Marine biogeography and ecology: invasions and introductions

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ABSTRACT

Although biogeography and ecology had previously been considered distinct disciplines, this outlook began to change in the early 1990s. Several people expressed interest in creating a link that would help ecologists become more aware of external influences on communities and help biogeographers realize that distribution patterns had their genesis at the community level. They proposed an interdisciplinary approach called macroecology. This concept has been aided by the advent of phylogeography, for a better knowledge of genetic relationships has had great interdisciplinary value. Two areas of research that should obviously benefit from a macroecological approach are: (1) the question of local vs. regional diversity and (2) the question of whether invader species pose a threat to biodiversity. The two questions are related, because both deal with the vulnerability of ecosystems to penetration by invading species. Biogeographers, who have studied the broad oceanic patterns of dispersal and colonization, tend to regard isolated communities as being open to invasion from areas with greater biodiversity. It became evident that many wide-ranging species were produced in centres of origin, and that the location of communities with respect to such centres had a direct effect on the level of species diversity. Ecologists, in earlier years, thought that a community could become saturated with species and would thereafter be self-sustaining. But recent research has shown that saturation is probably never achieved and that the assembly of communities and their maintenance is more or less dependent on the invasion of species from elsewhere. The study of invasions that take place in coastal areas, usually the result of ship traffic and/or aquaculture imports, has special importance due to numerous opinions expressed by scientists and policy-makers that such invasions are a major threat to biodiversity. However, none of the studies so far conducted has identified the extinction of a single, native marine species due to the influence of an exotic invader. Furthermore, fossil evidence of historical invasions does not indicate that invasive species have caused native extinctions or reductions in biodiversity.

Keywords

Biodiversity change, biogeography, community relations, ecology, macroecology, marine invasions, species diversity, species extinctions.

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INTRODUCTION

It has been observed that ecologists are virtually all reductionists (Brown, 1995). They use a deductive, usually experimental, approach to take apart small, well-defined ecological systems and try to understand how they work. On the other hand, biogeographers use inductive, non-manipulative methods to study single lineages or assemblages of many species distributed over continental or global space and through evolutionary time. Fortunately, there are now some signs that ecologists have become more interested in external influences that may affect community structure, and that biogeographers are paying more attention to community events that may have a broader significance. The advent of macroecology has encouraged ecologists to look beyond the community level and biogeographers to examine communities for the genesis of some widespread geographical patterns. At the same time, the rapid progress of research in palaeobiology has enhanced both

ecology and biogeography. These developments should result in a coalescence of interests between the two disciplines but such a mutual appreciation appears to be slow in developing.

Brown & Maurer (1989) introduced the term 'macroecology' and applied it to the division of food and space among species on a continental scale. This was followed by the book *Macroecology* by Brown (1995). In that work, Brown described macroecology as a non-experimental approach that can identify patterns of abundance, distribution and diversity on spatial and temporal scales much larger than those of traditional ecological studies. Five years later another significant book appeared, *Pattern and Process in Macroecology* by Gaston & Blackburn (2000). This was followed by a symposium volume *Macroecology: Concepts and Consequences* edited by Blackburn & Gaston (2003). By this time, a multitude of journal papers referring to the subject of macroecology had been published.

Recently, it has been observed that although ecology and historical biogeography have much to offer one another, exchanges between these fields have been limited (Wiens & Donoghue, 2004). Theoretically, macroecology, with its emphasis on the importance of large-scale patterns, should provide a bridge for cooperation between the two. The opportunities for interdisciplinary research may be most promising within research areas devoted to the causes of: (1) local vs. regional species and (2) the biodiversity threat that may be posed by invader species. These areas are interrelated and have important consequences for marine conservation.

LOCAL VS. REGIONAL DIVERSITY

According to the traditional Volterra–Gause viewpoint, the number of species in ecological communities ought to be controlled mainly by species interactions within the community. But Cornell & Lawton (1992), in their review of theoretical evidence for saturation in various community models, suggested that the principal direction of control for species richness is from regional to local. They speculated that, if this suggestion was correct, then the key to community structure may lie in extrinsic biogeography rather than in intrinsic local processes.

