COMMENTARY

The natural history of Chiloé: on Darwin's trail

La historia natural de Chiloé: en la senda de Darwin

MARY F. WILLSON¹ and JUAN J. ARMESTO²

¹ Forestry Sciences Laboratory 2770 Sherwood Lane Juneau, AK 99801 U.S.A.
 ² Lab. Sistemática & Ecología Vegetal, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile E-mail: iiech@codon.ciencias.uchile.cl

ABSTRACT

This article reviews the wiritings of Charles Darwin during his visit to Chiloé Island in southern Chile in 1834-35, focusing on his observations on the climate, plants, landscapes, animals and people. We compare Darwin's impressions with our views of the natural history of the Island 150 years later.

Key words: Biogeography, Chiloé, plant-animal interactions, history of science, Chile.

RESUMEN

En este artículo revisamos las descripciones de Charles Darwin durante su visita a la Isla Grande de Chiloé en 1834-35, con referencia especial a sus observaciones sobre el clima, la vegetación, el paisaje, la fauna y los habitantes de la Isla. Contrastamos las impresiones de Darwin con nuestra propia visión de la historia natural de la Isla 150 años más tarde.

Palabras clave: Biogeografía, Chiloé, interacciones animal-planta, historia de la ciencia, Chile.

INTRODUCTION

The Beagle brought Charles Darwin to Isla Grande de Chiloé and its subsidiary islands in southern Chile in 1834 and 1835. Darwin recorded his impressions first in his diary and, briefly, in his correspondence, and later in "The Voyage of the Beagle". Over 150 years later, we began our ecological studies on Chiloé and so had occasion to reread Darwin's comments on this austral region. Judging from what he wrote, we think that Darwin's impressions of Chiloé Island were often quite different from ours. Our goal in this paper is to contrast Darwin's commentary with our observations, in the course of recording the major transformations of the biota and the landscape that have occurred in the past 150 years.

In the interest of brevity, we reference Darwin's writings as follows: B = Voyage of the Beagle (Darwin 1860); C = Correspondence (Burkhart & Smith 1985), and

D = Diary edited by Keynes (1988). First we provide annotated Darwin's quotes, and our comments follow.

CLIMATE

Darwin: "Chiloé, situated on the West coast, enjoys a very uniform temperature, & an atmosphere saturated with moisture..." (D). "I do not suppose any part of the world is so rainy as the Island of Chiloé" (D). Forced by a winter storm to seek shelter in Ancud harbor, Darwin remarks that "Such weather utterly destroys for every good end the precious time during which it lasts" (D). "In winter the climate is detestable, and in summer it is only a little better. I should think there are few parts of the world, within the temperate regions, where so much rain falls. The winds are very boisterous, and the sky almost always clouded: to have a week of fine weather is something wonderful" (B).

"Pigs and potatoes are as plentiful as in Ireland. With the exception of this weighty advantage, Chiloé, from its climate is a miserable hole" (C). Almost three days of good weather in July led Darwin to note that "...the inhabitants themselves wonder[ed] at such an event." "I believe every one was glad to say farewell to Chiloé; yet if we could forget the gloom and ceaseless rain of winter, Chiloé might pass for a charming island" (B). "We were all glad to leave Chiloé; at this time of year nothing but an amphibious animal could tolerate the climate. Even the inhabitants have not a word to say in its favor; very commonly I was asked what I thought of the Island; no es muy mala?.." (D). In spring (November), the Beagle returned to Chiloé: "The island wore quite a pleasing aspect, with the sun shining brightly on the patches of cleared ground & dusky green woods. At night however we were convinced that it was Chiloé, by torrents of rain & a gale of wind" (D). In January (austral summer), "during the night it rained as if rain was a novelty; the rain in this country never seems to grow tired of pouring down" (D). And in February, stopping again in Ancud on the way north, "We have arrived on the right day, for in the evening heavy rain commenced" (D).

Armesto/Willson: The stormy weather that so impressed Darwin during his two visits to the island has presumably changed rather little since then, although a weak drying trend has been suggested for some localities in south-central Chile since the end of the nineteenth century (Aceituno et al. 1993). Chiloé Island remains one of the rainiest places in the world, particularly within the temperate zone. Although few long-term meteorological records have become available for the Island since Darwin's visit, the estimated annual precipitation for different sites varies between 2000 and 3000 mm/yr (Di Castri & Hajek 1975). The longest records are available only for the drier areas on the east coast of the Island, in the rain shadow of the Cordillera de Piuchué, which rises up to a maximum elevation of nearly 800 m on the west coast. For the summits of this coastal range, however, annual rainfall is likely to be considerably

higher than 3000 mm (Hedin & Armesto, unpublished data), leading to the occurrence of moorland plant communities and peat accumulation (Ruthsatz & Villagrán 1991).

Summers (late December to early March) in Chiloé may be quite dry, however, due to the extended influence of the mediterranean climate that is strongly developed in the regions to the north of the Island (di Castri & Hajek 1975). Over more than a decade of field work in Chiloé, we have experienced several rainless periods, often lasting up to one month in summer. A recent drought, in January and February 1994, lasted nearly two months, and the town of Ancud on the northwestern coast of Chiloé experienced a shortage of drinking water. January temperatures can be quite pleasant, reaching a maximum of about 25°C in the lowlands. Local people take advantage of the dry and warm conditions in summer to burn the forests and create agricultural lands. During clear days, the snow-capped Andean volcanoes in the adjacent mainland, ordinarily hidden by the clouds, can be seen from high places around the island. This magnificent view is a splendid reward to those who must endure the island's harsh climate.

