



Why are there so few evolutionary transitions between aquatic and terrestrial ecosystems?

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Insects and flowering plants have rarely invaded the sea. Explanations for this have traditionally centered on the unique shortcomings of these groups in the marine environment. We show, however, that transitions among terrestrial, freshwater, and marine environments are infrequent in all major plant and animal clades except tetrapod vertebrates. In general, well-adapted incumbents are at a competitive advantage over would-be invaders from a physically different habitat. Data on the times and places of transition are consistent with our contention that evolutionary transitions among physically different environments are most likely when incumbents in the recipient environment exist in a regime of low-intensity competition and predation, as in terrestrial communities of the middle Paleozoic or the land biotas of oceanic islands. Freshwater environments, in which inferred intensities of predation are lower than in most marine and terrestrial environments, offer less biotic resistance to invaders than do communities in the sea or on land. Most invaders respond to novel physical circumstances by shutting down their metabolic machinery, and therefore add to their subordinate status as competitors with active incumbents. Only active tetrapods, particularly those with high and endothermically driven rates of metabolism, have successfully overcome this limitation.

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INTRODUCTION

Why are there so few insects in the sea? Of a minimum of 1 million living insect species, only about 1400 (0.14%) live in marine settings, mainly in the intertidal zone (Cheng, 1985). Explanations for this dearth of marine insects have centered on respiratory, osmoregulatory, defensive, and competitive shortcomings of marine insects compared to other groups in the sea (Carpenter, 1901; Buxton, 1926; Mackerras, 1950; Usinger, 1957; Hutchinson, 1967; Cheng, 1976; Maddrell, 1998; Hynes, 1984; Foster, 1986; Ward, 1992).

Similarly, why are there so few flowering plants in the sea? Of some 300 000 living species of flowering plants, only about 60 (0.02%) are marine (Les & Cleland, 1997). The low frequency of marine flowering plants has often been ascribed to osmoregulatory problems and especially to difficulties of pollination by water currents (see van der Hage, 1996; Les & Cleland, 1997; Ollerton & McCollin, 1998; Raven, 1998). We believe, however, that these explanations have been cast too narrowly. Insects and flowering plants are by no means alone among land organisms in having few marine representatives. With the exception of some groups of tetrapod vertebrates, no group of primarily terrestrial plants or animals has penetrated marine environments with a high frequency. Moreover, very few marine groups have been able to colonize terrestrial environments.

Explanations for the rarity of such transitions between the sea and the land must therefore go well beyond the particulars of individual clades, and must instead apply very broadly to many groups in all parts of the world and at most times in the history of life. Although osmotic challenges and the great physical differences between life in water and life on land are important and affect all clades making the transition, part of the explanation must reside in the biological context in which invasion occurs, that is, the conditions of life in the donor, transitional, and recipient environments.

After reviewing the patterns of transition between land and sea, we propose a general explanation for the rarity of major ecological transitions. We suggest that, because most newcomers are not as well adapted to the target environment as are established incumbents, the newcomers operate at a clear disadvantage. Furthermore, solutions involving a metabolic slowdown during times of physiological stress in the new medium will predispose newcomers to remain subordinate to well-adapted natives. Hynes (1984) proposed a version of this hypothesis for insects, but he did not evaluate his ideas with respect to other groups that have invaded between the sea and the land, nor did he examine the geographical and historical dimensions of the problem.

PATTERNS OF INVASION

Sea to land

There have been astonishingly few invasions of the land by marine clades with or without freshwater intermediaries. Early instances include the ancestor of

