PATTERNS OF SPECIES RICHNESS, ENDEMISM, AND DIVERSIFICATION IN OCEANIC ISLAND FLORAS

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Summary

Oceanic islands present special conditions for plant evolution. Their geographic isolation, small size, relatively young geological age, and a host of other factors have led to the development of the unique floras occurring in insular environments. Floristic richness varies greatly, with the Mascarene Islands and Hawaii possessing the most native flowering plant species (ca. 1300 and 1000, respectively), followed closely by the Comoro Islands—far less, however, than in continental areas or on older continental islands. Many oceanic islands have a high proportion of endemic species (reaching 89% in Hawaii), although endemism tends to be lower in islands and archipelagoes that are situated close to source areas such as continents. Geographic relief and related climatic and habitat diversity, as well as greater island age, all generally contribute to increased richness and endemism.

Insular floras are exclusively derived from plants that arrived via long-distance dispersal over a water barrier, and this has selected for small, easily transported diaspores, thus usually favoring groups initially adapted to open environments. As a result, the floras of

oceanic islands are disharmonic, with some taxa over-represented compared to source areas and others absent. Once established, certain groups have undergone adaptive radiation, often evolving into a tremendous number of species, each adapted to a particular habitat and exhibiting distinctive morphological features and ecological requirements. Island environments have particularly favored the evolution of a woody habit in groups that are typically herbaceous in most areas. Adaptive radiation has also resulted in a reduction or loss of dispersal capacity in many groups as they underwent an ecological shift to more stable, closed habitats such as forests.

Oceanic islands offer biologists with unparalleled opportunities to study evolutionary processes and ecological phenomena. However, widespread human impacts have already dramatically altered or completely destroyed many insular environments, and have driven countless species to extinction. Land conversion, fire, and the introduction of non-native plant and animal species have severely endangered the flora and vegetation of most oceanic islands, which are far more fragile and vulnerable than in older, continental areas. Unless urgent measures are taken to protect island biotas, native species and unique habitats will continue to disappear at an alarming rate, and an especially important component of global biodiversity will be irreversibly lost.

1. Introduction

Oceanic islands have fascinated biologists and natural historians for well over two centuries, and botanists, like our zoologist colleagues, have long been intrigued by the unique and sometimes bizarre taxa found in these isolated lands scattered all over the world. In addition to the almost mythical attraction of far-away islands and archipelagoes, which differ in so many striking ways from the places most of us call home, oceanic islands are in many respects true “living laboratories” of evolution—places where a remarkable range of processes and phenomena can be studied, hypotheses can be formulated and (in some cases) tested, and explanations for the wonders of nature can be sought. Because the biotas of most oceanic islands are relatively simple and species-poor compared to those of older, continental areas, they may make it easier to develop an understanding of how the members of various plant groups have adapted to their surrounding environments and diversified into the spectacular variety of forms we see today.

Isolated oceanic islands also present botanists and conservationists with a special set of challenges because insular floras are particularly sensitive to perturbation and vulnerable to the effects of introduced, non-native species, as well as to a wide range of other human caused or induced environmental changes. Moreover, the processes leading to population decline and extinction are often exaggerated and accelerated on oceanic islands, and since many of these areas have high proportions of endemic taxa, this has especially important implications for the conservation of global biodiversity.

Oceanic island floras today comprise both indigenous and non-native elements, and in most cases (unfortunately, in my view) the former are gradually being replaced by the latter. While the study of introduced plants in insular environments can be of real interest and may have important practical applications for conservation biology and some other scientific disciplines, it is the native component of an island’s flora that is of particular interest to botanists, ecologists, and evolutionary biologists. For this reason, nearly all of the discussion in the present chapter will focus on the indigenous portion of oceanic island floras.

A broad array of plant groups contribute to an area's flora, ranging from algae, mosses, and other nonvascular taxa, to ferns, gymnosperms, and angiosperms (flowering plants). While "lower" plants are often very interesting and can play an important role in various ecological processes, they tend to be more ubiquitous, in large part because they are more easily dispersed and can thus reach oceanic islands without difficulty. Considerations of floristic richness, diversity, and endemism are therefore generally limited to vascular plants, which have the added advantage of being far better documented and for which the taxonomic framework (i.e., the definition of species, genera, and other taxa) is more refined—although far from complete. Gymnosperms are absent or rare in nearly all oceanic island floras (the consequence of poor dispersal ability), whereas ferns and angiosperms are generally well represented. However, the detail and reliability of information on fern diversity varies widely from one island or archipelago to another, making it difficult to undertake broader comparisons. Thus, the following discussion will only make use of information on flowering plants occurring in oceanic island areas.

