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AN HISTORICAL APPROACH TO PLANT EVOLUTION.

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Last year, in a German article of this magazine, I demonstrated that the neo-Darwinian theory about the origin of new species is not confirmed by the great experiment of Nature: there is nothing creative in selection, its rôle being restricted to the sifting out of actually existing species.

The present article is meant to give an idea of how the problem of plant evolution may be approached in a positive way. The subject matter, to speak in terms of scholastic philosophy, remains the same as in the above mentioned discussion: the history of the South Brazilian phanerogamic flora; and the negative conclusion reached at then, viz., that there has been, in at least two great formations, and since their immigration into the present area, no production of new species, is one of the cornerstones of my argument.

My formal thesis is that **plant evolution intimately depends upon the historical conditions of an area at the time of its occupation by the vegetable kingdom;** the appearance of new units of a given taxonomic degree represents nothing else but a natural and necessary consequence of flora history throughout geological times.

1. Space occupation.

Plant life, plant dispersion, and plant distribution all over the face of the globe are governed, like all other living beings, by a basic principle which is simply factual, prior to any scientific investigation and resisting to any ultimate analysis: the principle of space occupation.

All living things, plants more than animals, produce much more offspring than can survive. This is the sound starting point of Darwin's theory and the basic condition for space occupation. **Every plant tends to conquer the greatest possible area within its natural limits.** These limits are defined by: the plant's inborn tolerance as to the conditions of climate and soil; the plant's degree of dependence upon its native formation; and, as an external but often decisive factor, the plant's limitations by geographical barriers such as mountain ranges, deserts, wide stretches of open sea.

So it comes to be that no plant species whatwever actually occupies the whole of its possible area: it always strives to do so, but never reaches its final goal.

From this it **follows that the plant kingdom, like life itself, is always on the move.** This is a factual difference compared with non-living things, which cannot be explained by any "mechanism" in terms of physico-chemical processes. Life means moving, life means progressing, life means conquering, life means dying out or renewing itself either by reproducing the same species or, if necessary, by transforming the old units into new ones.

The final result, in present and past times, is always the same: space occupation as full, as wide, and as permanent as possible. Actually, there is no single area capable of plant life on the surface of the earth devoid of its convenient vegetation and, as far as our fragmentary knowledge goes, never lacked it.

As a consequence both of the innate principle of space occupation and the utmost diversity of life spaces lying within the general range of the plant kingdom, **there follows an enormous amount of life forms and systematic units.** If plants, by some hidden destiny unattainable to biological research, but non the less real and factual, are bound to occupy all of the habitable lands and waters, including the whole gammut of ecological conditions from tropical jungles through temperate forests and steppes to semideserts and polar nunataks: their adaptadness and life forms must needs vary along the same line; and if, as it is the case, their close bonds to their native formations and areas allied to physical barriers impose a severe limitation to random migration, there must needs be a great floristic diversity in areas widely separated from each other although similar in life conditions.

This is not the place for a lengthy demonstration and discussion of the principle established above: every perusal of the pertinent literature, percursory as it may be, and every field observation adds ample evidence to it.

Thus, all basic features of the vegetable kingdom can be derived from one general principle: there exists, prior to all discussion and beyond the respected limits of Natural Science, the general law that plants are bound to cover the whole of the habitable earth.

Every investigation in plant history and plant evolution which does not start from this fundamental fact is doomed to operate in a vacuum; and every theory on the historical formation of new units which does not take into account this inborn quality will never reach beyond very limited partial results or, worse than that, wild-running speculation.

2. Space occupation and area.

On their migrational move over the face of the planet, the plants, bound together in natural societies and formations, find themselves confronted with a vast variety of areas to be occupied. For practical purposes, I subdivide them into two main categories: areas entirely unoccupied, and areas partially or fully stocked with plants.

a. **Occupation of present-time new areas.** — This category comprises all recent areas, small or large, natural or artificial, that are devoid of a native vegetation but surrounded by a fullfledged flora with a sufficient variety of species to occupy all essential niches of the new life space. Such areas partially are natural, like the bare stretches of deeply eroded soil left in the wake of landslides, the ever-changing deposits at the bends of the rivers, the recent layers of lava and volcanic ashes; or man-made, like the deep cuts opened by road construction, the trodden ground near dwellings, stables and corrals; and, in a gigantic scale, the agricultural soil.

Let us examine the latter of these cases, being by far the most common and most important.

In Southern Brazil, the slash-and-burn system of agriculture has destroyed, in less than 150 years, most of the native rain forest and a considerable part of the Araucaria woods and low grass steppes. Due to the extensive method of mere exploitation, the fertility of the soil, very high during the first years, rapidly declines leaving the cultivated fields in a condition of utter exhaustion. It is highly instructive to observe the definite steps by wich the abandoned agricultural areas are repopulated by the native flora.

During the period of cultivation, all species, except for the cultivated ones, belong to the category of the **weeds**. There are, estimatively, around 300 species of weedy plants infesting the crops of which one third is of European origin; the other two thirds are mostly American. Some of them are dangerous pests like Digitaria sanguinalis, Bidens pilosus, several species of Amarantus; but the great majority of them can easily be maintained under control.

This first occupation wave, as is is the case in every part of the world, preserves its specific identity down to varieties, for instance Anagallis arvensis with the varieties brick and blue. The weeds come and go with the crops. Five years after a field has been abandoned, there remains no trace of them.

The second wave of plants immediatily setting in, after a cultivated area has been left, belongs to two categories of plants: **half-weeds and ruderal elements** of American extraction like Solanum aculeatissimum, S. atropurpureum, S. sisymbrifolium, Xanthium cavanillesii, Tagetes minuta; and **native species from the steppe** or similar formations on dry soil: Andropogon virgatus, A. condensatus, Cortaderia argentea, Baccharis dracunculifolia, and a wealth of species of Baccharis, Eupatorium, Vernonia, Stipa, Aristida. The gigantic bunches of Cortaderia argentea and the tall shrubs of Baccharis dracunculifolia are, throughout the whole country, the dominant species of this brushwood formation.

Under the shelter of this brushwood and on the quickly improved soil, there soon appear the first representants of the third successional wave in the shape of **rain forest elements** which occupied the area before its agricultural transformation. Generally, the species belong to the edge of the forest, like Bauhinia candicans, Inga marginata, Ocotea puberula; among them, a variable number of species foreign to the rain forest may occur, like Escallonia montevidensis from the Araucaria woods, Erythroxylum argentinum from the gallery woodlets of the steppe, Lithraea brasiliensis from the park formations all over the State. Locally, Piptadentia rigida, a tall hardwood of the

After some ten or fifteen years, the **high trees of the rain forest** begin to make their appearance, mostly species dispersed by wind or birds: Cordia trichotoma, Patagonula americana, Phytolacca dioica, Inga sessilis, and many others. In this stage of re-occupation, the second wave (half-weeds and native steppe elements) has entirely disappeared; the second (Cortaderia-Baccharis formation) is dying out leaving behind a much improved soil; the third (Bauhinia-Inga) is being crowded out or pushed towards the edge of the growing forest. Where the depletion of the soil by agriculture and erosion lies within tolerable limits, after some 25 or 30 years, a **vigorous secondary rain forest** is in full development. Under the canopy of the high trees, the lower stories of the subtropical forest, herbs, small brushes and middle-sized trees, spread in their damp and shadowy habitat.

Creepers and epiphytes complete the structure of the original forest which is, in all essentials, equivalent to a formation never touched by an ax.

This exemple demonstrates that artificial new areas, no matter how large, are, at least under the rain forest climate of southern Brazil, re-occupied by the former climax formation; although the successional waves and the final result may be different under different conditions of soil and climate, the general statement has a universal value: **Present-day artificial new areas are always occupied by an already existing flora without any change towards evolution**.