embryophytes during or possibly before the Ordovician (Stebbins & Hill, 1980; Gray, Massa & Boucot, 1982; Shear, 1991), millipedes perhaps by the Late Ordovician (Retallack & Feakes, 1987), arachnids (oribatoid mites) and apterygote insects no later than the Early Devonian (Shear, 1991; Störmer, 1976, 1977; Rolfe, 1980; Shear, Gensel & Jeram, 1996), tetrapod vertebrates during the Viséan stage of the Early Carboniferous (Ahlberg & Milner, 1994; Ahlberg, 1995; Paton, Smithson & Clack, 1999), scorpions by the Early Carboniferous (Sissom, 1990), and molluscs (two or perhaps three gastropod clades) in the Late Carboniferous (Solem & Yochelson, 1979; Bandel, 1994). Post-Paleozoic invasions have occurred among crustaceans and gastropod molluscs. Crustacean invaders include members of the Isopoda, Amphipoda, Brachyura, and Anomala. These taxa colonized the land during the Cenozoic era, and in one case (a Jamaican sesarminine ocypodid crab) as recently as the late Pliocene (Schubart, Diesel & Hedges, 1998). At least seven post-Paleozoic gastropod clades contain terrestrial members (see Solem, 1979; Rosenberg, 1996). Cyclophoroids arose in the Late Jurassic, terrestrial littorinoids in the Late Cretaceous or earliest Cenozoic, and carychiid basommatophorans in the early Cenozoic. Four clades of rissooideans invaded the land probably during the Cenozoic. One of these, the Truncatellidae, colonized the land at least four times independently, three of which occurred within the last one million years on West Indian islands (Rosenberg, 1996). We do not know when planarian flatworms, roundworms, oligochaete annelids, and onychophoran velvet worms invaded the land. Several of these primarily marine clades have become extraordinarily diverse on land, and particularly so for the groups that invaded during the Paleozoic era.

Land to sea

Secondarily marine organisms occur among arthropods, tetrapod vertebrates, and flowering plants. With the exception of tetrapods (especially birds and to a lesser extent mammals and reptiles), the number of transitions has been small. Only about 0.14% of insects are found in marine ecosystems. Most of these marine insects are flies, whose immature stages inhabit estuarine, salt-marsh, or mangrove habitats; and beetles, which along with some adult and larval flies occur in rocky and sandy intertidal habitats (Carpenter, 1901; Usinger, 1957; Cheng, 1976; Norris, 1991). Additional salt-water insects are known among true bugs (Heteroptera) and Collembola, and there are even two caddisflies (Trichoptera) whose larvae are marine (see also Winterbourn & Anderson, 1980). Some Lepidoptera alight on the sea surface but are not in any real sense marine. Only five species of the gerrid heteropteran genus *Halobates* are epipelagic (Cheng, 1985). We know of no permanently submerged marine insects, nor of any marine members of such large groups as Orthoptera, Isoptera, Hymenoptera, Ephemeroptera, Mecoptera, Plecoptera, Odonata, Homoptera, Lepidoptera, Raphidioptera, Megaloptera, Diplura, and Protura (see also Norris, 1991). Without detailed phylogenetic knowledge of all the clades involved, it is difficult to estimate how many invasions from land to sea have occurred among insects. Very roughly and conservatively, we estimate 70 instances of invasion at the family to genus level from fresh water to the sea, and at least 42 instances from land to sea without freshwater intermediaries (compiled from data in Cheng, 1976; Norris, 1991).

The timing of marine invasion of insects is essentially unknown. Fossil *Halobates*

have been reported from the Middle Eocene of Italy (Andersen *et al.*, 1994). Major radiations of Diptera and Coleoptera occurred in the Jurassic to Early Cretaceous (Wootton, 1988; Labandeira, 1998), and the earliest shorebugs (Saldidae, Heteroptera) are of Late Jurassic age. Marine invasions by these groups are therefore no older than Late Jurassic.

With the exception of halacarid mites, of which some 300 species are known (Krantz, 1978), other groups of terrestrial arthropods have invaded the sea as infrequently as have insects. For example, only ten of 1400 living scorpion species (0.7%) are intertidal (Polis, 1990), and these represent four independent invasions. At the family level, arachnids of terrestrial origin have invaded the sea at least 47 times (compiled from Roth & Brown, 1976). Myriapods have invaded the sea about 15 times independently (Roth & Brown, 1976). The only arthropods of terrestrial origin that live submerged in the sea are the halacarids, some of which have been found down to abyssal depths of 4000 m (see Krantz, 1978).

Despite the large diversity of land snails (about 25 000 species according to Solem, 1979), we know of no case of secondary marine invasion in this group. Davis (1979) suggested that the pomatiopsid rissoidae genus became secondarily adapted to a high-shore environment in northeast Asia, and Ponder (1998) hesitatingly inferred that the northeast Asian rissoidae family Falsicingulidae presents a case of secondary marine invasion, but the phylogenetic evidence in both cases is equivocal.

