolfi 1996), differences in reef coral community composition during successive high stands of sea level were greater among sites of the same age than among reefs of different ages, even though global changes in sea level, atmospheric CO<sub>2</sub> concentration, tropical benthic habitat area, and temperature varied at each high sea-level stand (Pandolfi 1999). One question this study raises is what communities might have looked like during low sea-level stands. Were they the same and so faunal persistence merely reflects “habitat tracking” (*sensu* Brett et al. 2007): “lateral migration of species or biofacies in response



**Fig. 1** Three-phase model for variability in coral community structure with respect to spatial and temporal scale of study. Studies conducted on small spatial and temporal scales show the greatest degrees of variability in coral composition and those completed at the largest scales within biogeographic provinces show intermediate variance. However, studies conducted at intermediate spatial and temporal scales show high degrees of order in coral composition (From Pandolfi 2002)

to shifting environments” p. 231) or were they different and the recurrent high-stand communities represent multiple niche assembly of similar communities? Tager et al. (2010) investigated this problem and showed that not only were low-stand communities distinct in coral species composition from their high-stand counterparts, but that successive low-stand coral assemblages, in contrast to the high-stand assemblages, showed directional change in coral community composition through time. Thus, it appears that simple habitat tracking does not provide a reasonable explanation for the ecological processes involved in sustaining similar ecological communities over successive intervals of re-assembly of high-stand reefs.

Perhaps, one of the most significant advances of the past 50 years of ecological research has been our ability to formulate null models to help explain species distribution patterns (Gotelli and Graves 1996). One of the most influential of these has been the formulation of the Unified Theory of Biodiversity and Biogeography (Hubbell 1997, 2001), which predicts species abundance distribution using a small number of demographic variables. While simulations over time characterize tests of the theory, there are still relatively few studies that utilize the fossil record (Olszewski and Erwin 2004; McGill et al. 2005). Earlier studies of fossil corals (Pandolfi 1996, 1999) informed the theory to accommodate high levels of similarity in community structure through time [see (Chave 2004) for discussion of neutral theory maturation and fossil corals].

Niche theory has also been discussed in the context of the ecology of ancient reefs. Watkins (2000) interpreted patterns in morphology related to feeding (corallite size and spacing)

in associations of Silurian (425 mya) tabulate corals as niche-partitioning, which was also used to explain the ecological dynamics of Pleistocene scleractinian corals (Pandolfi et al. 2002).

## 6 Global Change: Environmental Influences on Species Distribution Patterns

### 6.1 Reef Growth and Global Change

Some of the physical changes that are projected to occur in the coming century (Solomon et al. 2007) have occurred repeatedly throughout both the past two million years of the Quaternary period and in the more distant past (e.g. sea-level and temperature rise), while others have not (e.g. rates of CO<sub>2</sub> rise) (Pandolfi and Greenstein 2007). Reef coral communities in the distant past rebounded from decimation by climatic events that affected the global marine biota. Recovery intervals varied from 4 to 100 my, during which time framework building organisms were largely absent from reef ecosystems (Newell 1971). More recently, Quaternary coral reef development either proceeded undeterred throughout climatic changes or recovered so quickly as to leave no record of their demise (Pandolfi et al. 2006; Pandolfi and Greenstein 2007). One major difference between Quaternary reefs and those confronting climate changes in the coming decades is that today's reefs have been preconditioned by human impacts such that the frequency of anthropogenic disturbance might have decreased their resilience to perturbations (Hughes et al. 2003; Pandolfi et al. 2006). Another is that the rates and magnitude of CO<sub>2</sub> concentration change appear to be unprecedented over millions of years.

### 6.2 Range Expansions/Contractions

One of the most critical challenges facing ecologists today is to understand the changing geographic distribution of species in response to current and predicted global warming. Range movements in living coral communities have begun to be documented (Marsh 1993; Vargas-Angel et al. 2003; Precht and Aronson 2004). However, it is not yet clear whether such shifts represent ephemeral or more permanent change. The fossil record can be used to assess the effect of climate change on coral communities over a temporal scale unavailable to studies conducted solely on modern communities, to determine how labile reef coral species are in the face of sustained changes in climate.