LANDSCAPE AND FOREST

Darwin: "This island is about ninety miles long, with a breadth of rather less than thirty. The land is hilly, but not mountainous, and is covered [near Ancud] by one great forest, except where a few green patches have been cleared round the thatched cottages" (B). Near Chacao, in the northern coast of the island, "the land in this neighbourhood has been extensively cleared, and there were many quiet and most picturesque nooks in the forest" (B). "The whole of this eastern side of Chiloé has one aspect: it is a plain, broken by valleys and divided into little islands, and the whole thickly covered with one impervious blackish-green forest. On the margins there are some cleared spaces, surrounding the high-roofed cottages" (B). As for the Chonos Islands (Guaytecas), "...the surface of the land in all these islands is all but impassable. The coast is so very

rugged that to attempt to walk in the directions requires continued scrambling up and down over the sharp rocks of micaslate..." (B).

Viewing Chiloé from the ocean, Darwin writes: "From a distance the view somewhat resembles that of Tierra del Fuego; but the woods, when seen nearer, are incomparably more beautiful. Many kinds of fine evergreen trees, and plants with a tropical character, here take the place of the gloomy beech of the southern shores" (B). "The woods are incomparably more beautiful than those of T. del Fuego, instead of the dusky uniformity of that country we have the variety of Tropical scenery; excepting in Brazil I have never seen such an abundance of elegant forms" (D). "This resemblance to Tropical scenery is chiefly to be attributed to a sort of arborescent grass of Bamboo, which twines amongst the trees to the height of 30 or 40 feet & renders the woods quite impervious – to this may be added some large ferns, the trees also are all evergreens, & the stems are variously coloured white, & red & c." (D). Attempting to climb the San Pedro mountains (part of the coastal range), "The general aspect ... was more like that of Tierra del Fuego than of Chiloé. In vain we tried to gain the summit: the forest was so impenetrable, that no one who has not beheld it, can imagine so entangled a mass of dying and dead trunks. I am sure that often, for more than ten minutes together, our feet never touched the ground, and we were frequently ten or fifteen feet above it, so that the seamen as a joke called out the soundings. At other times we crept one after another on our hands and knees, under the rotten trunks. In the lower part of the mountain, noble trees of the Winter's Bark, and a laurel like the sassafras with fragrant leaves, and others, the names of which I do not know, were matted together by a trailing bamboo or cane. Here we were more like fishes struggling in a net than any other animal...We ultimately gave up the attempt in despair" (B). In the Chonos, "...as for the woods, I have said enough about them; I shall never forget or forgive them; my face, hands, and shin-bones all bear witness what maltreatment I have received in simply trying to penetrate into their forbidden recesses" (D). Even in

summer (January), "The day was beautiful, and the number of trees which were in full flower perfumed the air; yet even this could hardly dissipate the effect of the gloomy dampness of the forest. Moreover, the many dead trunks that stand like skeletons, never fail to give to these primeval woods a character of solemnity, absent in those of countries long civilized" (B).

About the paths and roads, "Even where paths exist, they are scarcely passable from the soft and swampy state of the soil. The inhabitants... move about chiefly on the beach or in boats" (B). "The road [from Ancud to Castro] is the only one which goes directly through the interior of the country. About two miles from [Ancud] it enters the forest, which covers the whole country & has only been rendered passable by the aid of the axe...From the gloomy damp nature of the climate, the wood had a dreary aspect; in the Tropics such a scene is delightful from the contrast it affords with the brilliancy & glare of every open spot" (D). "...the ground is so damp from the suns rays never penetrating the evergreen foliage, that neither man nor horse would be able to pass along" [without the road of logs] (D). "The road is a very singular affair... almost entirely composed of logs of wood... Being summertime & fine weather the road is not so very bad; but in winter, when the wood is slippery with rain, by all accounts the travelling becomes quite dangerous...In winter the road on each side of the line of logs is a perfect swamp & is in many places overflowed... On either hand of the road we have the forest of lofty trees, their bases matted together by the Canes... The first opening of this road must have cost considerable labor.- I was told that many people had lost their lives in attempting to cross the forest, & that the first who succeeded was an Indian who cut his way through the canes in 8 days..." (D). On the west coast, "We had some difficulty in reaching the point owing to the intolerably bad paths; for every where in the shade, the ground in Chiloé soon becomes a perfect quagmire" (D).

Armesto/Willson: The arborescent bamboos and canes are species of *Chusquea*, known locally as quila or colihue, that occur

frequently in the understory of the evergreen forests. They form dense thickets, and could grow up to reach the tree crowns, especially where the forest canopy has been opened by disturbances, such as tree falls or logging. Like other bamboos, these species flower and fruit at long intervals (20-30 yrs in Chiloé species), and soon after fruiting the entire plant senesces and dies over the course of one or two years. The most recent die-off occurred in 1993-1994. These species of arborescent grasses produce large seed crops that are consumed by many local granivores (many rodents and birds, including both finch-like species and the large pigeon or torcaza, Columba araucana). This fruiting strategy has been called mast-fruiting (Janzen 1986) and may have evolved as a means of reducing seed damage by generalist granivores. In some areas of Chile, the fruiting of quila may be followed by huge outbreaks of rodents (Pacheco 1993, R. Murúa, pers. comm.) that damage crops and stored grains, and sometimes pass leptospirosis disease organisms to cows (Péfaur et al. 1979).

The "red-stemmed" trees to which Darwin refers are probably myrtles (most likely, Luma apiculata or arrayán, and possibly Amomyrtus luma or luma whose trunks are also red within the forest), and "whitestemmed" trunks may be laurel (Laureliopsis phillipiana) or meli (Amomyrtus meli), all of which occur in lowland forests in Chiloé Island. Bamboos (Chusquea spp.) and the tree fern Lophosoria quadripinnata (ampe) often form a dense understory. The variety of evergreen trees and the bamboos, as well as the great abundance of epiphytes and vines are responsible for the "tropical aspect" of the forests of the islands, as described by Darwin. Among the epiphytes, filmy ferns (genus Hymenophyllum) and bromeliads (Fascicularia bicolor) grow profusely on the trunks and branches of large (30-40 m tall) emergent trees (e.g., Nothofagus nitida, Eucryphia cordifolia). Frequent vines include two endemic species of Gesneriaceae and Campsidium valdivianum (Bignoniaceae), notable for their conspicuous red flowers (Smith-Ramírez 1993). The tropical appearance is also due to the fact that all tree species are broad-leaved and have a dark

evergreen foliage, in contrast to northernhemisphere temperate forests that are dominated by deciduous trees. The lavish old-growth forests that so impressed Darwin are now a rare sight on the island, because of the increasing rates of logging, burning and land clearing.

