

When Biotas Meet: Understanding Biotic Interchange

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When the barrier between biotas with long separate histories breaks down, species invade from one biota to the other. Studies of episodes of marine and terrestrial biotic interchange that have occurred during the last 20 million years show that large-scale extinction of species before the onset of interchange renders biotas especially prone to invasion. As environments and species are being exploited and eliminated on an ever increasing scale in the human-dominated biosphere, the geographical expansion of species from biotas in which evolution of high competitive, defensive, and reproductive abilities has proceeded the furthest will become more frequent. Historical events and interactions are essential ingredients for understanding the current and future structure and composition of the world's biota.

THE GEOGRAPHICAL LIMITS OF SPECIES AND BIOTAS ARE SET by physical and biological barriers. The position and effectiveness of these barriers vary through time as climates change and as tectonic upheavals in the earth's crust alter the configuration of water bodies and land masses. If a barrier separating two biotas with long independent histories breaks down, species may invade from one biota (donor biota) to the other (recipient biota). This biotic interchange has occurred frequently during the Neogene period, the last 25 million years of earth history. In the human-dominated biosphere, barriers are being breached on an unprecedented scale. Not only are species being transported piecemeal through human commerce around the world, either deliberately or by accidental introduction (1), but humans are bringing about wholesale biotic interchange by creating avenues of dispersal in the place of former barriers. Construction of the Suez Canal has enabled hundreds of marine species to enter the Mediterranean from the Red Sea since 1869 (2). Large numbers of estuarine and nearshore species from Japan are being established on the western coast of North America thanks to the transport of larvae in huge volumes of ballast water in ships (3). The potential for extensive interchange exists in tropical America as well. Only a few marine plants and animals have crossed between the eastern Pacific and western Atlantic oceans through the freshwater Panama Canal (4–6), but construction of a sea-level canal across the Central American isthmus or the augmentation of the present canal's freshwater supply with seawater would re-establish a marine connection between the rich biotas of western and eastern

tropical America, a connection that was interrupted by the emergence of a land bridge during the Pliocene about 3.1 million years ago (5, 7).

Besides providing the foundation for predicting the pattern and consequences of invasions still to come, studies of past episodes of biotic interchange have an important bearing on several basic questions in ecology and evolutionary biology. They enable us to investigate how new species are accommodated in existing biotas, what factors determine the geographical ranges of species, whether species (including invaders) are important as agents of extinction, whether biotas are saturated with species, how selective regimes are altered by new arrivals, and whether such changes stimulate or are accompanied by speciation.

Documentation of range expansion of species from one biota to another rests on historical evidence. A species may be recognized as a participant in biotic interchange if it occurred as a fossil in the donor biota before it appeared in the recipient biota, or if there is cladistic evidence that it descended from ancestors in the donor biota. Because of their good fossil record, mammals and molluscs have figured prominently in studies of biotic interchange. Advances in taxonomy, phylogenetic reconstruction, and biogeography of these and other groups, together with refinements in stratigraphic correlation, are revealing details of many episodes of biotic interchange. Although much remains to be learned, empirical and theoretical studies are yielding several principles of historical ecology. I shall elaborate on these in the context of Neogene biotic interchanges.

Biotic Interchange During the Neogene

Climatic changes and geographical rearrangements have made the Neogene a time of extensive biotic interchange (Fig. 1). Interruption of the Tethys seaway across the Middle East during the late early Miocene (18 million years ago) led to interchange between the land biotas of Asia and Africa (8, 9). Northward movement of the plate carrying Australia and New Guinea brought the isolated land biota of those two continental islands into contact with the rich biota of southeast Asia (10–12). The Pliocene epoch witnessed the completion of the Central American land bridge, accelerating the great American interchange between the land biotas of North and South America that had begun during the late Miocene (13–16). The middle Pliocene opening of the Bering Strait between Asia and North America initiated the trans-Arctic interchange between the cold-water marine biotas of the North Pacific and Arctic-Atlantic basins (17, 18). Intensifying oceanic circulation associated with these changes in geography (19) led to interchange between the temperate marine biotas of the Northern and Southern hemispheres in the eastern Pacific (20, 21) and, to a lesser extent, between the marine biotas of the temperate eastern and western Atlantic (18).

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Interchange by long-distance larval dispersal between the western and eastern tropical Pacific began in the Pleistocene, perhaps as the result of the northward motion of the Line Islands into the path of the eastward-flowing North Equatorial Countercurrent in the central Pacific (22). Circum-Antarctic currents associated with the West-Wind Drift resulted in interchange among the cold-water marine biotas of the Southern Hemisphere. Although this interchange began with the opening of Drake Passage between South America and Antarctica, it has become particularly intense during the Pleistocene or perhaps a little earlier (20, 24). Intermittent interchange has occurred during much of the Paleogene and Neogene between the land biotas of Asia and North America (25–27), between the temperate marine biotas of the western and eastern North Pacific (28, 29), and between the tropical marine biotas of the eastern and western Atlantic (30). Numerous smaller scale interchanges have occurred among biotas within Eurasia, North America, and other continents, and between river systems on many continents. These will not be considered further here.

