giant ocean island volcano collapses are rare, with a worldwide frequency of known events of around 1 every 20,000 years. Lateral collapses at island arc volcanoes are smaller, with volumes usually in the range of 1–10 km³, but they occur much more frequently. The most recent island arc volcano lateral collapses occurred at Ritter Island in 1888 and at Oshima-Oshima in 1741 (Table 1).

LANDSLIDE HAZARDS AND ECOSYSTEM EFFECTS DUE TO LANDSLIDES AT ISLANDS

In addition to destruction of areas covered by landslides themselves, large landslides at islands, especially volcano lateral collapse landslides, produce destructive tsunamis when they enter the ocean. Well-documented tsunamis produced by events such as the 1741 Oshima-Oshima and 1888 Ritter Island collapses provide key evidence to support computer models that predict catastrophic ocean-wide tsunamis as a result of giant ocean island volcano collapses. More locally, volcano collapses such as that of Ritter Island in 1888 can eliminate the pre-collapse island ecosystems, leading to instances of island recolonization.

SEE ALSO THE FOLLOWING ARTICLES

Canary Islands, Geology / Island Arcs / New Guinea, Geology / Taiwan, Geology / Tsunamis

FURTHER READING


LAND SNAILS

BRENDEN S. HOLLAND
University of Hawaii, Manoa

Land snails are surprisingly adept at dispersing across vast stretches of open ocean, a fact supported by their presence on virtually all tropical and subtropical islands globally. Island snail radiations make fascinating subjects for the study of biogeography and diversification, as many archipelagoes have well-developed and diverse endemic snail faunas.

WHAT MAKES A SNAIL A SNAIL

Land snails are familiar molluscs with several characteristics that make them easily identifiable. They usually have paired eyes located at the tips of tentacles, a second pair of sensory tentacles, and a single, coiled shell into which the animals can generally withdraw their soft bodies for protection from predators and desiccation. Beneath the head is a mouth equipped with a radula, a highly specialized, elongated, rasping tongue-like organ used to scrape plant or fungal material, or in some cases to bore holes in the shells of other molluscs. Hard, calcified snail shells are secreted by a specialized layer of tissue called the mantle. Most snails have a flattened, muscular, tapering foot on which the animals glide.

Land snails typically dwell on the ground or in or under bushes, shrubs, or trees; feed on decaying organic matter; and deposit eggs on or in damp soil. Taxonomically, snails are members of the Gastropoda, a globally distributed class that contains more species than all of the other classes in the phylum combined.

The often drab coloration of familiar snails from temperate continental Asia, Europe, and North America, with the notable exception of a few taxa, such as the Cepaea species of Europe, contrasts dramatically with the often beautiful, brightly colored, and intricately patterned and banded shells of many island snails, such as tropical tree-dwelling groups like the Achatinellinae of the Hawaiian Islands, Amphidromus spp. of Indonesia, Liguus spp. and Polyfusita spp. of Cuba, Pupauna spp. of Melanesia, and...
Partulidae of French Polynesia and the islands of the South Pacific (see Figs. 1 and 2 for selected examples).

**DIVERSITY OF ISLAND SNAILS**

Island snail diversity and biogeography have fascinated biologists since the time of Darwin, who wrote in a letter to A. R. Wallace in 1857, “One of the subjects on which I have been experimentising and which cost me much trouble, is the means of distribution of all organic beings found on oceanic islands and any facts on this subject would be most gratefully received: Land-Molluscs are a great perplexity to me.” In spite of weak active dispersal, a relatively sedentary lifestyle, and minimal seawater tolerance, a number of land snail families have distributions that span ocean basins. In fact, land snails constitute some of the major terrestrial species radiations on oceanic islands, offering excellent opportunities for the study of historical biogeography, microevolution, and the diversification of insular lineages. Examples of island snail species diversity estimates include the Canaries (350), the Caribbean (1200), the Galápagos (100), the Hawaiian Islands (750), the Marquesas (300), Micronesia (400), New Guinea (1000), New Caledonia (400), the Ogasawaras (100), Pitcairn (30), Rapa (100), Rota (40), the Samoan Islands (100), and the Society Islands (200).

