EFFECTS OF DISTURBANCE SIZE AND LOCATION ON EXTINCTION DYNAMICS

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ABSTRACT—Maps showing the modern distributions of 414 species (102 genera) of irregular echinoids were subjected to randomly placed disturbances of variable size, and total species lost per impact were counted. The results show that an environmental impact affecting ≥83% of the earth's surface will always cause a mass extinction, defined as a loss of 50% of the species. Conversely, it takes an environmental impact affecting ≥57% of the earth's surface to cause a mass extinction. The range of impact areas causing a mass extinction is due to the latitudinal gradient of diversity and the restricted diversity around the Caribbean and Malaysia.

Any mass-extinction event found in the fossil record implies an environmental impact. This paper extends the work of Raup (1982), who asked how large an area need be affected by an environmental impact to cause a mass extinction (defined as a loss of 50% of species diversity). Raup (1991) emphasizes extraterrestrial impacts as being a probable cause of mass extinction, but many other causes have been suggested in fossil mass extinctions (Donovan, 1989). The present paper deals only with the aerial extent of the disturbance, so the term impact herein will mean anything that kills individuals. The exact cause of the impact is not specified.

MATERIALS AND METHODS

The geographic ranges of 414 species of modern irregular echinoids were mapped using Ghiold (1989). Then, using randomly generated coordinates, disks representing environmental disturbances covering 11, 43, 78, and 92% of the earth's surface were placed on the coordinates on each of the maps, and the number of species and genera underneath the disks were counted. The assumption was that any species whose range was completely under one of the impact disks was eliminated.The data garnered from these counts, including latitude of disturbance, size of impact, and species and genera eliminated per impact, were tabulated, and graphs were made which were relevant to the species-area problem.

RESULTS AND DISCUSSION

The relationship between the maximum and minimum percentage of species eliminated and the percentage of area of the earth covered by the impact area is curvilinear (Fig. 1); the percentage of species eliminated increases at a faster rate than does the percentage of impact area. A loss of ≥50% of species diversity is commonly quoted as the definition of a mass extinction. Any impact area affecting roughly 83% or more of the earth's surface will consistently cause a mass extinction, whereas an impact affecting ≥57% of the earth's surface is necessary to cause a mass extinction (Fig. 1).

The larger an area of impact, the more species that can be eliminated. However, the ranges of species vary. Some have extremely restricted ranges, with some even being restricted to waters around one island. Others have ranges which span the globe, while still others exist in two distantly separated areas. Species of the latter two would not be eliminated by the smaller impact areas. The larger impact areas not only eliminate species with small ranges and restricted distributions but also those with large ranges and widespread distributions.

The number of species eliminated in any one impact area also depends on the geographical location of the impact area. A comparison of the percentage of species eliminated across different latitudes of the impact area revealed a trend of decreasing percentage of species eliminated as latitude is increased (Fig. 2). The slope of the relationships between latitude and impact areas of 11, 43, and 78% of the earth's surface are -0.0015, -0.0031, and -0.00023, respectively. The 92% impact area had sites only along the equator, so a latitudinal comparison was not possible for that percentage. The negative slopes show that the percentage of species eliminated by impact areas centered in the tropical latitudes (defined as between 20° north and south) is greater than that in impact areas centered at nontropical latitudes. This is due to the greater diversity of species in tropical regions (Stevens, 1992). The larger an impact area is, the greater the chance of it affecting a tropical area, no matter where it is centered. The two larger areas, 78 and 92% of the earth's surface, always affected some tropical waters, and, therefore, a greater percentage of species was eliminated per percentage of area for the larger impact areas than for the smaller areas.

Within the tropics, the species diversity is not evenly distributed. For the irregular echinoids used, there were two areas of higher specific concentration: the waters around the Caribbean; the waters around Malaysia. The larger an impact is, the more likely it is to affect one or both of these areas. In fact, the largest impact area always included both of these geographic areas of highest concentration.

