Chapter Title: OCEANIC ISLANDS
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Book Title: Encyclopedia of Islands
Book Editor(s): ROSEMARY G. GILLESPIE, DAVID A. CLAGUE
Published by: University of California Press. (2009)
Stable URL: http://www.jstor.org/stable/10.1525/j.ctt1pn90r.165

seem necessary for the maintenance of local diversity of oasis animal and plant communities. This system, however, has seen and is currently seeing dramatic changes, directly linked with the socioeconomic changes occurring in some oasis societies. For instance, new types of palm plantations have been established in Tunisia since the middle of the twentieth century as a means of maximizing the production and exportation of dates of the well-known Deglet Nour variety. Those modern palm plantations are actual monocultures of date palm trees, which lack the vegetation structure of traditional oases, notably the stratification of the vegetation. The agricultural production is done by employees and uses modern techniques and tools. Those modern palm plantations do not lead to a sharp climatic contrast between the oasis and the surrounding desert, and they do not host a wild biodiversity as rich as that of traditional oases. Moreover, those new oases are in competition with the traditional ones for limited fossil water. Hence, several springs that were irrigating traditional oases have dried up, leading to severe drought problems for those oases. In addition to these water-availability problems, socioeconomic issues linked with the abandonment of traditional agricultural practices are affecting oasis vegetation structure. The largest of such socioeconomic problems are the non-profitability of traditional agricultural production in the current economic context and the tendency for farmers to focus on a monocultural approach, such as date production, or to switch to more rewarding activities such as tourism and industry; the fragmentation of real estate within the oases over generations; the concurrent tendency for young people to move toward cities and to migrate to Europe; and the fast urbanization of some oases.

Overall, it seems that if oases are created by humans, then their possible disappearance can also logically be caused by humans. The case of oases illustrates how the development of modern agricultural practices, done to maximize profit, can represent an important threat to the biodiversity of precarious agro-ecosystems. As with other island and island-like entities that host specific and sensitive ecosystems, special efforts should be devoted to the protection of traditional oases. In this respect, a sound knowledge of their animal and plant communities is needed to better understand the dynamics of biodiversity in such systems. Any action plan for the conservation of these very original sociohistorical and ecological islands will have to consider the human aspect of things—economic, social, and cultural issues—as well as the physical and biological aspects.

SEE ALSO THE FOLLOWING ARTICLES

Continental Islands / Hydrology / *Lophelia* Oases / Metapopulations / Species–Area Relationship / Vegetation

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OCEANIC ISLANDS

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Those of us who live close to the edges of the world's continents are likely to be familiar with islands, often as places for recreation or retreat. In the past, they were sometimes places of refuge for people or other biota escaping continental calamities ranging from warfare to ice advance. In a geological sense, such islands are commonly slivers of continent, their connections drowned by the high-sea-level conditions in which we live today. Oceanic islands are quite different, often smaller and more remote, and to find them, the continental dweller generally has to travel much farther offshore, into the hearts of the ocean basins.

DEFINING AND UNDERSTANDING OCEANIC ISLANDS

The crust of the Earth is divisible into two distinct types: continental and oceanic. Relative to the ocean surface, the less dense continental crust rests higher—and therefore forms Earth's largest contiguous land masses—than the denser oceanic crust, most of which is covered by ocean. Only rarely does the ocean crust push above the ocean surface and form oceanic islands. Two further differences between the continental and oceanic types of crust are also important to mention.

The first is their age. The continental crust is old—in places as much as 5000 million years old—but the oceanic crust is almost nowhere older than 120 million years in age. The reason for this astonishing difference has, of course, to do with plate tectonics, widely acknowledged as the driver of the evolution of the Earth's surface. The mid-ocean ridges, mostly under water, steadily create new oceanic crust along their axes, pushing it laterally outward. At the other end of this oceanic "conveyor belt," the old oceanic crust is pulled down into the Earth's interior along ocean trenches, eventually perhaps to be regurgitated along mid-ocean ridges. So the oceanic crust is being continually moved sideways: pushed from one end, and pulled from the other.

The second important difference between continental and oceanic crust is composition. Understandably, given that continents have been around so much longer, continental crust is far more diverse in terms of its rock types than is oceanic crust, which—at least at its surface—is rarely anything other than a stack of basalt.

