Article

Invasions, adaptive radiations, and the generation of biodiversity

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Received 3 November 2013; *Accepted 8 December 2013*; *Published online 1 March 2014*

Abstract
When the subject of global biodiversity and its loss through human action became a focal point of conservation biology, there developed an increasing argument about the effects of the invasions of exotic species into native ecosystems. In order to place the current contention in a historical context, evidence from the geologic record has been examined. The record clearly indicates that numerous species invasions, extending from the Paleozoic through the Cenozoic, have led to adaptive radiations significantly increasing global biodiversity. Three invasion induced categories are recognized: (1) global radiations, (2) local radiations, and (3) single species effects. Together, the three may account for much of the biodiversity gain that has accumulated in the intervals between mass extinctions. In contemporary time, it has become apparent that exotic species colonizing a native ecosystem rarely cause extinctions. Instead, the invaders are accommodated by the native species that occupy the appropriate niches or habitats. The accommodation process results in a gain in the species diversity of the invaded area. Over time, local diversity gains can result in global gains as speciation among the invaders takes place. The majority of successful invasions occur via migration of species from centers of high species diversity to places of lesser diversity. The result is a dynamic world characterized by constant movement whereby the high diversity centers increase the diversity of outlying regions.

Keywords adaptive radiation; biodiversity; evolution; historic invasions; species invasions.

Environmental Skeptics and Critics
ISSN 2224-4263
URL: http://www.iaees.org/publications/journals/environsc/online-version.asp
RSS: http://www.iaees.org/publications/journals/environsc/rss.xml
E-mail: environsc@iaees.org
Editor-in-Chief: WenJun Zhang
Publisher: International Academy of Ecology and Environmental Sciences

1 Introduction

Adaptive radiation may be defined as the diversification of species to fill a wide variety of ecological niches. It occurs when a single ancestral species gives rise, through repeated episodes of speciation, to numerous kinds of descendents that remain or become sympatric (Lomolino et al., 2010). Although the initial cause is often attributed to development of a key innovation in the ancestral species, that appears to be a simple solution to a more complex process. Simpson (1953) proposed entry into an adaptive zone as a prerequisite for adaptive radiation. An adaptive zone could be entered in one of three ways: (1) evolution of a key innovation, (2) dispersal into a new habitat, and (3) extinction of antagonists. More recently, the causes and significance of the adaptive radiation phenomenon have been widely discussed. Prominent contributions have been a book by Schluter (2000) and a detailed review by Yoder et al. (2010). Currently, such radiations are most commonly attributed to ecological opportunity, meaning a relaxation of selection or an ecological release. While these general terms cover many possibilities, I find Simpson's original subdivisions still appear to be logical and useful.

An important question is, which of the three main causes of adaptive radiation (key innovation, invasion into a new habitat, extinction of competition) is the most important driver of biodiversity increase? This question has not been asked previously because the relationship between adaptive radiations and global biodiversity had not been explored in detail. Judging from observations in the paleontological literature, as well as those on contemporary species, it appears that species invasions are the initial step that precedes evolutionary change. Once a given species finds an advantageous new habitat, it begins the adaptation process which may result in significant or key innovations. Instead of one important driver, there is really a sequence: invasion to evolutionary innovation to radiation. The rapidity and the ultimate extent of the radiation may be influenced by the residual effects of previous extinctions.

Although the term "biodiversity" generally means the diversity of life in the broad sense, it is here employed as a synonym for species richness or species diversity. This is consistent with the meaning of the term in most works dealing with conservation issues. Species that colonize a new ecosystem or environment, as the result of natural or human introductions, are characterized as invasive. Otherwise, they possess no special attributes and may be undesirable or beneficial according to various economic or esthetic standards. Each species needs to be judged on its own merits, not whether it happens to be exotic or native (Davis et al., 2011). Invasive species, whether entering a new unoccupied environment or one that is well populated, appear to follow the sequence noted above. If the environment is unoccupied, there would no native opposition and the invasion would proceed rapidly.

The prevention of biodiversity loss has become the foremost conservation goal of the 21st century. It is the primary concern of many scientists and the focus of action among most conservation societies. The purpose of this paper is to first, explore the biodiversity effects of historic invasions and second, to compare those results to recent knowledge gained about contemporary invasions. The comparison process provides evidence bearing on the vital question of loss or gain in global biodiversity.