As a group, terrestrial tetrapod vertebrates have invaded the sea more often and more successfully than have arthropods. Among living reptiles (snakes, lizards, turtles, crocodiles, and their relatives), about 1.5% are marine (Greene, 1997). These include three major and three minor clades of snakes, one or two species of crocodiles, one small group of sea turtles and a few North American salt-marsh turtles, a marine iguana, and a few incidentally intertidal lizards (Pritchard, 1979; Steel, 1973; Greene, 1997). In addition, 15 or 16 fossil diapsid reptile clades became marine, as did four groups of turtles, one or more groups of pterosaurs, and even one group of amphibians (see Carroll, 1985; Pritchard, 1979; Collin & Janis, 1997).

Marine mammals have arisen at least seven times independently. They are known in the Cetacea (whales and dolphins), Sirenia (seacows), Desmostylia (a fossil group related to, but independent from, Sirenia), Pinnipedia (seals), the Pliocene Peruvian sloth *Thalassocnus*, the Holocene sea mink of the mustelid genus *Mustela*, and lutrid sea otters (see Waters & Ray, 1961; Gingerich *et al.*, 1994; Berta & Morgan, 1985; Wyss, 1987, 1988; Savage, Domning & Thewissen, 1994; de Muizon & McDonald, 1995; Thewissen *et al.*, 1996; Domning, Ray & McKenna, 1986).

At most, four of the reptilian and mammalian tetrapod groups entered the sea directly from the land. These are sea kraits (snakes of the genus *Laticauda*), the marine iguana *Amblyrhynchus*, the sea sloth, and seals (Wyss, 1987, 1988; Greene, 1997). All other marine clades of these tetrapod groups made the transition from land via fresh water.

By far the largest number of living marine tetrapod species is found among birds. It is difficult to estimate how often the transition from land (or fresh water) to the sea occurred among birds in view of the fact that many birds are flexible and variable according to where they feed. Such behaviour typifies ducks, geese, herons, sandpipers, plovers, gulls, terns, grebes, loons, coots, cormorants, spoonbills, ibises, stilts, rails, flamingoes, ospreys, pelicans, and skimmers, among others. Even if we restrict the survey to exclusively marine birds—penguins, petrels, sheathbills, auks,

living frigatebirds, tropic birds, boobies, albatrosses, and phalaropes, among others—the number of transitions is still potentially very high.

The history of tetrapod invasion to the sea began during the Late Permian, when as many as three initially terrestrial groups took to the sea. Excluding birds, there were eight invasions during the Triassic, six each during the Jurassic and Cretaceous, two during the early Eocene, four during the Miocene, and three (all highly local) in the Plio-Pleistocene. Birds fed in or near the sea from the Neocomian (earliest Cretaceous) onward (Olson, 1985; Chiappe, 1995). All Cretaceous invasions occurred during the early and middle part of the period (see Pritchard, 1979; Morales, 1997; Hirayama, 1998). In the North Pacific, at least four groups of birds and two groups of mammals became adapted to the sea during the late Oligocene to early Miocene interval (Berta, Ray & Wyss, 1989; Domning *et al.*, 1986; Saito, Barron & Sakamoto 1988; Warheit, 1992).

Several major clades of tetrapods lack marine members. Examples include rodents, perissodactyl and artiodactyl ungulates, bats, insectivores, marsupials, songbirds (the passerine songbirds *Anthus*, *Cinclis*, and *Corvus* occasionally feed in the intertidal zone but are not bound to it), parrots, owls, hummingbirds, and swifts. Amphibia are another major tetrapod lineage with no living marine representatives.

The only truly marine plants of terrestrial origin are the sixty or so living species of sea grasses, which are the products of three independent invasions via fresh water among members of the Alismatidae (Les & Cleland, 1997). Intertidal mangroves evolved an additional 15 times in 15 families and nine orders of dicots (Ricklefs & Latham, 1993). In addition, salt-marsh plants capable of temporary submersion in sea water evolved independently several times in each of at least five flowering-plant families.