In their road to San Pedro, Darwin and his companions apparently encountered a "tepual", a low-stature, dense forest, dominated by many-stemmed Tepualia stipularis (Myrtaceae), which is common in poorly-drained sites on the Island. This forest often had an emergent canopy of *Nothofagus* nitida (coigue de Chiloé) and presence of conifers: Podocarpus nubigena (mañío), Pilgerogendron uviferum (ciprés), and Fitzroya cupressoides (alerce). Tepualia has an unusual growth form with horizontal or creeping trunks, from which arise many vertical stems. These horizontal trunks often form an entangled mass, sometimes up to a couple of meters above the ground. The density of stems, the network of fallen logs and creeping stems, and the deep mud makes it very hard to walk through this kind of forest, as Darwin described. The tepual is commonly found in water-logged soils, in lowland or montane sites, and is commonly inundated for part of the year. Over much of the Island, selective cutting for lumber and firewood has eliminated the major canopy trees in these forests, and clear-cutting has opened much land for pastures or agriculture. The disappearance of the canopy presumably has led to increased levels of flooding in lowland areas, because of reduced transpiration by the vegetation, causing a loss of value of cleared land. Tepu is a valuable firewood, as it produces unusually high amounts of heat when burned. Massive harvesting of tepu wood from poorly drained areas, a process which is ongoing in many places around the island, should lead to increased land flooding and loss of valuable soil.

Many paths in remote areas of the Island are still as described by Darwin. Because of the dense shade casted by trees and bamboos, and the wet conditions of the soil, these paths may be impassable during most of the winter. Upland, well-drained, forests generally have a more open understory through which walking is easier.

At the present time, reaching the west coast of the Island, across the coastal Cordillera, remains a difficult and hazardous trip. Only two gravel roads provide access to the west coast, by way of Chepu, near the northern end of Chiloé National Park, and Cucao, about 100 km to the south. Crossing the Cordillera to the west coast is possible, by experienced hikers, using a single unmarked path, but the trip may take two or three days.

Many forests in Chiloé Island, especially on the western slopes of the coastal Cordillera, still remain in a nearly primeval condition, but they are now restricted to most inaccessible locations. Since 1985, a significant fraction of these old-growth forests have been protected within the newly created Chiloé National Park that covers around 40,000 ha, a large part of which is primary, old-growth forest. These great rainforests are a unique feature of Chiloé and a very rare sight in the temperate regions of the world. In contrast, lowland forests over large portions of the Island, from the foothills of the coastal Cordillera to the eastern shore, have been logged, cleared, and burned since Darwin's time, to be replaced by pastures and exotic plants. Large patches of forest burned by the settlers (probably early in the 20th century) around all the major roads are still identifiable by the solemn, upright, dead stems of coigue that still reach heights of 30-40 m. In the time since these burnings, abundant regeneration by canelo (*Drimys winteri*) and myrtles has occurred below the skeleton of the former forest canopy.

PLANTS

Darwin: Curiously, he wrote little about the biology of particular species of plants in Chiloé. He remarked on *Gunnera* (nalca or pangue), of "very noble appearance", like "rhubarb on a gigantic scale" (B). "There were also several extensive brakes of the *Fuchsia*, covered with its beautiful drooping flowers, but very difficult to crawl through" (B). A native type of potato was remarked for its ability to grow in the "sterile mountains of central Chile, where a drop of

rain does not fall for more than six months, and within the damp forests of these southern islands." To Darwin, the wild potatoes were abundant, but "watery and insipid" (B). He notes the decrease in plant species diversity from Chiloé southward and the richness of cryptogamic plants in the Chonos, and discourses on the formation of peat (B). On the western side of Chiloé, a hill was "covered by a plant allied I believe to the bromelias, with little recurved hooks on the leaves, and which the inhabitants call Chepones. In scrambling through the beds, our hands were very much scratched...This plant bears a fruit, in shape like an Artichoke; in it a number of seed-vessels are packed together which contain a pleasant sweet pulp..." (D).

Willson/Armesto: The giant leaves of Gunnera chilensis are very common in open areas, especially on recently bared ground. The base of the stems and rhizome of these plants are inhabited by symbiotic, nitrogenfixing blue-green algae, which facilitate the colonization of nutrient-poor, disturbed soils. This species has presumably become more common than it was at the time of Darwin's visit, because it occurs frequently on road cuts and in other areas heavily disturbed by people. Local inhabitants eat the stem (nalca) directly from the plant or in salads, and the leaves (pangue) are used to cover the fire-pit in which curanto, a characteristic celebratory dinner, is cooked.

More than 100 varieties of potatoes still grow on the Island and its surrounding archipelago, and at least some of these varieties are native to the region. Potatoes remain an essential component of the diet of Chilotan families, during both summer (fresh) and winter (stored). Some of the varieties that we have eaten in Chiloé have a flavor and texture superior to that of many varieties currently available in North America; indeed, they are anything but "watery and insipid".