The suggestion of Cornell & Lawton (1992) was carried a step farther when Brown (1995) observed that we could expect to understand the structure and dynamics of local populations and communities without studying the influence of large-scale historical and biogeographical processes. Three years later, Karlson & Cornell (1998) reported on local and regional effects on species richness in reef-building corals. They found that the relative sensitivity of community richness to local and regional variables was 61% and 39%, respectively. However, when only depauperate regions of the Indo-Pacific were considered, regional influence rose to 95%. Their results indicated that Indo-Pacific coral assemblages in both speciose and depauperate regions are unsaturated, and that local richness consistently increased with the size of the regional species pool.

In a review of the evidence for local vs. regional influences, Cornell (1999) concluded that local richness frequently correlated with the regional number, and did not become independent of the latter in the richest regions as would be expected if the community had become saturated. As the result of further work on coral assemblages, Karlson & Cornell (2002) found that local richness was relatively insensitive to regional richness when sampled in small (1 m^2) quadrats but highly sensitive when sampled with 10-m line transects. They concluded that coral assemblages are generally open to immigration from regional species pools and are regionally enriched rather than being saturated with species. Using experimental microcosm communities, Fox et al. (2000) tested for local species saturation and found that strong species interactions did not necessarily set an upper limit to the number of locally co-existing species.

More recently, Witman et al. (2004) reported on the results of a global research programme to test the effects of latitude and regional richness by sampling local diversity in marine, epifaunal invertebrate communities. The sampling efforts took place in 12 locations that ranged from 63° N to 62° S latitude (from Iceland to the Antarctic). Species identifications were made from photographic transects taken across vertical rock walls. Regional pools were assembled from published lists and by consulting taxonomic experts. Biogeographical regions were said to be selected to represent at least three replicates of low, intermediate and high species richness. The results were demonstrated by a series of species accumulation curves for a total of 49 sampling sites within the 12 locations. Overall, the richness of the regional species pool appeared to explain 73–76% of local species richness. The proportion of regional biota represented in local communities seemed to increase from low to high latitudes, and species richness was seen to decrease from low to high latitudes.

The wide-ranging sampling programme undertaken by Witman et al. (2004) was potentially very important because it was the first attempt to examine the local vs. regional relationship on a global scale. Although the general results are in line with findings from smaller areas, the design of the sampling programme left much to be desired. Of the 12 locations where species richness was evaluated, seven were established at oceanic islands. In fact, all of the five tropical stations were at oceanic islands. The shallow water faunas found around oceanic islands are invariably depauperate in comparison to those of the nearest mainland shores. Future comparative studies should be conducted in locations where fauna is more diverse and would be more representative of the region as a whole.

Sampling programmes devoted to marine regional vs. local species diversity need to be planned with respect to known areas of maximum diversity and to the characteristics of the regions in which the communities of interest are located. In the short term, a community may build or maintain its diversity by means of recruitment from a nearby regional pool but, in the long term, it will be influenced by other factors, i.e. rates of speciation, immigration and extinction and environmental events. Immigration to a given community may be influenced by the dispersal of dominant species from centres of origin. An outward evolutionary flow apparently extends from three

principal centres of origin: the tropical East Indies Triangle, the cold-temperate North Pacific and the cold Antarctic (Briggs, 2003). A secondary, tropical centre exists in the southern Caribbean Sea. Some extinction patterns apparently also originate in centres of origin (Briggs, 1999). Depending on location, the species composition of a given community is apt to reflect the influence of one of the centres.

Another recent paper by Karlson *et al.* (2004) demonstrated regional influence on local coral communities along a 10,000-km transect from the East Indies out to French Polynesia. In this case, the research programme was designed to begin in the area of maximum regional diversity and to follow a gradient of decreasing diversity. Local richness and the size of the regional component both declined significantly across the 15 islands spanning the gradient. A strong linear relationship between local and regional richness was demonstrated throughout. The authors concluded that regional enrichment was pervasive and influenced both rich and poor communities. These results may be compared to a biogeographical study (Mora *et al.*, 2003) that analysed the distribution of reef fishes from 70 locations across the Indo-Pacific, about two-thirds of the way across the globe. The latter authors concluded that speciation in and dispersal from the East Indies played the major role in assembling communities throughout the Indian and Pacific oceans.