2 Historic Global Invasions

Although the following invasions have all been identified in the fossil record, new information exists about most of them and listing them, in order of habitat invaded, should provide a useful comparison when evaluating Recent events. That is, current invasions may take on an added importance when viewed through the lens of history. Information is presented in a sequence: organisms - origin - invasion - time - reference - remarks.

1. Green algae - freshwater - land - 468 to 472 Ma (million years ago) - Rubenstein et al., 2010. Perhaps *the* most important invasion in Earth history. Locality was in Gondwana (Argentina).
2. Progymnosperm seed ferns - swamp - dry land - 385 Ma - Taylor and Taylor, 1993. Gave rise to sister clades of gymnosperms and angiosperms.
3. Angiosperms - equatorial region - high latitudes - 140 Ma - Magallon and Castillo, 2009; Benton, 2010. Major diversity increase took place 125 - 80 Ma.
4. Insects (Hexapoda) - sea - land - 433 Ma - Wheat and Whalberg, 2013. Rapid radiation to possibly two million species.

5. Tetrapod amphibians - aquatic - land - 395 Ma - Niedzwiedzki et al., 2010; Clack, 2012. Clack's review notes the many morphological changes that lobe-fin fishes underwent in order to become adapted to terrestrial life. There is no indication of a key innovation that provided the ability to climb out of the water and survive on land. Brief subaerial exposures (invasions) were apparently followed by a multitude of innovations that provided an increasingly better survival on land. As indicated in the introduction, the process consisted of a sequence: invasion to innovation to radiation.

6. Amniotes - swamp - dry land - 318 Ma - Laurin and Gauthier, 1996. The early amniotes diverged into two lines, one line (Synapsida) culminated in living mammals, and another line (Sauropsida) embraced all living reptiles (including birds). The evolution of the amniotic egg was the ecological equivalent of the development of the seed in vascular plants. In each case, protection of the early embryo from excessive water loss permitted a great invasion into dry, upland habitats.

7. Insects - land - air - 325 Ma - Wheat and Whalberg, 2013. The adoption of flight, and the numerous morphological and physiological changes it required, marked the next invasion into a foreign habitat. It was successful to the extent that more than 98% of modern insects have wings.

8. Pterosaurs - land - air - 251 Ma - Hone, 2012. Pterosaurs, the largest flying animals of all time, were extant from the Triassic until the Cretaceous (251 – 66 Ma). Their decline has been attributed to the rise of the birds, but there seems to be no evidence of direct competition (Prentice et al., 2011).

9. Birds - land - air - late Jurassic? - Brocklehurst et al., 2012; Jetz et al., 2012. There was a strong increase in diversification rate from about 50 Ma to the present.

10. Bats - land - air - 52 Ma - Simmons et al., 2008. Bats (Chiroptera) represent one of the largest and most diverse orders of mammals, accounting for about one-fifth of extant species.

11. Monocotyledon plants - freshwater - sea - 70 Ma - Vermeij, 2004. About 60 extant species.

12. Marine reptiles - land - sea - 250 Ma - Thorne et al., 2011. A major radiation resulted in the long-necked fish-eating eosauropterygians, mollusk-eating placodonts, serpentine thalattosaurs, and stream-lined ichthyosaurs. Marine crocodilians appeared in the Jurassic and mosasaurs in the late Cretaceous (85 Ma). Marine turtles appeared about 150 Ma (Bowen et al., 1993).

13. Sea snakes (Elapidae, Hydrophiinae) - land - sea - 10 Ma - Sanders et al., 2008. The subfamily includes more than 100 terrestrial species plus 60 species of completely aquatic sea snakes. The entire radiation took place within the past 10 Ma. Even more remarkable, the genus *Hydrophis*, with more than 40 species, evolved within the past 5 Ma.

14. Marine mammals - land - sea - 55Ma - Uhen, 2007; Berta, 2012. Mammals did not enter the sea until they had evolved on land for about 300 Myr (million years). Four different lineages (Cetacea, Sirenia, Desmostylia, Pinnipedia) invaded the sea in the Lower Eocene. The whales (Cetacea) evolved into about 70 genera within the following 50 Myr. Living whales include 83 species, pinnipeds 33 species, sirenians 4, and desmostylians 0.

15. Marine insects - freshwater - sea - 45 Ma - Andersen and Cheng, 2004. The genus *Halobates* includes five species of sea striders that are completely oceanic.