Two kinds of bromeliads are found on the Island. The large, ground-growing *Greigia sphacelata* is common in second-growth and open areas; it is often cultivated as part of living fences. It produces fruits with a sweet and juicy pulp, known as "chupones", which

are harvested not only by people, but also by frugivorous birds and foxes that contribute to seed dispersal (Armesto et al. 1987). A second species of bromeliad, not mentioned by Darwin, is the poe (Fascicularia bicolor), a common epiphyte in montane and coastal rainforests. The drooping narrow leaves of these epiphytes in the crown of large trees also contribute to give the forest its tropical aspect. This plant is remarkable because the base of the rosette of leaves acquires a bright red color during the flowering period. The red color attracts hummingbirds, which are the major pollinators of its flowers (Smith-Ramírez 1993), and later, it may be a signal for avian frugivores which feed on the fleshy fruits of Fascicularia, thereby dispersing the seeds to other trees.

Darwin made few observations on the natural history of plant-animal interactions, which are particularly striking in the temperate forests of Chiloé (Armesto et al. 1987, Willson 1991, Smith-Ramírez 1993, Willson et al. 1994, Armesto et al. 1996). Some of the bestdocumented interactions are those of birds as seed dispersers of the many fleshy-fruited plants (Armesto & Rozzi 1989, Sabag 1993). Recent work has established that the migrant fio-fio (Elaenia albiceps) is the dominant frugivore in the rainforest, providing seed-dispersal 'services' for many fleshy-fruited plants (Sabag 1993). Most of the fleshy-fruited species in the forest are angiosperms, but some gymnosperms (e.g., mañío, Podocarpus nubigena) are also dispersed by vertebrates. The large black seeds of mañío are attached to a sweet and juicy red aril that is eaten by many species of birds (Willson & Sabag, unpublished manuscript). Many consumers nibble the aril and drop the seed below the parent female tree. The zorzal (Turdus falcklandii) often swallows both seed and aril, but soon regurgitates the seed, often below the parent. However, in some cases, zorzales carry the arillate seed to a neighboring tree and deposit the seed one or two tree canopies away; quite often they fly long distances with an ingested seed.

In addition, the seeds of several species are dispersed by lizards (*Liolaemus* spp.). The tiny orange fruits of the herbaceous *Nertera granadensis* and *Relbunium hypocarpium* are frequently eaten by these small lizards, which pass intact seeds

through the digestive tract (Willson & Sabag, unpublished manuscript).

Other well-documented interactions include the importance of fire-crowned hummingbird (Sephanoides galeritus) as the principal pollinator of many species of flowering plants. Although the red, tubular flowers of hummingbird-pollinated plants are conspicuous all year round (Smith-Ramírez 1993), they went unnoticed by Darwin. Among the hummingbird-pollinated species, the drooping red and purple flowers of Fuchsia magellanica, which Darwin noted, are a common sight in lowland areas, forming dense thickets in forest edges, especially along the coastline. A common pioneer tree, Embothrium coccineum, produces an unusually large display of brilliant red flowers that attract not only hummingbirds, but also at least six species of nectarforaging passerines (including the fio-fio), some of which carry pollen between flowers (Smith-Ramírez & Armesto, unpublished).

ANIMALS

"... y el Chucao lanza su lanza, su largo grito desbordante: él rompe con su grito de agua mil años de silencio en que sólo cayeron hojas y las raíces ocuparon como invasores este reino."

P. Neruda. Arte de Pájaros

Darwin: The endemic birds of the family Rhinocryptidae received his attention. "In all parts of Chiloé and Chonos, two very strange birds occur, which are allied to, and replace, the Turco and Tapacolo of central Chile." The chucao (Scelorchilus rubecula) is "an odd red-breasted little bird, which inhabits the thick forest, and utters very peculiar noises..."; "it frequents the most gloomy and retired spots within the damp forests. Sometimes, although its cry may be heard close at hand, let a person watch ever so attentively he will not see the cheucau; at other times, let him stand motionless and the red-breasted little bird will approach within a few feet in the most familiar manner. It then

busily hops about the entangled mass of rotting canes and branches, with its little tail cocked upwards. I opened the gizzard of some specimens: it was very muscular, and contained hard seeds, buds of plants, and vegetable fibres, mixed with small stones. The cheucau is held in superstitious fear by the Chilotans, on account of its strange and varied cries... The Chilotans assuredly have chosen a most comical little creature for their prophet." The related but larger hued-hued (Pteroptochos tarnii) was said to have the English name of "the barking bird". "This latter name is well given; for I defy any one at first to feel certain that a small dog is not yelping somewhere in the forest...Its manner of feeding and its general habits are very similar to those of the cheucau" (B & D).

In his notes, he describes "the strange noises, which, although frequently heard within these gloomy forests, yet scarcely disturb the general silence. The yelping of the guid-guid [hued-hued], and the sudden whew-whew of the cheucau, sometimes come from afar off, and sometimes from close at hand; the little black wren [presumably Scytalopus magellanicus] of Tierra del Fuego occasionally adds its cry; the creeper [rayadito, Aphrastura spinicauda] ...follows the intruder screaming and twittering; the humming-bird [Sephanoides galeritus] may be seen every now than then darting from side to side, and emitting, like an insect, its shrill chirp; lastly, from the top of some lofty tree the indistinct but plaintive note of the white-tufted tyrant-flycatcher [fio-fio, Elaenia albiceps] may be noticed." Darwin reacts with surprise that taxa, such as finches, so common elsewhere are here less common than "the peculiar forms above enumerated" (B). "When finding, as in this case, animals which seem to play so insignificant a part in the great scheme of nature, one is apt to wonder why they were created. But it should always be recollected, that in some other country perhaps they are essential members of society, or at some former period may have been so." He found a dusky churrete (Cinclodes patagonicus) living on the beach, "like a sandpiper" and footnotes the three-month delay in breeding phenology compared to populations 700 miles to the north (B).

