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The glacial limit in south america and its role in biogeography: darwin's observations

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ABSTRACT

Darwin was confused by the abrupt contrast in vegetation he found near Chiloé, in which the southern forests were replaced by those of a more tropical character. The contrast he observed coincides with the Pacific limit of the Cordilleran Ice Sheet, and is partly responsible for the vegetation contrast. Part of Darwin's apparent confusion may have been due to his erroneous understanding of glacial deposits.

Introduction

Charles Darwin had his first opportunity to investigate the flora and fauna of South America at San Salvador, Brazil on February 29th, 1831. Here, he describes the experience: "The day has passed delightfully. Delight itself, however, is a weak term to express the feelings of a naturalist who, for the first time, has wandered by himself in a Brazilian forest. The elegance of the grasses, the novelty of the parasitical plants, the beauty of the flowers, the glossy green of the foliage, but above all the general luxuriance of the vegetation, filled me with admiration.... To a person fond of Natural History, such a day as this brings with it a deeper pleasure than he can ever hope to experience again."

Three years later, on June 29th, 1834, Darwin landed at Ancud (formerly San Carlos) on the northwest coast of Chiloé, a large island that includes the southernmost extent of Coastal Range in Chile. In his diary Darwin wrote: "The woods [of northern Chiloé] are incomparably more beautiful than those of Tierra 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." A second version of this same experience is contained in the Voyage of the Beagle "From the distance the view [of the forest] somewhat resembles that of Tierra del Fuego; but the woods 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." In this second passage, which is more restrained and scientific than the original version, Darwin informs us that, beneath the obvious similarities in the forest flora, there lies a dramatic difference.

Why was Darwin so struck by the vegetation on the northwest coast of Chiloé? In this article, I argue that it is because northern Chiloé (and all of the Chilean coast to the north) escaped recent glaciation. In contrast, southern and eastern Chiloé (and all of the Chilean coast to the south) were buried by ice for thousands of years. Darwin, the keen naturalist that he was, apparently recognized the biogeographic effects of this glacial limit, even though he knew it did not coincide with a sharp climatic transition. Part of Darwin's confusion may have arisen because he adhered strongly to the erroneous "drift" theory for the origin of glacial sediments; that they were deposited as icebergs "drifted" about the ocean, dropping their sediment in unusual places.

The purpose of this article is not to document the presence of a recognizable boundary between the flora of northern and southern Chiloé. If such a phytogeographic difference exists at all, it is likely to be found in the accessory elements of the flora and fauna rather than in the dominant forest taxa, which form a complex mosaic at the level of existing mapping (Otero et al., 1996). Nor is the purpose of this paper to discuss the paleobotany of the coast of Chile with respect to climatic change, a subject that has been thoroughly reviewed by Villagrán and coworkers (1996), who demonstrate that ecosystems were displaced northward along the coast during glacial ages, where they survived in relict populations. Rather, my purpose is to show: (1) that Darwin noticed an abrupt change in the landscape and flora each time he unknowingly crossed the glacial limit, (2) that during one of these crossings on Chiloé he noted a remarkable floristic contrast, and (3) that the abruptness

of the landscape changes at the glacial limit took place within a context of more gradual climatic transitions. These sharp contrasts in biogeography may have contributed to Darwin's later thinking about disjunct and endemic populations.

