

40,000 or so people go there to marvel at the megaliths. About a thousand Chileans live on Rapanui, employed by the extensive government bureaucracy and taking advantage of the relative prosperity of the island. This has resulted in considerable intermarriage and a blurring of ethnic lines: Over the last four decades of freedom, there has ceased to be a sharp distinction between Chilean and Rapanui; the language of the island is heard rarely in public, and increasingly, Chilean Spanish is the home and school language as well, although official policy is to promote the indigenous culture.

A sign of the vibrancy of Rapanui culture, in spite of the language decline, is the annual “Easter Island Week” (*Tapati Rapanui*) around the end of January or beginning of February; in this festival, nearly every Islander is either on stage or in the enthusiastic audience, and anyone on Rapanui at the time is invited without charge. The celebration is a delight for tourists, but it is not intended for that outsider audience. Instead, it is a cultural production demonstrating Rapanui values and ideals.

The dominant industry for Rapanui is tourism: People will always want to visit the place. The Islanders are excellent guides (since 1722!) and are pleased that people make such sacrifices to visit the place where they live. The rich volcanic soil provides European and some Polynesian crops in sufficient abundance to subsist on a traditional diet, however, and some few Rapanui choose to do just that, leading a simple country life (with selected European artifacts such as clothing), in contrast to their town-dwelling urbanite counterparts, who live by and around the tourist services.

In song and story Rapanui is often called *Tepito ote henua*; it was so called in the 1888 Chilean annexation treaty. In the Rapanui language this name means “the navel [i.e., center] of the Earth,” and in some sense all of us think of the place where we live as being the center of our world at least, but another meaning flavors the place for the Rapanui: “the end of the world”: the most remote place, the last place, even the isolated place. Some rueful Rapanui readily give that sort of translation to the place where they live, work, entertain visitors, and seek to end their days.

SEE ALSO THE FOLLOWING ARTICLES

Archaeology / Exploration and Discovery / Human Impacts, Pre-European / Missionaries, Effects of / Peopling the Pacific

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ECOLOGICAL RELEASE

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Ecological release is the expansion of range, habitat, and/or resource usage by an organism when it arrives in a community from which some members are lacking (Fig. 1); effectively, it indicates the difference between the fundamental and realized niche of a species. The phenomenon has frequently been described for species upon initial colonization of islands, where communities may have lower species diversity, or where the existing predators/parasites are not yet capable of exploiting the newly arriving species. For example, Puercos Island (Pearl Archipelago off Panama) has far fewer species of resident birds compared to the mainland, though the density of individuals is generally slightly higher. Here, island colonists have expanded their habitat (wider ranges of vertical foraging, Table 1); density compensation varies between islands depending on the relative effects of (i) replacement of missing mainland species by island colonists less well adapted to the vacated habitat, tending to lower densities; and (ii) relatively fewer large species on islands, tending to increase population densities.

HISTORIC EVIDENCE AND ADAPTIVE RADIATION

A species radiation almost invariably starts when a population moves into a novel and unoccupied set of niches. In the absence of competitors or predators, the popula-

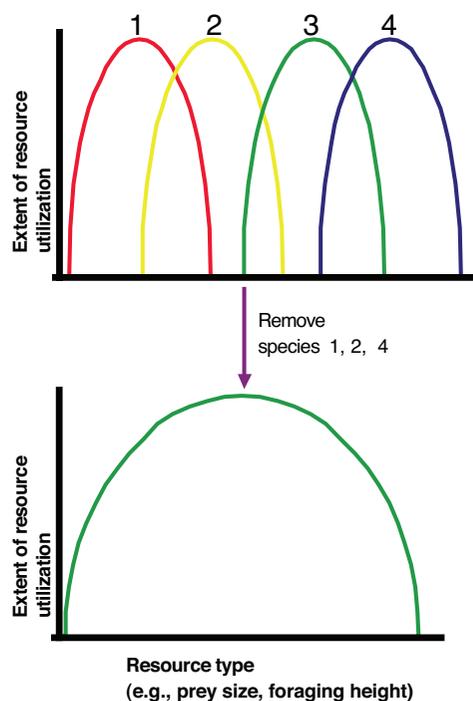


FIGURE 1 Diagram illustrating how ecological release might occur on an island. For species (3), the diagram on the top indicates the realized niche in its original habitat. When (3) colonizes a new area (e.g., an island) from which species (1), (2), and (4) are lacking, it can expand its range to include not only its own niche but also the niches of species (1), (2), and (4), as shown in the diagram below.

tion may undergo ecological release and expand its range, adopting a more generalized habit, the degree to which expansion occurs being a function of preadaptation to that environment. During this period of release, differentiation may occur rapidly as a consequence of diversifying selection (natural or sexual) in the novel and expanded environment.