3 Global Consequences

Although species diversity in the marine environment showed considerable gains from the Mesozoic through the Cenozoic, despite the loss at the K/T boundary, it failed to keep up with the enormous increase in terrestrial diversity that began in the mid-Cretaceous period. The Cretaceous Terrestrial Revolution (CTR) (Benton, 2010) took place as the angiosperm flora invaded the higher latitudes about 125-80 Ma (Magallo and Castillo, 2009). As the angiosperms dispersed, the advanced eudicots underwent an explosive radiation (Heimhofer et al., 2005) causing a huge increase in primary productivity (Brodripp and Feild, 2010). Beginning about 100 Ma, the eudicot clade increased its biomass production three to four times over that of their earlier relatives (Boyce et al., 2009).

The expansion of angiosperms was accompanied by huge radiations in insects, especially among the genera of Coleoptera, Hymenoptera, and Lepidoptera, along with comparable increases in plant-associated fungi (Vermeij and Grosberg, 2010). The productivity increase of the CTR also had notable effects on vertebrate radiation. For example, the four principal mammalian groups (Marsupialia, Laurasiatheria, Euarchontoglires, Afrotheria) diverged around 90-80 Ma (Meredith et al., 2011). It was during the CTR that biodiversity on land finally exceeded that in the sea, an event called “The Great Divergence” (Vermeij and Grosberg, 2010). Today, there are far more species living on land; in the sea, non-microbial species account for a small fraction of the global total, estimated at anywhere from 2% (Briggs, 1994) to 5% (Benton, 2009) to 15% (May, 1994).

Mass extinctions appear to cause a collapse of ecospace which must be rebuilt to create new opportunities and redirect the course of evolution. After an extinction, there is usually a survival interval during which there is a lack of speciation. This interval is generally followed by a rapid innovation, often consisting of “bloom taxa” that abruptly diversify and then decline. After the K/T extinction, angiosperm plants began to recover their diversity after about 1.5 Myr, and marine productivity returned after a few hundred thousand years (Erwin, 2001). In mammals, several crown-group orders, including Primates and Rodentia, evolved before the K/T boundary, some rose in the Eocene- such as the Perissodactyla and Carnivora- and others in the later Cenozoic. But these diversifications were spread out over considerable time and were not as dramatic as those of the CTR (Meredith et al., 2011). In regard to global biodiversity, it may be observed that mass extinctions produce losses that are not recovered for hundreds of thousands or millions of years. But in the eventual aftermath, rapid speciation takes place in some regions that may effect others by means of species invasion, as will be noted in the case of Cenozoic mammals.

There has been considerable speculation about the evolutionary effects of mass extinctions. These once provided a consistent message that a “wiping out of the old forms to make way for the new” had evolutionary benefits. Eldredge (1987) expressed the firm belief that, without extinctions to free up ecological niches, life would still be confined to a primitive state somewhere on the sea bottom. Stanley (1987) stated, “Had the dinosaurs survived, there is no question that we would not walk the earth today. Mammals would still be small and unobtrusive, not unlike the rodents of the modern world.” The idea that major extinctions convey evolutionary benefits was developed into a new theory of evolution by Hsü (1986). He would substitute the concept of evolution by means of global extinctions for Darwin’s mechanism of natural selection. In his “new catastrophism” evolutionary advances would take place as survivors adapted to spaces created by extinction events. In his view, “it is time to wake up to the absurdity of the idea of natural selection.” Recent advances in paleontology have made these ideas of the 1980s untenable.

4 Historic Regional Invasions

Some palaeontological works have dealt with regional invasions and may have relevance to contemporary events. Patzkowsky and Holland (2007) investigated a Late Ordovician marine biotic invasion linked to a warming event. They found the increase in species diversity caused by the invasion was not ephemeral but lasted for at least 1 Myr. Another Ordovician study (Heim, 2008) found evidence of a global richness equilibrium dictated by a combination of invasion, origination, and extinction rates. But, Devonian studies (Stigall and Liberman, 2006; Stigall, 2012) found a long-term biodiversity decline combined with a preferential survival of invaders and a drop in speciation rate.

In regard to the fossil evidence, it seems to me that recent (Cenozoic) data are more applicable to current invasions than events that took place in the Paleozoic some 300 to 500 Ma. There is the example of the trans-Arctic invasion of molluscs between the North Pacific and the North Atlantic (Vermeij, 2004). That migration took place in the Pliocene about 3.5 Ma and the results are apparent in the living fauna. Invasion into the Atlantic involved 265 species and 24 species invaded the North Pacific. The molluscan fauna of the North Atlantic now consists of large numbers of species that have evolved from Pacific ancestors. In the Northwestern Atlantic,118 species or 45% of the molluscs have such ancestry, indicating a long-term effect of invasions and, via speciation, an increase of global biodiversity. The superior diversity of the Pacific (twice as many molluscan species) and its greater resistance to invasion probably accounted for the difference in invasion success. In each recipient area there were no native extinctions attributable to the invaders.

