WOODINESS IN ISLAND FLORAS

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Abstract: The idea that woodiness in otherwise largely herbaceous genera is a basic feature of the ecosystem of oceanic islands is found to be redundant. Woodiness in such genera is also not confined to islands; a scanning of all cases in Hawaii learned that of all these genera woodiness is also found in continental areas. The wrong impression of its uniqueness has probably originated because, as with many other so-called characteristic island features, no comparative studies were made with situations in continental areas. Ratios of woodiness on islands and continents cq. continental areas must still be computed.

It is sometimes advanced that woodiness in oceanic islands is due to the notably moderate climate of such islands permitting continued growth and that there is a natural selecting active for plants that are of longer duration, suiting the year-long growing season of such insular islands, an explanation recently phrased by Carlquist in a study on the endemic species of *Echium* in Macaronesia.

In my experience it is in these two island groups as varied as it can be imagined to be on any place of the same size anywhere in the world. And I object against the use of the term natural selection here as it is in these volcanic areas precisely the lack of competition; the prevelance of bare soil and open niches provides natural opportunity for the origin of different life forms unhampered by competition and genomes may show what they are capable of to produce in the patio ludens of form making. In agreement with this is the occurrence of striking, rare life forms in the volcanic areas of East Africa and the Andes.

Already long ago it has attracted attention that in oceanic islands sometimes woody species occur of otherwise largely herbaceous genera and in some island (groups) occur a proportionally large number of woody genera in largely herbaceous families, e. g. *Compositae* and *Campanulaceae.*

This occurrence of woodiness has rather been inflated beyond proportion in accepting this as a characteristic of the flora of such islands. It should be at once made clear that such woodiness is by no means at all restricted to islands, and that conversely a number of oceanic islands do not show it, for example New Caledonia, New Zealand, the Marianas, etc. In continents or continental areas the same phenomenon occurs in various biotopes and elsewhere in the world there occur also woody *Campanulaceae* and *Compositae*, even in the tropical rain forest. In Malesia there are for example in the large herbaceous genus *Vernonia* some very tall trees, *V. arborea et al.* attaining some 45 m height, forming part of the canopy. Another random example is *Phytolacca dioica* L. which becomes an enormous tree.

Thus it appears that great attention has been focussed on and given to a phenomenon in islands without comparing the frequency of the same phenomenon in continental areas, by which onesided approach much of its importance is simply

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lost. A thorough scanning of relative frequency of life forms is still to be made in various floras; such a survey would be very interesting indeed and could well serve as the subject for a thesis.

In such an analysis it should also be considered whether the occurrence of woody species found in islands of a genus is also found in continental areas in the same genus. That in Hawaii *Euphorbia* is represented by 7 woody species is not particularly significant as trees of this genus occur also in Malesia and are also found elsewhere in other continental areas. Woody *Echiums* occur for example also in NW. Africa.

Furthermore, it should also be noted whether in addition to woody species in islands there are also herbaceous species of the same genus in such islands or districts.

A rapid scanning of Hillebrand's Flora of Hawaii does not come up to the inflated abundance of woodiness of the flora of these islands, in the sense that they have a 'uniqueness' in ligneous species. Of *Solanum* there are 5 woody and 1 hebaceous species, but the genus *Solanum* has woody species in many other non-insular parts of the world. In *Plantago* the ratio is 1:1, in *Chenopodium* 1:1. In some genera there are intermediate stages between herbaceous and woody, becoming woody at the base, thus in *Viola* 6 are woody, 1 semiwoody, and 1 herbaceous. The relation in *Lysimachia* is 3:2:1. In *Senecio* which produced many wood species in other non-insular parts of the world Hawaii has only 1–2 herbaceous species, none woody. Only in 3 genera there is completely woodiness, notably *Geranium* (6 sp.), *Lepidium* (3 spp.) and *Euphorbia* (7 sp.). But in the latter genus woodiness is not at all specific ally insular. And the same holds for *Geranium* of which there is a *G. lignosus* forming sect. *Fruticulosa* in the paramos of Colombia. In *Plantago* there are various frutescent species in sect. *Leucopsyllium* (*P. albicans, bismarckii, caulescens, polyclada, fiebrigii*, ect.) in Mexico, Argentina, Peru and even in the Mediterranen. In *Viola* there are small shrubs in Africa (sect. *Xylinosium*), the Mediterranean (sect. *Delphiniopsis*) and Chile (sect. *Rubellium*). In *Lysimachia* the wide-spread coastal species *L. mauritiana* may become fruticose and so is *L. glaucophylla* from Mexico. In *Chenopodium* woody species occur also in Juan Fernandez (sect. *Skottsbergia*) and a suffrutescent sect. *Rhagodioides* in Australia. In *Lepidium* woody species are also recorded from South America and South Australia.