Setting

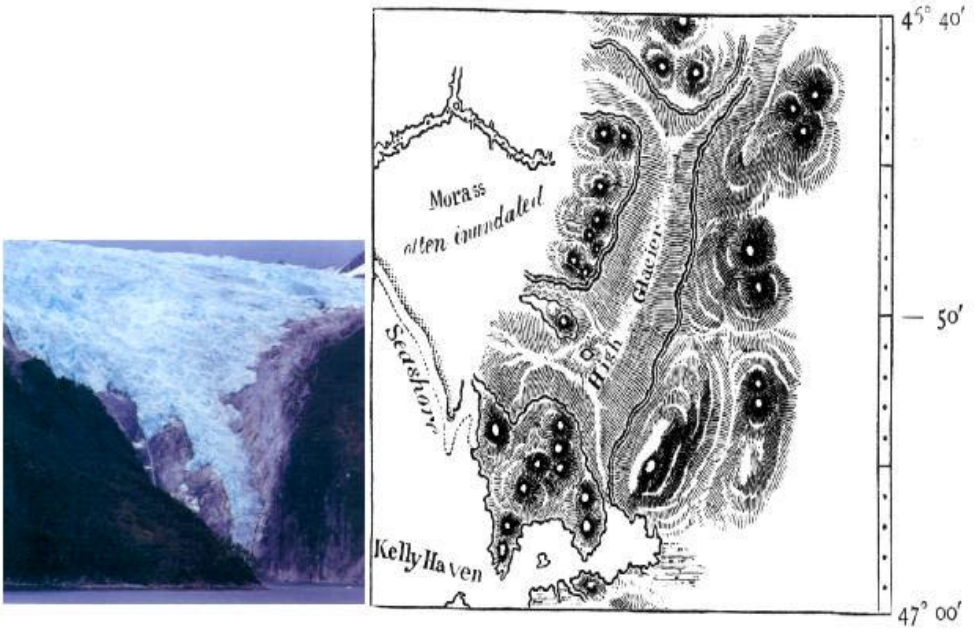

Figure 1. Patagonian glaciers. Left, Glacier on Beagle channel. Right, Glaciers map of Golfo de Penas by FitzRoy.

Chiloé is an archipelago of islands along the coast of south-central Chile at 42^{o} and 43^{o} South latitude (Figure 1). The major island in the group is approximately ninety miles long and thirty wide. Darwin first saw the northwest part of the island near Ancud. From there he travelled overland to its northeastern tip at Chacao. He then voyaged down the eastern side of the island by sea as far as San Pedro, frequenting many ports and taking inland excursions along the way. Later, he made a second, more extensive overland crossing between Castro and Cucao, on the rugged Pacific coast.

Now an island, rather than the tip of a peninsula, Chiloé is separated from the remainder of the coastal range to the north by the narrow Canal de Chacao, which was an exposed meltwater stream during the peak of the last glaciation when sea level was approximately 120 meters lower than at present. Geologically, the western side of Chiloe contains the southernmost limit of the coastal range in Chile, a belt of ancient Paleozoic rocks mantled by Tertiary sedimentary and volcanic rock which crop out intermittently along the coast for more than a thousand miles (Veit & Karsten, 1996; Servicio Nacional de Geología y Minería, n.d.). The Coastal Range on Chiloé is dominated by two resistant massifs of ancient rock, the Cordillera de Pirulil to the south, which was overridden by glaciers and the Cordillera de Piuchén to the north, which remained an ice-free refugium. The eastern side of Chiloé is part of Chile's longitudinal valley. Consequently, it is low country continuously mantled by Quaternary glacial deposits (Heusser & Flint, 1977).

The outer limit of the Cordilleran Ice sheet at the scale of the continent is summarized by Hollin and Shilling (1981). Essentially, the extensive glacierization of the Andes during the Pleistocene was caused by a northward shift of the convergence zone between polar and subtropical air masses by as much as 5-7 degrees of latitude (Kerr & Sugden, 1994). Associated with this change was a drop in the Andean snowline by nearly a kilometer (Porter, 1981), which coincided with a northward migration in the precipitation belts in central and southern Chile (Heusser, 1981). The last significant expansion of glaciers, the Llanquihue Glaciation (Heusser & Flint, 1977), took place between about 40,000 and 15,000 years before present (BP), and culminated about 20,000 years ago. At least three earlier glaciations are recognized, but remain un-dated; they predate the last interglaciation, which took place sometime between 80,000 and 125,000 years ago.