Another case involves the Miocene to early Pleiostocene molluscan invasions between the Caribbean and Florida (Vermeij, 2005). Some 40 species invaded from the Caribbean, which possessed the richest molluscan fauna, but only four moved in the opposite direction. During the Pliocene, the invasion accounted for almost all of the increase in standing diversity in Florida, and about 90% of the invaders underwent speciation. The long-term consequences of this and many other regional exchanges were enrichment of the local and global species pool.

Aside from the marine examples, there is an extensive literature devoted regional invasions and adaptive radiations by birds, mammals, and amphibians. In regard to mammals, the details of their Cenozoic increase in diversity indicate more than a simple replacement for the dinosaurs. Mammals tended make evolutionary advances in certain regions and then invaded others where they underwent rapid diversification. For example, placental mammals invaded South America from North America, marsupials and rodents invaded Australia from South America and Asia respectively, various African mammals invaded Eurasia, and North American ungulates reached Eurasia (Lomolino et al., 2010). Similar examples may be found among the amphibians where the advanced frogs (neobatrachians) may have originated in Africa-India, salamanders in East Asia, and the caecilians in Triassic Pangaea (Zhang et al., 2005). In regard to birds, rapid local radiations took place in Asia, North America, and southern South America (Jetz et al., 2012). All of these regional invasions and numerous others resulted in immediate gains in local biodiversity, followed by speciation providing long-term gains in global biodiversity.

5 Contemporary Invasions

A review of contemporary invasion ecology was recently published in this journal (Briggs, 2013). It was concluded that, on land and in the sea, invader species added to local diversity. In the sea, it seemed that the addition process must have a competitive component because successful (colonizing) invasions took place almost entirely from areas of high species diversity to those of lesser diversity. On land, various kinds of plant competition had been described but the relationship between regional and local species diversity was not quite as clear. But almost all successful invasions were apparently made possible by accommodations on the part of the native species. The accommodation process can include the provision of space, shelter, or physical support (Briggs, 2010). Although some reference was made to fossil evidence, space did not permit a detailed analysis.

6 Current Opinions

Although the geologic record indicates that biological invasions are a driving force for global biodiversity, such a conclusion may seem incongruous in the light of many current opinions on species invasions. During the past 20 years, invasive species have usually been described in detrimental terms. Queries to yahoo or google about invasive species will bring up a multitude of postings by a variety of organizations, including the

United Nations (IUCN), Wikipedia, Encyclopedia of Earth, UN Environment Program, Global Issues, The World Bank, Institute for European Environmental Policy, U.S. Environmental Protection Agency, Foundation for Research and Sustainable Development, Eco-Question, Green Facts, Eco-Pros, and Actionbioscience. In addition, many individual nations and conservation organizations have web sites emphasizing the danger of invasive species. These sources provide a consistent message saying that nonnative species cause native extinctions resulting in biodiversity loss, as well as various kinds of ecological damage. The organizations and individuals that continue to bemoan biodiversity loss are misleading the public and are directing conservation support away from the real problem, the precarious existence of small populations that are the results of human habitat destruction and over exploitation.

7 Discussion

In light of the present day concern about invasion-caused extinctions and loss of biodiversity, it seemed worthwhile to examine evidence about historic invasions and their biodiversity effects. The greatest adaptive radiations were caused by several invasions that took place in the early Paleozoic. Most of the terrestrial world's present biodiversity can be traced back to the invasions of green plants about 470 Ma, the insects about 433 Ma, and the amphibians about 395 Ma. Beyond these beginnings, there have been numerous subsequent invasions and radiations that have also involved large portions of the globe and, through the millennia, have continued to add to the general biodiversity increase.

After the early Paleozoic, two of the most notable events were invasions of the dry parts of the Earth made possible for: (1) plants by the development of seeds, and (2) vertebrates due to their evolution of the amniote egg. Invasions of the aerial environment induced major radiations in insects about 325 Ma; pterosaurs by 251 Ma; birds by 150 Ma (*Archaeopteryx* or before); and bats by 52 Ma (but perhaps earlier). Terrestrial animals and plants returning to the sea also caused rapid radiations: several clades of Mesozoic reptiles arose about 250 Ma, turtles by 150 Ma, mosasaurs by 85 Ma, mammals by 50 Ma, and sea snakes at 10 Ma.

