1

Introduction

In 1846 Sir Joseph Hooker delivered an intriguing paper to the Linnaean Society in London on the flora of the Galapagos Islands, the results of a study he had undertaken at the request of his friend Charles Darwin. Subsequently published in 1849, the paper raised and discussed issues that remain at the heart of most research on island plants. He described the Galapagos Islands as being of rather recent volcanic origin, and the flora as remarkable for its paucity of species, believed at the time to number around 265; over 20% of the species were ferns (Pteridophytes) and sunflower relatives (Asteraceae = Compositae). The paper compared the islands' flora to those of other tropical archipelagoes, which at that time were becoming better known botanically: the Cape Verde and Sandwich (Hawaiian) Islands, St. Helena in the South Atlantic, and the Juan Fernandez Islands and New Zealand in the southern Pacific Ocean.

Hooker singled out for special consideration two components in the Galapagos flora, one of species endemic to the islands and comprising over 50% of the species list, and the other of taxa having wide distributions on other islands and in continental regions over a broad range of tropical latitudes. The means of dispersal by which plants reached an archipelago across nearly 1000 km of ocean was a subject of enlightened speculation; transport by water and wind, by birds, and most recently by humans were seen as the chief options. The implied loss of dispersal ability in weedy Galapagos *Ageratum conyzoides* (Asteraceae), which show reduced awns and scales on the pappus of the achenes and thence presumably a reduced dispersal capacity by wind (anemochory), elicited Hooker's surprise and interest. Indeed, similar morphological changes are found to accompany a loss of dispersal ability in a wide range of island plants. Hooker examined the relationships of endemic species to their nearest known continental relatives and noted the prevalence of endemics in the vegetation at higher island elevations. He reported also the presence of new genera and species of "curious arborescent Compositae which have no near allies in other parts of the globe," foreshadowing the so-called weeds-to-trees theme for oceanic islands that has been widely developed and documented since Hooker's time.

It seemed quite reasonable to Sir Joseph that larger islands, islands more centrally located in the archipelago, and those reaching higher elevations, should support larger numbers of plant species. But the differences in species composition from one island to another, particularly the representation on different islands of endemic genera by different species, were a significant source of wonder, a "mystery which it is my object to portray, but not to explain." An explanation based on the adaptation of local isolates, all derivatives of a single ancestral immigrant to the archipelago, was, however, not long in the offing. In fact, a new theory of species formation via descent with modification from a common ancestor gave Hooker's introductory essay to his *Flora Tasmaniae* (1859) added perspective and insight. This enhanced understanding was deployed just a year after Darwin and Wallace presented the essence of the new theory at the Linnaean Society meetings, and its publication date is the same as that of Darwin's *The Origin of Species*.

Studies of plants on islands, with Hooker's initial contributions providing a foundation, are an ongoing, vigorous, and productive branch of biology, and contribute in major ways to the fields of ecology, evolutionary biology, and biogeography. A key impetus to their synthesis was Sherwin Carlquist's classic *Island Life,* with its wealth of information on origins and adaptations of island plants. This 1965 book remains an invaluable compendium of the novelties produced on remote islands by plants that differ from known or putative ancestors in diverse and often startling ways. Now, of course, most oceanic or partly oceanic archipelagoes, such as the Canary, Galapagos, Hawaiian, and Cape Verde Islands, have their own published floras, and their origins, diversity and endemicity have been examined in great detail. A major attraction of remote islands for both plant and animal ecologists and evolutionary biologists lies in their isolation and their lack of past connections to continents. As a consequence, their floras and faunas are derived from mainland ancestors that successfully reached the island by oversea dispersal and, moreover, succeeded in establishing and persisting there. Further, with increased isolation comes a reduction in the number of successful colonists and thence reduced diversity, followed by increased opportunities for the development of novel morphology and ecology in a new selective regime.

Islands in general have diverse origins and histories. This diversity can be seen even within islands of a single region, such as the Sea of Cortés between Baja California and mainland México, a contact zone between the North American and Pacific Plates (Carreño and Helenes 2002). Variously composed of volcanic or granitic substrates, or of old seafloor or more recent sediments, some were formed by block faulting off the trailing edge of shifting plates, some by seafloor spreading and subsequent uplift, some by fluvial outwash deposits, and some by submarine tectonic and volcanic activity that continued structural deformations inexorably brought to the light and air. In some, past continental connections are ancient, severed by their slower movement relative to that of the parent rocks, while in others continental connections are as recent as a few thousand years. In many instances, the islands still bear the imprint of these diverse origins and histories, which are reflected in present-day differences and discrepancies, as well as similarities, in their floras and faunas (Case et al. 2002).