For most interchanges, invading species make up only a small proportion of the potential pool of invaders in the donor biota. Only 2 to 11% of North American mammal genera, and 2 to 7% of their South American counterparts, took part in the great American interchange during any one land-mammal age (14). About 4.3% of Red Sea fishes overall, and 24% of sand-dwelling fishes in the northern Gulf of Aqaba, have colonized the eastern Mediterranean (2). Estimates for other groups in the trans-Suez interchange are lacking, but the proportions are not likely to differ much from those in fishes. Of approximately 250 gastropod species in the Line Islands, only 33 (13%) have invaded the offshore islands in the eastern Pacific, and 11 (4.4%) have penetrated to the Pacific coast of the American mainland (36). Among corals, the proportion of Line Islands species reaching mainland tropical America is a little higher

(11 of 70 species, 16%) (22). Species taking part in the trans-Arctic interchange account for 23 to 46% of the shallow-water molluscan species in the cool-temperate North Pacific, depending on habitat and geographical location, and less than 1% of comparable North Atlantic assemblages (18). Data for other donor biotas do not exist because estimates of the number of invading species and of the number of potential invaders in the donor assemblages are not available.

The contribution of invaders to recipient biotas varies widely. In the eastern Pacific, 100% of the corals but less than 5% of the molluscs are of western or central Pacific origin (7, 22, 36). Invaders from the Red Sea make up 9.4% to 20% of eastern Mediterranean assemblages, depending on the taxonomic group (2). Nonflying placental mammals derived from Asian ancestors make up about 41% of the mammal fauna of Australia and New Guinea (10). Slightly more than 50% of the 120 mammalian genera from the late Pleistocene (Lujanian) of South America is derived from North American ancestors (14). Gentry (16) estimates that more than 90% of the angiosperm species of lowland rain-forests in Central America (geologically part of North America) are identical to or derived from

Key

1. Terrestrial interchange between Africa and Asia
2. Terrestrial interchange, chiefly from south-east Asia to Australia and New Guinea
3. Marine interchange across the tropical Atlantic
4. Marine interchange across the North Pacific, mainly from west to east
- 5a. Great American interchange for lowland rain-forest organisms, chiefly from south to north
- 5b. Great American interchange for savanna and upland organisms, symmetrical during the Pliocene, mainly north to south subsequently
6. Transequatorial marine interchange in the eastern Pacific, mainly from north to south during the Pliocene, of unknown directionality subsequently
7. Marine trans-Arctic interchange
8. Marine interchange across the North Atlantic, mainly from east to west
9. Transequatorial marine interchange in the eastern Atlantic
10. Circum-Antarctic marine interchange
11. Marine interchange across the tropical Pacific, mainly from west to east
12. Trans-Suez interchange (Recent only)