Contemporary, invasion-caused adaptive radiations have been known to occur on both small and large scales. Many small radiations have taken place in freshwater lakes or on terrestrial archipelagos. Extraordinary assemblages of related species are often called "species flocks" and are known to occur among many different animal groups. Some, such as the cichlid fishes of the African lakes, serve as textbook examples of rapid speciation and diversification (Salzburger and Meyer, 2004). Other species flocks have been detected in marine waters: the gastropod fauna of the Cape Verde archipelago contains 47 endemic and only three nonendemic *Conus* species (Duda and Rolánd, 2005), rockfishes of the genus *Sebastodes* are concentrated in the Northeast Pacific (Johns and Avise, 1998), and notothenioid fishes dominate the ichthyofauna of the Antarctic (Eastman and McCune, 2000). Terrestrial species flocks are numerous including such well known examples as those in the Hawaiian, West Indian, and Galapagos islands. Despite their limited geographic size, these radiations have occurred over many parts of the world and produced endemic species that have made significant additions to the global total. On an even smaller scale are the continuing invasions by individual species. Over 300 species have invaded the Eastern Mediterranean via the Suez Canal (Galil, 2007), more than 200 have become established in San Francisco Bay (Ruiz et al., 1997), and many others are found in estuarine and coastal environments around the world. Contemporary single invasions continuously add to local diversity and, via speciation, have the potential of adding to the global total. All of the foregoing information, both fossil and Recent, provides support to Simpson (1953) who thought that adaptive radiations could explain all of life's diversity, and to Schluter (2000) who observed that much of life's diversity, perhaps even most of it, arose from such episodes.

8 Conclusions

Multiple invasions of animals and plants into contrasting habitats have occurred on a major and minor scale from the early Paleozoic to Recent time, and have made notable contributions to global biodiversity. The land and aerial invasions of the insects, by themselves, accounts for most of the world's terrestrial species diversity. However, the major radiations were not all confined to ancient times. The Cenozoic era, which began 65 Ma, has seen evolution of most modern birds (Neornithes), including the origin of about 9,000 species. Mammalian invasion of the sea, including the origin of the whales, pinnipeds and sirenians, has taken place within the past 50 Myr. Evolution of our present terrestrial mammal diversity, involving numerous regional invasions, also took place within the Cenozoic. The radiation of sea snakes began only 10 Ma.

Over the course of the Phanerozoic, there have been evident decreases in the magnitude of adaptive radiations and the size of their contributions to global biodiversity. This indicates that, despite the setbacks caused by the five major extinctions, radiations became more restricted as ecological opportunity became less. Even so, species invasions leading to biological innovation still occur and new habitats caused by tectonic and climatic changes will continue to become available. Depending on size and complexity, the new habitats will offer platforms for large or small adaptive radiations.

In our dynamic world, species are continually migrating, most commonly from high diversity areas to those of lesser diversity. Species that successfully invade (colonize), add to local diversity. Over time, many of the invaders will speciate, thus increasing global diversity. If we combine the diversity gains produced by the three invasive catagories, i.e., global adaptive radiations, local radiations, and single species effects, that total may account for much of the biodiversity gains that have taken place in the intervals between mass extinctions. The present high level of the world's biodiversity had its beginning with the advent of the CTR which took place 125-80 Ma. The CTR was fueled by a huge increase in primary production provided by angiosperm plants as they invaded the temperate zones of the Earth. The impetus from the CTR continued through the Cenozoic despite a temporary setback caused by the K/T extinction. If we value and protect the individual species that comprise the total biodiversity, it should continue to rise until the next mass extinction. A small minority of invasive species are pests to human endeavors and need to be controlled, but for the sake of biodiversity conservation, it would behoove us to judge each species on its own merits.

The positive contributions of historic and contemporary invasions to global biodiversity may be contrasted to the claims of biodiversity loss that dominate the current literature. These claims have little validity and species invasions, combined with ongoing allopatric, parapatric, and sympatric speciation, are continually adding to biodiversity. The world's primary conservation problem is not the loss of biodiversity, it is the loss of habitat and over exploitation through human activity that has reduced thousands of formerly widespread species to small remnant populations. Many of these vulnerable populations can still be rescued if there is sufficient interest in doing so.

Acknowledgments

I wish to thank E.A. Hanni, M.K. Chew, A.L. Stigall and M. Dawson for discussion and helpful comments.

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