"A fox (Canis fulvipes) [now called Pseudalopex fulvipes], of a kind said to be peculiar to the island, and very rare in it, and which is a new species, was sitting on the rocks [of San Pedro]. He was so intently absorbed in watching the work of the officers, that I was able, by quietly walking up behind, to knock him on the head with my geological hammer. This fox, more curious or more scientific, but less wise, than the generality of his brethren, is now mounted in the museum of the Zoological Society" (B).

North of Tres Montes (apparently a point west of Chacao), "...the number of seals which we saw was quite astonishing: every bit of flat rock, and parts of the beach, were covered with them. They appeared to be of a loving disposition, and lay huddled together, fast asleep, like so many pigs; but even pigs would have been ashamed of their dirt, and of the foul smell which came from them. Each herd was watched by the patient but inauspicious eyes of the turkey-buzzard. This disgusting bird, with its bald scarlet head, formed to wallow in putridity, is very common on the west coast, and their attendance on the seals shows on what they rely for their food" (B).

Finding a "singular little mouse" on some of the islands caused Darwin to write "What a succession of chances, or what changes of level must have been brought into play, thus to spread these small animals throughout this broken archipelago!" He also speculates that small mammals might be spread to scattered islands by raptorial birds that bring to their nests live prey that occasionally escapes.

Willson/Armesto: The Chilote forests in spring are anything but generally silent. The far-carrying calls of hued-hueds and chucaos characterize large stands of both primary and secondary forest. At any point in a wooded stand, one can often hear six or eight fio-fios singing; this species is by far the most common in the forest. The rayaditos are indeed the local watchdogs, sounding a chorus of conversational curiosity at the presence of an intruder. The fio-fio is the only neotropical migrant in the community, although some of the other species make more local seasonal movements. Both the fio-fio and the picaflor are pivotal mutualists

in plant reproduction (Armesto et al. 1996) and seem to be relatively insensitive to forest fragmentation (Willson et al. 1994). As a result, mutualistic interactions in this forest community may be quite resilient to the effects of fragmentation – as long as these two pivotal species remain abundant.

The level of endemism in the avifauna of the south-temperate rainforests is high (Vuilleumier 1985), although the species richness of the community is not very great. These Patagonian forests are separated from other South American forests by over 1000 km, such that they constitute, in effect, an ecological island (Vuilleumier 1985). Many of the forest birds seem to be able to occupy a range of habitats, perhaps as a result of insularity and low species richness (Vuilleumier 1985).

Many endemic bird species are sensitive to forest fragmentation, among them the Rhinocryptids (Willson et al. 1994). Preliminary evidence indicates that all the understory endemics can use corridors between forest fragments, if the corridors provide sufficiently dense cover (Willson et al. 1994). The Rhinocryptids are far more than "odd", "peculiar", and "strange". The chucao is often sufficiently calm that observers can watch the nests at close range, while the adults deliver food to nestlings, and it is often possible to follow individuals as they forage through the forest. Calmness in the presence of humans is sometimes taken to mean stupidity, as seen in the common name "booby" for seabirds (Sula spp.) that failed to flee early sailors with murderous intentions, and as seen in our Victorian's comments about the Chiloé fox. It seems unfortunate that humans should so despise animals that lack experience with our sooften malignant attitudes; perhaps it is the ultimate arrogance to suppose that all creatures should naturally fear us.

Clearing the forest has wrought predictable increases in the abundances of open-country birds, such that some species that must have been uncommon during Darwin's visit are now among the most frequently encountered. For example, the nearly ubiquitous tiuque (Milvago chimango) scavenges the placentae of cows and sheep, ravages the eggs (and probably the nestlings)

of birds nesting in and near open areas, and patrols the beaches with the gulls. Almost every field has several queltehues (or - in Chiloé - treiles, Vanellus chilensis) that scream alarms at the slightest provocation, providing a continuous vocal backdrop all day long and into the night. The mirlo (Molothrus bonariensis), which feeds in pastures and fields, has surely increased in numbers and will probably continue to do so as more and more forest is cleared. This species is a brood parasite, laying its eggs in the nests of chincoles (Zonotrichia capensis), diucas (Diuca diuca), and other species. Population increases of the mirlo are bound to have negative effects on their host species, perhaps especially since the local populations have little historical experience with this parasite.

The birds of the south-temperate rainforest generally have small clutches (Willson et al. 1996), but the reasons are not known. Many species produce only two or three eggs per clutch. Species with close relatives in North America often have smaller clutches than their northern counterparts. Small clutches in birds sometimes have been attributed to competition with migrants, but this explanation cannot apply in southern Chile, where few birds are regularly migratory (Johnson 1965, Jaksic & Feinsinger 1991).

The "little black wren" or Magellanic churrín is interesting in several respects. First, until recently, it was considered to range from Colombia to Tierra del Fuego, but the species called *Scytalopus magellanicus* is restricted to southern South America and is distinguished from its northern relatives by voice and behavior. Plumage patterns are variable and interesting: Adult males are typically black, but females often begin breeding while still in an "immature" brownish plumage. Both sexes sometimes bear a silver crown patch, but many individuals lack it, at least in northeastern Chiloé.

There are a number of scavenging birds in Chiloé, including two caracaras and two vultures. The vultures indeed have bald heads, perhaps as a hygienic adaptation to foraging on carrion, although the caracaras are not bald. However, wallowing in putridity (see above) is hardly a scientific

description of their foraging habits! Vultures may sometimes be associated with seals and sea lions, perhaps especially in pupping season. However, seal populations have been greatly reduced in recent years, because they are considered to be a threat to the salmon farms and fisheries now established around the Island. Large seal colonies are now restricted to very remote and inaccessible locations. With the increasing agricultural development, both vultures and caracaras forage on placentae of domestic animals.

Churretes often forage on the beaches, apparently functioning much like shorebirds in terms of their foraging. They nest in burrows in seacliffs and cutbanks, and can often be seen at quite high density in the intertidal, as well as in pastures. The "finches" that Darwin found to be curiously rare, may have become more common, as more and more land is deforested. His attitude seems to have been that common creatures may be readily accorded a place in nature, but that rarer beings need special explanations for their existence, a view curiously at variance with his later ideas on interactions between organism and environment.