Recent work in coastal Western Australia has provided preliminary data on how such range movements might affect the long-term ecological dynamics of coral reef ecosystems. Pleistocene coral reefs were established throughout the length of the Western Australia coastline for several reasons. First, sea-surface temperatures were at least 2°C warmer than today (Kendrick et al. 1991). Second, the Leeuwin Current, which bathes the coast of Western Australia with warm, relatively low salinity water derived from the western central Pacific via the Indonesian throughflow, was present and may have been more intense as a result of the southward migration of the west wind drift and subtropical convergence during Late Pleistocene time (Kendrick et al. 1991; McGowran et al. 1997; Li et al. 1999). Wells and Wells (1994) used transfer functions derived from planktic foraminifera to show that the Leeuwin Current was intensified during the last interglacial maximum (Marine Isotopic Substage 5e). Third, higher sea levels pushed warmer water down from the Indonesian throughflow facilitating the extension of the warm-water Leeuwin Current along the western Australia coastline. Hence, the gradient in community composition of Late Pleistocene reef corals exposed along the west Australian coast was not as strong as now occurs in adjacent modern reef coral communities, which show a pronounced gradient in coral composition over their latitudinal range (Greenstein and Pandolfi 2008).

Comparison of reef coral community composition between adjacent modern and fossil reefs along 10° of this environmental gradient revealed that coral taxa expanded their latitudinal ranges during warmer Late Pleistocene time compared with today. Tropical-adapted taxa contracted their ranges north since Late Pleistocene time as temperatures cooled, emplacing two biogeographic provinces in a region in which a single province had existed previously. Beta diversity values for adjacent communities also reflect this change. Modern reefs show a distinct peak in beta diversity in the middle of the region; the peak is not matched by Pleistocene reefs. Beta diversity is correlated with distance only for comparisons between modern reefs in the north and the fossil assemblages, further supporting change in distribution of the biogeographic provinces in the study area. Coral taxa present in modern communities clearly expanded and contracted their geographic ranges in response to climate change during the Pleistocene.

One interpretation from this work is that those taxa that distinguish Pleistocene from modern reefs are predicted to migrate south in response to future climate change, and potentially persist in "temperature refugia" as tropical reef communities farther north decline. However, sea-level changes and ocean acidification as well as anthropogenic impacts on habitat degradation need to be incorporated into such predictions.

## 7 Diversity Through Time: Evolutionary Ecology and Biotic Turnover

The analysis of taxonomic abundance data embedded within a detailed and precise environmental context is enabling paleontologists to rigorously explore the dynamics and underlying processes of ecological and evolutionary change in deep time (Klaus and Budd 2003; Jackson and Erwin 2006). To ensure success, paleontologists now work with other geologists to obtain extensive new collections of fossils tied to detailed and independent records of stratigraphic correlation and changes in climate, oceanography, tectonic events, and other aspects of the physical–chemical environment. Analysis of the history of diversity and evolutionary turnover of fossil corals provides context for understanding both the present standing diversity of modern corals and the rates and magnitudes of any future changes in coral diversity.

### 7.1 Cenozoic Patterns

Perhaps one of the best examples of the insights gained through such interdisciplinary synergy is the response of tropical marine communities to the oceanographic events associated with the rise of the Isthmus of Panama three to five million years ago (Jackson and Johnson 2001; O’Dea et al. 2007). Here, extinction occurred one to two million years after the environmental event, while the collapse of coastal upwelling and primary productivity corresponded with an upsurge in carbonate production in the tropical western Atlantic (Collins et al. 1996). Knowledge of the environmental events and corresponding development of tropical marine ecosystems in the Indo-West Pacific (IWP) is embryonic when compared with the detailed view of tropical ecosystem development for the Caribbean and the eastern Pacific (Jackson et al. 1996). However, the rise of the modern IWP biota is thought to have occurred in the critical interval spanning the transition from the Late Oligocene to the Early Miocene (Wilson 2002) during large fluctuations in global ice volume (Zachos et al. 2001), regional changes in tectonics, and major shifts in the genesis of carbonate build-ups. It has also been proposed (Renema et al. 2008; Williams and Duda 2008) that increased basin complexity, driven by tectonics, resulted in increased habitat availability and heterogeneity in tropical Neogene faunas, driving higher species origination rates. The unraveling of the interplay between biotic turnover, ecological change, and environmental history is fundamental to understanding the likely ecological response of modern tropical marine biotas to predicted global change.