We can differentiate between two major types of novel niches that a species might colonize at the outset of a radiation: First, new habitat may become available, as in the formation of new (and isolated) islands: Here, colonization is a rare event (because of the isolation), and new arrivals are presented with the opportunity to expand their ecological range (undergo ecological release), which may then allow populations to start diverging. The rate of differentiation will depend on the extent of gene flow between diverging populations and/or the strength of disruptive local selection. Such geographic events may be the most common mechanisms in the initiation of species diversification. Alternatively, species may enter a new “adaptive zone,” either because it was preadapted for a niche(s) that becomes available or because it evolves a

“key innovation,” enabling it to use resources from which it was previously barred. The evolution of key characters or ecological shifts has repeatedly been invoked to explain the initiation of species radiations. Under such conditions a population of a given species may escape the constraints of its current ecological dimension and expand its range across the new dimension (for example, insects may develop resistance to a toxic chemical in potential host plants, allowing them access to an entire suite of new hosts).

After a variable amount of time, the expanded ecological range of the taxon in the new environment will tend to decrease. Reasons for this include (i) enhanced ability of predators or pathogens to exploit the new colonist, leading to reduced numbers in part or all of its range; (ii) competitive displacement from part of its original range by new colonists (close relatives or otherwise); and/or (iii) adaptation of a taxon to different specific local environmental conditions, which may allow evolutionary divergence between populations (and may ultimately lead to adaptive radiation). These tendencies are not mutually exclusive (for example, selection as a result of predation pressure may lead to greater ecological specialization).

Evidence for historic ecological release can often be found in examining phylogenetic histories of lineages that have undergone adaptive radiation: For many of these, the most extensive ecological range expansion has occurred at the outset of the radiation. For example, planthoppers in the genus *Nesosydne* (Delphacidae) are represented by a radiation of approximately 80 species in the Hawaiian Islands. Phylogenetic analysis shows that the lineage diverged from an ancestral group restricted to monocotyledonous plants (especially grasses and sedges) to feed on a total of 28 plant families, mostly dicotyledonous plants, in the Hawaiian Islands.

TABLE 1
Forage Layers of Birds on Puercos

	Puercos	Mainland
Antshrike	3.95	1.24
Wren	3.01	2.55
Yellow-Green Vireo	2.09	1.78
Bananaquit	2.00	1.33

NOTE: On the island of Puercos, off Panama, there are very few antbirds (foliage gleaners) compared to the mainland. Birds on the island have undergone ecological release in habitat and foraging range (height). The table lists the number of layers in which birds were found to forage. From MacArthur *et al.* (1972).

ISLAND COLONIZATION AND TAXON CYCLES

Early studies on land birds showed an increased population density and greater habitat breadth, together with increased diversity of feeding strategies, in birds that had colonized Bermuda, Puerto Rico, and other islands in the Caribbean, as compared to their mainland counterparts. Different studies of ecological release have shown that an island population may occupy a wider range of elevations, more vegetation types, or forage more broadly as compared to the mainland population. However, considerable differences exist between species in their colonization ability and tendency to undergo ecological release. In some groups, ecological release appears to be the first step in a cycle of distributional change following colonization of islands. E. O. Wilson coined the term “taxon cycle” to describe such a progression in Melanesian ants: The ants initially expand their ecological range upon colonization of the island and occur as widespread, dispersive populations (“Stage I”). These give rise to many more restricted and specialized populations (“Stage II”) or species (“Stage III”). Stage I species reflect ecological release; they are “generalist” and dominate in marginal habitats. At Stage II the ants have moved into the forest and specialize on specific substrates. Stage III species show development of the process of becoming local endemics. The concept of the taxon cycle has been adapted for carabid beetles in the related “taxon pulse” hypothesis.

A similar cycle of distributional change has been described for Caribbean birds. Most birds appear to have colonized the islands through a similar process, from ecological release in marginal habitats to more specialized inner forest and montane species. Also, it appears that habitat shifts can intermittently occur in reverse (i.e., from specialized species), associated with colonization of new islands, thus restarting the taxon cycle. As with the broader phenomenon of ecological release, one of the primary drivers of taxon cycles may be coevolutionary responses of predators and prey or of pathogens and hosts: Upon arrival on an island, colonists escape their predators or parasites and expand their ecological amplitude. Over evolutionary time, resident predators or pathogens may adapt to, and hence exploit, the new colonists, which may therefore undergo selection for greater ecological specialization.

INVASIONS

When invasive species first colonize a new area, the rates of population growth and range expansion can vary considerably, with some species showing an immediate and rapid rate of local population growth and range

expansion, whereas others show a long lag time between initial introduction and population growth. Explanations for such a lag time are not well understood. However, once populations of an invasive species start to expand, they frequently undergo ecological release, and this phenomenon has now been well documented. Indeed, successful establishment of introduced species is often attributed to ecological release from competitors or predators/parasites in their native range. A related concept is that of “enemy release,” in which invasive species gain an advantage over native species by escaping many of their natural enemies upon colonization of a new area. Escape from predators and parasites may also explain the frequently observed increased size and vigor of some invasive plants.

SEE ALSO THE FOLLOWING ARTICLES

Adaptive Radiation / Invasion Biology / Taxon Cycle

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ENDEMISM

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Island organisms are often not found elsewhere and are taxa distinct from their closest relatives on continental landmasses. This phenomenon is called island endemism. Island endemics may be relicts (paleoendemics) or may be of more recent origin (neoendemics). The evolutionary processes leading to endemism often involve evolutionary