Land plants may have begun to invade shore environments as early as the Late Carboniferous, when the gymnosperm *Amyelon* perhaps formed mangroves (reviewed in Gray, 1988). Additional mangrove-forming plants are known from the Late Jurassic (the fern *Weichselia*), the Early to Late Cretaceous (two conifer genera), and Cenomanian middle Cretaceous (*Acerites*) (Retallack & Dilcher, 1981; Shinaq & Bandel, 1998). There were at least two invasions of land plants into mangrove environments in the Late Cretaceous, three during the Eocene, and four in the Oligocene and Miocene (Ricklefs & Latham, 1993). At least two sea-grass genera are known from the latest Cretaceous, and others had arisen by the Eocene (den Hartog, 1970; Ivany, Portell & Jones, 1990). We do not know anything about the history of salt marsh plants, but their wide distribution implies origins no later than the Early Cenozoic.

FRESH WATER AS INTERMEDIATE AND RECIPIENT ENVIRONMENT

Many terrestrial clades that have colonized the sea, and many marine clades that have invaded the land, made the transition via fresh water. Among invaders to fresh water, however, the clades that made the transition either to the sea or to the land constitute a small minority. About 1 to 2% of living flowering plants are aquatic, representing 50 to 100 independent invasions of fresh water (Cook, 1996); whereas only 60 species in three clades have become fully marine. Living freshwater molluscs belong to 15 gastropod and 14 bivalve clades, all of marine origin (compiled from

Vermeij & Dudley, 1985; Gray, 1988; Houbriek, 1988; Ponder, 1988; Harasewych *et al.*, 1998). Among fossil molluscs, an additional five clades of gastropods and three of bivalves contain freshwater representatives (compiled from Gray, 1988). All but one of these (the late Miocene succineid stylommatophoran *Papyrotheca*) are of marine origin. The 41 freshwater molluscan clades with marine ancestors rarely contain terrestrial members. Only five family- to order-level clades (all gastropods) contain terrestrial as well as freshwater members. Thus, only about 12% of molluscan clades that invaded fresh water from the sea made the transition to dry land. The proportion is probably similarly low in insects. There are some 45 000 living aquatic insect species, representing roughly 4.5% of extant insect diversity. All of these are likely to have had terrestrial ancestors (Wootton, 1988; Messner, 1988; Pritchard *et al.*, 1993; Resh & Solem, 1996).

The fact that many aquatic clades of insects, including groups in inland saline lakes, have no marine members (Hynes, 1984; Ward, 1992) indicates that transitions from land to fresh water or inland salt water have been more frequent than have transitions from either land or fresh water to the sea. This trend seems to be general. Among fossil and living mammals, we estimate conservatively from D. W. Taylor and Gray's compilation (in Gray, 1988) that 24 clades entered the aquatic environment, of which 7 (29%) have also become marine and 17 (69%) have remained in fresh water. At least two of the secondarily marine clades (Cetacea and Pinnipedia) have reinvaded fresh water one or more times. Among crustaceans, we know of no cases of transition from fresh water to the sea or from land to fresh water. Of the 30 suborder- to order-level clades that have invaded fresh water (Gray, 1988), only four contain terrestrial members as well (13%). All these numbers undoubtedly underestimate the actual number of transitions, but they indicate a general pattern: invasions to fresh water are far more numerous than are invasions of terrestrial animals by way of fresh water to the sea or of marine animals by way of fresh water to the land. This conclusion would be even stronger had we considered fishes, which have made the transition between the sea and fresh water in numerous clades throughout their long history.

DISCUSSION

Although data on the frequencies of transition by clades among marine, freshwater, and terrestrial habitats are incomplete, we draw the following conclusions from them: (1) In most groups of plants and animals, transitions among physically different habitats—sea, land, and freshwater—are rare; (2) transitions from sea to land are generally less frequent than are transitions from land to sea; (3) invasion of fresh water from the land or from the sea is more frequent than invasion via fresh water between land and sea. The analysis demonstrates that insects and flowering plants are not alone among terrestrial groups in being poorly represented in marine ecosystems.