Paleoecological insights into the timing and antiquity of modern-day biodiversity can also feed into genetic studies and conservation strategies. Many genetic studies on modern-day corals and other tropical marine organisms have focused on Pleistocene sea-level changes as speciation “pumps.” However, new data from a number of recent molecular studies, as well as calibration curves and new fossil finds are revealing that Indo-Pacific marine diversity is much older, commonly extending millions of years into the geological past (Renema et al. 2008; Williams and Duda 2008).

Finally, investigations into the relationship between reef growth and biodiversity through time highlight the capacity for coral reefs to engage in reef growth as biodiversity loss occurs at local and regional scales on living coral reefs (Johnson et al. 2008). Modern ecologists can only speculate on the relationship between coral biodiversity and potential for reef growth. In fact, rates of reef growth are broadly similar among regions where coral diversity may vary up to ten-fold (Montaggioni 2005), leading to the question of just how important diversity might be for reef development. Johnson et al. (2008) found that reef development did not correlate with coral diversity within the tropical western Atlantic over the past 28 my. Moreover, the largest reef tracts formed after extinction had reduced diversity by as much as 50%. Similar to the spatial patterns found on many modern reefs (Riegl 2001), these temporal patterns suggest that high coral diversity is not essential for the growth and persistence of coral reefs (see review in Kiessling 2009).

### 7.2 Deep Time

A complement to the specimen-based and genetic studies noted above are a considerable number of studies that have tracked the biodiversity of corals through various intervals of deep time, including the 540 my of the Phanerozoic Eon (summarized in Kiessling 2009). A significant number of challenges face coral paleontologists in estimating broad patterns of global diversity through time. Besides taxonomic uncertainties, there are mineralogical differences among the three major coral groups (Rugosa, Tabulata, Scleractinia). However, even though chemical alteration occurs frequently, especially within the scleractinian corals, who build their skeletons from the unstable aragonite, corals form a major group of fossilized organisms throughout the history of life. There is little evidence to suggest that the diversity of Paleozoic rugose and tabulate corals, which likely built their skeletons from calcite, was preferentially enriched by skeletal mineralogy in relation to their Mesozoic and Cenozoic scleractinian counterparts. Challenges for future work

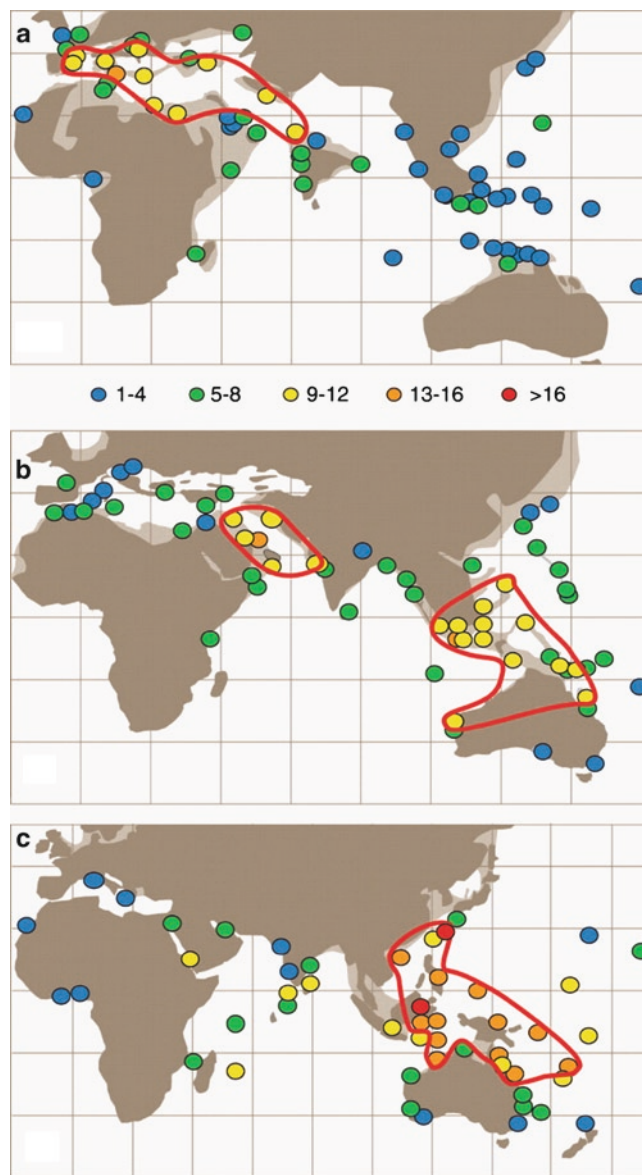
include quantifying patterns of biotic change in carefully dated and correlated stratigraphic sections in the context of multiscaled environmental change in order to test whether patterns of faunal turnover are random or clumped in time, and whether they correlate with tectonic or climatic events.