It may be noted that the results from the latter two papers complement one another. Both reflect the pervasive influence of the East Indies centre of origin. In the account devoted to coral species, Karlson *et al.* (2004) referred to a strong regional relationship as indicated by their linear regressions showing that species in the sampling sites averaged about 27% of the regional pool. On the other hand, in the study on the fish species, Mora *et al.* (2003) found that, on average, about 86% of the species in their samples also occurred in the East Indies – their evident area of origin. The difference in regional effects may be due to the difference in life cycle mobility between fishes and invertebrates.

MARINE INVADERS

As noted, information about the local vs. regional relationship indicates that invasions into individual communities are commonplace. In fact, it appears that community biodiversity may be largely dependent on continuous invasions from regional or more distant sources. On the other hand, the introduction of alien species of animals and plants has been identified by some ecologists and policy-makers as a major threat to biodiversity in marine ecosystems (Amborgi, 2001; Bax *et al.*, 2001; Perrings, 2002; Dawson *et al.*, 2005). The World Conservation Union (IUCN, 2003) rated invasive species as one of the four greatest threats to the world's oceans and published a set of guidelines for '…the prevention of biodiversity loss caused by alien invasive species'.

The marine invasions that have attracted the most publicity are those that have taken place in the vicinity of harbours that accommodate large vessels. Along the Pacific, Gulf and Atlantic coasts of the United States, more than 400 invasions

by non-indigenous species have been recorded (Ruiz *et al.*, 1997), and hundreds more have been reported from other parts of the world. Most of them have taken place in estuarine habitats and have been attributed to the release of ballast water by ships. Another important source of invaders is the community of fouling organisms attached to the hulls of ships. Other alien species have been imported for aquaculture purposes. Some of the alien species have turned out to be pests and have inflicted economic damage, while others have proved to be beneficial. However, an important ecological question is: are marine introductions actually a threat to biodiversity?

Biodiversity is an ambiguous but frequently used term in reference to the relative abundance of life. It has been used to describe many different levels of organization. But, in terms of its use in conservation biology, biodiversity distils down to one simple goal: maintaining the diversity of species (Lomolino *et al.*, 2006). It is most commonly employed to describe abundance at the species level. Therefore, one would expect that a major threat to biodiversity would be in the form of an invading species that would cause the extinction or the expulsion of one or more native species from an area or community. In the terrestrial and freshwater environments, invaders have driven many hundreds of geographically restricted, native species to extinction (Lockwood, 2004). These events have horrified many conservationists and have resulted in the formation of organizations whose primary purpose is to detect and eliminate invading organisms.

A large-scale invasion from the Red Sea to the Mediterranean has been taking place, and it is unusual because most of the documented introductions involve megafaunal species that are usually not attributed to ship traffic. Since the opening of the Suez Canal in 1869, more than 300 Red Sea organisms have invaded and apparently become established. According to the website being maintained by the Mediterranean Science Commission (CIESM), some of the invaders that have been positively identified include 59 fish species, 46 crustaceans and 129 molluscs. Only a few of the interactions between native and equivalent alien species have been studied, but they provide significant results. Along the Mediterranean coast of Israel, two invading goatfish (Mullidae) species *Upeneus moluccensis* and *Upeneus pori* were accommodated by the native species *Mullus barbatus* and *Mullus surmuletis* by means of niche sharing (Golani, 1994). The invading goatfishes appear to dominate the shallow waters while the natives are most abundant below about 55 m.

Many of the invaders from the Red Sea are fishes that have commercial value and their relative abundance over time has been reported in the Israeli fishery statistics. This information has been analysed in a review of fish assemblage changes by Goren & Galil (2005). Nearly half the trawl catches along the Israeli coast, about half the fish biomass in rocky shore habitats and 50–90% of the fishes in shallow sandy habitats, are now of Red Sea origin. The invasions of the barracuda, *Sphyraena chrysotaenia*, and two clupeids, *Dussumieria elopsoides* and *Herklotsichthys punctatus*, were primarily responsible for a shift in trawling activity from deep to near-shore waters of less than 50 m.