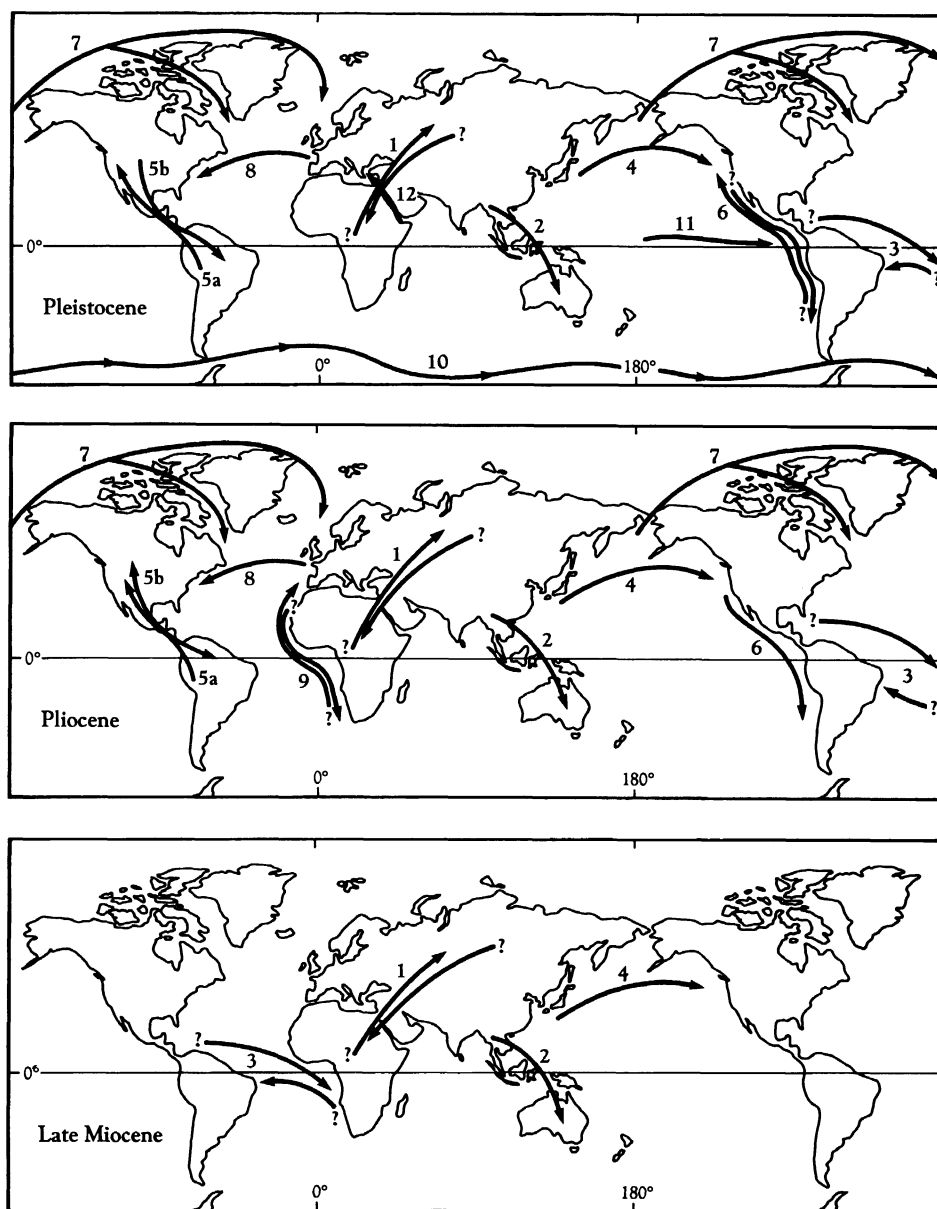


Fig. 1. World maps showing major episodes of biotic interchange during the late Miocene, Pliocene, and Pleistocene-Recent. Question marks indicate uncertainties about the directionality of interchange. Symmetrical interchange is indicated by a two-headed arrow. For asymmetrical interchanges, the predominant direction of invasion is indicated by single-headed arrows.

invaders across the Panama land bridge from South America. By contrast, the great majority of montane plant species in South America are of North American origin (16). Trans-Arctic invaders from the Pacific make up only 10% and 22% of northeastern Atlantic and northwestern Atlantic molluscan faunas, respectively, but on rocky shores in northeastern North America, invaders account for 83% of molluscan species (18).

Asymmetry of Invasion

The pattern of biotic interchange is often highly one-sided, with movement in one direction across a former barrier predominating over that in the other direction. The trans-Suez interchange, for example, has been overwhelmingly from the Red Sea to the Mediterranean. At least 91 molluscs, 15 crabs, and 41 fishes have invaded the Mediterranean from the Red Sea, as compared to only three molluscs, no crabs, and six fishes in the opposite direction (2). Invasion across the Bering Land Bridge was predominantly eastward during the Pleistocene, but apparently was even-handed during the Pliocene and earlier (25, 26, 31). The great American interchange during the Pleistocene was mainly southward for savannah-adapted mammals and montane plants (14, 16, 31). During this interval, about 11% of North American mammal genera invaded South America, whereas only 2% of South American genera extended to North America. Late Miocene and Pliocene phases were symmetrical for these mammals (14, 31). Invasion of rain-forest groups (birds, mammals, and plants) was overwhelmingly from south to north during the great American interchange (16, 31). Invasion of marine species across the central Pacific was almost entirely from west to east, there being no convincing case of invasion in the opposite direction (22, 32, 36). The Pliocene phase of the transequatorial interchange in the temperate eastern Pacific involved at least six taxa extending southward from North to South America and only two extending northward from South to North America (21). For the North Pacific, my preliminary data indicated that nine genus-level molluscan taxa invaded from North America to Asia beginning in the late Miocene, whereas 47 invaded in the opposite direction from west to east. Earlier episodes of interchange across the temperate North Pacific were probably less lopsided (29). The trans-Arctic interchange heavily favored invasion from the Pacific to the Atlantic (18, 33). Among shell-bearing molluscs, 261 species in the Arctic-Atlantic basin are of Pacific origin, whereas only 34 species in the North Pacific originated in the Atlantic (18). Other groups of invertebrates and algae show a similar pattern. Within the North Atlantic, almost 100 shell-bearing molluscan species invaded from Europe to North America during the Pleistocene, and only five (all introduced by humans) moved in the opposite direction (18). Only three marsupial mammals have extended their range beyond Australia and New Guinea to eastern Indonesia, whereas rodents and lowland tropical plants invaded and diversified extensively in the Australo-Papuan region (10, 12, 16). Other Neogene episodes of interchange have been insufficiently documented to establish quantitative estimates of the pattern of invasion. In all cases of asymmetrical interchange, the per-species probability of invasion is significantly higher for one donor than for the other (2, 14, 18, 22, 31).

Passive transport by unidirectional currents may contribute to the explanation for asymmetrical interchange through the Suez Canal (2) and across the tropical Pacific (21), but fails as an explanation for most marine interchanges and for all terrestrial cases (17). Even in the tropical Pacific, passive transport could in principle occur westward by the North and South Equatorial Currents, just as it does in the tropical Atlantic, but all Pacific invasions are eastward via the North Equatorial Countercurrent (22, 32, 36).

Asymmetrical patterns of interchange have often been taken to imply that species in the biota providing most of the invaders are, on average, superior in competition, defense, or reproduction to species in the biota receiving the bulk of the invaders (7, 25, 32–34). The great success of placental mammals of Asian origin in Australia as compared to the limited penetration of marsupials and monotremes of Australian origin into East Indian faunas is correlated with the generally lower metabolic rates and lower life-time fecundities of the indigenous Australian mammals (12). In South America, native predaceous marsupials may have been competitively replaced by invading North American carnivores, and some of the extinctions among native ungulates and other mammals may have been the work of North American predators, which are thought to have been faster and more powerful than their South American counterparts (35).