The same holds true in present-day natural new areas such as are produced by landslides, river deposits, volcanic ashes and lava sheds.

b. **Occupation of geologically new areas.** — More important than the foregoing observation is the statement that even the stocking of new areas reaching back several hundred thousand years has followed the same line of simple immigration without producing any novelty.

This may be exemplified by **the flora of the South Brazilian coastal plain.** The area of this plain amounting to about 30.000 square kilometers in Rio Grande do Sul is of Quaternary age, emerging from the retreating ocean as a consequence of the isostatical upheaval of the mainland. Its phanerogamic flora, as far as my investigations of more than 20 years go, amounts to 1072 species in 530 genera and 132 families. As to its geographical and historical relationships, this flora may be subdivided into the following elements: Subtropical rain forest — 176 species; mountain flora (eastern rim of the South Brazilian highlands) — 25; western flora (related to the Chaco with a considerable percentage of "Sonoran" elements) — 36; campos flora (South Brazilian steppe element) — 677; insular flora (a mixture of Brazilian and Andean elements with many endemics on the granitic hills of southeastern Rio Grande do Sul and eastern Uruguay) — 234.

A thorough discussion of this flora, whose beginnings reach as far back as the final stages of the Tertiary period, yields the surprising result that **there is not a single species which must, of necessity, be considered as a local neo-endemic;** on the contrary, the whole of the evidence points to simple immigration, streaming in from the older areas that lie contiguous to the coastal strip: rain forest on the escarpment of the near-by highlands, steppe on the more elevated areas of southern Brazil already present in Tertiary times, and granitic hills emerging from the sea as an archipelago, before the uplifting of the coast united them with the old mainland to the north.

Thus, we have a convincing proof that a large body of plants embracing 132 families out of 152, 530 genera out of 900, and 1072 species out of 4500 of the total floral of Rio Grande do Sul, during the last half to one million years, did not produce a single new species. Evidently, the occupation of the Quaternary area took place in the same manner as that of contemporaneous new areas within the reach of a highly diversified flora. The existing species in the neighboring areas being fit to take possession of the new sea-born soil, and with no barrier preventing their always active tendency to spread all over the habitable land, simply occupied it by common immigration.

The two exemples cited above, especially the last, may give a clue as to how the occupation of new areas has taken place in the earth's past history. Although the lay-out of the factual foundation is, perhaps, too narrow for a general statement, is suggests to us a somewhat revolutionary idea about plant evolution, which may be formulated as follows: **Whenever there is a new area lying within the general range of life requirements and migration of an already existing flora, its occupation is accomplished without any evolutionary change**.

Correctly seen, this static behaviour of the plant species under the aforesaid historical circumstances means nothing else but a concrete formulation of the principle of space occupation: The first and foremost task to be accomplished is the replenishment of every area capable of plant life; if this can be done by the already existing species there is no reason for creating new ones. It may be stressed, once for all, that the driving force in space occupation is reason and finality, not chance; and that, consequently, there emerges a second general principle which will become clearer during the following discussion: the principle of parsimony.

c. **The behaviour of saturated areas** — One third of the total area of Rio Grande do Sul (285.000 square kilometers) was originally covered with **subtropical rain forest.** As far as I can judge from my own research, this formation contains about 1000 phanerogams in 367 genera and 37 families, which correspond to more or less 20% of the total flora of southernmost Brazil.

Although severely depleted in comparison to the Amazonian jungles, the Riograndean forest preserves the typical 6 stories as may be collected from a partial analysis of the forest at the Upper Uruguay River in northwestern Rio Grande do Sul, southwestern Santa Catarina and the Argentine Territory of Misiones. Among 400 species — less than one half of the total — analised, 46 = 11,5% belong to the low terrestrial herbs; 75 = 18,25% to the small brushes up to 2 meters high; 90 = 22,5% to small trees up to 15 meters; 50 = 12,5% to the tall trees forming the general canopy up to 35 meters; 116 = 29% to the climbers and half-climbers; and 25 = 6,25% to the epiphytes and parasites.

As to the different zones of maturation, 21 = 5,25% species are limited to the banks of the rivers, 124 = 31% to the edge of the forest, and 525 = 63,75% to the inner and most charasteristic part of the formation.

The general structure remains the same throughout the whole area, but the floristic composition in the two main centers, Upper Uruguay and Atlantic coast, varies very notably. Although most of the species are common to both centers, the floristic differences clearly define two main streams of immigration. The western center represents the southernmost fringe of the tropical forests in the great basin of the rivers Paraná and Paraguay; it contains a huge number of very characteristic species absent in the east, like Balfourodendron riedelianum, Peltophorum dubium, Chorisia insignis among the trees; Britoa sellowiana, Trichilia catigua, Cordyline dracaenoides among the small trees; Dichorisandra aubletiana, Hamelia patens, Hybanthus communis among the brushes and herbs. The eastern center is strongly, defined by a great number of purely tropical elements: Euterpe edulis, Heliconia biahi, Cecropia adenopus and, more than all, epiphytic and terrestrial Araceae, Bromeliaceae, Orchidaceae.

There cannot be the slightest doubt as to the **Quaternary immigration** of the Riograndean rain forest into its present area: in several articles, not to be repeated here, I have assembled irrefutable proofs of this fact which is going on up to the present time.

Now, the most remarkable feature of this rain forest is that **it does not contain**, in its present Riograndean area, **the slightest trace of neo-endemic species production.** Several very painstaking analyses carried out both for given taxonomic groups (Compositae, Leguminosae, Asclepiadaceae) and for the flora as a whole have made it evident that there are no more than 40 Riograndean rain forest species — less than 5% — which so far have not been found north of the Uruguay River or along the coast of Santa Catarina. Significantly enough, all of them belong to the small gap-stoppers, notably epiphytic orchids of the genera Pleurothallis and Octomeria, or genera lying in an utter confusion, like the terrestrial and epiphytic genus Peperomia. It may be said in passing that those gap-stoppers living under the rather equable conditions of the inner forest are the last group in which neo-endemics can be expected. As an example of the wide-ranging dispersion of purely tropical species under the dense canopy of the Araucaria forests, may be cited the fact that out of 266 species composing the Araucaria groves on the highest part of the highlands (eastern rim) 84 — 32% are purely tropical herbs, shrubs and epiphytes from the coastal forests: protected by the dense story of middle-sized trees they thrive perfectly in a climate 4-5 degrees colder than in their original home, with cold nights all the year round and snowfalls every winter.

Thus, it is certain that the South Brazilian rain forest in Rio Grande do Sul, which must be considered as the highest expression of plant life under the present conditions, **has produced no novelty** since the first beginning of its immigration. This fact gives strong evidence against all random and mechanical evolution; on the other hand, it perfectly harmonizes with the general principle of space occupation guided by reason and finalism, not by chance meaning absence of a definite cause and, therefore, a philosophical nonsense.

d. **The behaviour of undersaturated areas.** — Two thirds of Rio Grande do Sul, that is to say, about 200.000 square kilometers were, at the time of the oldest white settlements, covered with **"campo"**.

The meaning of this Portuguese word throughout Brazil is a rather shifting one. In its most general acception, it is used for designating a natural formation where there is grass for pasture. The Central Brazilian "campos cerrados" (closed campos) are park steppes due to seasonal lack of rain; the South Brazilian "campos gerais" (general campos) are low or bunch grass steppes thriving under a rainfall of 1500-2500 mm per year which is much too high for their ecological requirements. Locally, distinction is made between "campos limpos" (clean pastures) and "campos sujos" (dirty pastures more or less interspersed with swamps or invaded by brushwood). Most of the confusion as to the origin of the Brazilian campos has arisen from the faulty definition deeply rooted in the older literature: actually, the campos cerrados of Central Brazil are a consequence of present-time climatic conditions, whereas the South Brazilian ones (Paraná, Santa Catarina, Rio Grande do Sul) are an immense Tertiary relic formation, originated in a much drier climate and, in our days, subject to invasion and outcrowding by the forest.