The broad distribution of snails on oceanic Pacific islands contributed to the development of early biogeographic theories including the “mid-Pacific continent”

**FIGURE 1** Images of a number of conspicuous endemic island land snail shells from several Pacific diversity hotspot regions including Melanesia (New Guinea with over 1000 species) and Polynesia (Hawaiian Islands with over 750 species). A number of species represented are extinct, some are endangered, and the remainder are surviving but threatened. These images are shown at approximately accurate relative sizes and provide just a hint of the tremendous diversity and dazzling beauty of endemic island land snail faunas. Species identifications and geographic origins are as follows: (A) Placostylus albersi, New Caledonia; (B) Papuina micans, Solomons; (C) Placostylus hargravesi, Solomons; (D) Achatinella decipiens, Oahu; (E) Placostylus strangell, Solomons; (F) Achatinella fulgens, Oahu; (G) Laminella sanguinea, Oahu; (H) Oxio sp., New Guinea; (I) Parahylyda dictyodes, New Caledonia; (J) Papuina pulcherrima, New Guinea; (K) Trocomorpha sp., Fiji; (L) Carelia sp., Kauai; (M) Carelia sp., Kauai; (N) Amastra spirzona, Oahu; (O) Succinea kuhnii, Hawaii; (P) Papuina mendana, New Guinea; (Q) Partulina proxima, Molokai; (R) Papustyla hindei, New Guinea. All photographs by B. S. Holland. See also Fig. 2.
hypothesis, which proposed that a massive continent stretching across the South Pacific had once existed and had subsequently sunk beneath the ocean.

Origins of most island snail faunas are poorly understood. Multiple dispersal events from multiple geographic source regions, in which the nearer the potential geographic source, the higher the probability of colonization, is thought to be the predominant mode of origin for oceanic island snail faunas. Rafting attached to drifting tree trunks and other floating items, aerial dispersal including by tropical storms and hurricanes, and transport attached to birds have all been suggested as mechanisms of dispersal to and among oceanic islands. For long-distance dispersal, most malacologists agree that rafting is not likely to have been an important passive vector because of a general inability of land snails to tolerate saltwater. Small stones and pebbles of the mass of certain snails have been sampled in aerial plankton studies. Transport of land snails attached to the feet and feathers of migratory birds has been documented. To complicate the understanding of dispersal pathways and history further, founding propagules may not have originated on islands that are currently emergent but may have come from those that, because of erosion and or subsidence, no longer exist.

The dynamic geological and climatic processes that build up, tear down, and profoundly transform volcanic islands have no doubt influenced the diversity of land snail faunas that have persisted through long periods of island evolution. But vicariant processes such as island separation and coalescence, sea-level fluctuation, and lava flows do not hold the potential to generate novel lineages. Such processes fragment populations and have therefore played a role in enhancing allopatric speciation on a local scale, resulting in complexes of closely related sister taxa. Thus, although there is evidence that vicariance has impacted island snail species diversity, the results
of island vicariance are phylogenetically relatively shallow (affecting only more recent tip clades), compared with the effects of long-distance dispersal and multiple colonizations by divergent, independent lineages, from various geographic sources. Deeper phylogenetic divisions, and therefore more ancient levels of diversity, are driven and shaped by passive long-distance dispersal. Therefore, both dispersal and vicariance have played important roles in shaping island snail faunas, but to differing degrees and at different phylogenetic levels.

Although no single compilation of the overall numbers of non-marine island snail species exists, species lists are available for various geographic regions, including most island groups, some recent, others more than 100 years old. Such lists are notorious for taxonomic inaccuracy, including the fact that many species remain undescribed, whereas others have been described multiple times as different species. Nevertheless, using these compilations, it is possible to arrive at rough estimates of diversity. One such recent estimate suggests that there are perhaps 24,000 described species of terrestrial snails, although estimates as high as 80,000 species have been published. Likewise, a rough estimate of the total number of snails that have evolved on islands (excluding New Zealand, Papua New Guinea, and Madagascar) is about 6000, or 25% of the lowest total global estimate of snail species. In light of the minute fraction of global land area constituted by islands, this estimate shows the disproportionately important role played by islands in the generation of land snail biodiversity. For example, a comparison of the number of species in all of North America with the species diversity of the main Hawaiian Islands reveals that, in spite of the fact that the land area of North America exceeds that of the Hawaiian Islands by about a thousandfold, snail species diversity is roughly equivalent between the two regions.

The presence of diverse endemic assemblages of land snails on islands, including oceanic island groups that are thousands of kilometers from the nearest neighboring island or continent, is a testament not only to the extraordinary ability of these molluscs to passively disperse over long distances and establish new colonies, but also to their tendency to radiate into large numbers of species from relatively rare initial propagules, often in
adaptive species complexes (see Fig. 3). Because of these characteristics, island land snail radiations are increasingly valued as informative systems in illuminating and advancing the general understanding of the processes and patterns of evolution and adaptive radiation on islands.

Factors considered most important in the generation of high species diversity include island area, latitude, age, elevation, rainfall, and plant community diversity. These factors are frequently interrelated, and probably influence species diversity on islands in concert, and in complex ways.