Oceanic islands are bits of the oceanic crust that have somehow reached above the ocean surface. The obvious difficulty of this achievement, given the comparatively short time available (120 million years maximum) and the height involved (perhaps 4 km from ocean floor to ocean surface), explains why there are so few oceanic islands. This in turn explains why, for decades, while geologists explored the continents in minute detail, oceanic islands were marginalized, typically regarded as unremarkable adjuncts to continents or—even more pejoratively—as the detritus left in the wake of drifting continents.

Not surprisingly, then, the earliest ideas about the evolution of the Earth's surface all had a continental bias, and because they effectively ignored the other 73% of the Earth's surface (the ocean basins), they have since been proven largely wrong. Some of the earliest investigations of oceanic islands and, more generally, of the ocean floor can today be read as full of pointers to the critical importance of these features in understanding the formation of the Earth's surface, but it was not until after World War II, when the U.S. Navy (among others) turned some of its resources and expertise to gathering scientific information about the ocean floor, that this breakthrough in perspective occurred. The results of these investigations, which led eventually to the formulation of the theory of plate tectonics in 1967, also underlined the importance of knowing about oceanic islands.

OCEANIC ISLANDS AND PLATE TECTONICS

Plate tectonics envisages the Earth's crust as divided into huge chunks (plates) that are generally rigid, interlocking, and continually moving. Plates include both continental and oceanic crust, but it is only the latter that moves independently. To understand the variety of ways in which oceanic islands form, it is helpful to classify their origin, as in Table 1. At the highest level, this separates oceanic islands formed along plate boundaries from those—far fewer—that form in the middle of plates.

Divergent Plate–Boundary Islands

In the scheme of plate tectonics, a single plate may have a divergent plate boundary—typically marked by a mid-ocean ridge—along which (sea-floor) spreading takes place. This is therefore marked by divergence or extension, and all the world's ocean basins have one main divergent plate boundary, on either side of which ocean floor (and the islands that rise from it) increases in age with increasing distance from the ridge axis.

Islands occur in places where (part of) a mid-ocean ridge rises above the ocean surface, an unusual occurrence best exemplified by Iceland in the North Atlantic.

TABLE 1
Genetic Classification of Oceanic Islands

Level 1 Classification	Level 2 Classification	Examples
Plate-boundary islands	Divergent plate boundary (mid-ocean ridge)	Iceland (North Atlantic) Niuafo'ou (Tonga, South Pacific)
	Convergent plate boundary (island arc)	Lesser Antilles group (Caribbean Sea) Solomon Islands (western Pacific) Sunda arc (Sumatra-Java, eastern Indian Ocean)
	Transform plate boundary	Cikobia (Fiji, South Pacific)
Intraplate (mid-plate) islands	Linear island groups (hotspot island chains)	Hawaii group (northeastern Pacific) Tristan da Cunha–Walvis ridge (South Atlantic) Réunion-Laccadive (Indian Ocean)

Here there is a plate triple junction where high heat flow has elevated the ocean floor, causing part of it to emerge above sea level. Much of what has been learned about divergent plate boundaries comes from Iceland, but there are smaller divergent plate-boundary islands. Among these are the island Niuafoʻou (Tonga) in the Southwest Pacific, whose doughnut shape is a result of a stretched caldera that has become filled with water and forms Lake Vai Lahi.

FIGURE 1 Oceanic islands forming. (A) The summit of Kavachi volcano in Solomon Islands lies 50–100 m below the ocean surface, but when it erupts, as here in October 2002, it forms a conspicuous sight. Kavachi occasionally forms islands, but these are short-lived, being eroded by waves when the eruption ends. (Photograph by Corey Howell). In 1453 the giant Kuwae volcano in Vanuatu blew itself to pieces in one of the largest eruptions by volume in the last 10,000 years. Today, an undersea caldera lies where Kuwae once stood, and occasionally a smaller volcano named Karua that has grown up from the caldera rim erupts. The eruption shown occurred on February 22, 1971, (B) and formed an island one day later (C). (Photographs by Don Mallick, used with permission of the Vanuatu Cultural Centre.)