The Riograndean campos both on the northern highlands and the south-eastern lowlands predominantly appartain to the "clean pastures" with narrow belts of brush or half-high gallery woods along the water-courses; on the highlands, the proximity of large bodies of rain forest makes itself felt by numerous islets of wood with rain forest character.

The native flora of the Riograndean campos numbers, at least, 3500 species of which one third belongs to four great families: Compositae — 500 (Baccharis 100, Eupatorium 70, Vernonia 50), Gramineae — 350 (Paspalum, Panicum, Andropogon, Eragrotis, Stipa, Aristida), Leguminosae — 219 (Mimosa, Desmodium, Phaseolus), Cyperaceae — 120 (Cyperus, Rhynchospora, Scleria, Carex). There are, besides, many other genera with a strong local development, like Petunia — 27, the erect species of Oxypetalum — 24, the erect Mikaniae — 10, Eryngium — 40 mostly in the swamps.

As to its geographical and historical origin, 75% of the campos flora stems from Central Brazilian tropical roots, 25% from a temperate stock highly developed in the Andean space and nearly related to the northern hemisphere (Vicia, Lathyrus, Lupinus, Salvia, Eryngium — about 120 genera). It may be mentioned in passing that the Araucaria woods contain about the same percentage of "Brazilians" and "Andeans" whilst the flora of the rain forests is purely Brazilian without the slightest vestige of Andean elements.

As mentioned before, the South Brazilian Campos are, under present climatic conditions, "out of place" or, in terms of historical plant geography, despite of their vast extension, a **relic formation.**

Whereas the campos cerrados of Central Brazil and the Argentine Pampas are typical formations disfavoured by a rainfall below the threshold of forests, the South Brazilian steppe receives, at least, twice as much as needed by its formational requirements. There is ample geological evidence as to a much drier climate in former times, although the beginning and the causes of the present-day rain period cannot be ascertained yet. Evidently, it is, at least, as remote as the first appearing of the migrating rain forest in Rio Grande do Sul, and probably much older.

As it is generally known, the plant formations behave in a different manner relatively to climatic changes: If the conditions fall down towards the minimum threshold of their exigencies, the formations thin out and eventually disappear; but if they increase beyond the requirements, the plant cover remains unchanged although richer in individuals and volume.

This is certainly the case with the South Brazilian campos. They reacted and continue reacting to the bettered rain conditions by a general improvement of their steppe features. But, from all we can ascertian, they did not evolve new species better or fully adapted to avail themselves of the improved conditions. On the contrary, the general ecological features of the campos species are decidedly xerophytic, much in opposition to their present home: small, needlelike or leathery leaves, abundant hairs or strong odoriferous substances, procumbent habit, sturdy rootstocks.

Although there is no means to prove that the campos flora remained specifically unchanged despite the changing climate, this becomes highly probable if we proceed to study its behaviour in contact with the immigrating rain forest.

e. **Contact phenomena between saturated and unsaturated areas.** — The South Brazilian campos lie, for many thousands of kilometers, in direct contact with the advancing forest. As we have seen, on its advance over nearly 100.000 square kilometers of original grassland, they have not produced a single new species; what interests us here is the question of whether the campos, on their slow retreat, succeeded in salvaging some of their stocks transforming them into forest forms.

The progress of the forest, as it can be observed in a thousand of local variations, is always essentially the same: At the heads of the water-courses, along the borders of the creeks, in the gulches opened by violent downpours, in the shelter of outcropping rocks — in one word where there is abundant moisture and disturbed soil the first settlers from the rain forest make their appearance. They invariably come from the edge of the forest, many of them, especially Myrtaceae, being common elements of the gallery belts along the rivers and streams of the campos region. The second step is made by some tall trees, commonly with flying or bird-dispersed seeds: Cordia trichotoma, Patagonula americana, Phytolacca decandra, whose seedlings, unable to thrive in the highly mineralized soil of the campos, find a much improved home under the protection of the first invasion wave.

As the high trees develop and close their canopy, the light-loving brushes and small trees die out in the center and become restricted to the fringe of the growing forest. Much in the same manner as in the re-occupation of abandoned farmland, the three lower stories of the rain forest, herbs, brushes and small trees, begin filling up the gaps between the high trees.

The creepers and the epiphytes, as it always happens where a rain forest comes into being, are the last two stories giving the final finish to the new forest.

The ultimate result is a "capão" (Guarany-Portuguese word meaning "round forest") which continues advancing concentrically and preserving its roundish circumference until it enters into contact with other similar nuclei, fusing with them and constituting more or less large and solid bodies of forest. In the final stage, there is no perceptible difference between those forests on former campos soil and the much older portions in the river valleys; in their mature sections, there is not the slightest trace left of the original campos vegetation.

Let us consider this fact more closely. The rain forest contains about 1000 species in 362 genera and 87 families; as to the campos flora, on may not be far from truth in admitting 3500 species in 600 genera and 140 families. Three distinct conclusions emerge from the foregoing facts:

First, there are occupied but not saturated areas, whose present flora cannot avail itself of the resources brought about by an ecological improvement. Within a certain margin of tolerance, which may be very wide as it is in the case of the South Brazilian campos, they do not react by producing new species but become liable to invasion by better fitted communities lying within immigration range.

Secondly, there are fully saturated formations which do not develop any novelty whilst invading, in a very slow and methodical progress, unsaturated areas.

Thirdly, the contact between the two precedent categories of formations is of a radical character: The invading forest does not make its advance by evolving new species, but with the aid of its already existing resources; and the campos flora, in its struggle which literally means existence, does not make the slightest effort for survival, either by producing species fitter for taking profit of the increased resources of its habitat, either by salvaging, at least, some of its units adapting them to the victorious forest.

3. The concept of space occupation.

The foregoing examples give us a strong hint, not only as to how space occupation really proceeds, but also as to the true meaning of the concept.

With reference to the fully saturated areas — the subtropical rain forest in our present case — nothing remains to be added; in their mature sections, they are absolutely closed societies resistant to any kind of immigration.

The same does not obtain with undersatured areas under the edaphic and climatic conditions of Southern Brazil: they are occupied but not to their maximum capacity. Still, they do not produce new forms better adapted to avail themselves of the substantially increased potentialities of plant existence. Much on the contrary, they become liable to suffer invasion down to complete extermination by stronger communities within range of immigration.

Hence, there are **naturally undersatured areas** which remain so during an indefinite period of time; in other words, the concept of space occupation does not necessarily include the concept of saturation. Every habitable area naturally lays claim to a convenient plant cover but this claim does not forcibly include saturation.

There exists, evidently, an enormous difference, both in life forms and mass of vegetable substance, between the one-storied grasslands that actually spread over most of southern Brazil and the six-storied rain forest that potentially can develop in the same area: neither does the forest produce anything that might speed up its advance, nor does the campo offer any effective resistance.

One would perhaps object that this behaviour is but a peculiar feature of the areas and formation under study and, consequently, dismiss the subject as of no general significance. Nevertheless, I suspect that we are here at grips with a universal law of plant migration and plant evolution, and that it is worth while insisting upon its main features.

a. Space occupation means the presence of a plant cover **within very broad limits** of intensity and effectiveness. The lower boundary of occupation, that is to say, the line wherefrom an area must be considered as just occupied, can hardly be drawn, not being for this less real and factual; the upper boundary, saturation, lies open to observation. All empty, and occupied but undersatured areas lie open, in a measure that is a function of the intensity and effectiveness of their occupation, to foreign invaders: saturation, in its turn, means exclusion of any immigration.

b. A saturated area never produces a new species. The static behaviour of saturated formations is put in full evidence by the south-migrating rain forest in Rio Grande do Sul. Once a vegetational unit, no matter of what taxonomic groups it is made up, has acquired its final finish, no reasonable grounds remain for further changes. It may thin out, as it happens at the southernmost fringe of the South Brazilian rain forest in Uruguay, down to a few dozens of species, but it maintains its identity **up to the last.**

c. **Neither do empty areas, and occupied but not saturated ones,** provided there are, within immigration range, enough species and vegetational units capable of answering to their claim **—produce any novelty.** Leaving aside all artificial and small natural new areas, this is more than clear from the history and composition of the Riograndean coastal flora, and the behaviour of the campos in contact with the immigrating rain forest.