Whether biological superiority in fact played a decisive role in these asymmetrical interchanges remains a matter of conjecture. The first step in demonstrating this role is to show that the incidence or expression of traits correlated with high competitive, defensive, or reproductive performance is greater among invaders than among ecologically comparable native species in the recipient biota. Such indirect evidence is available for the shell armor of molluscs taking part in the asymmetrical interchanges through the Suez Canal and across the tropical Pacific (7, 36). This does not, of course, prove that the interactions among species affect the success of invasion, nor does it follow that invaders are the best protected, the most fecund, or the most adept competitors among the potential invaders in the donor biota (7).

The strongest evidence for the role of organisms in controlling the pattern of interchange comes from invasions of oceanic islands and non-Eurasian grasslands by human-introduced species. Island biotas and the grassland biotas of South America, Australia, and parts of western North America contain species that are highly susceptible to herbivory, predation, and disease resulting from the introduction of continental species, especially warm-blooded birds and mammals (37–39). It is possible that the diseases carried by invading plants and especially by vertebrates provide the most potent mechanism for the competitive success of invaders in these and other recipient biotas (37). Species evolving in diverse continental and marine biotas may carry, and be adapted to, a larger array of pathogens and parasites than species from biologically less “sophisticated” assemblages.

That levels of adaptation to enemies are not alone in controlling patterns of invasion is demonstrated by the great rarity of interchanges between tropical and temperate marine biotas. Enemy-related adaptation is generally more common and better expressed in tropical species than in allied temperate ones (7). If this difference were decisive as a determinant of susceptibility to invasion, temperate biotas would be highly susceptible at all times to invasion from the tropics. Although such invasions can be documented for the Paleogene and perhaps the earliest Neogene, when the cold climates of the present northern oceans gradually developed (29), there is little evidence of subsequent invasion of temperate marine biotas by tropical taxa. Similarly, there are few if any well-documented instances of temperate to tropical invasion during the Neogene. These points are well illustrated by the late Neogene transequatorial interchange in the eastern Pacific (20, 21), which involved mostly warm-temperate marine species that traversed the intervening tropics.

The magnitude of extinction before the onset of interchange also strongly affects a biota's susceptibility to invasion. The Indo-West Pacific biota, which serves as the source for most or all of the species participating in the interchange across the tropical Pacific, lost few or no molluscan and coral genera during the Pliocene, before interchange began, whereas the tropical eastern Pacific biota, which was at the receiving end of the invasion, suffered extinction of most of its corals and about 15% of Pliocene molluscan subgenera (22, 40). The generally southward invasion of marine species during the Pliocene

phase of the transequatorial interchange is consistent with the fact that the temperate fauna of the southeastern Pacific suffered more extinction than did that of the northeastern Pacific near the end of the Miocene (21). Within the North Pacific, the predominantly eastward invasion of temperate molluscs from Asia to North America is correlated with higher late Miocene and Pliocene magnitudes of extinction on the North American side. The trans-Arctic interchange provides another good example. Invaders from the Atlantic make up less than 4% of the molluscan faunas in the North Pacific, where the magnitude of species-level extinction since the early Pliocene was 20% to 40%, whereas in the northeastern and northwestern Atlantic, invaders from several biotas make up 21% and 36% of the living faunas, respectively, and extinction affected 50% and about 75% of species, respectively, since the early Pliocene (17, 40). The trans-Suez interchange also exemplifies invasion from an area in which few taxa became extinct to one in which major faunistic losses have occurred episodically since latest Miocene time (2). Data on mammal genera (14) show that asymmetrical invasion from North to South America during the Pleistocene is linked to higher rates of extinction of South American as compared to North American mammals during the preceding Pliocene epoch. Too little is known about the history of extinction and the extent of invasion to evaluate the role of prior impoverishment in other episodes of biotic interchange.

These results have several implications for biogeography. First, the resistance of biotas to invasion is reduced by prior extinction of species in that biota. The presence of incumbent species in the recipient biota evidently inhibits the establishment of invaders (41, 42), even if potential invaders occasionally disperse into that biota. This may be the biogeographical equivalent of the well-documented ecological phenomenon that undisturbed communities of competitive dominants resist recruitment of other species, which typically require newly opened space to gain a foothold (43).

A related point is that the limits of geographical range of species are set not only by topographic features and climate barriers, but to an important degree also by other species. This conclusion is supported by Hallam's (44) observation that Tethyan ammonoids did not penetrate the Boreal realm during several epochs of the Jurassic until native Boreal species had disappeared, by Geist's (45) contention that the southward penetration of Asian mammals into western North America during the Pleistocene took place mainly after many native mammals had become extinct, and by the interpretation that the establishment and expansion of European freshwater fishes in the American Great Lakes and of European birds in New Zealand were facilitated by human-caused disturbance and impoverishment of the native recipient biotas (46). As environments around the world are being disturbed and as species are being exploited and eliminated on an ever increasing scale, this phenomenon of geographical release is likely to become more common.

These empirical conclusions are broadly in accord with predictions from theoretical models of communities in which competition is the most important interaction among species (47). According to these models, communities that should be most difficult to invade are those in which interactions among species are strong and in which the number of species is large. These conditions are evidently met in biotas in which the evolution of enemy-related traits has been little affected by extinction and in which circumstances were favorable to diversification and the evolution of high biological performance.