Convergent Plate–Boundary Islands

As well as a divergent boundary, a plate may also have a convergent boundary, one type of which involves an oceanic plate pushing down into the Earth's interior beneath another oceanic plate. In terms of island formation, these are the most productive places in the ocean basins. This ocean–ocean convergent plate boundary is generally marked by an ocean trench with parallel lines of islands, sometimes along both sides. Ocean trenches are asymmetrical, with the more gently sloping side being that of the downgoing plate, and the steeper side—along which collapses often occur, generating tsunamis—being that of the overriding plate.

Along convergent plate boundaries, islands can form and emerge in one of three locations: along the volcanic island arc on the overriding plate, along the non-volcanic island arc on the overriding plate, or along a crustal flexure on the downgoing plate.

VOLCANIC ARC ISLANDS

At a convergent plate boundary, the downgoing plate is pulled down into the Earth's interior, where—because of the intense heat—it melts. The liquid rock (magma) is lighter than the solid rock, so it tries to rise back to the Earth's surface. Where it succeeds, it will erupt on the ocean floor and may eventually build a line of volcanoes (which may grow into volcanic islands) parallel to the associated ocean trench. The composition of the volcanic rocks in these islands can be linked to the type of material being pulled down into the trench, particularly whether or not this includes significant amounts of the sediments that accumulate in the bottoms of trenches.

Because ocean trenches are usually arcuate in plan, the lines of associated volcanic islands are likewise arc-shaped; hence, they are referred to as volcanic island arcs. Examples come from the Caribbean (Lesser Antilles) and western Pacific (Marianas–Izu). In youthful volcanic island arcs, there are typically many underwater islands; some of these occasionally erupt just beneath the ocean surface, making their presence manifest (Fig. 1A), and may form islands of unconsolidated pumice that are washed away when the eruption ends (Figs. 1B and 1C).

Under many volcanic island arcs, particularly when they have grown comparatively large, much of the rising magma may not reach the surface of the crust, so it solidifies below it and forms intrusive igneous rocks. Recent work, particularly in the Canary Islands, has demonstrated that the importance of intrusive rocks to the growth of oceanic islands in such locations is far greater than once suspected.

ISLANDS OF NON-VOLCANIC ARCS

It is clear that, along convergent plate boundaries in the ocean basins, not only is one plate being pulled down, but the other is being thrust upward over the top of it. This overriding plate is therefore being pushed not only sideways but also upward as it rides over the downgoing one, a process that is amplified when the surface of the downgoing plate is highly irregular.

The uplift of the overriding plate often causes its edge to emerge above sea level, typically producing a line of islands, parallel to both the volcanic island arc and the adjacent ocean trench (Fig. 2A). Although these islands have volcanic basements, when they emerge, the basements are draped with thick piles of ocean-floor sediments. If they emerge within the coral seas, the emergent islands will commonly exhibit a thick cover of coral reef, testimony to their journey through the uppermost layers of the ocean. Examples include parts of several larger Caribbean islands (Hispaniola, Jamaica, Puerto Rico), the Mentawai Islands of Indonesia, and islands such as Choiseul in the northern Solomon Islands in the western Pacific.

Such islands are generally not visibly volcanic, and therefore form a non-volcanic arc, distinct from its volcanic counterpart, which is farther away from the trench axis. Some of the most distinctive types of non-volcanic islands of this kind are those whose form is that of a staircase of broad limestone steps, each of which represents an emerged coral reef. The highest emerged coral reef is expected to be the oldest—the first to emerge above sea level—whereas the lowest is the most recent (Fig. 2B).

ISLANDS ALONG THE CRUSTAL FLEXURE ON A DOWNGOING PLATE

Oceanic crustal plates are stiff, 15-km thick slabs of solid rock that naturally resist being forced upward or downward at convergent plate boundaries in the ocean basins. One clear manifestation of this resistance to be found on the downgoing plate is the way in which it rises upward slightly before being thrust down. This upward rise produces a flexure (or bulge) in the ocean floor up which submerged islands rise and sometimes poke their heads above the ocean surface when they get close to the flexural crest. Thereafter, it is all downhill, with many formerly emergent islands being pulled down into the bottoms of the ocean trenches where they are eventually dismembered and destroyed. Examples associated with the Tonga trench in the southwestern Pacific include the emergent island Niue, which is rising up the flexure, and the underwater Capricorn seamount, which is presently on its way down the trench slope.