Summing up: All areas hitherto examined have nothing to do with plant evolution. It would be of the highest importance to examine the flora of other great regions of the world where, as is proves possible in southernmost Brazil, a hard and fast line can be drawn between the different vegetational units and their respective historical background. Although the South Brazilian flora with its 4500-5000 species in 900 genera and 154 families represents but a small fraction of the earth's vegetable kingdom, I feel confident that we have to do here with a general feature of plant history and plant evolution. As a prerequisite of studies of this kind, one must, once for all, put aside the various theories that have been invented for explaining the "mechanism" of plant evolution, from the crudest Lamarckism down to the brand new genetically minded forms of Darwinism. Before we know where and under what historical circumstances of space and time the upsurge of new life forms comes about, speculating as to how the "mechanism" of evolution works cannot go beyond useless armchair theorizing.

It seems, therefore, to be certain that the production of new species of plants, if there be any such process depends upon some very peculiar historical circumstances of the area, circumstances that are absent from the areas hitherto examined.

4. **The principle of parsimony.**

Before we proceed to analise those peculiar circumstances of space and time, it is necessary to devote our attention to the second general principle governing plant dispersal, plant distribution and, as a matter of fact, plant evolution.

There was a time when plant distribution all over the face of the globe was attributed to random dispersal of the propagules by wind, water, animals, and similar external agents. This thoroughly unhistorical way of thinking, one of the most outstanding characteristics of the golden period of Darwinism, has since been upset by the fact that there is no chance migration of plants, at least between areas already stocked with their convenient vegetation. Except for a few hundreds of weeds — less than 1% of the phanerogams and near to 0% of the cryptogams — the species cling to their native formation and area, their migrations depending upon movements of their home society as a body, and being slow in time and limited in space. This is so much true that disrupted areas more or less widely separated in local disjunctions constitute one of the most valuable resources of paleography.

It is all the more remarkable that most of modern evolutionists, whose supposed vocation would be the clearing up of life's past history and future prospects, work under the guidance of methods that are downright sterile in any kind of historical research. Whilst other historical disciplines, like human prehistory and comparative ethnology, depending upon indirect evidence similar to that of plant history, have long since discarded the mechanistic scheme of extreme evolutionism, evolutionists continue thinking along lines that may prove useful in physics and chemistry but not where life is concerned.

As all history develops in space and time, **there must be, and there really is, a way from space to time and relative chronology**. The first thing to be done is to put into evidence the guiding principles that factually govern the spread of plant kingdom over all habitable lands, in order to understand the historical behaviour of the plants under the concrete circumstances of space and time.

Despite the prodigious dissipation of pollen, seeds, and other propagules observed in many species of plants, there decidedly is a strongly accentuated **parsimony in life forms.** This may be shown by a few corollaries emerging from the foregoing chapters.

a. There are uncountable millions of habitable niches in a given area, all more or less different as to their local micro-conditions of soil, climate and plant associations; but there are, all in all, less than 200.000 species of phanerogams constituting the bulk of the earth's vegetation. The fact is that **every species has its individual range of adaptibility**, sometimes rather narrow, sometimes very wide, thus substantially restricting the number of wanted occupational units.

b. The same principle is valid as to the secondary transformations evolutionary or not — present in most plants: roots into respiration organs, branches into thorns, leaves into tendrils, and thousands of others. **A new necessity does not lead to an entirely new organ but conveniently transforms an old one**.

c. What is true with each individual species cannot but rule the behaviour of any given flora and, therefore, of the plant kingdom as a whole. **The principle of parsimony prevents a flora from producing new units as long as the already existing ones can occupy a given area**.

This, beyond any doubt, is the case with present-day new areas, artificial or natural; and this, as far as indirect testimony goes, in past-time new areas like the coastal plain of Rio Grande do Sul. For the same reason, areas stocked up to the very summit of saturation, like the subtropical rain forests, remain static in their floristic composition.

The principle of parsimony goes even so far as to impede the production of new species in undersaturated areas like the South Brazilian campos, provided there exists, within immigration range, a full-fledged flora that can take advantage of the environmental conditions. Parsimony, from all we can collect, keeps the base-line of occupation very low leaving the full stocking of an area to immigration. This explains why all insular floras, although rich in endemisms, are liable to violent invasions; and why the species density per square kilometer, even under similar environment conditions, is incomparably less on oceanic islands than on mainlands. Take, for instance, the flora of New Zealand with around 1000 species only, and the flora of the surroundings of Porto Alegre in Rio Grande do Sul — only 1500 square kilometers — with 1300 phanerogams; or the flora of the Juan Fernandez Islands with 146 phanerogams on 90 square kilometers with that of the flat top the Morro Sapucaia near Porto Alegre with about 200 phanerogamic species on scarcely 3 hectares. The reason must evidently be sought in the fact that on the big mainlands, with their rich diversity of developing centers and open wandering paths, the gaps in any local flora can easily be filled up with immigrants, whilst the oceanic islands are severely curtailed as to immigration.

d. A very important corollary emerges from the contact phenomena between the campo and the rain forest in southernmost Brazil. Let us remember that the final outcome is the radical victory of the forest and the no less radical extermination of the campo. **Nature, evidently, is not in the least interested in preserving this or that species, this or that vegetational unit,** its only scope being to have a given area conveniently occupied by plants. There is no trace of struggle for survival, no trace of evolutionary selection of the fittest.

These anthropomorphisms have done, and continue to do, more harm to sound evolutionistic thinking than any other original sin committed by the fathers of the theory.

Nature goes even so far as to destroy hundreds and hundreds of species where, if it had slightest care for their transformation along Lamarckian or Darwinian lines, is would be a simple "mechanism" to mutate them into species able, at least, to inhabit the edge of the forest. See, for this purpose, the 24 erect Oxypetala, or the 10 erect Mikaniae or other genera with closely related species among the creepers of the rain forest and the erect half shrubs of the campo (Ipomoea, Convolvulus, Gonolobus, etc.): there is no reason apparent why those slender erect species could not have been salvaged by their transformation into climbing ones. Although the campos of southern Brazil are not very rich in endemics, more than thousand species would entirely dissappear from Nature's checkbook, if the immigration of the forest came to its final end.

ε. The more or less wide **margin of tolerance** present in every individual, every species, and every local flora and vegetation as a whole, is the concrete expression of the principle of parsimony.

No hurry, no chance, no random instability chases the plant species along diverging paths later to be disentangled and rectified by the most business-minded of all goddesses, namely, Selection. Plant life, plant migration and, if there be any such phenomenon, plant evolution are full of sense, full of definite finality.

By depriving the plant kingdom of these inherent qualities, one would throw it into the utmost chaos, and Chaos cannot beget Order.

5. Direct creation and evolution.

The reader may live under the impression that the foregoing chapters mean a radical opposition to plant evolution; this, however, is not the case. Let us examine, in the light of the facts and not in the mist of the tenets of conflicting theories, the scattered pieces of evidence speaking in favour of plant evolution.

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a. First and foremost, there are three facts easily standing all attempts of attack: The plants of our present geological period did not exist in the earliest of life's history. The species and most of the higher units present at the dim beginning of plant kingdom do not survive in our days. The nearer to each other the systemic units of past geological periods stand in their relative chonological succession the more similar they generally are in their physiognomical features.