Glacier expanded outward from the Andes in all directions, but reached their greatest extent on the west, the direction of Pacific moisture. On the eastern side of the Andes the glacier limit lies within the foothills of Argentina, and is defined by moraines of east-draining ice lobes in glacial valleys. Further south, but still on the eastern side of the continent, the glacier cover was more extensive, reaching the eastern side of the Straits of Magellan. To the west and north glaciers extended well beyond the present coast, where they calved into the sea. The boundary between this marine terminus and a terrestrial terminus to the north in the Lake District of Chile occurs at Chiloé, where the edge of the last ice sheet is very evident in the topography,

especially between Castro and Ancud, a transect covered by Darwin on one of his overland voyages, and described in some detail. The limit also parallels the north side of the valley of Lago Huillinco-Lago Cucao, where it was crossed by Darwin on his way to Point Huentemo, on the Pacific coast.

The last glaciation was not the most extensive. That distinction is reserved for a discontinuous series of moraines and glacial deposits called the Rio Llico drift by Porter (1981) which apparently covered all of Chiloé, and terminated just north of the Canal de Chacao where it abutted against the coastal range (locally the Cordillera de Zarao). The age of this limit is not known. Its importance rests with the fact that the terrain north of the outermost limit has been continuously available for plant growth since the origin of the southern flora during the Cenozoic Era.

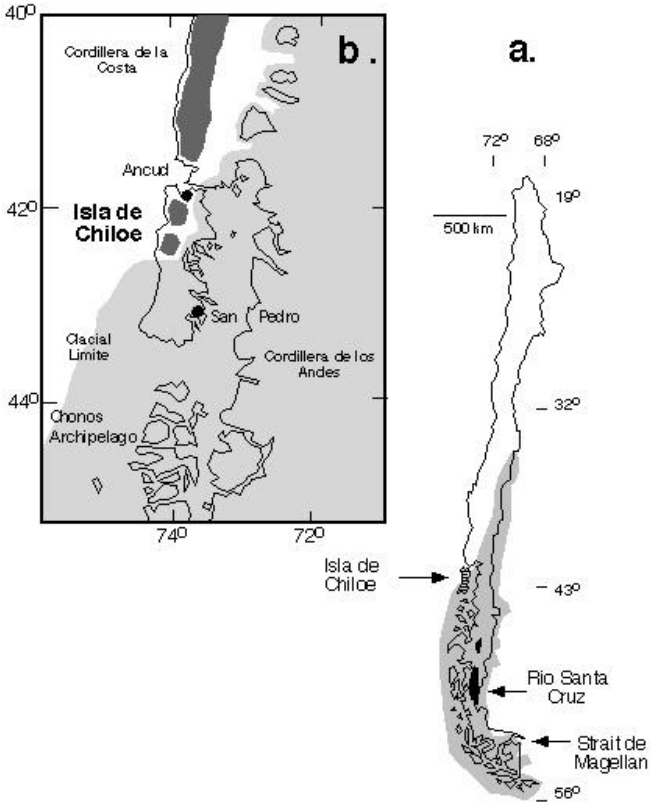

Figure 2. Maps illustrating Darwin's movements across the limit of the last glacial maximum. (a.) Outline of the Cordilleran Ice Sheet in South America (shaded gray) and the distribution of modern glaciers (black) after Shilling and Hollin, 1981. Darwin's three crossings of the glacial limit are shown by arrows. (b.) Expanded view of the area between 40 and 45 degrees latitude showing the glacial limit on Chiloe and adjacent parts of the Coastal Range, after Heusser and Flint, 1977 and Porter, 1981. Unglaciated lowlands (white) were subject to the drainage of cold, dry air from the ice sheets.