The Chiloé fox is now known to occur also in a restricted area of the coast range of mountains on the mainland (in the Cordillera de Nahuelbuta, Medel et al. 1989). This endemic species is the smallest of the three Chilean foxes. Its presence in Nahuelbuta and Chiloé may be an indication of the conservative character of these two regions during the last glacial period (see Villagrán et al. 1993). This fox has a broad diet, often consuming large quantities of fruits of forest plants such as luma and canelo and dispersing their seeds (Jiménez et al. 1990). They may be significant predators on eggs and nestlings of understory birds, as well. The species in now much less common than in Darwin's time, because of predation by humans.

The spread of small mammals in the Chiloé Archipelago may be accounted for in part by historical considerations. It is now well established that the landscape of the archipelago has been shaped by both glacial and tectonic forces acting over several thousand years (Villagrán 1985). The inland

marine channels to the east of the islands is the southward continuation of the central depression of the Lake District, sunk by the weight of accumulated glaciers and by subsidence due to earthquakes. Some areas of Chiloé Island and the surrounding mainland were uplifted, while others subsided during the large earthquake of 1960 in the Lake District. It is likely that the Island was connected to the mainland during glacial times, when the ocean level was 100-200 m lower than at present. The ocean to the north and east of the Island is generally (50-150)shallow m deep). very Consequently, the forest was once a continuous habitat between the mainland and the Island. However, some islands south of Chiloé, such as Isla Guafo, may have been separated for a long period, as they lack important forest species including the chucao (Rozzi et al. 1995).

Additional notes on Darwin's contribution to the natural history of animals in other regions of Chile may be found in Jaksic & Lazo (1994).

HUMANS ON THE LANDSCAPE

Darwin: "The inhabitants, from their complexion and low stature, appear to have three-fourths of Indian blood in their veins. They are an humble, quiet, industrious set of men" (B). Despite the fertile soil, the lack of sunshine limits the kinds of crops that can be grown and "there is very little pasture for the larger quadruped; and in consequence, the staple articles of food are pigs, potatoes, and fish" (B). "...the obtaining these requires labor, & has consequently induced a different set of manners from what is found in other parts of S. America" (D). "The people all dress in strong woollen garments, which each family makes for itself, and dyes with indigo of a dark blue colour. The arts, however, are in the rudest state; -as may be seen in their strange fashion of ploughing [the breastplow], their method of spinning, grinding corn, and in the construction of their boats... Although with plenty to eat, the people are very poor: there is no demand for labour, and consequently the lower orders cannot scrape together money sufficient to purchase even the smallest luxuries. There is also a great deficiency of a circulating medium. I have seen a man bringing on his back a bag of charcoal, with which to buy some trifle, and another carrying a plank to exchange for a bottle of wine" (B). "Although with plenty to eat, they are excessively poor; there is little demand for labor, & from the scarcity of money nearly all payments are made with goods" (D). "I cannot give a better idea of the poverty of Castro, than the fact that we had great difficulty to buy a pound of sugar; & a knife which we wanted was quite out of the question" (D).

On Isla Lemuy, "the people... live chiefly on shell-fish and potatoes. At certain seasons they catch also, in 'corrales', or hedges under water, many fish which are left on the mudbanks as the tide falls. They occasionally possess fowls, sheep, goats, pigs, horses, and cattle" [listed in order of decreasing frequency (B). Island inhabitants eat the stalks of Gunnera, "tan leather with the roots, and prepare a black dye from them". "During the summer, many of the Indians wander about the forests (but chiefly in the higher parts, where the woods are not quite so thick), in search of the half-wild cattle which live on the leaves of the cane and certain trees" (B).

"In Chiloé the inhabitants possess a marvellously short method of making an orchard. At the lower part of almost every branch, small, conical, brown, wrinkled points project; these are always ready to change into roots, as may sometimes be seen, where any mud has been accidentally splashed against the tree. A branch as thick as a man's thigh is chosen in the early spring, and is cut off just beneath a group of these points; all the smaller branches are lopped off, and it is then placed about two feet deep in the ground. During the ensuing summer the stump throws out long shoots, and sometimes even bears fruits: I was shown one which had produced as many as twentythree apples, but this was thought very unusual. In the third season the stump is changed (as I have myself seen) into a wellwooded tree, loaded with fruit" (B).

The lack of cleared land "is partly owing to their own negligence in not clearing the woods, and partly to restrictions by the government..." (B). "In most countries, forests are removed without much difficulty by the aid of fire; but in Chiloé, from the damp nature of the climate, and the sort of trees, it is necessary first to cut them down. This is a heavy drawback to the prosperity of Chiloé" (B). On a trip to Cucao, Darwin notes that 'the whole of Chiloé took advantage of this week of unusually fine weather, to clear the ground by burning. In every direction volumes of smoke were curling upwards. Although the inhabitants were so assiduous in setting fire to every part of the wood, yet I did not see a single fire which they had succeeded in making extensive" (B).

"The capital [Ancud] itself is worthy of the island, it is a small straggling dirty village; the houses are singular from being entirely built sides, roofs, partitions &c of plank. The Alerce [Fitzroya cupressoides] or cedar from which these planks are made grows on the sides of the Andes; they possess the curious property of splitting so evenly that by planing the planks are nearly as well-formed as if sawed.— These planks are the staple export of the Islands, to which may be added potatoes & hams" (D).