This means, beyond all possible doubt: first, that there has taken place, at several times during life's history, a **production** of new systemic units, not only species but genera, families, orders, and even entire classes, like the phanerogams emerging in the late Mesozoic era; secondly that this production has happened, at least in its broad outlines, along the **likeness and similarity** of each preceding period of plant life.

Far from underestimating the strong hint as to evolution which the above facts imply, I must again stress my purposely chosen terms: production to the likeness and similarity of older units; for, in terms of clean thinking, **they do not necessarily mean evolution**. If there is, besides natural history, an independent science under the name of philosophy; if this kingly science having recourse to its own laws and methods, can reach truth even on an higher level than observation, induction and mathematics; and if the most outstanding result of philosophical inquiry tells us that there must be, as the ultimate cause of all things, a Creator, lest the whole Cosmos falls into a Chaos of nonsense; the possibility of direct creation cannot be dismissed from any kind of serious research as to the origin of the units of living beings.

It has been and, infortunately, continues to be the "proton pseudos" of evolutionism as a spiritual phenomenon of the last hundred years that the natural sciences are apt to absorb and dominate the whole of man's spiritual and cultural world, superseding the "myths" of former times. This fundamental error has led to a catastrophic narrowing down of all horizons, imprisoning man amidst the mechanistic machinery of an all-determining "evolution". No wonder that all attempts to explain the "mechanisms" of evolution have, finally, ended in a blind alley.

b. Maintaining, therefore, the possibility of direct creation as an alternative within the rights of spiritual liberty, I freely concede that evolution, within limits that do not concern us here, is by far the most satisfactory solution of this "mystery of mysteries". Even from a purely methodological standpoint, namely, that recourse to the ultimate cause should not be taken before all possible secondary causes have proved inefficient, evolution presents itself as the most natural explanation to be critically analised.

Evolution, as I conceive it, is **an inherent quality of the plant kingdom.** It follows, naturally and necessarily, from the rôle the plants play, by a destination beyond the reach of biological sciences, on the surface of the planet.

It follows, first and foremost, from the principle of space occupation. If the plants are bound to inhabit all areas suitable to life; if these areas, as to their concrete conditions, vary between the most astonishing extremes; and if one only or a few species cannot be adapted to all possible niches: there must be a great variety of plants.

Now, some original flora of the earth could not fulfill its mission without changing its life forms. As areas go and new ones come, their requirements vary in such a degree that, whithout substantial changes, the plants cannot stand on even terms with their inborn task: space occupation. Each individual plant, in order to withstand lesser changes, possesses its own range of adaptability; each individual species, in order to survive the natural death of its representants, has its natural means of propagation: it is, therefore, only logical that the plant kingdom as a whole has its innate and effective devices preventing destruction, by evolving, under the pressure of necessity, new units.

Even from the viewpoint of a strict believer, this situation is by far more convenient than the idea of repeated direct creations. If there was, as it must have been, a definite purpose in plant creation; if we can touch this purpose at every corner of the earth; if there be a sense and a fundamental harmony in all manifestations of plant life: then the original plan of the Creator cannot have forgotten so essential a requirement as age-long survival by evolution.

6. **The threshold of occupation.**

The final result of our inquiry in several categories of areas in southernmost Brazil has proved negative and rather disappointing, since there were no novelties produced in at least three areas where one must, according to the tenets of the current theories, reasonably expect them: coastal plain, migrating rain forest, and contact belt between forest and grasslands.

On the other hand, there emerged the general principle of parsimony which may furnish us with a very valuable clue as to how proceed further.

a. In the first place, this principle gives additional evidence or, perhaps better, a solemn confirmation, to the logical deductions of the preceding chapter. **It explains us why the new units,** in the long course of life's history, **have been produced to the likeness of older ones.** The whole of the more or less obscure and entangled relationships pervading the natural system of plants is concerned here. The same severe parsimony that prevents any random production of new species, even in undersaturated areas, has been at work impeding the limitless multiplication of sistemic patterns. The plant world, producing new units under the sheer pressure of its inborn task, adheres to the accepted models shunning, as it were, any superfluous innovation.

b. The very concept of space occupation receives its correct circumscription by that of parsimony. Occupation does not necessarily mean saturation: even undersaturated areas are truly occupied and, therefore, without a trace of production of new species.

The crucial question now is: **Where does the lowest threshold of space occupation lie** or, in other words, the boundary line, below which the principle of parsimony is superseded by that of space occupation? First of all, this limit, like all historical events, although real and scientifically ascertainable, escapes from all mechanistical and mathematical formulation. Life, in the innermost sanctuary of its essence, is a process of its own, not a mechanical one.

The existence of such a border line can safely be deduced from the following syllogism: There has been a production of new species governed by the principles of space occupation and parsimony; now the areas examined before, new or old, saturated or not, do not produce novelties: consequently, we must seek a specially circumstantiated area in which the two guiding principles necessarily lead to the production of new units.

c. Before entering into generalizations, let us see whether the South Brazilian flora can furnish us a clue as to this peculiar category of areas.

As mentioned before, southernmost Brazil, owing to its rather uniform conditions of life and to its openness toward the west and the north, is predominantly occupied by an immigration flora; this, at least, is absolutely true with reference to the coastal plant carpet and the rain forest. Notwithstanding this general situation, three areas can be singled out where production of species of has taken place.

The first is the **steppe.** Although the great majority of its species show a very wide distribution south of the Equator or, at least, south of the Capricorn, there are, in a percentage not yet exactly ascertained, hundreds and hundreds of more or less restricted endemics. Leaving aside all isolated species, which may be considered as stray immigrants or remnants of an older flora (this being the case with the Araucaria-bound community), I call attention to the erect Mikaniae (about 10 species), the genus Petunia (about 20 species), the genus Eryngium (about 40 species, one half of them endemic), and many others. From all we can collect, these "species-swarms" have originated by local production.

The second is **the eastern rim of the South Brazilian highlands**. Out of 742 phanerogams known from the Riograndean section, 134 = 20% are restricted to this mountainous region: 67% of them belong to the tropical Brazilian stock, 33% to the Andean element. The percentage of endemics on the eastern rim is the highest one in southern Brazil; as far as my collections go, one can expect about 2% of novelties in this quarter of the country.

Now it ought not be passed in silence that the Andeans probably represent nothing else but relics of a very old temperate flora which I named "The Old Southern Flora in Brazil"; the weak development of the genera (1-3 species per genus) points to the same direction.

On the other hand, the Brazilian genera possess a relatively rich production of endemics: Leandra 4, Eryngium 5, Mimosa 5, Tibouchina 6, Baccharis 12. The most striking example of a strongly developed group along the rim of the highlands are the Melastomataceae: out of 53 Riograndean species, 25 are restricted to the northeastern highlands, among them 7 endemics on the very rim of the precipices; no less than 12 belonging to the genera Leandra, Miconia, Ossaea, and Tibouchina are novelties recently collected by the author.

As to the origin of the Brazilian endemics, they have been derived, partly form rain forest elements like the Melastomataceae, partly from campos stock like Baccharis and Eryngium. Some very characteristic species of Baccharis in the peat bogs and Sphagnum swamps even retain unmistakable evidence of their dry steppe ancestors: Baccharis illinita abundant on marshy pastures, belongs to the Cuneatae group with thick leathery leaves and a very sturdy rootstock; Baccharis villosa, although exclusively found in more or less open Sphagnum swamps appartains to the dry campos group of the Alatae with broadly winged stems instead of normal leaves.

All in all, there is strong evidence that species production has been at work on the highest and wettest section of the South Brazilian highlands.