Two invasive, herbivorous siganid (Siganidae) species, *Siganus rivulatus* and *Siganus luridus*, comprise a third of the total fish biomass along Israeli rocky shores (Goren & Galil, 2005). Before the arrival of the siganids, the algae entered the food chain by the slow process of decomposition. The siganids grazed on the algae, grew rapidly in numbers, and began to provide the major food source for three species of grouper (Serranidae) (Aronov, 2002). The more rapid turnover of algal resources augmented the production of the large carnivorous fishes and changed the community structure to resemble that of more tropical seas.

Among the invertebrates, the snapping shrimp *Alpheus* provides an example. The immigrant snapping shrimp, *Alpheus rapacida*, occurs between 15 and 50 m, apparently having replaced the native *Alpheus glaber*, which now occurs at depths of 45–145 m (Galil, 1993). It has been noted that the littoral and infra-littoral of the Levantine Basin are dominated by invader species and that the eastern Mediterranean is gradually becoming a Red Sea Province (Goren & Galil, 2005). In his book on biological invasions, Williamson (1996) stated that Suez Canal invaders have not obviously affected the native species. But, the siganid invasion has had beneficial results in terms of an increased production of native carnivorous fishes, and other invaders have also augmented the fishery resources. Apparently no native species have become extinct as a result of the invasions.

Elsewhere, other studies of invading species have shown beneficial effects. In northern Patagonia, the introduced Pacific oyster, *Crassostrea gigas*, increased the population densities of epifaunal and infaunal organisms, and also the feeding rates of local and migratory bird species (Escapa *et al.*, 2004). In the Pacific north-west, the Asian hornsnail, *Batillaria attramentaria*, provided a substrate that was utilized by two other exotic and two native species (Wonham *et al.*, 2005). Along the coast of Chile, invasive bio-engineer species, such as the ascidian *Pyura praeputialis* and the seagrass *Heterozostera tasmanica* have created new habitats for nursery grounds and biodiversity enhancement (Casilla *et al.*, 2005). In the same region, three algal invaders have provided new resources that are exploited by coastal food gatherers.

The effects of exotic species invasions were studied in estuarine, strandline plant communities in Narragansett Bay, Rhode Island, USA (Bruno *et al.*, 2004). Established exotics comprised 79 out of a total of 147 species. Information from 24 sites in the bay indicated that native and exotic species richness was positively correlated and that the invaders appeared to pose little threat to the native plant diversity. The authors concluded that their results did not support earlier predictions of ecosystem damage.

On the other hand, authors of some invader reports have expressed alarm because a few exotic species have proven to be pests that cause economic damage and other exotics have had adverse effects on native populations. For example, the American slipper limpet, *Crepidula fornicata*, was introduced to Europe in the 1870s and has significantly reduced the growth rate and survival of the native blue mussel (Thieltges, 2005). San Francisco Bay has been invaded by an alien green crab,

Carcinus maenas, that has reduced the abundances of several native invertebrates, including a shore crab and two clam species (Grosholz *et al.*, 2000). But, at the same time, there were significant increases in the populations of tanaid crustaceans and two polychaete taxa. None of the recent studies devoted to effects of marine invaders have indicated any species extinctions or loss of biodiversity. So far, it appears that predictions of such losses may not be applicable to the marine environment.

HISTORICAL INVASIONS

Admittedly, it is difficult to forecast the eventual results of invasions that have taken place in recent years. However, the fossil record does provide information about historical invasions and their long-term consequences. The opening of the Bering Strait permitted the Great Trans-Arctic Biotic Interchange that apparently began about 5.4 Ma, but with the bulk of migrations taking place about 3.5 Ma. Information on the Pacific molluscan species that invaded the North Atlantic (Vermeij, 2005a) indicates that at least 143 species colonized European shores while 176 settled in eastern North America. On the American rocky shores, the invaders now comprise the majority of common species. Although the invaders have replaced the incumbents in some of the preferred habitats, apparently none of the natives have been driven to extinction.