Armesto/Willson: The economy of rural Chiloé is still primarily a subsistence economy rather than one based on currency, although this is slowly changing. Seafood (fish, locos, other shellfish) and livestock (including sheep, pigs, chickens, geese) provide meat, and carefully tended gardens provide vegetables. Major crops in the fertile soils of the Island include peas, habas, onions, giant garlic, and several varieties of potatoes. Potato fields are cultivated with a single-share plow pulled by a team of oxen, which are also used to pull logs from the forest for sale or for firewood. Successful fruit trees are apples (used to make cider), plums, and cherries. The short growing season and summer storms are sometimes serious limitations on the success of fruit crops. The rural people obtain currency, when needed, by selling crafts or fish or by taking a short-term job. However, rural electrification is underway, and television sets are found with increasing frequency in rural homes, and it seems likely that the

conditions of country life in this area will change with ever-increasing speed.

Pastures, apparently rare in Darwin's time, are now predominant in the landscape of the eastern side of the Island. Near Ancud, a growing milk industry has been established. Although cattle are now abundant, sheep are still the most common livestock on the Island. Woolen garments continue to be used by many Chilotans, but sweaters and gorros are also much appreciated now by visitors to the Island who buy them in local markets. Native plants (lichens, canelo, *Gunnera, Rhaphithamnus spinosus*, among others) provide a number of 'earth-tone' dyes, which are favored by local people, but imported gaudy hues are often used for tourist sales.

As noted by Darwin, Chilotans are skilful builders of boats, houses, and many craft objects made of wood (e.g., tinajas and barrels). Hundreds of shingles of alerce needed to cover the outside of a house are cut directly from the tree bole with an ax. Fishing boats and skiffs are built on the beach, with hand tools and a trained eye, without 'benefit' of electricity or blueprints. In addition, Chilotans use other natural materials (reeds, vines) to make baskets (Smith-Ramírez 1994).

From the point of view of the amount of cleared land, Chiloé Island has greatly 'prospered' since Darwin's time. The lack of cleared land that was a 'drawback to the prosperity of Chiloé' is not a problem any more. Much of the forest has been cleared in the past 150 years. Fire, that seemed to Darwin so difficult to use in the damp climate, has been the major agent used to destroy thousands of hectares of forest, taking advantage of the summer droughts. Although fires are rarely extensive, as Darwin observed, they certainly have been effective in rapidly clearing the land. During the dry summer periods, hundreds of fires burn, clearing ground for pastures and fields, and producing 'volumes of smoke' that often become a hazard to drivers because the smoke reduces the visibility along sections of the main road. Indeed, the whole island seems to be on fire at such times.

Once the land is cleared, maintenance work is needed to keep it clear. Many species of shrubs and trees are early invaders of open areas, recruiting both from seed banks and freshly dispersed seed. Also, many trees are able to resprout after cutting. Many pastures are studded with spiny Berberis bushes (B. buxifolia and B. darwini) that thrive in early succession. Compared to oldfields in the northern hemisphere, exotic weeds are not widespread or abundant in second-growth sites on the Island (Villagrán & Armesto, unpubl.). However, gorse (*Ulex-europea*) has become a major pest in many places where forests have been cleared, spreading rapidly and resistant to control measures. Many forest fires are due to the futile efforts of land owners to remove the dense Ulex cover from fields.

Alerce and ciprés, so frequently seen in Chiloé in the time of Darwin's visits, have become rare, as the natural forest has disappeared from all accessible sites in the mainland and on the Island. Alerce and ciprés grown from seed originally collected by Darwin are growing in the Royal Botanical Garden at Edinburgh (M. Gardner, pers. comm.). In Chiloé, both species occur on the inaccessible summits (above 600 m) of the coastal Cordillera, now largely protected within Chiloé National Park. Alerce forests historically known to have occurred in lowland areas between Puerto Varas and Puerto Montt in the Lake District (Donoso 1993. Armesto et al. 1994) are now nearly extinct. Ciprés, highly valued for its aromatic wood, has nearly disappeared from all the accessible lowland sites, where once it was common. A few remnant saplings of ciprés can now be seen, growing in the midst of dense, second-growth, Baccharis shrublands on both the sides of the main highway between Ancud and Chacao. The exploitation of alerce has recently been prohibited by law, and the species is now included in the red list of vulnerable Chilean flora (Benoit 1989). Ciprés is not included in the 1989 list, although it is clearly vulnerable over much of its range, and especially in northern Chiloé.

At present, a major threat to the remaining forests on private lands in Chiloé is the increasing demand for woodchips. Chips are made by a forest-products company based in Puerto Montt and exported to Japan. The company purchases cut trees (by cubic meter) from land owners and also obtains permits from landowners to extract trees, in exchange for clearing the land. The volume of these operations is such that most forests in accessible places in Chiloé are likely to disappear in the coming decades.

CONCLUSION

Darwin went on from Chiloé to contribute concepts that changed biological sciences forever. But there is no indication that his Chilotan experiences contributed to his later theories or that he ever reconsidered these experiences in the light of his later insights. He found 'grandeur in this view of life' at the end of the Origin of Species, but there was little grandeur for him in Chiloé. The reasons for his largely negative impressions of the Island can be left for speculation by historians of biology. Perhaps he was simply not yet mentally prepared to take the best advantage of his visit.

However, present-day Chiloé offers the curious naturalists many opportunities for investigation. While the forests last, the many species and their interactions have only begun to be studied seriously. As they disappear, they provide an outdoor laboratory for understanding the effects on the native flora and fauna and, potentially, developing ways of facilitating their coexistence with the human users of the landscape.

ACKNOWLEDGMENTS

Joint work by the authors in Chiloé has been supported by NSF International Programs, Fundación Andes, and Fondecyt grants 92-1135, and 1950461. This is publication No. 1 of Estación Biológica "Senda Darwin", Instituto de Investigaciones Ecológicas Chiloé.

LITERATURE CITED

ACEITUNO P, H FUENZALIDA & B ROSENBLUTH (1993) Climate along the extratropical west coast of South America. In: Mooney HA, ER Fuentes & BI Kronberg (eds) Earth system responses to global change. Contrasts between North and South America: 61-69. Academic Press, San Diego.