The size of the slopes does not increase with the size of the area of impact. The slope of the line representing 11% of the earth's surface is less negative than for that representing 48%, but both are more negative than the slope of the line representing 78% of the earth's surface. These relationships show the effect of size of the impact area. More species

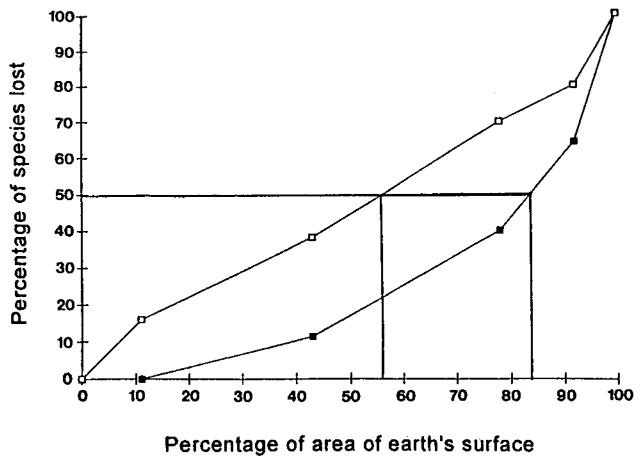

FIG. 1. The maximum (open squares) and minimum (closed squares) probable percentage of species lost for four impact areas (range within 2 *SD* of the mean of the four areas). The line representing a mass extinction is drawn at 50% loss of species.

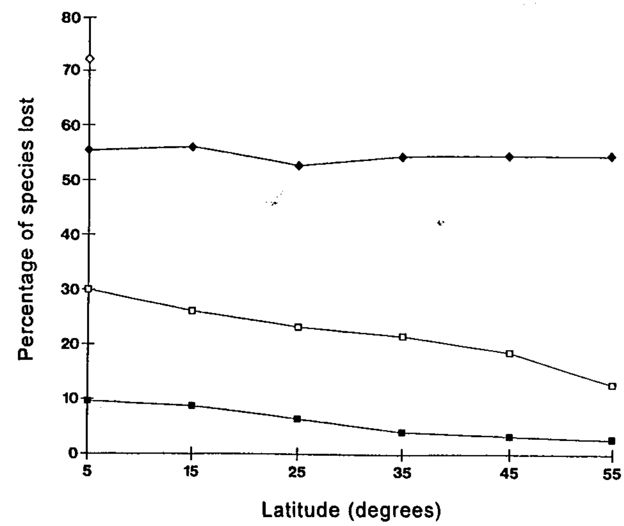

FIG. 2. Percentage of species lost at various latitudes. The open diamond represents an impact area of 92% of the earth's surface; no line was possible since all of its points were on the equator. Closed diamonds represent an impact area of 78% of the earth's surface; open squares represent 43% of the earth's surface; and closed squares represent 11% of the earth's surface.

can be eliminated in the 48% impact area than in the 11% impact area. Even when the 11% impact area includes the most diverse geographic areas of the tropics, only those species with small, geographically restricted ranges can be eliminated. The higher diversity of the tropics affects the percentage of species eliminated in the 43% impact area more than that in the 11% impact area. Because of its sheer size, the 78% impact area, no matter where it is centered, will include the tropics and at least one of the two areas of highest diversity within the tropics. Thus, the slope of its line is less negative than the slope of the line for the 43% impact area.

In order for an impact area of 57% of the earth's surface to cause a mass extinction, it would have to include the tropics and affect either one or both of the two areas of highest diversity within the tropics. Therefore, a mass extinction (50% loss of species diversity) could occur with a minimal global loss of habitat of 57%; however, a mass extinction is more likely to occur when the loss is approximately 70%. Habitat destruction would be much more effective at causing a mass extinction if it included the tropical areas of the world.

There are important implications for the continuing habitat destruction in the world today. For example, approximately 50% of the world's tropical rain forests have been destroyed (Groombridge, 1992). If the area considered in determining the percentage of species loss per percentage of area of the earth's surface is limited to only tropical areas, it becomes apparent that a "mass extinction" of tropical species is imminent at the current rate of habitat loss.

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