The third is the southeastern quarter of Rio Grande do Sul where the **Azoic granitic hill-lands,** beginning near Porto Alegre and extending, far south into Uruguay, constitute a large and very characteristic area. Its flora, as it is known from the hills near its northern end, amounts to 1238 phanerogams with no less than 164 = 13% endemics.

Discarding, for the same reasons as mentioned for the mountain flora, the Andean element, there remain, at last, 90 endemic species derived from the South Brazilian campos stock, notably Baccharis, Eupatorium, Croton, Euphorbia, Paspalum, Eugenia, Polygala, and many others. A lot of them, like Croton ericoides, Cr. gnaphalii, Cr.

helichrysum, Polygala leptolopha, etc., seem to have a rather narrow area, the same being the case, even in a much higher degree, with the endemics of Andean descent.

c. There has been, then, in at least three different areas, a local production of new units which, in a very low number of cases, reach the generic level; all that is left for us to do is to examine what peculiar historical circumstances determined the behaviour of the plants in these areas.

A commonplace argument, deeply rooted in evolutionistic thinking although faulty in its very core, ascribes the production of new species to **time**. Perhaps no other methodological error better illustrates the downright unhistorical mentality of the "historians of life". Time, as they put is, means simple duration as physicists and chemists use it in their formulae. This kind of time is reduced to its bare skeleton of meaning, precedented, repeatable, reversible; but is in nowise applicable to any kind of true history, which is, by its very concept, unprecedented, unrepeatable, irreversible. Time as such, that it to say, mere duration, cannot be a factor of plant evolution which is, like all historical events, intimately tied up with all happenings of the past and all circumstances of the present; lastly. historical time represents but a moment's fraction in the cosmic clock of universal history.

Thus, the fact that the geological stage on which most of the South Brazilian campos develop their play reaches far down into Mesozoic times; the fact that the upheaval of the eastern rim of the highlands responsible for its peculiar ecological conditions is probably contemporaneous to the Tertiary uplift of the Andes; and the fact that the southeastern granitic hills belong to the oldest portions of undisturbed soil in Brazil: cannot be invoked as an evidence for their having produced new vegetable units. The Age-and-Evolution theory tacitly or openly held by most of the evolutionists, belongs to the same mechanistic brand as Willis' Age-and-Area.

There is, on the other hand, one common historical circumstance that applies to the areas under study: **At the time of their occupation, they lay out of reach for a fullfledged immigrational flora**.

This was the case with the highland area. Geological evidence shows that the gigantic basalt flows, forming its present floor to an extension of more than one million of square kilometers happened towards the end of the Triassic period; and the desert climate so characteristic of the South Brazilian Triassic went on even after the lava eruptions had come to their end. All evidence we can gather points to the fact that the dry campos formation represents the oldest plant carpet on the highlands. From all we know about South America's past, there existed, at this time, no other steppe area within migration range from which so enormous a new space could be occupied. Thus, under the always active pressure of the principle of space occupation, old Andean roots from the one side and old Central Brazilian ones from the other evolved into new units which, significantly enough, never go beyond the generic level.

The same obtained, although in a smaller scale, on the eastern rim of the highlands. By the beginning of the Tertiary period or so, the whole eastern wing of the highlands broke off submerging in the Atlantic; the remaining western wing, due to an isostatical upward movement going on until today, was uplifted to 1000-1800 meters above sea level, forming an immense tilted block with a gentle slope towards west and south.

The natural consequence of these geological events was, within the old dry steppe, the formation of an entirely new climate and soil, bringing about an altitudinal belt near timberline. The average temperature lies 4-5°C. lower than that of the near seacoast; condensation along the line of the steep precipicies radically erased the former dry grasslands.

It is more than evident that, neither the dry steppe, nor the tropical rain forest immigrating along the coast, were in possession of elements for occupying, without far-going changes, such new habitats as cloud belts, Sphagnum swamps, peat bogs and a soil highly oversaturated with water, and that there could not be expected an immigration from the only area in South America with similar habitat conditions, namely, Southern Chile and Fuegia.

It is only natural that, under the all-ruling pressure of space occupation, the adjoining floras of the grasslands and the rain forest produced new units fitting into the new area. This is even true if we leave aside the rather mysterious presence of "Chilean" elements, like Araucaria, Gunnera, Podocarpus, Fuchsia, Griselinia, Orites and others; the special problem presented by this relic flora has been examined in the German written article in this present year-book.

The comparatively rich endemism of the southeastern granitic hills can be interpreted along the same line of thinking. They were, in Tertiary times up to the very dawn of the Quaternary period, separated from the mainland and partially from each other by a shallow sea that covered all the present-day lowlands of Rio Grande do Sul: a large archipelago beginning at 30.° SL and stretching far down to the mouth of the La Plata.

As we have seen, the local endemics both from Andean and Brazilian stock perform the highest percentage in all southern Brazil. Although separated from the main body of the South Brazilian steppe by no more than 50-100 kilometers of open water, a true insular flora evolved on the old archipelago, poor in number but clean-cut in taxonomic characters. The only reasonable cause of this upsurge of new units is the following: The old archipelago lay beyond the range of simple immigration from the campos, not because of its edaphic and climatic environment, which may be considered as almost identical, but because of the intervening arm of open sea; chance newcomers from the northern campos and the western Andean region, in response to the principle of space occupation, brought about the typical insular flora, whose features, although blurred by the Quaternary mass immigration of campos and rain forest elements, remain clearly distinguishable up to now. Whilst the recent immigrants are scattered all over the area or limited, like the rain forest, to the bottom of the valleys, the old insular elements are, preferently, found on the hilltops, in rock crevices, and on the **grassy slopes** along the upper third of the hills.

This may suffice to make clear what is meant by the **threshold of plant occupation.** The only category of areas where plant evolution has taken place are **unoccupied ones without the range of immigration of an already existing flora fitting into the new habitat.** They may be entirely new and empty areas; and they may be areas which, after having been truely occupied, better their life conditions in such a degree that they can no longer be considered as occupied by their former plant cover. As we had occasion to observe in the case of the contact between steppe and rain forest, this latter category does not produce anything new if there is, within immigration range, a flora fitting into the changed environment; but if such is not the case, as we learned from the example of the South Brazilian mountain belt, the present flora reassumes evolution.

I frankly confess that my present theory contains some bones hard to crush. Its very mainstays, that is to say, the principles of space occupation and parsimony; my confessedly vitalistic and finalistic philosophy of life; my exemplification by means of the South Brazilian flora being far from complete: may lend themselves, I fear, to violent criticism. This all the more as the very mentioning of "myths" like vitalism, finalism, direct creation sounds to the ears of many exponents of evolutionism as downright profanity. Moreover, the fundamental statement that there must be a threshold ou space occupation rests on a conclusion, not on direct observation.

Students of evolutionism may ask why never mention the current articles of the Lamarckian, Darwinian and other creeds. So here goes my greatest heresy: I do not accept any of them. They are hostile brothers, sons of the same mother whose name and essence is Biological Materialism.

7. **Insular areas.**

It is highly significant that the first idea of evolution arose from the peculiar features of insular faunas and floras. Indeed, the ultimate foundation of the present study stems from the same source. In reality, an unoccupied area beyond the reach of a fitting immigration flora always has an insular character, be it an island in the geographical sense or an otherwise isolated space.

a. Now, it need not be demonstrated that all oceanic islands possess a highly peculiar flora: take, for instance, **Juan Fernandez**. Out of 147 species of phanerogams in 89 genera and 42 families, 101 species, 17 genera, and 1 family are endemic. A similar situation obtains as to the pteridophyta: out of a total of 53 species in 23 genera, 18 species and 1 genus are endemic. Among the mosses, 9 species out of 14 are endemic, among the Lichenes, 5 out of 23.