Most oceanic islands and archipelagos were formed by tectonic activity at the submarine contact zones between major plates and have no history of connection to larger or mainland land masses. In contrast, so-called continental or inshore islands are those that lie on the continental shelves and have experienced past mainland connections, perhaps on many occasions. During glacial maxima, when sea levels were lowered by more than 100 m and the continental ice sheets were at maximum depth and extension, present-day continental islands separated by current channel depths of less than about 130 m were connected to the adjacent mainland by land bridges. Thus the islands were formed, split into smaller islands, and separated sequentially with rising sea levels according to the current submarine depressions between them, until the present island size distribution was reached by about 7000 years BP.

Continental islands lack a number of the features that often distinguish oceanic islands. Their proximity to continents and history of continental connections via land bridges are reflected in their having similar floras of relatively similar sizes living under similar abiotic conditions; in general, these characteristics preclude selection for island novelties, the evolution of endemics, and adaptive radiations. Many oceanic islands, especially larger islands (such as Madagascar, New Caledonia, and New Zealand) and archipelagoes, are conservatories for plant relicts, more primitive species that have been replaced or supplanted on continents by more advanced species of later evolutionary lineages. Among many examples of ancient plants that retain high diversity on islands are primitive gymnosperm families, such as the magnificent podocarp-dominated (Podocarpaceae) forests of New Zealand and the Araucariaceae and Austrotaxaceae of New Caledonia. These same old but large islands are also havens for the more primitive angiosperm families, such as Winteraceae and laurels (Lauraceae), the latter being especially well represented also in the Canary Islands, Madeira, and the Azores. Relicts of more ancient, pregymnosperm, radiations in cycads (Cycadaceae) are perhaps best represented today on islands in the Pacific Ocean (Sachs 1997).

Since the subject of this book is plants on continental rather than oceanic islands, it will say little about endemism, radiations, or relicts, which are classical themes of oceanic islands. But on the other hand, the lower degree of isolation of continental islands and greater proximity to source floras is reflected in much higher colonization rates relative to oceanic islands, and typically the dynamics of colonization and extinction they display are more apparent. As these processes can take place over short-term ecological time, for example, over decades, rather than much longer evolutionary or geological time scales, they can be documented and studied with relative ease. Thus, several of Hooker's concerns, such as species numbers and species turnover between islands, dispersal means, and characteristics and morphological changes on islands, can be studied with much greater resolution on continental islands; the dynamical aspect of island biotas can be revealed only with difficulty and inference on oceanic islands. Further, the proximity of the source floras to large numbers of available and accessible continental islands make for attractive and practicable research programs. Haila (1990) classified islands over space and time scales and pointed out the relevance of different ecological and evolutionary processes over these continua; certain aspects of island biogeography can best be pursued on small, continental islands, and other aspects on oceanic islands, especially large, old, and isolated islands and archipelagoes. On the latter, a range of phenomena occur, from the preservation of relictual taxa often long extinct on mainlands, to adaptive radiations of new taxa; on rather less isolated archipelagoes infrequent but repeated colonization drives taxon cycles that also produce endemic forms (Fig. 1.1). On the former, the dynamics of colonization and extinction rates take precedence, with questions relating to local adaptation, niche shifts, community assembly, and composition lying somewhere between.

This monograph describes a study of plants on the continental islands in Barkley Sound, British Columbia. It can be considered an island biogeography case history, constrained by taxon and region. It covers the statics of the patterns of plant distribution and diversity and especially emphasizes the dynamics of at least some components of the island floras. While the study can illustrate some aspects of local adaptation, niche shifts, and interspecific influences on community assembly, it has little or nothing to say about speciation. The work, in fact, was not begun as a long-term island biogeography study of plants; I first visited the area in 1981 with the notion that it might be suitable for short-term research on the islands' landbirds!