Invasion, Extinction, and Saturation

If asymmetrical patterns of interchange result in part from differences between biotas in the average biological performance of species, the arrival of invaders in the biologically less sophisticated

biota might lead to the extinction of many native species (48). This has indeed been commonly observed when continental invaders (especially predators) colonize lakes and oceanic islands (39, 49). Invasion-induced extinction has also been claimed for some South American mammals during the great American interchange (35) and for North American multituberculate and plesiadapiform mammals following the Eocene invasion of rodents from Asia (50). Human-caused introductions usually result in the ecological restriction of active continental and marine species (51) or even in the provision of new resources (52). The reduction in population size associated with invasion-induced ecological restriction might render species more prone to extinction from causes unrelated to invasion, but such an effect would be indirect. No invasion-related extinctions have been documented in studies of the marine trans-Suez, transequatorial, trans-Arctic, or trans-Pacific interchanges (18, 21, 22, 41), or in Asian mammal faunas following invasion by species from Africa and North America (9, 27). Sometimes, new arrivals even provide new resources or enhance existing ones, as in the case of the introduction of nitrogen-fixing trees in Hawaii, European *Littorina littorea* shells for northwestern Atlantic hermit crabs, and Asian eelgrass (*Zostera japonica*) on the tidal flats of the northeastern Pacific (52).

A major open question in ecology is whether living biotas and communities are saturated with species. Can a given community support more species than are actually found there, or would the addition of species be counterbalanced by extinctions? The fact that biotas in which there was little prior extinction have been largely unaffected by invasion may mean that these "intact" biotas are close to saturation. On the other hand, it may imply only that none of the species in the available pool of potential invaders happens to "fit in" to the recipient biota. Moreover, invasion usually results in the enrichment of biotas of continents and oceans. In some biotas, such as the mammal faunas of South America and Asia, interchange has pushed diversity to levels higher than the pre-extinction number of species (9, 13, 27). Most extinctions that result from invasions in continental biotas affect, or are caused by, species with high per capita energy requirements, especially endothermic vertebrates. Evidence from biotic interchange therefore supports the view (53) that saturation is more likely to apply to species with high metabolic requirements than to most assemblages of plants, invertebrates, and ectothermic vertebrates.

A Sea-Level Panama Canal

What kind of biotic interchange would occur if a saltwater connection were re-established between the Pacific and Atlantic oceans across the Central American isthmus? The marine biotas on opposite sides of the isthmus differ both in the development of enemy-related traits and in their history. Eastern Pacific gastropods, especially those found on rocky bottoms, show a higher incidence and greater expression of armor, are more likely to die as a result of shell breakage, and are susceptible to crushing at larger shell sizes than are their western Atlantic counterparts (7, 54). Predation on corals and grazing of algae are more intense in the eastern Pacific than in the western Atlantic (5-7). The difference in armor came about in part because of selective extinction. In the western Atlantic, where about 32% of late Miocene and Pliocene molluscan subgenera are no longer found living, gastropods with well-armored apertures were more prone to extinction than were less specialized forms, whereas in the eastern Pacific, which has lost only 15% of molluscan subgenera since the early Pliocene, armored gastropod taxa were underrepresented among the extinct groups (40). For corals, the interoceanic difference in extinction was reversed, with nearly all eastern Pacific and less than half the Caribbean genera

disappearing from their respective basins following the uplift of the land bridge (22). Briggs (32, 55), assuming that the biotas on the two sides of the isthmus are essentially saturated with species, suggested that interchange would be largely from the Atlantic to the Pacific and would lead to many extinctions, because the fish fauna of the Atlantic is richer than that of the Pacific and because competition was thought to be more intense in richer biotas. Topp (56) argued that interchange would be relatively minor, and without strong directionality, because he assumed that neither biota had suffered much prior extinction. The data referred to above, however, imply that biotic interchange through a sea-level canal or its equivalent across Central America would be asymmetrical, with the bulk of the participants invading from the less impoverished but still biologically more sophisticated eastern Pacific to the more impoverished and less sophisticated western Atlantic. This may be true even for the corals, despite the fact that the eastern Pacific coral fauna suffered more than did the coral fauna of the Caribbean. In the eastern Pacific, the original corals present during the Neogene were replaced by species from the central Pacific, and these corals in turn invaded from a fauna of highly sophisticated corals, a fauna that was less affected by extinction than was the reef biota of the Caribbean. Glynn (5) has, moreover, warned of the likelihood that the voracious coral predator *Acanthaster planci* (the crown-of-thorns sea-star) would extend its current range in the Indo-West Pacific and eastern Pacific to the Caribbean region. If the Central American marine interchange conforms in pattern to other marine interchanges, it should result in ecological shifts but few extinctions of western Atlantic species.

Conclusions and Prospects

What little we know about biotic interchange implies that the history of extinction and the adaptational attributes of species in the affected biotas strongly influence the pattern and extent of interchange. The available evidence points to three tentative conclusions: (i) many (perhaps most) episodes of interchange are strongly asymmetrical; (ii) biotas providing the bulk of the invading species in asymmetrical interchanges contain species that have evolved high competitive, defensive, and reproductive performance in comparison with native species in the recipient biotas; and (iii) biotas in which the magnitude of extinction before the onset of interchange was high are especially vulnerable to invasion.

An interesting but unexplored possibility is that the greater than average susceptibility of species of high biological performance to extinction provides exceptional opportunities for invaders with similar qualities. To test this idea further will require information on selectivity of extinction and of subsequent invasion.