Leaving aside all other discussion, which may me looked up in Skottsberg's classical report, I beg to call attention to the very excellent confirmation my theory receives from the oceanic insular floras. First, there is the general principle of space occupation taking care that all oceanic islands, although far out of the range of mass immigration, receive their convenient plant cover: secondly, there is at work the principle of parsimony producing an unbalanced and undersaturated flora later to be completed by immigrants; in the third place there is an unmistakable hint as to the threshold of species evolution lying between complete absence of plants in the beginning and undersaturated occupation at the present time.

In other words, the historical background of the different behaviour of the plants in different areas, which in southern Brazil is severely blurred by recent migrations, stands out in all desirable clarity where the original insular characters of an area have been preserved. True local endemism (not relics!) meaning species production in the area they occupy up to the present can be conceived as a direct function of time and space: time, meaning a historically circumstantiated situation, not mere duration; space, meaning distance in terms of migration range, not mere separation by a given number of kilometers.

b. The flora of Juan Fernandez, the same being true with the South Brazilian areas of endemism, gives us a clue to the origin of such floras. Out of 147 phanerogams in 89 genera and 42 families, 46 species in 72 genera and 41 families are in common with other parts of the southern hemisphere, notably Chile (46,9% of the total), the route Australia-New Zealand-Hawaii (17,7%), Magellania (10%), Neotropics (12,9%).

From this we learn that all floras staying in the area where they have developed, or emigrated from there as a body, contain, in a very variable percentage, two fundamental elements: species immigrated with unchanged identity, and newly produced ones from an immigrated stock.

c. This peculiar fact shows us, perhaps better than any other observation, the paramount importance of the principle of parsimony. The 72 genera in common with other southern areas put in relief, in the strongest possible manner, the enormous **stability** of the taxonomic units, resistant to any stray and random change. Where production of new genera has taken place, like the Cichoriaceous group on Juan Fernandez, they not only belong to world-wide families but also to well defined tribes within their family. Even in the case of the endemic and monotypic family of the Lactoridaceae, the general kinship to the Magnoliaceae is out of question.

The ultimate meaning, evidently, is that Nature has no interest at all in producing more and more novelties; and that there is a sense and a finality in restricting the production of new units to the rigid but moderate exigences of the principle of space occupation.

d. Finally, **the principle of parsimony,** always chosing the new patterns from older ones; always taking its motives from the nearest older areas (not to be forgotten: in terms of migration range at the time of the first settlement!); always preserving the hierarchical order that pervades and binds together to whole natural system of the plant world: **is,** in my opinion, **the strongest argument in favor of evolution** as opposed to direct creation. Without entering into philosophical technicalities, it seems to me that the only correct method to extricate this problem is to follow the hints that Nature itself gives us, and to interpret the facts, as far as possible, without taking a cheap recourse to the Ultimate Cause. I cannot imagine, like Darwin and long before him St. Augustine, the Creator as a narrow-minded petty artisan always mending his wonderful cosmic machinery. The plant, or plants, he has put into being at the very start of life, had in them, as a constitutional feature of their essence, all that was necessary to fulfill their inborn task: space occupation within the general plan of the universal Cosmos.

By the way, exception made for the first beginning of plant life, the heated controversy about the alternative Creation-Evolution seems to me, as the German popular saying goes, "ein Streit um des Kaisers Bart". God, by his very definition, lives and acts beyond the level of time. What is seen by man as past, present and future, is, before him, one eternal and non-successional Now. Direct artisan-like production, or evolution under guiding principles in harmony with the whole of the Cosmos are, in the last analysis, the same: creation. Whether this creation is direct, or indirect cannot be ascertained on an aprioristic basis. Nature's factual ways have to be tracked before; and Nature's factual ways point, with overwhelming emphasis, to indirect creation, that is, evolution.

8. A mental experiment.

The principles of space occupation and parsimony are innate qualities of the plant world; consequently, the past, the present and the future are ineffugibly ruled by them. They are not established a priori but on factual observation. They are able to explain why plants conquer all habitable land, and why evolution proceeds in an orderly way. The example of Juan Fernandez — if one would reject these islands as possibly being the remainder of a drowned continental mass, take St. Helena or some other oceanic island never connected with any mainland — teaches us under what historical circumstances and from what stock an insular flora arises.

It seems, then, perfectly within the limits of sound speculation to undertake a mental experiment like the following:

The Antarctic continent, with roughly 14 million square kilometers, is by far the biggest area on our planet that, except for two or three species, is entirely devoid of phanerogamic life. Plant fossils teach us that there has existed, in former times, an Antarctic flora not unlike that of southern Chile.

Now, in view of the enormous changes that have, in the geological past, affected almost every area of the earth, it seems not unreasonable to admit that Antarctica, in some dim future, would again become a habitable area for phanerogams. In order to stress the issue, let us suppose the whole continent as a thoroughly habitable area, with a climate like that of southernmost Brazil. What would then happen with reference to its plant life?

First of all, Antarctica would be occupied by a convenient plant carpet. There has never arisen a new area, no matter how big or how small, which has for ever remained devoid of plants. Stray immigrants from all areas within migration range would be the first settlers.

But, given the wide stretches of open sea; given the relative impoverishment of the sub-Antarctic flora; and given the countless types of local habitats forcibly present in so huge an area: the immigrants, neither in number nor in adaptations would be able to occupy the whole continent; in other words, the flora of Antarctica would lie, perhaps for hundreds of thousands of years, well below the occupation threshold. As a consequence, evolution on a gigantic scale would enter into play blurring but not erasing the bonds with the original homes of the immigrants.

Moreover, as occupation begins not only in one spot spreading from there all over the continent, but in as many local centers as there would have been successful landings, an intermigration and intermingling of the different primary, secondary and multiple centers would soon begin, giving the new flora its richess and final finish.

The end result would be, as it is in extratropical South America, an astonishing variety of units, of which, to judge from other isolated areas, no more than 25% would belong to unchanged immigrants. At least three fourths of the species, more than half of the genera, and a well defined percentage of families or secondary units of them would be endemic. The most perplexing "extravagances" of the category of the wind-pollinized Pringlea, the tree-like Cichorioideae, the monstrous Gunnera would flourish among slightly changed species of Nothofagus, Drimys, Araucaria and dozens of other southern genera.

This mental experiment, which is in perfect accordance with all we can observe and conclude from the behaviour of present and past floras, gives us a clue to the meaning and the final goal of plant life on the face of the globe. Plant life was present as long as the surface of the earth could bear it, and it will be present as long as life conditions persist within the general range of vegetable beings. There is no "evolution to death" as orthogenesis puts it; there is no evolution out of a nebulous, more or less anthropomorphic "will to adaptation", as Lamarck suggested; and there is no evolution out of mechanical change and utilitarian selection as neo-Darwinism, the poorest of all theories on evolution, wants to make us believe.

Order, sense, finality in evolution come from without. All that happens with plants is imbedded in the cosmic stream of events, flowing, for aeons uncounted, through the Universe.

Where Natural Science reaches its dead point, Philosophy enters into its right.

Conclusion.

The present study has been directed to **where and when** evolution of plants takes place. No attempt has been made as to **how** its "mechanisms" are operating. No one of the current theories has, so far, explained anything, despite their phraseology and "mathematically" formulated "laws of evolution". Frankly speaking, I feel little confident with reference to any merely biological explanation of evolution; before proceeding to this, life itself must have been explained.

The best we can do, for the time being, is to record the historical circumstances under which evolution enters into play; to describe the reflex of these factors on the face of the plant kingdom; and to state the general principles under whose guidance evolution goes on. If there could be any real opposition between the factual Science of Life, and History, the study of Evolution would belong to History, **not to Biology**.

Pôrto Alegre, May 5, 1958.

Resumo.