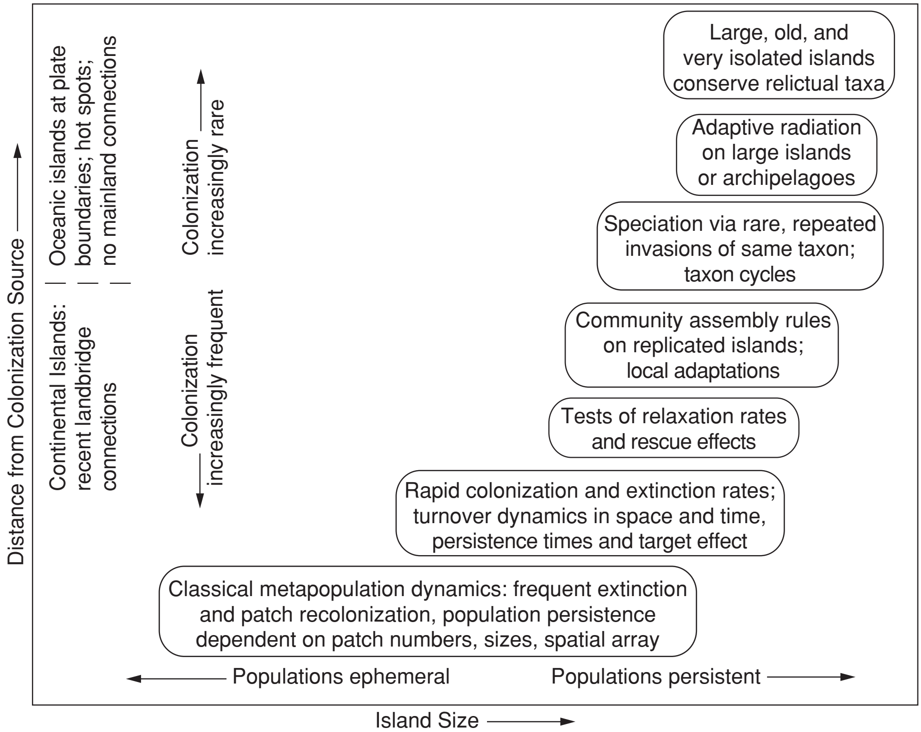


FIGURE 1.1. Phenomenological overview of island biogeographical processes and their realization over island size (abscissa) and isolation (ordinate) scales. Different processes are prevalent and are best studied, on different regions of these two scales.

I soon realized that both analytical scope and statistical power would be much enhanced by switching my focal taxon to plants, since islands of a quarter hectare or so support at most a few pairs of one of two bird species but house dozens of plant species. Even bird-free tiny islets have substantial populations of many different plants. Not only would this change of focus allow me to include in the study the numerous smaller and birdless islands and utilize a species pool more than an order of magnitude larger, but my sample sizes, sampling proficiency, data accumulation rate, and replication potential would all benefit.

Over the years this feathers to fronds, crows to crowberries, and fox sparrows to foxgloves downshift in trophic level has proved increasingly engaging and productive. While the course of the study has incorporated a number of exploratory sidetracks, as will be described later, the basic data set is a matrix of species by islands by calendar years. With an island flora of around 300 species, with over 200 islands surveyed, and with census results from 15 different years, the matrix potentially has nearly one million elements (though actually fewer, as not all islands were visited in each census year). While small portions of the data set have been aired in previous publications, the advantages (and satisfaction) of reporting the study in single monograph seemed obvious from early days, and I hope readers will enjoy a similar satisfaction.*

As a document on a specific case history, this book focuses closely on the Barkley Sound plant data and is in no way intended to be a review, or

* "It is the same thing with our publications; they are sown broadcast over the barren acres of Journals and other periodicals which none of us can afford to buy and then weed." J. D. Hooker to T. Huxley, 1856, from *Life and Letters of Sir J. D. Hooker,* L. Huxley (London: John Murray, 1918), 1:369.

overview, of island biogeography, ecology, or evolution, or of island plant biology. A vast primary literature, as well as a burgeoning secondary literature, exists on the ecology, evolution, and biogeography of island taxa. My personal favorites in this latter phylogeny are A.R. Wallace's *The Geographical Distribution of Animals* (1876) and *Island Life* (1881; dedicated to Sir J.D. Hooker), P. J. Darlington's *Zoogeography* (1957), S. Carlquist's *Island Life: A Natural History of the Islands of the World* (1965) and *Island Biology* (1974), R. MacArthur and E.O. Wilson's *The Theory of Island Biogeography* (1967), M.L. Rosenzweig's *Species Diversity in Space and Time* (1995), J. Brown and M. Lomolino's *Biogeography* (2nd ed., 1998), and R. J. Whittaker's *Island Biogeography* (1998). There are of course many additional more specialized texts and compilations, and sparing reference will be made to them, and to other relevant papers, throughout the text.