North of the glacial limit

The Atlantic shore of South America north of Tierra del Fuego, is unglaciated country dominated by coastal plains. On its southern voyage, the Beagle moved across two climatic gradients, both of which are clearly evident in the climatic, vegetation, and soils mapping. (FAO-UNESCO, 1971). The first was the general decrease in temperature with increasing latitude (The Beagle crossed more than 40 degrees latitude on the Atlantic shore). The second, more complicated changes, were those involving effective climatic differences resulting from both the global pattern of atmospheric circulation as well as more local effects of orography and continentality. En route, Darwin encountered a nearly continuous spectrum of forest types ranging from the tropical wet evergreen forests of Brazil to the frigid Patagonian steppes before heading west into the realm of Pacific moisture. As the Beagle moved southward across these latitudinal and precipitation gradients, Darwin noted that the diversity and density of forest taxa and forest cover, respectively, declined. Documenting these changes in vegetation, particularly as they pertained to climatic changes governing them, was one of the general themes of Darwin's observations, although he was highly anecdotal and unsystematic in this regard. For example, on December 23rd, 1833, Darwin noted at Port Desire that "The zoology of Patagonia is as limited as its Flora". Several weeks later, on January 9th, he was at Port St. Julian, 110 miles further south, observing that "The country is nearly similar to that of Port Desire, but perhaps rather more sterile." At the latitude of the Falkland Islands (Islas Malvinas) he wrote, on March 1st, 1833 "The theater is worthy of the scenes acted on it. An undulating land, with a desolate and wretched aspect, is everywhere covered by a peaty soil and wiry grass, of one monotonous brown colour."

As the flora became less interesting, Darwin's writings shifted away from plant taxonomy to other subjects, notably vertebrate paleontology, marine biology, tectonic and glacial geology, to the human inhabitants (particularly the gauchos and the Fuegans), and to the unusual vertebrates (condors, guanacos, cougars). This part of his diary and the Voyage of the Beagle, are fascinating in their indiosynchratic nature. Then something happened when Darwin crossed into the Strait of Magellan. In his own words:

“In the end of May, 1834, we entered for the second time the eastern mouth of the Strait of Magellan. The country on both sides of this part of the

Strait consists of nearly level plains, like those of Patagonia. Cape Negro, a little ??? within the second Narrows, may be considered as the point where the land begins to assume the marked features of Tierra del Fuego. On the east coast, south of the Strait, broken park-like scenery in a like manner connects these two countries, which are opposed to each other in almost every feature. It is truly surprising to find in a space of twenty miles such a change in the landscape. If we take a rather greater distance, as between Port Famine and Gregory Bay, that is about sixty miles, the difference is still more wonderful. At the former place, we have rounded mountains concealed by impervious forests, which are drenched with the rain, brought by an endless succession of gales; while at Cape Gregory, there is a clear and bright blue sky over the dry and sterile plains."

Within the glacial limit

Darwin attributed this abrupt contrast in the landscape to a change in the atmospheric circulation, which, indeed, is clearly present across of the Strait of Magellan. But the abruptness in the landscape transformation has a more specific and local cause. For it is here that Darwin first entered the glacial landscape of the Pacific Cordillera by crossing its eastern limit. Although he did not know it at the time, he was observing the effects of glacial erosion beneath a wet-based marine ice sheet, the effect of which was to round the summits of the low mountains, deepen and steepen the valley sides as fiords, to replace the ancient soils with freshly scoured rock, and where the oldest ecosystem was younger than the time the ice sheet withdrew. Essentially, this description applied to everything he would see between the eastern side of the Strait of Magellan and northern Chiloé, more than a thousand miles to the north. It is self evident that the climatic contrasts controlling vegetation today are also those responsible for the past distribution of glacial ice. However, the sharpness of the landscape boundaries noted by Darwin on both sides of the ice sheet, which we now know coincide with the glacier limit, suggests that this keen naturalist appreciated the effect of the ice limit on the landscape.

He had encountered it earlier, on the eastern flank of the Andes, during his excursion up the Santa Cruz River. In describing the change in the river he noted: "The well-rounded pebbles of porphyry were mingled with many immense angular fragments of basalt and of primary rocks. The first of these erratic boulders which I noticed, was sixty-seven miles distant from the

nearest mountain; another which I measured was five yards square...the plain here was not quite so level as that nearer the coast, but yet it betrayed no signs of any great violence. Under these circumstances it is, I believe, quite impossible to explain the transportal of these gigantic masses of rock so many miles from their parent-source, on any theory except by that of floating icebergs [April 29, 1833]." We now know that he was wrong; that the boulders were evident in places that the Santa Cruz River cut through its outermost moraines. It is evident from this passage, especially in its earlier unquoted sections, that Darwin thought of a glacial limit as a zone of transition, rather than as an abrupt boundary.