It is rare to have a line of islands form along the crustal flexure on a downgoing plate, because usually not very many seamounts (or guyots) are appropriately positioned, but some do occur. One of the best-studied examples is the Loyalty Islands of New Caledonia in the southwestern Pacific. Of these, the largest (Maré) is close to the flexural crest, whereas the two smaller ones (Ouvéa and Lifou) are on their way upward.

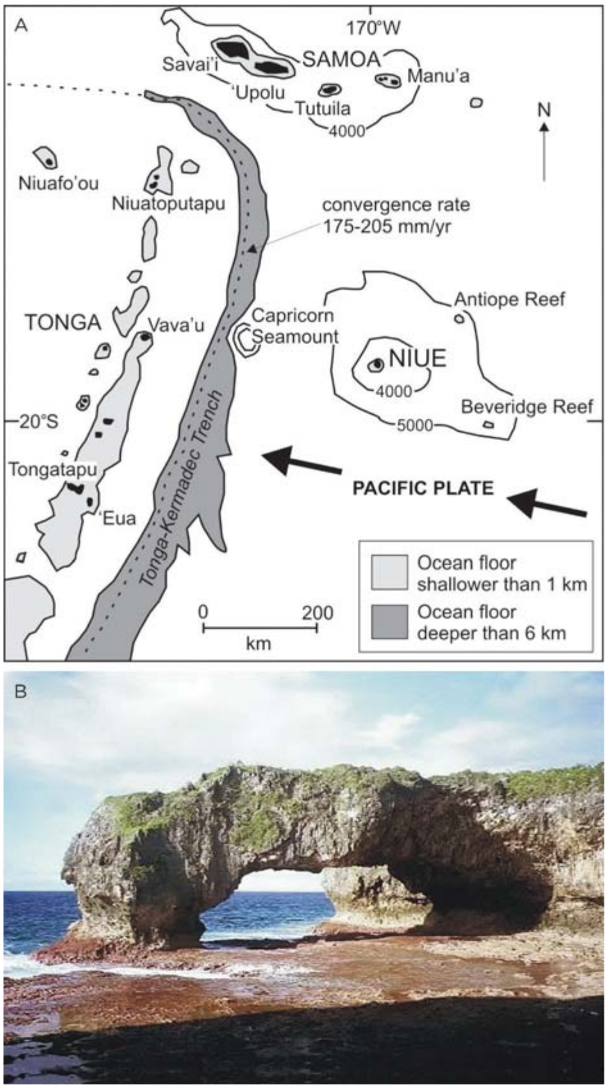

FIGURE 2 Islands close to convergent plate boundaries. (A) Map of part of the South Pacific showing the form of the ocean floor in the area where the Pacific plate in the east is converging with the plate in the west along the Tonga–Kermadec Trench. The non-volcanic arc is represented by a line of high uplifted reef-limestone islands from ʻEua in the south through Vavaʻu to Niuatoputapu in the north. The volcanic arc runs parallel 30–50 km to the west. To the east of the Tonga-Kermadec Trench, Niue Island is rising up the crustal bulge, whereas Capricorn seamount is on its way down into the trench. Niuafoʻou Island formed along a small divergent plate boundary, whereas the Samoa islands are a chain of hotspot islands. (B) View of the Talava Arches in northwest Niue Island. The flat top is formed by the emergence of a fringing reef since the last interglaciation about 120,000 years ago. (Photograph by the author.)

Transform Plate–Boundary Islands

If a rectangular plate has one divergent boundary and one convergent boundary, then its movement (from divergent to convergent) is fixed, which means that the other two boundaries can be neither of these. They are, in fact, places where one plate slides past an adjoining plate, theoretically with no net divergence or convergence: a type of boundary termed transform (or strike-slip). These are notorious as sites of large earthquakes—the San Andreas Fault is the best-studied—but they are not generally thought of as places where islands form.

Islands form along transform plate boundaries only where there are slight irregularities (kinks) in these that lead to localized convergence. The Fiji island of Cikobia may be an example of just such an island, formed at a kink in the Fiji fracture zone, a transform plate boundary in the southwestern Pacific.