Following this introductory preamble, I next describe the islands and their history, together with that of surrounding area, the climate of the region, its flora and vegetation, and the approaches this monograph takes to various island biogeographic themes. The results of the research, which spans nearly a quarter century now, are presented in subsequent sections.

2

Islands in Barkley Sound, British Columbia

GEOGRAPHY AND HISTORY

Vancouver Island (Fig. 2.1) lies between 48° and 51° N latitude. The largest island on the west coast of North America, it is part of the western Canadian province of British Columbia and the home of the provincial capital, Victoria. The island was named after George Vancouver (1757–1798), the English navigator who completed its first circumnavigation in 1792. This achievement was not Vancouver's first voyage to the region, though. He had served earlier with Capt. James Cook (1728–1779) on Cook's second (1772–1775) and third (1776–1780) voyages to the Pacific. On this last voyage, Cook sought the fabled Northwest Passage that had been the goal of expeditions for the previous two centuries, but discovered instead Vancouver Island's fabulous sea-otter pelts; the Russians further north were by the 1770s already trading these pelts to China at enormous profit. James Cook and company spent a month in early 1778 (Vancouver was 18 years old at the time) on the outer coast of Vancouver Island in Nootka Sound, likely first seen by the Spaniard Juan Perez in 1774. It was April, too early in the season for the mariners to appreciate the utility of the local plants; "of the Vegetables this place produceth, we benefited by none except the Spruce tree of which we made beer, and the wild Garlic" (James Cook, *Journals.* Pt. 1, pp. 310–311). Cook traded amicably with the natives, exchanging iron and copper for furs, and his reports to the Admiralty on the marvelous quality and value of these pelts triggered a veritable flotilla of English traders to the region. Serious commerce began in 1785 with James Hanna, and subsequent entrepreneurs included James Strange, John Meares, Nathaniel Portlock, and George Dixon. Charles William Barkley arrived in 1787, the Americans John Kendrick and Robert Gray followed in 1788, and the Spaniards Estévan José Martínez in 1789 and Pedro Alberni in 1790. Nootka must have been a very busy harbor in the last decades of the eighteenth century; fascinating accounts of these and earlier coastal explorations are given by Speck (1954) and Arima (1983).

It seems fitting that the Sound, situated about one-third of the way up the outer coast of Vancouver Island, bears Barkley's name, as he was one of the more reputable traders (though not above changing his ship's names and papers