Once inside of the glacial limit at Tierra del Fuego, monotonony, rather than variety, became the general theme of Darwin's writings. There, profound erosion, rather than the deposition of colossal boulders or gravel terraces was the dominant theme of the landscape. Darwin held particular scorn for the simplicity of the coastal forest. Here are some examples, arranged in chronological order: "I never saw a more cheerless prospect. The dusky woods ... I have already mentioned the somber and dull character of the evergreen forests, in which two or three species of tress grow, to the exclusion of all others [June 1, 1832]. The zoology of Tierra del Fuego, as might have been expected from the nature of its climate and vegetation, is very poor ... The gloomy woods are inhabited by few birds ... in the most gloomy, wet, and impenetrable ravines. [June 1, 1832]. Our course lay due south, down that gloomy passage ... as appearing to lead to another and worse world. [June 8, 1832]. The mountain sides, except on the exposed western coast, are covered from the water's edge upwards by one great forest ... The trees all belong to one kind, the *Nothofagus betuloides*, for the number of other species of Fagus and of Winter's Bark, is quite inconsiderable. This beech keeps its leaves throughout the year but its foliage is of a peculiar brownish-green color, with a tinge of yellow. As the whole landscape is thus colored, it has a somber, dull appearance, nor is it often enlivened by the rays of the sun [December 17, 1832]. There was a degree of mysterious grandeur in mountain behind mountain, with the deep intervening valleys, all covered by one thick, dusky mass of forest [Dec. 20, 1832]."

Darwin considered this miserable climate, with its monotonous forest, to extend for much of the way up the west coast of south America. "The equable, humid, and windy climate of Tierra del Fuego extends, with only a small increase of heat, for many degrees along the west coast of the continent.

The forests, for 600 miles northward of Cape Horn, have a very similar aspect. [June 10].

North of the glacial limit, again

We can contrast Darwin's view of the southern coastal forests to the one he found near Chiloé "Although the humid and equable climate of Chiloé, and of the coast northward and southward of it, is so unfavourable to our fruits, yet the native forests from latitude 45^{o} to 38^{o}, rival in luxuriance those of the glowing intertropical regions. Stately trees of many kinds, with smooth and highly colored barks, are loaded by parasitical monocotyledonous plants; large and elegant ferns are numerous, and arborescent grasses intwine the trees into one entangled mass to a height of thirty or forty feet about the ground. [June 10]." In my interpretation of this statement, Darwin identifies Chiloé as the place where the tropical forms are characteristic, while simultaneously indicating that the main climatic change takes place at about 45^{o} South, which he recognizes as the northern limit at which peat can accumulate. Darwin also recognized a third climatic zone in central Chile, one generally north of Concepción, and of a Mediterranean character. Climate and vegetation of this region do not concern us here.

Although not specific about the transition between these climatic zones, Darwin was quite specific about the location of the change in the landscape. When comparing the heavily glaciated southeastern part of Chiloé (San Pedro Island) with the non-glaciated northwestern part (Ancud), he had this to say: "The woods here [San Pedro] had rather a different appearance from those on the northern part of the island. The rock, also, being micaceous slate, there was no beach, but the steep sides dipped directly beneath the water. The general aspect in consequence was more like that of Tierra del Fuego than of Chiloé. [December 1]." In a subsequent passage on the same day, Darwin reinforces his comparison between southeastern Chiloé and Tierra del Fuego by documenting the presence of the southern beech, "I was also pleased to see, at an elevation of a little less than 1000 feet, our old friend the southern beech. They were, however, poor stunted trees; and I should think that this must be nearly their northern limit." From this pair of statements, I draw the conclusion that Darwin knew, perhaps instinctively, that he was very near a major biogeographic boundary. It is a curious aspect of his writings that his first mention of the southern beech took place as he crossed the glacial limit in the Strait of Magellan. And it is here, at the

northern limit of the ice sheet, is his last mention of this great tree, which he now regards as an old friend.