Linear Groups of Intraplate Islands

Away from the edges of oceanic plates, in places where crustal quiescence rather than crustal activity is the norm, islands also form, although these are generally smaller and fewer and have less complex histories than their plate-boundary counterparts. Most such islands occur in approximately straight lines, something much remarked upon in early accounts of oceanic islands. Later work showed something even more remarkable: namely, that the age and size of these islands generally increased uniformly from one end to another of the island chain. And at the younger, larger end, there always seemed to be an active volcano.

The combination of these observations led to the formulation of the hotspot hypothesis, the idea that lines of intraplate islands were produced when an oceanic plate passed over a hotspot—a fixed place in the Earth's crust thin enough for underlying magma to punch its way through to the surface. The movement of the oceanic plate led to the volcano over the hotspot being gradually pulled away from it, eventually becoming extinct and being replaced by another volcano. In time, this process gives rise to a line of volcanic islands whose age increases with greater distance from the hotspot and that will slowly subside and thereby become smaller (Fig. 3).

Lines of hotspot islands are common in intraplate locations and include the Hawaii–Emperor island and seamount chain in the northern Pacific and the Samoa–Tuvalu island chain in the central Pacific. Réunion Island in the Indian Ocean and Tristan da Cunha Island in the South Atlantic are both volcanic islands built on top of active hotspots.

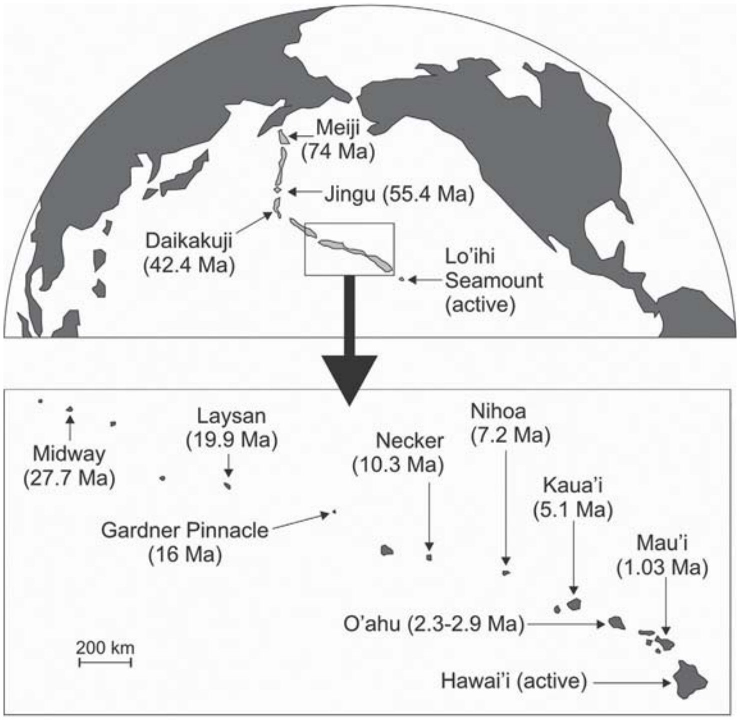

FIGURE 3 Ages of the most recent eruptions of island volcanoes along the Hawaii–Emperor island seamount chain (dates in millions of years ago). The upper map shows the location of the Hawaiian Ridge within the northern Pacific, and the oldest part of this hotspot chain (Meiji Seamount: 74 million years old). The lower map shows the younger, largely emerged part of the island chain from Midway Atoll (27.7 million years old) to still-active Hawai'i Island. Note the presence of newly active Lo'ihi Seamount, which is growing directly above the hotspot while Hawai'i moves away from it.

VARIETIES OF OCEANIC ISLANDS

The classification of oceanic islands given in Table 1 tells us about island origins but not necessarily about the way these islands look now. This is far less easy to generalize about systematically because various processes have caused islands to emerge or submerge relative to the ocean surface (which itself changes), irrespective of their origin. Thus, current appearance is an unhelpful guide to the origin of an island. But it is something worth knowing about, not least to help explain the nature of island biotas and—something highly topical at present—the vulnerability of particular oceanic islands to erosion, even erasure, by sea-level rise.

Every oceanic island began life as an ocean-floor volcano, but not all retain an immediately recognizable volcano form. When we look at the appearance of oceanic islands, three major groups can be identified: volcanic islands, high limestone islands, and atoll islands. There are other, more complex, types, often composites of volcanic rock and limestone, but their environments are generally reflective of the dominant rock types.