## 8 The History of Modern Biogeographic Patterns

Through study of the fossil record of the major carbonate-producing organisms, the biogeographic dynamics of reefs and their constituent organisms can be understood. For example, Miocene (24–5 mya) to Pleistocene (last 2 mya) interchange of molluscan species between biogeographic provinces in the subtropical equatorial Atlantic resulted in the enrichment of the regional and global species pool and the spread of adaptations reflecting intense competition and predation (Vermeij 2005).

Unlocking the history of modern geographic patterns of biodiversity relies on two fundamental data sets – the fossil record and molecular phylogeography. These data sets often appear in conflict, but recent work in the Indo-Australian Archipelago (IAA) has shown remarkable congruence that indicates a series of marine biodiversity “hotspots” in different places over the past 50 my (Fig. 2) (Renema et al. 2008). These “hopping hotspots” have a birth, life, and death that is closely tied to regional (tectonic) and global (paleoclimatic) environmental variation. Data were derived from alpha-diversity expressed in the fossil record of corals, large benthic foraminifera, mangroves, and molluscs, and from molecular studies of fish and molluscs. These combined paleontological/molecular data sets show that the modern biodiversity hotspot found in the present Indo-Australian Archipelago is not so much unique in its biodiversity as its present position (see also Harzhauser et al. 2007). The movement of the Earth’s tectonic plates is strongly associated with hotspot history (Renema et al. 2008). Understanding the history of biodiversity hotspots informs us that there always have been, and probably always will be, hotspots; it is vital to understand why they form, what drives them, and how they maintain their integrity. For this, our only recourse is the fossil record.

One of the major controversies surrounding Indo-Pacific coral biodiversity hotspots has concerned the mechanism by which they are formed – in situ as a “center-of-origin” (e.g. Briggs 2003), as a “museum” where species accumulate (Jablonski et al. 2006), and how they arrive – rafting (Jokiel 1984), and the role of dispersal and vicariance (Pandolfi 1992); see Rosen (1988) for an earlier review. All of these theories and mechanisms can be informed through a richer understanding of the Indo-Pacific fossil record, and



**Fig. 2** Generic (alpha)-diversity of large benthic foraminifera in (a) the late Middle Eocene (42–39 ma), (b) the Early Miocene (23–16 ma), and (c) the Recent. Solid lines delimit the West Tethys, Arabian, and IAA biodiversity hotspots. Note the relocation of hotspots across the globe (From Renema et al. 2008)

future research in this area should prove to be especially insightful.

## 9 Reef Paleoeology, Historical Ecology, and Conservation Biology

The diversity, frequency, and scale of human impacts on coral reefs are increasing to the extent that reefs are threatened



globally (Wilkinson 2008). Until recently, the direct and indirect effects of overfishing and pollution from agriculture and land development have been the major drivers of massive and accelerating decreases in abundance of coral reef species (Moberg and Folke 1999; Abram et al. 2001; Jackson et al. 2001; Gardner et al. 2003; Hughes et al. 2003; Pandolfi et al. 2003). These human impacts and the increased fragmentation of coral reef habitat are unprecedented and have the possibility to undermine reef resilience (Bellwood et al. 2004), raising the likelihood that modern coral reefs might be much more susceptible to current and future climate change than is suggested by their geologic history (Hughes et al. 2003; Bellwood et al. 2004).

One of the many pressing issues in conservation science is what was natural in the world before humans impacted it. By combining ecologists, oceanographers, archeologists, and social scientists, it has been possible to document global-scale changes in the sea (Jackson et al. 2001). The work documents in broad terms the history of human alterations in the sea, identifying overfishing as the first and farthest-reaching anthropogenic cause of decline in coastal marine ecosystems.

