APES LARSH NAME:________________________

***Annotate article, answer questions, & read ch.4 at home for Monday's discussion**

Island BioGeography Theory

Why do many more species of birds occur on the island of New Guinea than on the island of Bali? One answer is that New Guinea has more than fifty times the area of Bali, and numbers of species ordinarily increase with available space. This does not, however, explain why the Society Islands (Tahiti, Moorea, Bora Bora, etc.), which collectively have about the same area as the islands of the Louisiade Archipelago off New Guinea, play host to many fewer species, or why the Hawaiian Islands, ten times the area of the Louisiades, also have fewer native birds.

Two eminent ecologists, the late Robert MacArthur of Princeton University and E. 0. Wilson of Harvard, developed a theory of "island biogeography" to explain such uneven distributions. They proposed that the number of species on any island reflects a balance between the rate at which new species colonize it and the rate at which populations of established species become extinct. If a new volcanic island were to rise out of the ocean off the coast of a mainland inhabited by 100 species of birds, some birds would begin to immigrate across the gap and establish populations on the empty, but habitable, island. The rate at which these immigrant species could become established, however, would inevitably decline, for each species that successfully invaded the island would diminish by one the pool of possible future invaders (the same 100 species continue to live on the mainland, but those which have already become residents of the island can no longer be classed as potential invaders).

Equally, the rate at which species might become extinct on the island would be related to the number that have become residents. When an island is nearly empty, the extinction rate is necessarily low because few species are available to become extinct. And since the resources of an island are limited, as the number of resident species increases, the smaller and more prone to extinction their individual populations are likely to become. The rate at which additional species will establish populations will be high when the island is relatively empty, and the rate at which resident populations go extinct will be high when the island is relatively full. Thus, there must be a point between 0 and 100 species (the number on the mainland) where the two rates are equal -- where input from immigration balances output from extinction. That equilibrium number of species would be expected to remain constant as long as the factors determining the two rates did not change. But the exact species present should change continuously as some species go extinct and others invade (including some that have previously gone extinct), so that there is a steady turnover in the composition of the fauna.

That is the essence of the MacArthur-Wilson equilibrium theory of island biogeography. How well does it explain what we actually observe in nature? One famous "test" of the theory was provided in 1883 by a catastrophic volcanic explosion that devastated the island of Krakatoa, located between the islands of Sumatra and Java. The flora and fauna of its remnant and of two adjacent islands were completely exterminated, yet within 25 years (1908) thirteen species of birds had recolonized what was left of the island. By 1919-21 twenty-eight bird species were present, and by 1932-34, twenty-nine. Between the explosion and 1934, thirty-four species actually became established, but five of them went extinct. By 1951-52 thirty-three species were present, and by 1984-85, thirty-five species. During this half century (1934-1985), a further fourteen species had become established, and eight had become extinct. As the theory predicted, the rate of increase declined as more and more species colonized the island. In addition, as equilibrium was approached there was some turnover. The number in the cast remained roughly the same while the actors gradually changed.

The theory predicts other things, too. For instance, everything else being equal, distant islands will have lower immigration rates than those close to a mainland, and equilibrium will occur with fewer species on distant islands. Close islands will have high immigration rates and support more species. By similar reasoning, large islands, with their lower extinction rates, will have more species than small ones -- again everything else being equal (which it frequently is not, for larger islands often have a greater variety of habitats and more species for that reason).

Island biogeographic theory has been applied to many kinds of problems, including forecasting faunal changes caused by fragmenting previously continuous habitat. For instance, in most of the eastern United States only patches of the once-great deciduous forest remain, and many species of songbirds are disappearing from those patches. One reason for the decline in birds, according to the theory, is that fragmentation leads to both lower immigration rates (gaps between fragments are not crossed easily) and higher extinction rates (less area supports fewer species).

Indications of such changes in species composition during habitat fragmentation were found in studies conducted between 1953 and 1976 in a 16-acre nature preserve in Connecticut in which a forest was reestablishing itself. During that period development was increasing the distance between the preserve and other woodlands. As the forest grew back, species such as American Redstarts that live in young forest colonized the area, and birds such as the Field Sparrow, which prefer open shrublands, became scarce or disappeared. In spite of the successional trend toward large trees, however, two bird species normally found in mature forest suffered population declines, and five such species went extinct on the reserve. The extinctions are thought to have resulted from lowering immigration rates caused by the preserve's increasing isolation and by competition from six invading species characteristic of suburban habitats.

Long-term studies of a bird community in an oak wood in Surrey, England, also support the view that isolation can influence the avifauna of habitat islands. A rough equilibrium number of 32 breeding species was found in that community, with a turnover of three additions and three extinctions annually. It was projected that if the wood were as thoroughly isolated as an oceanic island, it would maintain only five species over an extended period -- two species of tits (same genus as titmice), a wren, and two thrushes (the English Robin and Blackbird).

Island biogeographic theory can be a great help in understanding the effects of habitat fragmentation. It does not, however, address other factors that can greatly influence which birds reside in a fragment. Some of these include whether nest-robbing species are present in such abundance that they could prevent certain invaders from establishing themselves, whether the fragment is large enough to contain a territory of the size required by some members of the pool of potential residents, or whether other habitat requirements of species in that pool can be satisfied. To take an extreme example of the latter, a grass-covered, treeless habitat in California would not be colonized by Acorn, Nuttall's, Downy, or Hairy Woodpeckers, even if it were large and all four woodpeckers are found in adjacent woodlands. Ecological theory is designed to help us think about the real world, but it is not a substitute for an intimate knowledge of nature's ways.

Who developed the Theory of Island Biogeography?

Why do larger islands have more biodiversity?

Why do islands closer to the mainland have more biodiversity?

Why would the Theory of Island Biogeography help us understand the effects of habitat fragmentation?