Volcanic islands vary in appearance depending largely on their lithology (rock type composition) and their age. Basalt volcanoes that form over very productive hotspots, for example, tend to involve huge volumes of moderately viscous material piled up in shield volcanoes—by far the most common type on Earth—in a series of comparatively low-energy, effusive eruptions. In contrast, andesite volcanoes tend to be much steeper sided—a reflection of the high viscosity of the eruptive material—and to erupt comparatively explosively. In a similar fashion, youthful—maybe even active—volcanoes form islands that generally betray that fact, whereas older (long extinct) volcanic islands may have been thoroughly disguised by post-eruptive denudation and flank collapse.

Limestone is a rock that forms only beneath the ocean surface, so a high limestone island has by definition emerged. For this reason, the form of limestone islands tends to broadly reflect the flat-topped form of undersea deposits. Sharp risers (slopes) to the next flat surface indicate successive periods of island emergence.

Atoll islands (motu) are distinguished by their comparative lowness—they usually rise no more than 3 m above sea level—and their transient nature. Part of this is because they are largely composed of unconsolidated sediments that are comparatively easy for the sea to remove.

Oceanic islands are more numerous in the warmer parts of the world's oceans than in the cooler parts. This is because in the former exist coral reefs, which can build up above a sunken volcanic island. It is a moot point whether living coral reefs actually constitute an oceanic island because they cannot generally grow above low-tide level, yet on almost every reef, there are accumulations of debris, swept up from below sea level by waves, that indeed reach above it—and in some parts of the world form islands large enough to be habitable by humans. Such islands—commonly called motu—are accumulations of largely unconsolidated sand and gravel, typically cemented by beachrock or phosphate rock along their fringes.

LIFE CYCLES OF OCEANIC ISLANDS

For anyone who is interested in explaining the distribution of islands in the world's ocean basins, it makes no sense to confine a survey to those islands that are currently emergent (above sea level): There are many "islands" whose summits lie below the ocean surface.

Some of these islands may have once been emergent but have since subsided (sunk) and/or been drowned as a result of sea-level rise. Traditionally these islands are classified as guyots, characterized by a flat top beveled by wave erosion as the island was slowly submerged.

Conversely, there are many islands that rise from the ocean floor but have not yet pushed their heads above the ocean surface. Some may do so eventually, and some not. Irrespective of whether they attain the surface, they should be included in any survey of oceanic islands. Such islands are generally referred to as seamounts, characterized by a conical form, attesting to their volcanic origins.

As noted above, in contrast to continental crust, oceanic islands are transient entities, never more than 120 million years in age and rarely emergent (above sea level) for even 50% of that time. Of course, there are exceptions, including oceanic islands that have become scraped off along continental margins and now lie far above the reach of the ocean, their insides exposed for all to see. Good examples are found in the accreted Wallowa terrane (Oregon) and others along the western side of the North American continental core.

There are three main external influences on the life cycles of oceanic islands: first, island tectonics—the rises and falls of the island itself; then islands and sea-level changes; and finally, island landscape evolution.

Oceanic-Island Tectonics

In any part of the world, the solid Earth's crust can rise and fall, but in the ocean basins these processes are more widespread and are a major cause of oceanic island emergence and submergence. Long-term uplift and subsidence also affect islands as a result of changing water loads on the ocean crust. Particularly following land-ice melt during deglaciation, rapid inputs of water into the oceans can cause the ocean floor to deform. Yet the principal cause of individual island emergence and submergence over shorter time periods is vertical tectonics—movements of the Earth's crust resulting from the accommodation of stresses associated with plate movements.

The process of crustal rise is known as uplift, and many oceanic islands have been uplifted, especially near convergent plate boundaries. Uplift can be continuous, in which case it is usually slow; Maré Island in the Loyalty Islands of New Caledonia in the southwestern Pacific has been climbing the crustal flexure (described previously) at rates as high as 1.9 mm/year during the last half million years or so. Uplift can also be sporadic, however. This uplift type is typified by rapid bursts of uplift during large-magnitude earthquakes, typically causing ground level to rise 1–2 m, and is termed coseismic uplift. Yet between these infrequent bursts of coseismic uplift, there is often slow subsidence, so the net uplift over long time periods may be comparatively slow. A recent example comes from Ranongga Island in the Solomon Islands in the southwestern Pacific where, early in the morning on April 2, 2007, a large earthquake raised up the entire island 2 m exposing the surface of its fringing reefs. A similar event happened during the December 26, 2004, earthquake in Indonesia (which caused the devastating tsunami) when Simeulue Island off the coast of Sumatra was raised 1.5 m in a few minutes.