Having drawn the comparison between the southeastern part of Chiloé and Tierra del Fuego, Darwin then had an opportunity to continue southward to the Chonos Archipelago. There, after observing the abundance of southern beech and the conspicuous absence of "the arborescent grass of Chiloé" he drew the conclusion that "Here, within the Chonos Archipelago, the nature of the climate more closely approaches that of Tierra del Fuego than that of northern Chiloé. [January 7]." Note that Darwin is specific about which part of Chiloé he is referring to. Thus, based on Darwin's writings, the relatively gradual climatic transition along the Pacific coast lies near latitude 45^{o} S. But the biogeographic transition is more abrupt, taking place somewhere south of Ancud, on Chiloé. And this just happens to be the location of the glacial limit.

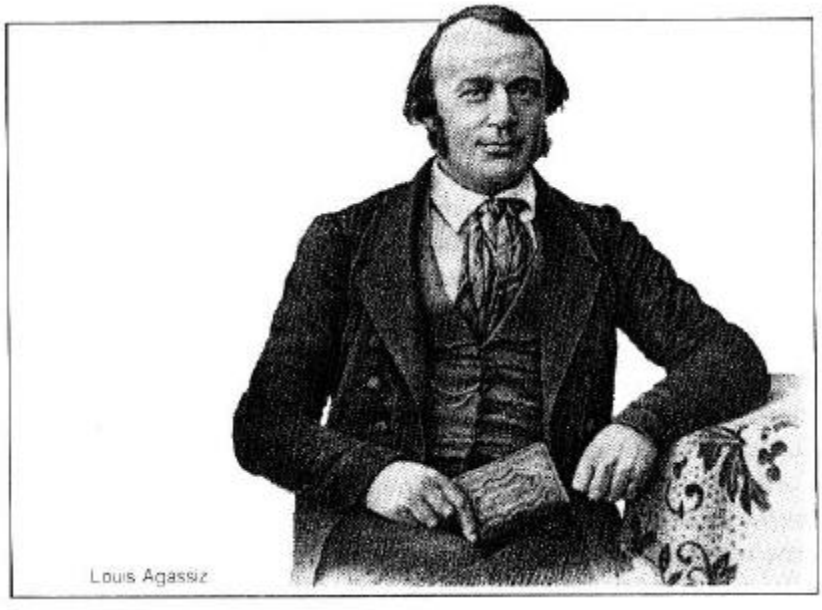

Figure. 3. Louis Agassiz

Darwin and drift

Darwin's voyage on the Beagle took place during the time when the glacial theory was being developed, primarily by Louis Agassiz in

Switzerland. The term "glacial theory" refers to the expansion of alpine and mid-latitude ice sheets in response to global changes in climate, and to the impact of such expansions on the landscape. An important impact of glaciers on landscape was the deposition of "till" a term used for the mixture of large, broken boulders, water-deposited layers, and massive stony mud that is deposited as the glacier passes over a landscape. Prior to our modern understanding of glacial deposition, this enigmatic mixture of deposits was referred to as "drift" because it was alleged to have been deposited by icebergs drifting about cold oceans. Charles Lyell, the prominent early 19th century geologist whose book "Principles of Geology" was a constant companion of Darwin's was an ardent advocate of the "drift" theory, rather than the so-called "glacial" theory. Based on Darwin's diary entries, as well as on a long footnote at the end of his chapter on the Strait of Magellan, Darwin remained a "drifter" throughout his lifetime.