2. General Characteristics of Oceanic Island Floras

Oceanic islands and archipelagoes comprise a remarkably diverse set of areas, and this is clearly reflected in their native floras. They differ tremendously in size, relief, climate, degree of isolation, and many other aspects that can have an important influence on species diversity and composition. Each island has a unique history and set of local conditions, and as a consequence no two insular floras are the same, even on adjacent islands separated by only a short distance. This complexity has long presented a challenge to botanists, who recognized early on many of the interesting characteristics of oceanic island floras, but initially had some difficulty developing broad concepts to explain the diversity and adaptations they were seeing.

Over the years many people have contributed to a gradual formulation and refinement of ideas on the origin and evolution of insular biotas. A better understanding of our planet's geological history played a critical role, allowing biologists to make an important distinction between relatively recent volcanic (i.e., oceanic) islands whose flora is derived exclusively from propagules transported over water, and generally much older islands derived from continental areas to which they were once connected. One of the most comprehensive and influential treatises of how plants and animals have evolved in insular environments is Sherwin Carlquist's landmark book *Island Biology*, published in 1974. Carlquist synthesized much of the current thinking and added many ideas and refinements of his own, in addition to providing detailed examples of the processes and phenomena he described. Thanks in large part to this volume, and to additional work that followed, it is now possible to characterize island floras broadly and to explain much of their variation in richness, composition and diversity.

Carlquist lists a series of principles that summarize the basic hypotheses regarding dispersal and evolution of island biotas. These led him to conclude that an "insular syndrome" exists, and that it is due largely to three main factors: (1) constraints associated with dispersal over a water barrier, (2) isolation following colonization, and (3) the presence of numerous ecological opportunities (i.e., "unoccupied niches") on younger islands. These three basic ideas provide a framework for understanding and explaining many aspects of oceanic island floras, including both the similarities they exhibit and the striking difference that occur among them.

In the following section, three main themes will be addressed, which together offer important insights into the principal characteristics of oceanic island floras—taxon richness, endemism, and floristic disharmony. While this list is far from exhaustive, an examination of these three subjects should give the reader a good feeling for how insular floras have become established and how they have evolved and diversified.

2.1 Taxon Richness

Floristic richness is usually measured in terms of the number of plant species that occur within a given area. While this is the most widely employed basis for analyzing and comparing floras (and the one primarily used here), in some cases it may also be instructive to consider taxonomic richness at other levels, including, for example, the genus or family, as well as at infraspecific ranks (subspecies and varieties). Certain oceanic islands have considerable richness at one or more of these levels.

Oceanic islands vary substantially with regard to the number of documented native plant species comprising their flora. The richest of these floras for which reliable data are available is that of the Hawaiian archipelago, with 956 angiosperm species reported in 1990, and several dozen added in the last decade. The Mascarene Islands probably have substantially more native species (perhaps 1300 in all), but the taxonomy of some large groups has not yet been revised so it is difficult to provide an accurate figure. The Comoros may also have more than a thousand native flowering plant species, although detailed field inventories and careful analyses of herbarium collections have only been done for Mayotte, and our level of knowledge concerning the three remaining islands is much lower.

Several other archipelagoes have relatively large floras as well, such as the Canary Islands (826 spp.), whereas at the other extreme, for example, the small island of St. Helena has less than 50 native angiosperm species (Table 1). Even the largest of these oceanic island floras, however, pales in comparison to those of numerous older, species-rich continental islands such as Madagascar (with an estimated 12 000 native species), Taiwan (ca. 3350 species and infraspecific taxa), and New Caledonia (ca. 3250 native species), among others. Some of the causal factors that explain the relative floristic impoverishment of oceanic islands will be explored below.

Island or archipelago	**Total native angiosperm species**	**Percentage of species endemic**	**Surface area (km^2)**
Oceanic islands			
Mascarene Islands	ca. 1 300	ca. 45	4 481
Hawaiian Islands	ca. 1 000	89	16 887
Comoro Islands (entire group)	ca. 1 000	ca. 15	2 236

Mayotte	546	6	354
Canary Islands	826	53	7 273
French Polynesia (entire region)	675	75	3 583
Society Islands	575	43	1 440
Marquesas Islands	228	48	1 050
Austral Islands	185	15	145
Tuamotu Islands	95	8	<1 000
Gambier Islands	71	13	<25
Saõ Tome	556	19	857
Samoan Islands	536	32	3 137
Galapagos Islands	431	51	7 844
Guam	330	21	450
Robinson Crusoe Islands	157	65	100
St. Helena	46	89	122
Continental islands			
Madagascar	ca. 12 000	88–90	587 040
Taiwan	ca. 3 350[a]	20–30	35 980
New Caledonia	3 250	76	16 890

[a] Includes species and infraspecific taxa.