Very recent work has sought to understand human impacts by developing time-series data archives that can be used to evaluate trends in the global decline of coral reefs since the arrival of humans (Pandolfi et al. 2003). The approach has been to use a number of different kinds of data during several time periods to examine the recent past history and present condition of coral reefs to provide a natural baseline for community ecology and coral growth rates. Archeological sites provide insight into the relationship between the development of civilization and its evolving impact on coastal marine resources over thousands of years. Historical records such as those found in ships logs, and publications of early naturalists and European colonialists provide a moving window of the natural history and inferred ecology of many coral reef inhabitants over a centennial time scale. Fisheries records and modern ecological surveys can be used in association with remote sensing data (going back the last 20 or 30 years) to provide a detailed picture of changing environments and biodiversity as human population and consumption, as well as economic globalization, have accelerated during the past several decades. Taken together, these databases provide a holistic view of changing environments and ecology on coral reefs that includes the onset of human disturbances and against which the acquisition of present-day data can be evaluated.

Study of the historical ecology of coral reefs, relying on the past history of corals and other components of the reef ecosystem documented the history of ecosystem change among tropical reef sites worldwide (Pandolfi et al. 2003, 2005). These findings showed the importance of

pre-industrial factors to reef health, and point to the immense importance of understanding historical events when attempting to tease out factors that have or may influence present coral reef biodiversity (Pandolfi et al. 2003). At 14 sites worldwide, early and effective overfishing appears to have been the major culprit in reef decline (Pandolfi et al. 2003). By considering these global “ecological trajectories” in the light of potential responses to projected global climate change, the history of human exploitation can be linked with global environmental parameters (Hughes et al. 2003). Knowledge of past ecosystem states provides at the minimum an understanding of what was natural and may even aid in assessing the success of management toward particular conservation goals.

An understanding of the history of reef coral communities can aid conservation initiatives by supplying information on natural baselines in the sea that are immune to the “shifting baseline syndrome” (Pauly 1995), where each new generation defines what it perceives to be “natural” or “pristine.” For example, in Barbados, coral community composition was very similar during four separate reef-building episodes between 220 and 104 ka (Pandolfi and Jackson 2006), and community structure is now very different in modern degraded habitats (Lewis 1984; Tomascik and Sander 1987). Similar results have been obtained from sedimentary cores from Belize and Panamá, where recently observed declines in the abundance of *Acropora* show no historical precedence (Aronson and Precht 1997; Aronson et al. 2004), and from coral death assemblages along the Florida reef tract (Greenstein et al. 1998) and the nearshore Great Barrier Reef (Perry et al. 2008; Roff 2010). Perspectives on baselines that do not include this longer-term data will be shifted to degraded habitats.

## 10 Proxies for Environmental Change

Corals and other reef inhabitants have long been studied as proxies for environmental change in earth history. Early work (Wells 1963; Runcorn 1966) uncovered a way to determine that the number of days in the year decreased through the Phanerozoic (review in Hughes 1985). More recent work has attempted to correlate skeletal trace element and isotopic composition to ambient seawater. Such variables as sea-surface temperatures, salinity, turbidity, and even paleo pH (Hönisch et al. 2004) are currently being ascertained to reconstruct the environmental history of both nearshore and oceanic coral reefs. And to document changing physical environments, coring of reef corals provides a proxy for sea-surface temperatures, rainfall, and river discharge (McCulloch et al. 2003) from the geological past to the present. These

studies have been extended back into the Quaternary, with work completed on both Pleistocene (Tudhope et al. 2001) and Holocene (Gagan et al. 1998) reef corals.

## 11 Summary

Coral reefs have a rich and illustrious history, going back to hundreds of millions of years. Living coral reefs have ancient counterparts that provide an almost continuous time series on scales ranging from millions to hundreds of years ago. Thus, the history of coral reefs can be reconstructed by examination of their skeletal remains and sedimentary record. Study of these deposits is the purview of coral reef paleoecology and much information has been gained, information that can be readily applied to a host of biological (and geological) problems and issues. Paleoecological study of coral reefs has informed modern ecology, environmental science, conservation biology, and climate change. In this chapter, we explore the rich history of contemporary coral reefs by summarizing the major paleoecological approaches applied to understanding patterns and processes over multiple time scales. Coral reef paleoecology is a vast and vibrant field with applications to a variety of natural history, evolutionary, ecological, environmental, and conservation fields. A comprehensive review could follow each of the major subjects I cover here, but this chapter is intended to provide a flavor for what has been and can be done in the paleoecological study of fossil coral reefs.

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