The results of the above and one other invasion provide information as to the fate of the invaders that became established. About 47% of the species of Pacific origin in the North Atlantic are now distinct at the species level from their North Pacific ancestors (Vermeij, 2005a). During the early Pliocene to early Pleistocene, 40 southern molluscan species invaded northward into Florida and the surrounding area. All but four or five eventually evolved into endemic species resulting in a rise in diversity for the region as a whole (Vermeij, 2005b). This information suggested that community relationships change as immigrants become assimilated, but most members survive and adapt. This is true because interactions among species tend to be numerous and flexible and adaptations arising from these interactions are often of a general nature and can apply to a variety of circumstances.

Considering that invasions by exotic marine species generally seem to result in increases in biodiversity, one may ask whether such increases are desirable from the standpoint of the invaded ecosystem. Experimental evidence from work on sessile invertebrates indicated that increased species richness significantly decreased the success of invasive species (Stachowicz *et al.*, 1999). More recently it has been observed that the scientific community has come to a broad consensus on the relationship between biodiversity and ecosystem function (Hooper *et al.*, 2005). An important part of the consensus stated (p. 2) that '…having a range of species that respond differently to environmental perturbations can stabilize ecosystem process rates in response to disturbances and variations in abiotic conditions'.

Among conservation organizations, there has developed a kind of militaristic attitude toward invading species, i.e. invaders are bad and must be repelled at all costs. This attitude

is somewhat understandable in view of the many terrestrial extinctions that have been caused by invaders, particularly on oceanic islands. Yet, even in those cases, invasions have generally resulted in an overall increase in biodiversity (Sax *et al.*, 2002). If the primary conservation goal is to preserve biodiversity, then the presence of exotic species does not appear to be detrimental, and often has a positive effect.

CONCLUSIONS

A major difficulty that one encounters in works on the local vs. regional relationships is that the region from which local recruitment supposedly takes place is seldom well-defined. Often there is simply a vague reference to a species pool without any further information. But, the oceanic world consists of recognized biogeographical regions (Briggs, 1995), each of which has an overall distinctive fauna. Moreover, the distribution of species within each biogeographical region is never completely homogeneous. This must be taken into account in the determination of what constitutes a regional species pool, i.e. the composition of the pool will vary depending on the location within a given region. In addition, the regional pool is likely to consist of at least some wide-ranging, dominant species that have come from a centre of origin. If comparisons of local vs. regional diversity are going to be made, they should be between a local community and a regional pool representing that part of the biogeographical region or province in which the community is located, and with due respect to influence from one of the centres of origin.

Local vs. regional relationship represents just one area of research in which ecologists can benefit from a macroecological viewpoint, including biogeographical input. But there are also many examples of biogeographical works that would be better if research at the community level had been taken into consideration. For example, considerable progress has been made that reflects the importance of ecological (sympatric) speciation, yet some biogeographers believe that only allopatric speciation has evolutionary significance. Speciation at the community level may have broad geographical and evolutionary consequences, so it belongs in the realm of macroecology. Similarly, many widespread patterns of extinction probably had their genesis at the community level but subsequently expanded into large geographical areas.

Another area that can benefit from a broader viewpoint is that generally termed 'alien invasions or introductions'. Invader species in coastal and estuarine areas tend to be considered dangerous and often become targets for destruction. There is little doubt that this general attitude is the result of the considerable publicity given to disasters caused by invaders into terrestrial and freshwater areas, especially into restricted areas such as islands and lakes where native species have little room to escape. So the idea that invaders are 'a threat to marine biodiversity' is attributable to well-known events that have occurred in other environments. As far as can be determined, marine invasions by alien species result in increases in biodiversity, not decreases.

In the long run, such increases help create stable ecosystems in which there is a higher level of competition and a greater resistance to invasion. Some invaders are considered to be pests and others are clearly beneficial, but the effects of the great majority are still unknown. So far, there is no reason for individuals or conservation organizations to maintain that marine invasions constitute a threat to biodiversity.

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BIOSKETCH

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