Subsidence can also be rapid and abrupt, perhaps coseismic, but more often it is an expression of the gravity-induced collapse of an island's flanks. On Hawai'i Island, during the Kalapana Earthquake on November 29, 1975, a 60-km stretch of the south coast sank 3.5 m and moved seaward some 8 m, causing a 10-m-high tsunami. Yet far more common among the global population of oceanic islands is slow, continuous, monotonic subsidence, typically the outcome of an island being carried on a moving plate into deeper water. Thus, islands that move away from the mid-ocean ridges or from hotspots usually subside as the underlying oceanic crust cools and comes to lie at increasing depths below the ocean surface. Some of these rates of subsidence are minute but continue for extremely long periods of time; the atoll island Enewetak (Marshall Islands, northwestern Pacific) has been sinking at an average rate of 0.03 mm/year for 45 million years.

Oceanic Islands and Sea-Level Changes

By comparing the maps of islands in the southwestern Pacific 18,000 years ago, when sea level was around 120 m lower than it is today, with maps from the present (Fig. 4), it is possible to get a sense of just how important sea-level changes are in causing islands to alternately emerge and submerge. Over the past 2–3 million years, sea level has oscillated between glacial (ice-age) low stands and interglacial high stands every 100,000 years or so. Today, in the middle of the Holocene interglacial period, which began around 12,000 years ago, we live in a drowned world; the ocean surface is higher than it has been for around 95% of the past 150,000 years. Thus, islands are far rarer today than they were during the last glaciation, something that has implications for various types of biota (including humans) that have dispersed across the oceans, as well as for islands themselves.

An island that is submerged is immune from many of the processes of erosion that affect its subaerial counterparts. Conversely, it also ceases to be a viable habitat for terrestrial biota, meaning that it has to be recolonized if it emerges again. Moreover, the process of alternate submergence and emergence may affect the stability of an oceanic island through the successive application of pressure and then the abrupt release of that pressure, which can accelerate the large-scale collapse of steep island flanks.

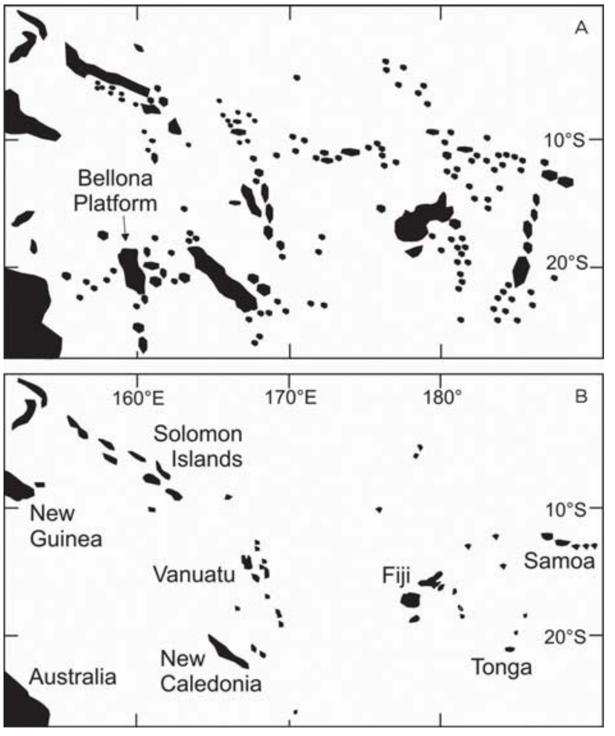

FIGURE 4 The changing geography of the southwest Pacific. (A) About 20,000 years ago during the lowest sea level (–120 m) of the last glaciation, much more land was exposed in this region. Note particularly the large island between New Caledonia and Australia, marked by the Bellona platform from which a few isolated reefs rise today. (B) The modern geography of the region for comparison.