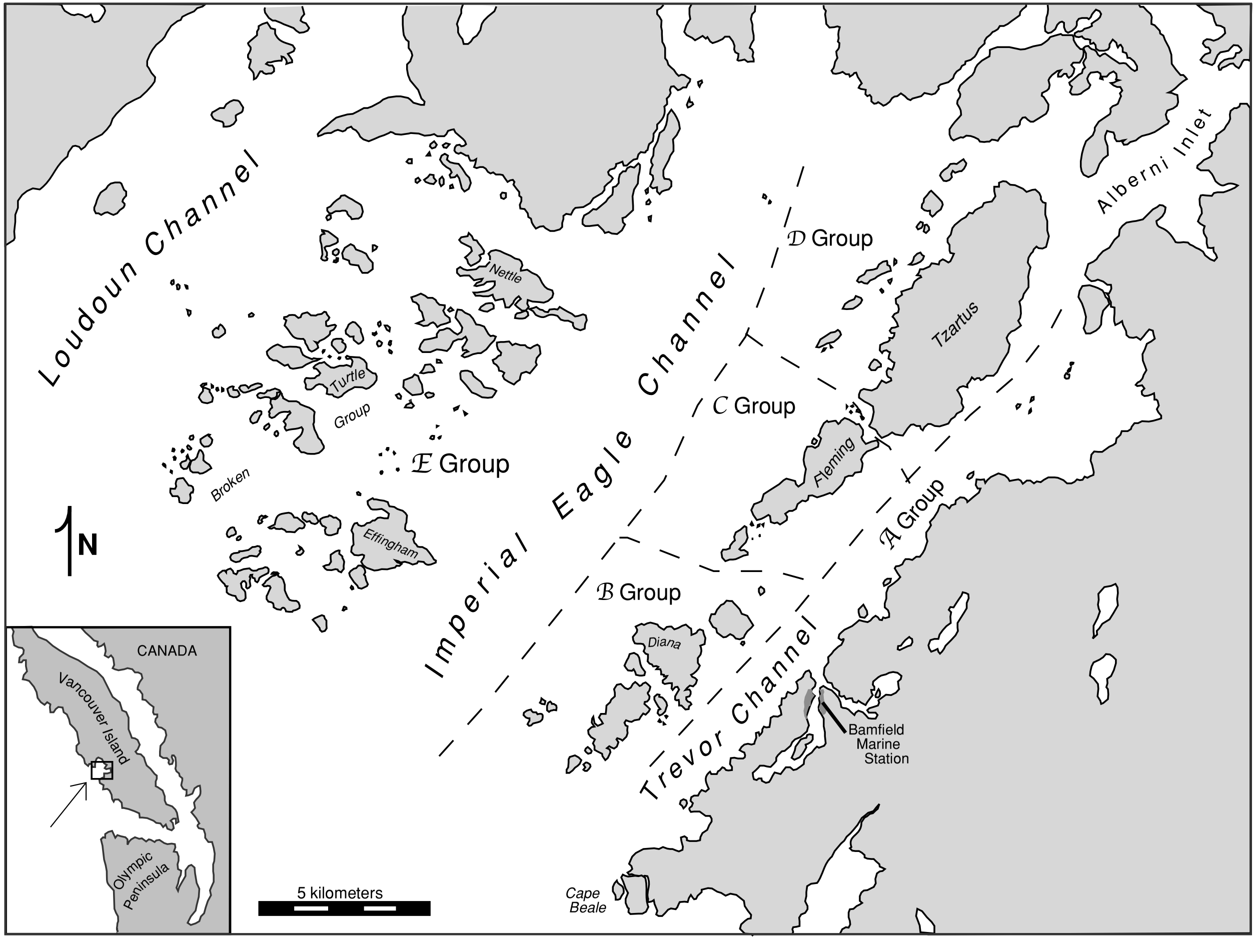


FIGURE 2.1. Barkley Sound islands and environs. Islands are grouped 𝒜–ℰ corresponding to isolation from mainland.

for tax evasion purposes). Charles Barkley found and named Barkley Sound in the summer of 1787, and his new teenaged wife, Frances, wrote that "this part of the coast proved a rich harvest of furs." Unfortunately, the voyage was not a financial success, as the Chinese markets were already glutted and the prices depressed by the time Barkley's furs reached them. However, Barkley and his wife (née Frances Hornby Trevor), his ship (*Loudoun,* later *Imperial Eagle*) and officers (Beale, King, Williams) all bequeathed their names to local features such as capes, channels, and islands. A regrettable legacy of the English, Spanish, and American traders was the utter depletion of the sea-otter populations by the beginning of the nineteenth century. In 1817 the French vessel *Le Bordelais* under the command of Camille Roquefeuil found that "the sea otters had long forsaken the area" (Scott 1970). I have yet to see a sea otter in Barkley Sound, though their reintroduction in the 1970s to Checleset Bay on the northwest coast of Vancouver Island was successful, and their range has been slowly extending southward since. By 2003, otters were established as far south as Clayoquot Sound and may be expected to repopulate Barkley Sound within the next decade.

Barkley Sound is centered at 48° 54′ N, 125° 17′ W and is a roughly rectangular indentation 24 km NW-SE by 18 km NE-SW on the coast of Vancouver Island, open to the Pacific Ocean to the southwest. The Sound encompasses a host of islands (Plate 1; Fig. 2.1), ranging in size from Tzartus (= Copper) at nearly 20 km^2 in area, down to many hundreds of tiny islets of a few or a few dozen square meters. Beyond and below these are rocks that are dry only at low tide, and thence submarine reefs representing drowned islands that were extant when pre-Holocene sea levels were lower. The shorelines of the islands, and the reefs and shallow waters around them, are extremely rich in marine life, from algae and invertebrates to fish, seabirds, and mammals such as seals, sea lions, dolphins, and whales.