**CONSERVATION CONCERNS**

Non-marine molluscs comprise one of the most threatened groups of animals on Earth and include 99% of all molluscan extinctions. Habitat loss, degradation, and fragmentation and environmental stresses such as climate change, pollution, and the introduction of invasive species such as black rats (*Rattus rattus*), the wolf snail (*Englantina rosea*), and the flatworm (*Platydemus manokwari*) all play important and often cascading synergistic roles in island land snail extinction. Although terrestrial vertebrate extinctions are well documented, invertebrate extinctions usually go unnoticed by the general public and undocumented by biologists and conservation agencies. Only a tiny fraction (less than 2%) of known molluscan species have had their conservation status scientifically assessed. Among the high-diversity island faunas, the Hawaiian land snails are relatively well studied, and species losses are daunting, estimated at 65–90%. Although most archipelagoes have not received the level of scientific scrutiny as have the Hawaiian Islands, similarly dire conditions probably exist on islands across all of the ocean basins.

Ecologists have begun to recognize important inputs to ecosystem function for a variety of invertebrate taxa, whether they be in the form of aeration of soils by earthworms, pollination of flowers by insects, decomposition of dead timber by termites, or other processes. Clearly, removal of such species has the potential to induce negative impacts on ecosystem balance, energy flow, health, and function. Although the precise roles of abundant, conspicuous terrestrial island snails in ecosystem function are not well understood, snails may play important roles in the maintenance of healthy forest ecological equilibrium (they may be involved in the calcium cycle, the carbon budget, and the breakdown of leaf litter and other organic material, and they may have a role as predator/prey in food webs and nutrient cycles).

Island snail assemblages are highly sensitive to habitat alteration and to the presence of invasive predatory species. On the majority of oceanic high islands, especially at elevations below about 300 m, native flora has been replaced by introduced weeds, ornamentals, and agricultural species. Most island land snails require native plants. We know from the notes of early twentieth-century expedition scientists that island floras were altered long ago; for example, Adamson in 1932 wrote of the Marquesas that “The native flora below 1000 ft has been replaced in large measure by immigrants, and to a considerable extent up to 2,500 feet.” Thus, in general, the native snail fauna is presently restricted to upper elevations of high islands, because these areas harbor the only remaining native forest in many island environments.

The degree of island land snail imperilment is poorly documented and almost certainly underestimated. This view is supported by the continual discovery of undescribed snails, especially on tropical island archipelagoes throughout the world, many of which have been largely deforested and on which numerous harmful invasive species have become established. For example, a multi-
year field survey of the terrestrial snails of the Papuan Peninsula and nearby islands by Florida Museum of Natural History biologists has recently uncovered dozens of undescribed species, suggesting that although the area has long been considered a biodiversity hotspot, the land snail fauna is far more diverse than was previously known. Surveys conducted in the southeastern United States focusing on small snails restricted to specialized habitats, including seeps and springs, are also uncovering previously undescribed species. Such surveys are also important in uncovering previously undocumented introduced species. Early detection of introduced species is crucial in the facilitation of efforts to control and prevent establishment, because after establishment, eradication is impossible.

CONCLUSION
This brief overview is intended to demonstrate that in terms of biodiversity hotspots, tropical and subtropical island land snails are important yet frequently overlooked components in terms of their contributions to unique island biodiversity. Ongoing efforts to preserve island land snails have had some success in recent years and have included captive rearing programs for rare Hawaiian achatinelline tree snails (University of Hawaii, Manoa) and French Polynesian partulid tree snails (mainly the London Zoological Society and the Jersey Zoo, but also the Detroit Zoological Park, the John G. Shedd Aquarium, and the San Diego Zoo); efforts to fence out, trap, or poison predators; habitat restoration; population translocation; and conservation genetics studies. However, the need persists for intensification of such efforts and for creative novel conservation strategies and solutions in the face of accelerating environmental change.

SEE ALSO THE FOLLOWING ARTICLES
Adaptive Radiation / Dispersal / Hawaiian Islands, Biology / Invasion Biology / Oceanic Islands / Vicariance

FURTHER READING

**LA VA AND ASH**

**KATHARINE V. CASHMAN**
University of Oregon, Eugene

Lava and ash are two different products of volcanic eruptions that cover the surfaces of volcanic islands. These two substrates have different volcanic origins and different physical properties, particularly with respect to their interaction with water (water transmission, storage, and susceptibility to erosion). The prevalence of one component or the other depends on the types of volcanic eruptions responsible for island formation. Eruption style, in turn, is determined primarily by the island’s location with respect to tectonic plates.

**LAVA FLOWS**
Basaltic lava flows cover much of the surface area of volcanic islands that form over hotspots, such as Hawai‘i. In these settings, the surfaces of active volcanoes are almost entirely composed of vast lava flow fields. J. D. Dana, an early geologist to visit Hawai‘i on Charles Wilkes’s U.S. Exploring Expedition, commented that “Areas, hundreds of square miles in extent, are covered with the refrigerated lava floods, over which the twistings and contortions of the sluggish stream as it flowed onward are everywhere apparent; other parts are desolate areas of ragged scoria.” Dana also noted that degradation of lava-mantled surfaces was dependent