One explanation for these patterns is that frequencies of invasion among environments reflect relative species richness in these environments. If the diversity of plants and animals on land is roughly ten times higher than is diversity in the sea, we should expect the number of invasions from land to sea to exceed the number of invasions from sea to land by an order of magnitude. At a superficial level, the

data are consistent with such an expectation. Among post-Paleozoic arthropods, for example, land-derived marine clades outnumber marine-derived terrestrial clades approximately 174 to 4. At least 37 post-Devonian clades of tetrapod vertebrates (excluding birds) have made the transition from land to sea, whereas no marine tetrapods (or any other marine vertebrates, for that matter) colonized the land since the Devonian. For clades in which the great majority of members are marine, the opposite pattern holds, as would be expected. Crustaceans and molluscs are primarily marine clades, whose terrestrial subclades have not reinvaded the sea. It is intriguing that transitions from land to fresh water are also unknown in these major animal groups, as are transitions from fresh water to the sea.

For vertebrates as a whole, however, the pattern of invasion between the land and the sea does not conform to expectations based on species richness. Marine vertebrates outnumber terrestrial vertebrate taxa by an approximate ratio of two to one, but the ratio of secondarily terrestrial to secondarily marine clades is 0 to 37. Even if only inshore marine clades were counted as being potential invaders to the land, diversity of vertebrates would still likely be greater in the sea.

One problem with the hypothesis that patterns of invasion reflect only species richness is that the data on diversity refer to Recent biotas. The enormous diversity of species on land is an almost entirely post-Jurassic phenomenon. Before flowering plants and their associated insects diversified during the Cretaceous, plant and animal life on land was probably no more diverse, and may have been less diverse, than that in the oceans. Yet, at least 17 clades of tetrapods of terrestrial origin invaded the sea before the Cretaceous, and a number of plants may have established pre-Cretaceous mangrove communities on marine shores.

A second problem is that total species richness on land or in the sea is a very crude and potentially misleading number against which to compare the number of invading clades. Transitions from one environment to another are most likely to occur in clades that live near the zone of transition between these environments. In order to test the null hypothesis that invasion reflects species richness, therefore, we would need data on the diversity of species in habitats adjacent to the terrestrial or marine ecosystems being invaded.

Even if the colonization of physically different habitats reflected only differences in the number of species in those habitats, we would still be left with the interesting question of why some clades invade whereas others do not. To answer such a question, we must understand the conditions of life in the ancestral, transitional, and recipient ecosystems, as well as the properties of potential invaders.

The physical properties of air and water are so different that the transition between terrestrial and aquatic habitats entails drastic changes in every aspect of life, from temperature regulation to gas exchange, foraging, sensation, locomotion, nutrient uptake in plants, and reproduction (for a comprehensive review see Denny, 1993). An organism that is well adapted for life in one medium is therefore likely to be poorly suited for life in the other. As a result, clades invading the land from an aquatic environment, or vice versa, will usually be at a distinct competitive disadvantage to those already present in the recipient ecosystem.

Invasions are likely only when incumbents are absent or of very modest competitive ability. This would have been the case on the dry land relative to the sea until Middle Carboniferous time, and may still be the case in fresh-water and insular habitats generally as well as in inland saline lakes.

During the Early and Middle Paleozoic, when multicellular plants and animals

were already well established in the sea, marine invaders to the land would not have had to meet high standards to offer significant competition to contemporaneous terrestrial incumbents. Early plants, for example, lacked leaves, phloem, roots, water-independent reproduction, and significant secondary growth. Until the Middle to Late Devonian, they had a xerophytic appearance, indicating that they experienced the dry land as a metabolically marginal environment (see Tiffney, 1981). Key adaptations to the land, resulting among other things in great increases in plant height, were achieved by land plants during the Devonian (Chaloner & Sheerin, 1981; Bateman & DiMichele, 1994a,b; Meyer-Berthaud, Scheckler and Vendt, 1999). When tetrapods became terrestrial during the Early Carboniferous, they encountered mainly small, wingless arthropods, which served as prey rather than as significant competitors. Winged insects and gigantic terrestrial arthropods evolved afterward, alongside tetrapods, during the Middle Carboniferous (see Shear, 1991). Continental terrestrial ecosystems have therefore offered substantial biological as well as physical barriers to invasion by aquatic organisms since the Late Carboniferous.