O presente trabalho constitui uma tentativa de explicar as circunstâncias históricas debaixo das quais se realiza a produção de novas unidades no reino vegetal. Examinando o comportamento da flora fanerogâmica sul-brasileira, o autor chega às seguintes **conclusões:**

1. A história do reino vegetal é governada por dois princípios fundamentais: o princípio da **ocupação do espaço**, segundo o qual nenhuma área habitável pode permanecer destituída de sua conveniente vegetação e o princípio da **parcimonia**, segundo o qual a ocupação se faz por meio de espécies já existentes, enquanto forem utilizáveis e estiverem dentro das possibilidades de imigração.

2. Ocupação não significa necessàriamente saturação: há um **limiar de ocupação**, acima do qual uma área está sujeita à imigração, ou mesmo invasão total, de formação já existentes, sem produzir qualquer novidade.

3. Conseqüentemente, as áreas novas, artificiais ou naturais, presentes ou passadas; e as ocupadas mas nao saturadas: enquanto estiverem nas condições de poderem ser preenchidas **com elementos de imigração**, não produzem novas unidades sistemáticas.

4. Produção de novidades não inclui necessàriamente evolução; entretanto, todos os indícios sugerem que a produção histórica de novas espécies é, de fato, **evolução**. Em última análise filosófica, criação e evolução não diferem na essência.

5. A evolução de novas unidades do reino vegetal se processa num único nitidamente definido tipo de áreas. **São as áreas insulares**, isto é aquelas, que no tempo da ocupação se acham fora do alcance duma flora e vegetação já existentes, seja por barreiras físicas à imigração, seja pelo caráter peculiar de suas condições de vida.

Concluindo, o autor se confessa adepto do vitalismo biológico e do finalismo filosófico; rejeita, como errôneas na base, tôdas as tentativas de explicar os "mecanismos" da evolução e estabelece que, antes de entrar em discussões sôbre o modo como a evolução se tenha efetuado, é necessário elucidar **onde** e **quando** se deu.

A ciência sôbre a evolução do reino vegetal é, antes de tudo, um capítulo da história da vida sôbre a face da terra; secundariamente, e dentro dos limites intransponíveis do método, é **objeto da biologia**.

Zusammenfassung.

Vorliegende Arbeit ist ein Versuch, die Entstehung neuer Einheiten im Pflanzenreich von der Florengeschichte her zu verstehen. Unter Zugrundelegung der südbrasilianischen Phanerogamenflora kommt der Verfasser zu folgenden Schlüssen:

1. Die Geschichte des Pflanzenreichs in ihrer Beziehung zu Raum und Zeit untersteht zwei grundlegenden Gesetzen: das Gesetz der Raumerfüllung, nach dem kein bewohnbarer Raum auf die Dauer ohne Pflanzendecke bleiben kann; und das Gesetz der Sparsamkeit, nach dem die Raumerfüllung, soweit nur immer möglich, von bereits vorhandenen Arten getätigt wird.

2. Raumerfüllung heisst nicht notwendigerweise Raumsättigung. Es gibt eine Schwelle, von der an die Entstehung neuer Arten stillsteht; die noch vorhandenen Möglichkeiten werden durch Einwanderung erfüllt, die bis zur völligen Vernichtung der ortsälteren Pflanzendecke führen kann.

3. Daraus folgt, dass keine Neubildung stattfindet, solange ein Raum wenigstens bis zur **Schwelle der Erfüllung** von unveränderten Einwanderern in Besitz genommen werden kann; das gilt nicht nur von völlig neuen Räumen, sondern auch von solchen, die zwar besetzt, aber nicht gesättigt sind.

4. **Entstehung neuer Einheiten heisst nicht notwendig Entwicklung**; nimmt man aber die zahlreichen Hinweise der Pflanzengeschichte zur Richtschnur, dann muss man sich vernünftigerweise für die Entwicklung entscheiden.

Das ist um so mehr erforderlich, als das Gesetz der Raumerfüllung die Entwicklung neuer Einheiten als Wesensbestandteil einschliesst. Ob ummittelbare Schöpfung oder Entwicklung, lässt sich nicht von vorneherein entscheiden; alle Fingerzeige deuten auf Entwicklung hin, das heisst, mittelbare Schöpfung.

5. Die Entwicklung neuer Einheiten im Pflanzenreich vollzieht sich in einer einzigen, klar umrissenen Art von Räumen.. Das sind die inselhaften Räume, das heisst solche, die bei ihrer Besetzung ausserhalb der Einwanderungsmöglichkeit einer bereits bestehenden und den Ansprüchen der Erfüllung genügenden Pflanzenwelt lagen. Dazu gehören nicht nur völlig neue Räume, sondern auch solche, die durch Änderung der Lebensbedingungen unterhalb der Erfüllungsschwelle zurückgesunken sind.

Der Verfasser bekennt sich zur Eigenständigkeit des Lebensprinzips und zum allgemeinen Zweckgedanken in der Natur; alle Versuche, die Entwicklung auf mechanistischem Wege zu erklären, sind daher von vorneherein zum Scheitern verurteilt. Bevor dieses Problem in Angriff genommen werden kann, müssen wir zuerst einmal wissen, wo und unter welchen geschichtlichen Bedingungen eine Entwicklung vor sich geht

Die Wissenschaft von der Entwicklung des Pflanzenreichs ist ein Ausschnitt aus der Geschichte der Lebensreiche auf Erden; ihre biologische Erklärung kommt erst an zweiter Stelle, und muss ihren Ausgang von den geschichtlichen Tatsachen nehmen.

Literature.

The subject matter of the present study has been treated in a series of articles written in Portuguese and German; the most important are the following:

1. **Rambo, B.**: O elemento andino no pinhal rio-grandense, Anais Botânicos do Herbário Barbosa Rodrigues 3 (1951), 3-39. Itajaí, Sta. Catarina, Brasil.
2. **Rambo, B.**: A imigração da selva higrófila no Rio Grande do Sul, ibidem, 55-91.
3. **Rambo B.**: Análise geográfica das Compostas rio-grandenses, ibidem 4 (1952), 87-161.
4. **Rambo, B.**: Análise comparativa das Leguminosas rio-grandenses, ibidem 5 (1953), 107-184.
5. **Rambo, B.**: História da flora do planalto rio-grandense, ibidem, 184-232.
6. **Rambo, B.**: Análise histórica da flora de Pôrto Alegre, ibidem 6 (1954), 9-112 (In this year, the Anais Botânicos do Herbário Rodrigues changed their name into "Sellowia").
7. **Rambo, B.**: História da flora do litoral rio-grandense, ibidem, 113-172.
8. **Rambo, B.**: Der Regenwald am oberen Uruguay, ibidem 7 (1956) 183-233.
9. **Rambo, B.**: A flora fanerogâmica dos Aparados rio-grandenses, ibidem, 235-298.
10. **Rambo, B.**: Regenwald und Kamp in Rio Grande do Sul, ibidem 8 (1957) 257-298.
11. **Rambo, B.**: O gênero Eryngium no Rio Grande do Sul, ibidem 299-353.
12. **Rambo, B.**: Die Gattung Oxypetalum in Rio Grande do Sul (unpublished).
13. **Rambo, B.**: Geografia das Melastomatáceas riograndenses (unpublished).
14. **Rambo, B.**: Die europäische Unkräuter in Südbrasilien, (unpublished).
15. **Rambo, B.**: Die Auslese im Naturversuch, Pesquisas 1 1957), 181-219.
16. **Rambo, B.**: Die alte Südflora in Brasilien, Pesquisas 2 (1958).
17. **Rambo, B.**: Notes, mostly unpublished, on the author's private Herbarium Florae Brasillae australis, Pòrto Alegre (63.000 numbers with about 4.000 native phanerogams).
18. **Skottsberg, C.**: The Vegetation of the Fernandez Islands. Uppsala 1953.
19. **Skottsberg, C.**: The Natural History of Juan Fernandez and Easter Island, Vol. 1 (1956), Part 3 ,Uppsala.