Ecologists traditionally emphasize energy flow, competition, predation, symbiosis, and recruitment in their attempts to understand how communities of species function and what factors regulate the distribution of species. It is clear, however, that history provides an additional critical element that has been poorly integrated into most studies of living communities and into predictions about the ecology of the future. Unfortunately, most of the available historical data come from only a few groups of organisms. Not only will it be important to extend the historical perspective to other components of the living biota, but we must be cautious about applying the results for one group to other groups. The differences in the extinction and invasion histories of molluscs and corals in tropical America illustrate this point well. In particular, interchanges showing asymmetry in one group may be more even-handed or even reversed in pattern for others, and the pattern and extent of interchange may vary widely according to habitat.

Studies of biotic interchange can also be rich sources for evolutionary biologists. If the time of arrival of an invading lineage can be pinpointed, invaders can serve as good models for the study of speciation and of changes in selective regimes. With invasion sure to play an increasingly important role in the ecology of the biosphere, a better understanding of the pattern and evolutionary consequences of biotic interchange is both theoretically interesting and practically useful.

REFERENCES AND NOTES

1. C. Elton, *The Ecology of Invasions by Animals and Plants* (Methuen, London, 1858); J. T. Carlton, *Conserv. Biol.* **3**, 265 (1989).
2. F. D. Por, *Lessepsian Migration: The Influx of Red Sea Biota into the Mediterranean* (Springer, Berlin, 1978); A. Barash and Z. Danin, *Spixiana* **9**, 117 (1986); M. Moraitou-Apostolopoulou and V. Kiortis, Eds., *Mediterranean Marine Ecosystems* (Plenum, New York, 1985).
3. J. T. Carlton, *Oceanogr. Mar. Biol. Annu. Rev.* **23**, 313 (1985); *Bull. Mar. Sci.* **41**, 452 (1987).
4. J. E. McCosker and C. E. Dawson, *Mar. Biol.* **30**, 343 (1975); H. R. Spivey, *Corros. Mar. Fouling* **1**, 43 (1976).
5. P. W. Glynn, *Adv. Mar. Biol.* **19**, 91 (1982).
6. M. E. Hay and S. D. Gaines, *Biotropica* **16**, 24 (1984).
7. G. J. Vermeij, *Biogeography and Adaptation: Patterns of Marine Life* (Harvard Univ. Press, Cambridge, 1978).
8. F. Rögl and F. F. Steininger, in *Fossils and Climate*, P. J. Brenchley, Ed. (Wiley, Chichester, 1984), p. 171; J. C. Barry, N. M. Johnson, S. M. Raza, L. L. Jacobs, *Geology* **13**, 637 (1985); F. D. Por, *The Legacy of Tethys: an Aquatic Biogeography of the Levant* (Kluwer, Dordrecht, 1989).
9. J. C. Barry et al., *Paleobiology*, in press.
10. A. Keast, *Q. Rev. Biol.* **43**, 373 (1968); *ibid.* **44**, 121 (1969); S. Hand, in *Vertebrate Zoogeography and Evolution in Australasia*, M. Archer and G. Clayton, Eds. (Hesperian Press, Carlisle, 1984), p. 905.
11. J. P. Kennett, G. Keller, M. S. Srinivasan, *Geol. Soc. Am. Mem.* **163**, 197 (1985).
12. J. A. Lillegraven et al., *Biol. J. Linn. Soc.* **32**, 281 (1987).
13. S. D. Webb, *Evolution* **23**, 688 (1969).
14. L. G. Marshall, S. D. Webb, J. J. Sepkoski, Jr., D. M. Raup, *Science* **215**, 1351 (1982).
15. F. G. Stehli and S. D. Webb, Eds., *The Great American Biotic Interchange* (Plenum, New York, 1985).
16. R. M. Schuster, in *Origin and Early Evolution of Angiosperms*, C. B. Beck, Ed. (Columbia Univ. Press, New York, 1988), p. 48; A. H. Gentry, *Ann. Mo. Bot. Gard.* **69**, 557 (1982).
17. D. M. Hopkins, Ed., *The Bering Land Bridge* (Stanford Univ. Press, Palo Alto, 1967).
18. G. J. Vermeij, *Paleobiology*, in press.
19. P. K. Weyl, *Meteorol. Monogr.* **8**, 37 (1968); W. A. Berggren and D. Hollister, *Tectonophysics* **38**, 11 (1977); A. G. Kaneps, *Science* **204**, 297 (1979).
20. J. D. Nations, *Nat. Hist. Mus. Los Ang. Cty. Sci. Bull.* **23**, 1 (1975); C. A. Repenning, C. E. Ray, and D. Grigorescu, in *Historical Biogeography, Plate Tectonics, and the Changing Environment*, J. Gray and A. J. Boucot, Eds. (Oregon State Univ. Press, Corvallis, 1979), p. 357.
21. D. R. Lindberg, *Paleobiology*, in press.
22. T. F. Dana, *Mar. Biol.* **33**, 355 (1975); K. L. Heck, Jr., and E. D. McCoy, *Mar. Biol.* **48**, 349 (1978); W. J. Zinsmeister and W. K. Emerson, *Veliger* **22**, 32 (1979); A. F. Budd, *Mem. Assoc. Australas. Palaeontol.* **8**, 219 (1989); N. W. Colgan, in (22, p. 183); R. H. Richmond, in (22, p. 127); W. K. Emerson, *Nautilus* **105**, 62 (1991).
23. P. W. Glynn, Ed., *Global Ecological Consequences of the 1982-83 El Niño-Southern Oscillation* (Elsevier, Amsterdam, 1990).
24. W. J. Zinsmeister, *J. Paleontol.* **56**, 84 (1982); B. Kensley, *Ann. South Afr. Mus.* **97**, 1 (1985); A. G. Beu and P. A. Maxwell, *N. Z. Geol. Surv. Paleontol. Bull.* **58**, 1 (1990).
25. G. G. Simpson, *Geol. Soc. Am. Bull.* **58**, 613 (1947); C. A. Repenning, in (16, p. 288); *Acta Zool. Fenn.* **170**, 173 (1985).
26. S. D. Webb, in (15, p. 201).
27. L. J. Flynn, R. H. Tedford, Q. Zhanxiang, *Paleobiology*, in press.
28. R. C. Allison, *Veliger* **21**, 171 (1978); Y. Honda, *Palaeontol. Soc. Jpn. Spec. Pap.* **29**, 3 (1986); *Tohoku Univ. Sci. Rep. (Ser. 2, Geol.)* **60**, 1 (1989).
29. A. I. Kafanov, *Can. Transl. Fish. Aquat. Sci.* **5052** (1984), p. 1.
30. H. B. Fell, *Oceanogr. Mar. Biol. Annu. Rev.* **5**, 317 (1967); R. S. Scheltema, *Biol. Bull.* **140**, 284 (1971); C. de Muizon, *Ann. South Afr. Mus.* **89**, 175 (1982); E. J. Petuch, *Palaeogeogr. Palaeoclimatol. Palaeocol.* **37**, 277 (1982).
31. S. D. Webb, in (15, p. 357).
32. J. C. Briggs, *Nature* **216**, 350 (1967); *Stud. Trop. Oceanogr.* **5**, 569 (1967).
33. J. W. Durham and F. S. MacNeil, in (16, p. 326); F. Strauch, *Abh. Senckenb. Naturforsch. Ges.* **531**, 1 (1972); A. I. Kafanov, *Sov. J. Mar. Biol.* **4**, 485 (1978).
34. C. Darwin, *The Origin of Species by Natural Selection or the Preservation of Favored Races in the Struggle for Life* (Colliers, New York, ed. 6, 1872); P. J. Darlington, Jr., *Evolution* **13**, 488 (1959); M. Moynihan, *Am. Nat.* **105**, 371 (1971); J. C. Briggs, *Syst. Zool.* **23**, 248 (1974).
35. L. G. Marshall, in *Biotic Crises in Ecological and Evolutionary Time*, M. H. Nitecki, Ed. (Academic Press, New York, 1981), p. 133; R. T. Bakker, in *Coevolution*, D. J. Futuyma and M. Slatkin, Eds. (Sinauer, Sunderland, MA, 1983), p. 350.
36. G. J. Vermeij, *Evolution* **41**, 1046 (1987).