Oceanic islands may offer less biological resistance to invasion from the sea than do most other terrestrial environments. The biota of small oceanic islands is characterized by the near absence of mammals (except bats), and by the abundance of insects and birds with reduced or no powers of flight and with low metabolic rates. The four cases of terrestrialization in truncatellid gastropods all took place on small islands (Rosenberg, 1996), as did the evolution of the large terrestrial hermit crab *Birgus latro* (the coconut crab) on islands in the Pacific and Indian Oceans (for a review, see Vermeij, 1987).

Freshwater environments may offer relatively little biological resistance to potential marine and terrestrial invaders. Strong circumstantial evidence shows that freshwater molluscs and crustaceans with mineralized external skeletons lack many of the morphological and behavioral specializations to predation when compared to their marine counterparts (Vermeij & Covich, 1978; Vermeij & Dudley, 1985; Vermeij, 1993). Gastropods and bivalves in fresh water have lower incidences and reduced expression of breakage-resistant sculpture, occluded or narrow shell openings, and shell features associated with rapid crawling or burrowing than do these groups in the sea. Some of this reduced specialization may reflect the greater cost of calcification in fresh water, where concentrations of calcium carbonate are often well below saturation, but they also reflect the absence of predators such as echinoderms and drilling gastropods that rely on distance chemoreception for detecting prey and danger (Vermeij, 1993). Many small, temporary bodies of fresh water are characterized by the absence of fish and other predators, and it is in these biologically undemanding environments where soft-bodied mosquito larvae (Culicidae) and perhaps other larval and nectonic adult insects, as well as predation-vulnerable leptostracan and anaspidid syncarid crustaceans, thrive (see also Ball & Glucksman, 1978; Hessler & Schram, 1984; Schram & Hessler, 1984; Maddrell, 1998). Thin-shelled pulmonate gastropod and sphaeriid bivalves are also most abundant in stagnant bodies of fresh water, as are weakly rooted and rootless vascular plants. Although stagnant inshore habitats also occur in marine settings, they are typically flushed by tides, and do not represent the kind of safe haven that temporary freshwater pools do. The biological barriers to invasion from the land or from the sea to fresh water should therefore be lower than it is between land and sea.

The reduced incumbent resistance of freshwater as compared to marine and terrestrial ecosystems is consistent with our data on the frequency of transitions. Of

the land-plant clades that invaded aquatic habitats, only 3–6% eventually spread from freshwater to marine habitats. For marine molluscs, only 12% of marine clades that penetrated freshwater ecosystems also produced terrestrial members. Among crustaceans, this proportion is about 13%. In mammals, for which the transition from the land to aquatic environments has been more frequent than in arthropods and molluscs, approximately 29% of the aquatic clades have marine members. No reliable estimates are available for other animal groups, but we suspect that the proportion of aquatic clades with secondarily terrestrial or marine members is low.

Perhaps the most dramatic indication that the biological environment is an important factor restricting the invasion of salt water habitats comes from inland saline lakes. Hynes (1984) and Ward (1992) point out that many aquatic insect groups unknown in the sea have colonized salt lakes in continental interiors. In such habitats, such typical aquatic groups as molluscs, fish, crustaceans (branchiopods excepted), and multicellular plants are absent. Clearly, insects can overcome osmotic and gas-exchange challenges in such saline environments. It is the array of highly adapted native species that prevents many would-be invaders from the land from establishing themselves in the sea.

Once clades have invaded a new medium, their speciation rates have not differed significantly from those of incumbent clades. Although vascular plants appear to have a very low diversity of about 60 living species, the fact that they represent only three independent transitions from land to sea since the Late Cretaceous means that, on average, each ancestor gave rise to 20 species in 70 million years. If angiosperms on land diversified at a comparable average rate, the approximately three hundred thousand living species would have descended from only about fifteen thousand Late Cretaceous ancestors. There is, of course, great variation in the diversification rates of secondarily marine and terrestrial clades, as there is in clades that did not make the great ecological transitions; but no evidence exists that invaders have lagged behind noninvaders in the production of biological diversity in the recipient environment.