Landscape Evolution on Oceanic Islands

Landscape evolution on oceanic islands is—as it is on continental landmasses—controlled largely by climate and lithology (rock type), and it is therefore difficult to generalize about. That said, it is clear that oceanic islands, largely because of their discrete nature (their boundedness) and their steep-sidedness—itself the outcome of their oceanic location—are susceptible to quite different processes of landscape evolution from those that operate on continents.

In terms of their discrete nature, it is the fact that most oceanic islands are comparatively small and not part of larger land masses that makes their landscapes evolve in isolation. Thus, for example, oceanic islands in the trade wind belts may have well-defined wet and dry sides, where different sets of geomorphic processes operate. Many oceanic islands are, on account of their comparative smallness, entirely coastal, which means that ocean-driven processes affect the entire island; thus, it may change far more rapidly as a result.

Next, there is the issue of the steep-sidedness of many oceanic islands, something that results from their having grown upward from the deep ocean floor. Like steep slopes anywhere, those that form the flanks of such oceanic islands are more prone to failure (collapse) than are gentler slopes, a process that is exacerbated for some islands by earthquake activity. The geological record is full of incidences of island flank collapse, ranging from the uncommon gigantic ones—such as the 5000-km^3 Nuʻuanu Slide on Hawaiʻi Island 2.1 million years ago—to more frequent, yet smaller, ones. Contained in the sedimentary (underwater) apron that surrounds the Marquesas Islands of the central eastern Pacific, there is many times more volcanic material than there is in the modern islands, suggesting that earlier islands collapsed and rebuilt themselves several times in the past.

SEE ALSO THE FOLLOWING ARTICLES

Coral / Earthquakes / Island Arcs / Island Formation / Plate Tectonics / Sea-Level Change / Volcanic Islands

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ORCHIDS

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Assisted by their dustlike seeds, orchids are among the first plant families to colonize islands, often speciating into the many unexploited niches on newly formed or newly disturbed islands. Reduced (or at least temporarily reduced) competition on some islands may allow more radical evolutionary shifts, as well as the establishment of new relationships between an orchid lineage and its necessary partners—animals for pollination and mycorrhizal fungi for germination and nutrition. Furthermore, the tendency of orchids to be pollinator-limited, and thus to occur as small populations, has resulted in orchids frequently evolving through founder effect and genetic drift.

SEED DISPERSAL

Orchids are well known for producing vast quantities of seeds, in some cases several million. This did not go unnoticed by Charles Darwin, who painstakingly recorded around 6200 seeds from a single capsule of *Orchis* (now *Dactylorhiza*) *maculata*. In his classic book *On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects, and on the Good Effects of Intercrossing* (1877) he stated whimsically that

> To give an idea what the above figures really mean, I will briefly show the possible rate of increase of *O. maculata*: an acre of land would hold 174,240 plants, each having a space of six inches square, and this would be just sufficient for their growth; so that, making the fair allowance of 400 bad seeds in each capsule, an acre would be thickly clothed by the progeny of a single plant. At the same rate of increase, the grandchildren would cover a space slightly exceeding the island of Anglesea; and the great grand-children of a single plant would nearly (in the ratio of 47 to 50) clothe with one uniform green carpet the entire surface of the land throughout the globe. But the number of seeds produced by one of our common British orchids is as nothing compared to that of some of the exotic kinds.

The exceptional dispersibility of dustlike orchid seeds in air currents over considerable distances has allowed successful colonization of islands hundreds or thousands of kilometers from the nearest seed source. Also, unusually for flowering plants, orchids have pollen that on average travels a shorter distance than the seed. However, most orchid seeds fall close to the mother plant. Orchids, particularly tropical species, are often pollinator-limited, resulting in low levels of fruiting success. Hence, tropical orchids have on average considerably lower fruiting success than do temperate species. In addition, many temperate species have several characteristics that maximize reproductive success under conditions of infrequent pollination.

COLONIZATION OF ISLANDS

Seed dispersal is only the first step in the successful colonization of an island. The seed must fortuitously land in a suitable place to germinate, on a surface that provides at least one compatible mycorrhizal fungal associate. An immigrant orchid seed may face not one fungally mediated barrier to colonization but two. There is an increasing body of evidence suggesting that, in many orchids, a member of one group of mycorrhizal fungi is necessary for successful