Long before Europeans arrived, the region supported large First Nations (or Native American) populations living in complex and sophisticated societies, based in coastal villages with economies largely dependent on the abundant marine resources. The Nuu-chah-nulth (Nootka) tribes occupied the west coast regions of Vancouver Island since postglacial times; the Barkley Sound affiliates belonged to the Huu-ay-aht (Ohiat) band (Arima 1983, Duff 1997). Population densities of indigenous peoples prior to European contact were likely higher in coastal British Columbia than anywhere else in Canada. Captain Meares in 1788 estimated the population of a single village on Effingham Island, a site traditionally occupied for summer fishing activities, at 2000 individuals. William Banfield, the region's first Caucasian settler and the government agent appointed in 1859, estimated the numbers of Huu-ay-aht indigenous peoples at around 550. First Nations populations declined precipitously as a result of the smallpox epidemics of the mid-1800ss and of the more lethal intertribal warfare that followed the acquisition of European weapons. While numbers recovered in the early 1900s (to over 200 Huu-ay-aht by 1963) and may now be close to precontact populations, traditional social, economic, and cultural activities have been largely lost. While the indigenous people originally made wide and ingenious use of many native plants and plant products, they did not maintain cultivated gardens (*fide* Mrs. E. Happynook, Anacla Village resident) and likely did not affect island plant distributions; their current usage of the native vegetation is minimal.

The area's European population grew rapidly in the 1800s by exploiting timber, salmon, and other marine resources. The village of Bamfield (from William Banfield) on the southeast edge of the Sound became the terminus of the Trans-Pacific Cable, a British Empire ("All-Red") project, directed by Sir Sanford Fleming and completed in 1902. The cable provided communications from Bamfield to New Zealand from 1902 to 1959. The Pacific Cable Company's original wooden building was supplemented by a three-story concrete structure in 1929, and this building, in its refurbished state, has housed

Bamfield Marine Science Centre (BMSC) since 1972, under the governance of the Western Canadian Universities Marine Biological Society. The station operates year-round and is particularly busy in the summer when courses in marine sciences, temperate rainforest ecology, and even island biogeography, are offered. The BMSC biologists, along with visitors to Pacific Rim National Park's coastal trails and natural wonders, sport and commercial fishermen, ecotourists, whale-watchers, and sea-kayakers, many of whom use the regular runs of the MV Lady Rose from Port Alberni for transportation, add substantially to Barkley Sound's summer recreational, educational, and commercial traffic.

At present, the islands in the Sound are under a variety of jurisdictions. The islands of the Broken Group lie in the center of the Sound and are part of Pacific Rim National Park Reserve, administered by Parks Canada. Several islands, together with parts of the larger islands, are First Nations reservations with tribal administration, and still others are claimed by the Huu-ay-aht tribe. Many of the remainder are so-called Crown lands (owned by the Province), and a few islands are in private ownership.

GEOLOGY AND TOPOGRAPHY

The western coast of North America, from California to Alaska, has a complex history of plate tectonics, vividly brought to life in John McPhee's (1993) book *Assembling California*. Only the eastern one-third of British Columbia is native North American Plate; the western two-thirds is an amalgam of highly diverse "alien" material, resulting from the formation, migration, and eventual accretion of numerous wandering terranes, essentially minicontinents, with very distant origins (Yorath 1990). Vancouver Island (excluding small southern and western portions) is the largest extant section of the terrane Wrangellia, named after the early polar seas and Alaskan explorer, and later czarist admiral, Ferdinand Petrovich Wrangell (b. 1796). Other parts of this terrane, sheared apart and rifted north, comprise the Queen Charlotte Islands and small areas of southeastern Alaska (Chichagof Island). Wrangellia originated in the ancient South Pacific Ocean, and its odyssey is recounted well by Ludvigsen and Beard (1994). By the early Permian (270 Ma [million years ago]), a substantial terrane had coalesced from volcanic eruptions above an island arc, become overlain with limestone generated by marine invertebrates, and isolated well west of the supercontinent Pangaea. More volcanics were added to the terrane in the Triassic, and granitic rock was intruded through the older volcanics during Jurassic times (200 Ma); accumulating further marine deposits meanwhile, the terrane rode across the paleo-equator into the northern hemisphere. By 130 Ma Wrangellia had completed a 10,000 km journey to collide with western Laurentia at the edge of the North American Plate. Thereafter and throughout the Cretaceous, Wrangellia, deformed by its North American contact, accumulated shales and sandstones in interior basins, and the main structural elements mapped by present-day geologists were assembled.