The role of incumbents in resisting invasion is potentially amplified by the way in which many plants and animals adapt to new physical circumstances. Perhaps the most common way of dealing with a new environment is to resist passively. This usually means shutting off the metabolic machinery as much as possible until conditions once again become more like those in which the organism's physiology evolved. In other words, many invaders are inactive. Although this method may be effective in ensuring survival, it is inimical to effective competition, which requires active acquisition of resources. Only those organisms that can remain active while making the great transitions can be expected to invade as reasonably good matches for already well adapted incumbents.

The role of incumbents in resisting invaders is amplified by the way in which many plants and animals adapt to the new medium. A very common means of dealing with a new medium is to isolate life functions from it, or to reduce metabolism temporarily. Intertidal insects, for example, often shelter in crevices or in air pockets while submerged. When exposed to air, molluscs of marine origin cease activity and often close the body off in a tightly sealed shell. Although inactivity is effective in ensuring survival, it is incompatible with effective competition, which requires active acquisition and defense of resources. Only those invaders that can remain active while making the transition to the new medium can hope to match well adapted incumbents. Adaptations replacing inactivity with mechanisms that continue life

functions under physically hostile circumstances are energetically costly, and potentially interfere with defence- and competition-related adaptations. Tetrapods are unusual among potential invaders from the land to the sea in remaining active in the new environment, and they have been much more successful than have other groups in making the land-to-sea transition. In fact, secondarily marine tetrapods have, since Mesozoic times, held important economic positions as high-energy consumers and competitors. For passive organisms, invasion of the land by marine clades or of the sea by terrestrial clades is interpretable as a response to intense predation or competition in the ancestral environment (Vermeij, 1987).

For many organisms, however, access to plentiful resources may provide additional opportunity, especially if productivity in the ancestral environment is low. Gingerich *et al.* (1983), for example, pointed out that marine cetaceans evolved during the early Eocene along the highly productive northern shores of the Tethys seaway (see also Lipps & Mitchell, 1976). Desmostylians, pinnipeds, and a number of bird groups made the transition to marine environments in the productive North Pacific during the interval from the Late Oligocene to the early Miocene (Berta *et al.*, 1989; Domning *et al.*, 1986; Warheit, 1992). The Pliocene sloth *Thalassocnus* exploited productive marine habitats nearshore on the Pliocene desert coast of Peru (de Muizon & McDonald, 1995). The abundance of decaying organic matter thrown up on temperate beaches and on the productive desert shores of the Gulf of California may similarly have provided opportunities for many invading terrestrial arthropods.

Some of these ideas can be tested further. Detailed phylogenies, together with refined estimates of divergence times and direct evidence from the fossil record, may enable us to constrain the time and place of transitions, so that the nature and importance of incumbency and productivity can be evaluated. More experiments are needed to evaluate relative intensities of predation and competition in terrestrial, freshwater, and marine environments.

Puzzles remain. It is unclear why so few vascular plants have colonized the sea. Compared to algae, vascular plants have the advantage of being able to tap nutrients from the sediment, and indeed to occupy sandy and muddy sea bottoms. Siphonalian green algae also occur in such settings, but vascular plants (seagrasses) are quantitatively more important. In effect, seagrasses and mangrove trees occupy parts of the nearshore marine environment that algae probably never exploited thoroughly (Vermeij, 1987). Given their competitive superiority and the apparently minor role of incumbents, it is surprising that only three clades of flowering plants became fully marine and that another 15 entered what are now mangrove environments. Moreover, biogeographical evidence strongly implies that most of the transitions to the mangrove habitat occurred in the Old World tropics (Ricklefs & Latham, 1993), as is also true for marine snakes (Greene, 1997). Why the very rich flora of the American tropics failed to produce marine species remains a mystery. Another puzzle resides in the absence of marine eusocial insects (Hymenoptera and Isoptera). Social insects are high-energy, quantitatively abundant, competitors on land, and their sociality has made colony-wide activity possible under a great variety of conditions. They have therefore achieved a level of environmental independence approaching that of tetrapods and quite unlike that of many other terrestrial arthropods; yet terrestrial social insects have invaded neither freshwater nor marine environments. Ants are common in the terrestrial parts of mangrove swamps, but

they are not subject to submergence and do not venture into parts of the forest under tidal influence.

In summary, the principal impediments to invasion from one environment to another physically contrasting one are passivity of potential invaders and the presence of well adapted incumbents in the recipient environment.

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