- ARMESTO JJ, R ROZZI, P MIRANDA & C SABAG (1987) Plant/frugivore interactions in South American temperate forests. Revista Chilena de Historia Natural 60: 321-336.
- ARMESTO JJ, & R ROZZI (1989) Seed dispersal syndromes in the rain forest of Chiloé: evidence for the importance of biotic dispersal in a temperate rain forest. Journal of Biogeography 16: 219-226.
- ARMESTO JJ, C DONOSO & C VILLAGRAN (1994) Desde la era glacial a la industrial: la historia del bosque templado chileno. Ambiente y Desarrollo (Chile) 10: 66-72
- ARMESTO JJ, C SMITH-RAMIREZ & C SABAG (1996)
 The importance of plant-bird mutualisms in South
 American temperate rain forests. In: Lawford RG, P
 Alaback, E Fuentes (eds) High-latitude rain forests
 and associated ecosystems of the west coast of the
 Americas: climate, hydrology, ecology, and
 conservation: 248-265. Springer, New York.
- BENOIT I (1989) Red List of the Chilean Terrestrial Flora. Corporación Nacional Forestal, Santiago.
- BURKHARDT F & S SMITH, eds. (1985) The correspondence of Charles Darwin. Vol 1. (letter to sister Catherine, 20 July 1834). Cambridge University Press, Cambridge.
- DARWIN C (1860) The voyage of the Beagle. (Natural History Library edition, 1962, edited by L. Engle; Doubleday, Garden City, NY). Chapters 8 and 9.
- DI CASTRI F & ER HAJEK (1976) Bioclimatología de Chile. Vicerrectoría Académica, Universidad Católica de Chile, Santiago.
- JAKSIC FM & P FEINSINGER (1991) Bird assemblages in temperate forests of North and South America: a comparison of diversity, dynamics, guild structure, and resource use. Revista Chilena de Historia Natural 64: 491-510
- JAKSIC FM & I LAZO (1994) La contribución de Darwin al conocimiento de los vertebrados terrestres de Chile. Revista Chilena de Historia Natural 67: 9-26.
- JANZEN DH (1976) Why bamboos wait so long to flower. Annual Review of Ecology and Systematics 7: 347-391.
- JIMENEZ JE, PA MARQUET, RG MEDEL & FM JAKSIC (1990) Comparative ecology of the Darwin's fox (*Psudalopex fulvipes*) in mainland and island settings of southern Chile. Revista Chilena de Historia Natural 63: 177-186.
- JOHNSON AW (1965) The Birds of Chile and adjacent regions of Argentina, Bolivia, and Peru. Platt Establecimientos Gráficos, Buenos Aires.
- KEYNES RD ed (1988) Charles Darwin's Beagle Diary. Cambridge University Press, Cambridge.
- MEDEL RG, JE JIMENEZ, FM JAKSIC, JL YAÑEZ & JJ ARMESTO (1990) Discovery of a continental population of the rare Darwin's fox, *Dusicyon fulvipes* (Martin, 1837) in Chile. Biological Conservation 51: 71-77.
- PACHECO N (1993) Floración de las quilas. Flora, Fauna y Areas Silvestres 7: 34-35.
- ROZZI R, D MARTINEZ, MF WILLSON & C SABAG (1996) Avifauna de los bosques templados de Sudamérica. In: Armesto JJ, C Villagrán & MK Arroyo (eds) Ecología de los bosques nativos de Chile. Editorial Universitaria, Santiago (in press).
- RUTHSATZ B & C VILLAGRAN (1991) Vegetation and soil nutrients of a Magellanic moorland on the Cordillera de Piuchué, Chiloé Island, Chile. Revista Chilena de Historia Natural 64: 461-478.
- SABAG, C (1993) El rol de las aves en la dispersión de semillas en un bosque templado secundario de Chiloé. M. Cs. Tesis, Facultad de Ciencias, Universidad de Chile.

- SMITH-RAMIREZ C (1993) Los picaflores y su recurso floral en el bosque templado de la isla de Chiloé, Chile. Revista Chilena de Historia Natural 66: 65-73.
- SMITH-RAMIREZ C (1994) Usos artesanales del bosque nativo: la extracción silenciosa. Ambiente y Desarrollo (Chile) 10: 71-76.
- VILLAGRAN C (1985) Análisis palinológico de los cambios vegetacionales durante el Tardiglacial y Postglacial en Chiloé (Chile). Revista Chilena de Historia Natural 58: 57-69.
- VILLAGRAN C, J VARELA, H FUENZALIDA, H VEIT, JJ ARMESTO & JC ARAVENA (1993) Antecedentes geomorfológicos y vegetacionales para el análisis del Cuaternario de la Región de Los Lagos de Chile. In: Villagrán C (ed) El Cuaternario de la Región de Los Lagos del sur de Chile: 1-50. Universidad de Chile, Santiago.
- VUILLEUMIER F (1985) Forest birds of Patagonia: ecological geography, speciation, endemism, and faunal history. Ornithological Monographs 36: 255-304.
- WILLSON MF (1991) Dispersal of seeds by frugivorous animals in temperate forests. Revista Chilena de Historia Natural 64: 537-554.
- WILLSON MF, TL DE SANTO, C SABAG, & JJ ARMESTO (1994) Avian communities of fragmented south-temperate rainforests in Chile. Conservation Biology 8: 508-520.
- WILLSON MF, TL DE SANTO, C SABAG, & JJ ARMESTO. (1996) Avian communities of temperate rainforest in North and South America. In: Lawford RG, P Alaback & E Fuentes (eds) High latitude rain forests and associated ecosystems of the west coast of the Americas: climate, hydrology, ecology, and conservation: 228-247. Springer, New York.