The recapitulation at the end of Darwin's chapter on the Strait of Magellan contains an undated recapitulation of his observations. In it, he states: "I will not here detail how simply the theory of icebergs being charged with fragments of rock, explains the origin and position of the gigantic boulders of eastern Tierra del Fuego, on the high plain of Santa Cruz, and on the island of Chiloé ... Few geologists now doubt that those erratic boulders which lie near lofty mountains, have been pushed forward the by the glaciers themselves, and that those distant from mountains, and embedded in subaqueous deposits, have been conveyed thither either on icebergs, or frozen in coast ice." In this statement Darwin mentions only three places as containing large boulders, erroneously interpreted to have "drifted" into their present position by sea ice. These three places, and only these three, are those where Darwin had a chance to inspect the glacier limit at its eastern, southern, and western extents. The Santa Cruz valley was occupied by a tongue of the glacier descending from the Argentine Andes. Eastern Tierra del Fuego is characteristic of the southern limit of the ice sheet. And Chiloé is its western limit. Erratic boulders occur elsewhere in moraines near the glacier limits, but Darwin did not have access to those localities. Thus, Darwin himself places the glacial limit at important biostratigraphic boundaries.

Time, terrain, and biography

The glacial limit near Chiloé represents an important biogeographic barrier. With respect to time, the boundary is sharpest at the time of

deglaciation, when land to the south would have been bare, free of soil, and rubbly, whereas the land immediately to the north was cold-adapted wet moorland (Villagrán, 1990). Over time, however, the boundary has become blurred as plants dispersed across it, and as plant and animal communities re-established their interdependencies. Provided that the substrate material is similar on both sides of an ice limit, 15,000 years of ice-free conditions may render a biogeographic contrast in the dominant taxa difficult to detect. Only at higher levels of complexity will it be present.

With respect to space, the glacial limit is not a sharp line, but a zone, perhaps a few dozen kilometers wide. The inner edge of this zone is the limit of the last glacial maximum. The outer edge of this zone is the outermost limit of glaciation of any age. Inside the Llanquihue limit, the maximum age of the surface on which plants could colonize is about 18,000 years. Local differences in edaphic conditions, essentially relief and drainage, represent the differential erosion of the previous landscape and the deposition of materials. On Chiloé this is extremely important because the well drained ridges are moraines, the flat plains are lacustrine basins, and the gravelly terraces are former meltwater outlets. The soils developed on these deposits are generally Dystric Cambisols and Humic Andisols, locally called Trumao soils. The only climatic changes experienced by these areas are those associated with the postglacial epoch, generally one of rapid warming and less wet conditions during the last 10,000 years, a period called the Holocene.

Beyond the limit of the Llanquihue Glaciation, but within the limit of the outermost glacial limit, the terrain has a more complex history. The complexity of edaphic habitats originally created by glacial action have been modified by burial of eolian material, by soil formation, and by erosion. Additionally, this zone has been subject to frequent pulses of abrupt changes in local climate associated with expansions of the Cordilleran Ice Sheet. Notable among these is the local effect of cold-air drainage in which density-driven westerly winds from the Andes would have been concentrated by the edge of the glacier (Figure 1).

Outside the maximum limit of Quaternary Glaciation, which lies just north of the Canal de Chacao, the maximum age of the surface exceeds the age of the flora itself. This terrain has been continuously available for a terrestrial ecosystem throughout the Cenozoic. Local differences in relief and drainage result primarily from the balance between the production of soils through long-term weathering, and their removal by erosion. The soils are

generally ancient, reddish, and rich in clay classified as Dystric Nitisols, and locally called Rojo Arcillosos.

It is here, in the southern part of the coastal range, north of the limit of glaciation, where one can find the maximum combination of variable lithology, local habitats, and pronounced climatic stresses, taking place on an ancient surface which has been continuously available to in-migration from the north, and to out-migration from the glaciated region. It is in this zone, near Valdivia, where the highest richness of forest species occurs and where narrow-range endemics are concentrated (Villagrán et al., 1996). Indeed, much work has been done by palynologists regarding the response of plant taxa to Quaternary climatic forcing. Darwin's recognition of the distinction between the forests of northern and southern Chiloé is not only a testament to his powers of observation, but it also provides us with a focal point on which to concentrate further research on the importance of the glacial limit itself to plant biogeography.

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Glossary

Edaphic condition: Physical, chemical and biological properties of the soil or substratum, which influence associated biota.

Lacustrine basin: low area in which lake sediments have accumulated.

Moraine: A mound or ridge of unstratified glacial drift, chiefly till, deposited by direct action of glacier ice.

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