Table 1. Number of native angiosperm species, percent endemism, and land surface area of selected islands and archipelagoes

It is important to note that in nearly all cases the documented flora of oceanic islands almost surely represents an underestimate (often a substantial one) of the total species richness that must have occurred prior to the arrival of humans. For example, although a thorough analysis of museum collections from Hawaii has revealed just under a thousand documented native plant species, large areas of vegetation had already been degraded or destroyed prior to the first visits made by explorers beginning in the late eighteenth century, especially in more accessible (and therefore vulnerable) lowland areas. By the time broader inventories were being made, mostly within the last century, far greater areas had been impacted, without doubt resulting in the loss of a large number of species before they became known to science. While it is impossible to estimate how many such extinctions took place, they probably number well into the hundreds, if not more. This same scenario has been repeated in virtually all other islands throughout the world, with the most dramatic consequences usually on oceanic islands. Indeed, this process is still being played out today, resulting in ever-decreasing native species richness.

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Bibliography

Carlquist S. (1974). *Island Biology*, 660 pp. New York: Columbia University Press. [This is probably the single most thorough and informative reference on the natural history and evolution of island biotas.]

Davis S. D. Heywood V. H. and Hamilton A. C. (1994). *Centres of Plant Diversity, a guide and strategy for their conservation.* Vol. 1: *Europe, Africa, South West Asia and the middle East*, 354 pp. Cambridge: IUCN Publications Unit. [Along with the following reference, this is part of a series summarizing important information on key areas of plant diversity, including many oceanic islands and archipelagoes.]

Davis S. D. Heywood V. H. and Hamilton A. C. (1995). *Centres of Plant Diversity, a guide and strategy for their conservation.* Vol. 2: *Asia, Australasia and the Pacific*, 578 pp. Cambridge: IUCN Publications Unit.

Florence J. (1997). *Flore de la Polynésie française*, Vol. 1, 393 pp. Paris: Editions de l'ORSTOM. [This is the first in a series that will treat the entire flora of French Polynesia. The introduction contains valuable information on the plants and vegetation of the region.]

Pascal O. Labat J. N. and Pignal M. (in press). *Diversité, affinités phytogéographiques et origines présumées de la flore de Mayotte*. Proceedings XIV AETFAT Congress, Meise, Belgium. [A detailed analysis of the flora of this member of the Comoro archipelago, focusing primarily on the woody component.]

Stuessy T. F. Swensen U. Marticorena C. Matthei O. and Crawford D. J. (1997). Loss of plant diversity and extinction on Robinson Crusoe Islands, Chile. In C.-I Peng and P. P. Lowry II, eds. *Rare, Threatened and Endangered Floras of Asia and the Pacific Rim*. Institute of Botany, Academia Sinica Monograph Series **16**, 243–257. [The latest in a series of studies on the flora of this oceanic archipelago, with interesting examples of human impacts and their effects.]

Wagner W. L. Herbst D. R. and Sohmer S. H. (1990). *Manual of the Flowering Plants of Hawai'i. Vol. 1*, 988 pp. Honolulu, Hawaii: University of Hawaii Press, Bishop Museum Press. [Part of a two volume series, with detailed introductory chapters on many subjects, including the flora, vegetation, geology, climate, etc., and a comprehensive treatment of one of the world's most intriguing floras.]

Biographical Sketch

Porter P. Lowry II is a curator at the Missouri Botanical Garden, where he serves as head of the Africa and Madagascar Department, working from his base at the Muséum National d'Histoire Naturelle in Paris, France. Dr. Lowry is a specialist on the systematics, evolution, and biogeography of the primarily tropical plant family Araliaceae (the ginseng family). He has conducted fieldwork on nearly a dozen islands and archipelagoes, including New Caledonia (where he did his doctoral research), Madagascar, Hawaii, Fiji, Tahiti, and Réunion. In addition to his work on Araliaceae, including taxonomic revisions of the family for many island areas, Dr. Lowry coordinates a large program in Madagascar that involves extensive botanical inventory (especially focusing on unexplored areas), combined with training activities for local botanists, support for local botanical institutions, and a major effort to compile and interpret reliable information on plants for use in conservation planning and implementation.