Most of the islands in Barkley Sound are composed of West Coast Diorites of late Paleozoic or early Mesozoic Era, with younger, mid-to-late Jurassic granodiorite intrusions toward the northeast of the Sound (Muller 1974). While most of the islands look rather uniformly "granitic," light colored with quartz and feldspar, some are bolstered and banded with darker, hornblend-rich volcanic rock into which the diorites have intruded. A few islands at interior locations, such as Nanat on the Trevor Channel's mainland coast, are composed of the characteristically clinkered rock of surface-cooled lava characteristic of the Bonanza Volcanics series. On some islands' beaches, these sharp and abrasive rocks seem almost volcano-fresh.

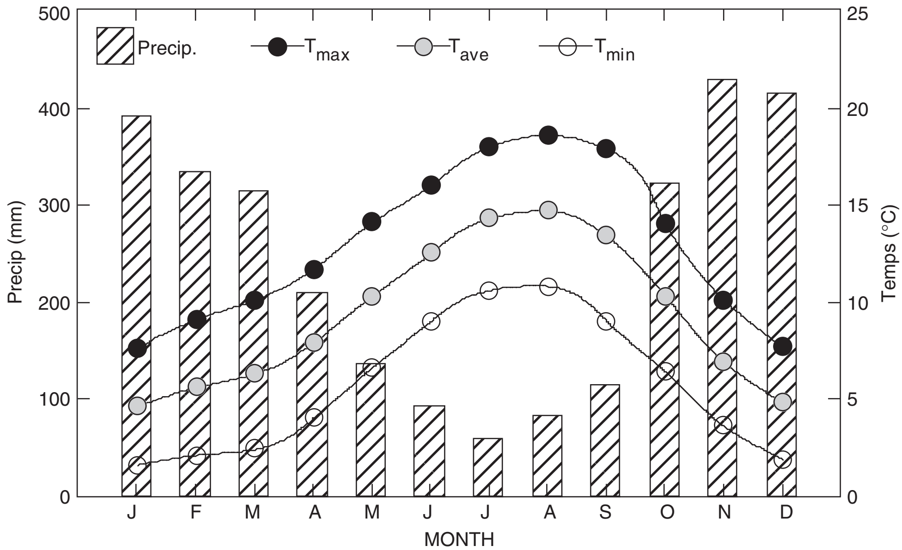
The Sound is rimmed by mountains reaching 1200–1500 m in elevation, and the vista to the north of the 2000 m peaks in Strathcona Provincial Park is especially impressive. At glacial maximum in the late Pleistocene, southeastern Vancouver Island was covered by a southwest-sloping ice sheet contiguous with the continental ice east across the Georgia Strait and south across the Juan de Fuca Strait (Muller 1974). Ice covered all but the highest mountains, reaching elevations of about 1500 m in the interior and having a thickness of 300 m or so at the outer coast; Barkley Sound was under ice sheets of perhaps 500–600 m thickness. With the passing of the successive glacial maxima, large glaciers descending from the highlands around the Sound incised valleys that are now deep fjords that cut into the interior, the longest of which (the 60 km Alberni Canal) makes Port Alberni a deepwater port and nearly transects Vancouver Island. The glacial sculpting of valleys and basins in Barkley Sound extends topographically in submarine features some 30 km out to sea and covers the inner half of the continental shelf. Here the shelf terminates 50–60 km from the present shoreline, at current ocean depths of around 200 m, and its smoother, outer half lacks the imprint of glacial activity.

Following the retreat of first the continental ice sheets and then the valley glaciers at the end of the last (Wisconsin) glacial episode, beginning around 18,500 years BP (before present), the landscape became revegetated in sequences that at some Pacific Northwest locations have been well studied. By using pollen records from lake-bottom sediments, vegetational stages can be reconstituted and representative plant species identified. First tundra, then parkland, woodland, and finally coastal forest reoccupied previously ice-covered terrain, spreading south to north and lowlands to highlands. The nearest source for the postglacial revegetation of Barkley Sound was the ice-free, lower Olympic Peninsula 150 km to the south, although the higher peaks on Vancouver Island stood as nunataks above the ice sheet and likely served as refugia for some northern plants. For example, the mountains of the Brooks Peninsula on the northwest coast of Vancouver Island gave refuge to several montane species that are disjunct from populations found in wider or more contiguous ranges elsewhere, including both southern disjuncts (with the greater part of the range further north) and northern disjuncts from Olympic Mountains populations to the south (Pojar 1980; Ogilvie and Ceska 1984). Several Brooks Peninsula plant species are otherwise Queen Charlotte Islands (Haida Gwaii) endemics, and the evidence for glacial refugia within the Queen Charlottes is substantial. However, none of these are species that revegetated the islands and coastal areas of Barkley Sound.