37. R. E. Warner, *Condor* **70**, 101 (1968); I. A. E. Atkinson, in *Conservation of Island Birds: Case Studies for the Management of Threatened Island Species*, P. J. Moors, Ed. (International Council for Bird Preservation, Cambridge, 1985), p. 35; P. W. Price, M. J. Westoby, B. Rice, *Am. Nat.* **131**, 544 (1988); R. N. Mack, in (37, p. 155).
38. J. A. Drake et al., Eds., *Biological Invasions: a Global Perspective* (Wiley, Chichester, 1989).
39. D. S. Simberloff in, *Biotic Crises in Ecological and Evolutionary Time*, M. H. Nitecki, Ed. (Academic Press, New York, 1981), p. 53; J. M. Diamond, in *Quaternary Extinctions: a Prehistoric Revolution* (Univ. of Arizona Press, Tucson, 1984), p. 824.
40. G. J. Vermeij and E. J. Petuch, *Malacologia* **27**, 29 (1986).
41. G. J. Vermeij, *Conserv. Biol.* **3**, 274 (1989); *Paleobiology* **15**, 335 (1989).
42. G. J. Vermeij, *Evolution and Escalation, an Ecological History of Life* (Princeton Univ. Press, Princeton, 1987); M. H. Rosenzweig and R. D. McCord, *Paleobiology*, in press.
43. P. K. Dayton, *Ecol. Monogr.* **41**, 351 (1971); H. S. Horn, *The Adaptive Geometry of Trees* (Princeton Univ. Press, Princeton, 1971); J. P. Sutherland, *Am. Nat.* **108**, 859 (1974); J. H. Connell, *Science* **199**, 1302 (1978); R. T. Paine and S. A. Levin, *Ecol. Monogr.* **51**, 145 (1981).
44. A. Hallam, in *Causes of Evolution: a Paleontological Perspective* (Univ. of Chicago Press, Chicago, 1990), p. 249.
45. V. Geist, *Wildl. Soc. Bull.* **13**, 351 (1985).
46. W. J. Christie, *J. Fish. Res. Board Canada* **31**, 827 (1974); J. M. Diamond and C. R. Veitsch, *Science* **211**, 499 (1981); M. D. Fox and B. J. Fox, in *Ecology of Biological Invasions*, R. H. Groves and J. J. Burdon, Eds. (Cambridge Univ. Press, Cambridge, 1986), p. 57.
47. J. Roughgarden, *Evolution* **41**, 1130 (1987); S. L. Pimm, in (37, p. 351); T. J. Case, *Proc. Nat. Acad. Sci. U.S.A.* **87**, 9610 (1990).
48. A. R. Wallace, *The Geographical Distribution of Animals* (Hafner, New York, 1876).
49. T. M. Zaret and R. T. Paine, *Science* **182**, 449 (1973); J. A. Savidge, *Ecology* **68**, 660 (1987); J. Murray, E. Murray, M. S. Johnson, B. Clarke, *Pac. Sci.* **42**, 150 (1988); J. H. Brown, in (37, p. 85).
50. D. W. Krause, *Contrib. Geol. Univ. Wyo. Spec. Pap.* **3**, 95 (1986); M. C. Maas, D. W. Krause, S. G. Strait, *Paleobiology* **14**, 410 (1988).
51. M. Ben-Yami and T. Glaser, *Fish. Bull.* **72**, 359 (1974); M. D. Bertness, *Ecology* **65**, 370 (1984); M. B. Usher, *Biol. Conserv.* **44**, 119 (1988).
52. N. W. Blackstone, *Biol. Bull.* **171**, 379 (1986); M. H. Posey, *Mar. Ecol. Prog. Ser.* **31**, 15 (1986); P. M. Vitousek, L. R. Waller, L. D. Whiteaker, D. Mueller-Dombois, P. A. Matson, *Science* **238**, 802 (1987).
53. R. H. MacArthur, *Geographical Ecology: Patterns in the Distribution of Species* (Harper & Row, New York, 1972); R. H. Whittaker, *Evol. Biol.* **10**, 1 (1977); P. W. Price, *Evolutionary Biology of Parasites* (Princeton Univ. Press, Princeton, 1980); K. Rohde, *Evol. Theory* **8**, 305 (1989). Many vertebrate assemblages are probably well below saturation [see also J. A. Wiens, *The Ecology of Bird Communities, Foundations and Patterns* (Cambridge Univ. Press, Cambridge, 1989), vol. 1].
54. M. D. Bertness, *J. Exp. Mar. Biol. Ecol.* **64**, 159 (1982); G. J. Vermeij, *Mar. Ecol. Prog. Ser.* **57**, 293 (1989).
55. J. C. Briggs, *Science* **162**, 511 (1968).
56. R. W. Topp, *ibid.* **165**, 1325 (1969).
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Vapor-Phase Fabrication and Properties of Continuous-Filament Ceramic Composites