CLIMATE

Late Quaternary climates in northwestern Washington, just south of the continental ice sheet, were considerably cooler, by about 4 °C, and 50% reduced in annual precipitation compared to the present regime (Heusser et al. 1980). Given the location of Barkley Sound close to both the seaward and southward edge of the continental ice sheet, glacial retreat must have occurred relatively early, with revegetation following shortly thereafter. A major shift to conditions more like the present occurred around 13,000 years BP, and nearly modern climates have prevailed for most of the last 10,000 years. Recent palynology data were obtained from Whyac Lake on the outer coast of southern Vancouver Island not far south of Barkley Sound. By 11,000 years BP, the major forest tree taxa (*Picea, Tsuga, Abies, Pseudotsuga, Alnus*) already had become abundant pollen contributors, and they have been represented in the pollen record at levels similar to those of modern times throughout this period. An essentially modern forest, by tree species composition, appears to have characterized the Barkley Sound region over at least the last 7000–8000 years (Brown and Hebda 2002; see also Heusser 1989). Note that the reconstitution of the forest flora began shortly after the second major melt-water period of the mid-11,000s BP, and thus it dates from a period when sea levels were about 45 m below present and nearly all of the Barkley Sound islands were then part of the mainland landscape.

The Sound is within Krajina's (1973) "Coastal Western Hemlock" biogeoclimatic zone, where a cool and wet climate supports what is often



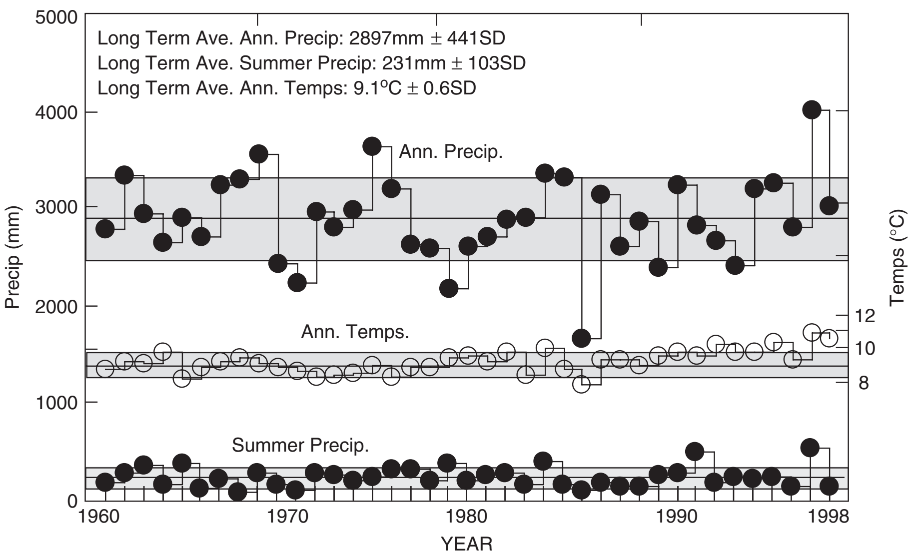


FIGURE 2.2. Climogram (upper) and yearly weather variations (lower) for Bamfield East, Barkley Sound, British Columbia. The vegetation under these climatic conditions is predicted to be temperate rainforest (Holdridge L.R. 1947 Determination of world plant formations from simple climate data. *Science* 105:367–368; Wright et al. 2004).

referred to as temperate rainforest. Indeed, this region's 3 m annual precipitation is similar to that of many tropical rainforests. A climogram summarizing data collected at the Bamfield East weather station, on the southeastern edge of Barkley Sound, is shown in Fig. 2.2 (upper). For six months of the year monthly precipitation averages over 300 mm, but the summer months of June, July, and August are considerably drier, with only 8% of the annual total falling in this period (Fig. 2.2, lower). October through March, inclusively, average 20 days per month with measurable rain, versus 10 days per month in June through August. Winter frosts are common, but snow is unusual and contributes negligible precipitation. Summer months are moderately, even benignly, warm and temperate (see monthly mean minimum, mean, and maximum