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The continuous-filament ceramic composite is becoming recognized as necessary for new, high-temperature structural applications. Yet because of the susceptibility of the filaments to damage from traditional methods for the preparation of ceramics, vapor-phase infiltration has become the fabrication method of choice. The chemical vapor infiltration methods for producing these composites are now being studied in earnest, with the complexity of filament weaves and deposition chemistry being merged

with standard heat and mass-transport relationships. Two of the most influential effects on the mechanical properties of these materials are the adhesion and frictional force between the fibers and the matrix, which can be controlled by a tailored interface coating. A variety of materials are available for producing these composites including carbide, nitride, boride, and oxide filaments and matrices. Silicon carbide-based materials are by far the most advanced and are already being used in aerospace applications.

UNTIL JUST A FEW YEARS AGO, VAPOR-PHASE SYNTHESIS was rarely thought of as a route to structural materials. The technology was restricted to the deposition of specialty coatings and, more recently, to the fabrication of thin-film electronic devices. Now, however, it is emerging as a method for the preparation of near-final-shape, continuous-filament ceramic composites (CFCCs) for advanced structural applications. Conventional techniques for the fabrication of ceramics such as hot pressing (in which a ceramic body is simultaneously subjected to high temperatures and pressures) involve fiber-damaging extremes of temperature and mechanical stress. For example, the popular SiC-based fiber Nicalon suffers degradation at processing temperatures above 1100°C (1, 2), a temperature well below that for sintering SiC. The high-modulus, small-diameter (15-μm) Nicalon fibers are also susceptible to mechanical damage from high-pressure consolidation methods. This

susceptibility has led to several novel approaches involving impregnation of fibrous preforms with matrix precursors. By far the greatest success has been obtained with vapor sources, leading to a class of techniques termed chemical vapor infiltration (CVI).

CVI originated in efforts to densify porous graphite bodies by infiltration with carbon (3). The technique has developed commercially such that half of the carbon-carbon composites currently produced are made by CVI (the remainder are fabricated by the curing of polymer-impregnated fiber lay-ups). The earliest report of the use of CVI for ceramics fabrication was a 1964 patent for infiltrating fibrous alumina with chromium carbides (4). During the past two decades, much of the development of CVI techniques has taken place at the University of Karlsruhe (5), the University of Bordeaux (6), and Oak Ridge National Laboratory (7, 8).

In CVI, gaseous reactants infiltrate a porous (typically fibrous) preform held at an elevated temperature, depositing matrix material on the substrate structure via a standard chemical vapor deposition (CVD) reaction. This CVD coating grows with continued deposition to form the composite matrix. CVD reactions are attractive in that they permit the use of a wide variety of ceramic matrix materials

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