The background of this problem concerns of course the distribution of life forms.

Distribution of life forms, by which I mean the occurrence of life forms in various environments, depends of course on finding suitable ecological conditions.

But first must come their origin, or better the *potential possibility of their origin*, their inheritance of this capacity from obviously mainly woody gymnospermous ancestors or newly acquired woodiness from latent potentials in herbaceous ancestors.

Potential capacity is capricious, in the sense that it cannot a priori be predicted that each family or ancestral line, say of originally woody descent, must a fortiori possess the potential capacity of producing somewhere under favourable conditions (habitats) herbaceous species, and the reverse; that an innate herbaceous group must be capable of producing woody forms.

A huge morphologically polymorphous genus like *Ficus* has obviously not been capable to produce any herbaceous species: small plants, yes, as some forms of *F. quercifolia, F. delotidea*, etc. but all remaining ligneous.

Huge families of the Magnoliales s. l. have obviously also a completely "ligneous genome". Within this compass they "have done what they can" in producing miniature trees and shrubs and lianes, but produce no herbs, except a parasite (*Cassytha*) in Lauraceae.

Thus I see the restriction of development of the plant kingdom as to life forms in the same way as the innate restriction of development by the great factor of ecological response to temperature: certain groups have simply not the capacity of developing forms standing cold, others can simply not adapt themselves to heat while there are also groups which have no such rigid restrictions.

The conclusion that these restrictions are bound to innate potentialities of the genome is proved by the fact that through the ages onwards of the Cretaceous all plant groups have been confronted with any ecological condition inviting them to show what they were worth conquering it; for which they had plenty opportunity and time. It is up to molecular biology to reveal the molecular secret behind this.

But let us return to development of woodiness: sometimes an 'ecological explanation' is given for it. Thus Carlquist in a study on woodiness in *Echium* of the Canary Islands (Aliso 7: 183–199. 1970) in agreement with some former authors (1c. 181) advanced that the tendency for Macaronesian species to be *woodier than their mainland relatives* suggests "herbaceous groups in which *the notably moderate climate of islands has permitted continued growth:* in these groups there is *a natural selection for plants that are of longer duration and increased woodiness, suiting the year-long growing season of such insular islands*".

I have had the privilege to visit two groups of such islands, Hawaii and Canary Is. and I feel just stupified by the generalisation of the statement of the "notably moderate climate", as contrarily both island groups show a grandiose panorama of various ecology, from almost tropical sealevel conditions to almost eternal snow and from mossy forest conditions to almost desert, as everybody who has visited these islands or studied the literature on their physiography can easily observe or learn. In fact I know no other physiography which is so varied within such small surface as the Canary Islands: open volcanic soils (screes, lavastreams, ash slopes) at any altitude to nearly 4000 metres altitude, windward and leeward slopes, sinuous huge barrancos, rocks and seepage, with streams and waterfalls, wind-swept crests, smothering high lauraceous rainforest in the cloud zone, windswept ridges with trimmed forest canopy, barren desert-like shores and plains of sand or lavas, in short a most astonishing variety. And as to the year-long growth season it should be remarked that each year the *Echiums* have only one flowering season.

The second part of his explanation concerns "natural selection", by which he means, or should mean obviously "competition" as it would otherwise be an empty term. This then is related to continued growth favourable to this competition. But what does it mean to Echium? Outcrowding other plants? This is distinctly not so, as most of these endemic species are distinctly rare local endemics and occur only in groups, similarly as some other pluri-annual monocarpic island plants as *Argyroxiphium* in Hawaii. And is pluri-annual growth in nature more favourable than being an annual? Is producing seeds at intervals a high-rated competition factor against being annual and producing seed each year?

Besides, as to *Echium*, I observe that besides the fantastic monocarpic *Echiums* there occur all sorts of *Echium* in the Canaries, also annual species.

In my opinion there is in these cases not in the least a matter of "*natural selection*", but of "*natural opportunity*". It is a thinking error (or a loose or pre-

judiced way of expression) to assume that the environment exercizes "selection pressure on development of plant life". Each plant species or group is confronted with a varied environment, where it can show up its genetical capacity of producing froms which can stand specialized conditions and occupy empty niches to which the original forms are not or less well adapted. Some show up, others not, as the Hawaiian *Senecio*.

I have to elaborate this somewhat further in observing that it is precisely the *volcanic* islands on which a number of forms is produced. And it is precisely the high *volcanic* islands which offer the greatest abundance of local endemism. This goes parallel with great variability of physiography, among which a *preponderance* of *bare soil*, hence with *absence of competition*. It has hence nothing to do with natural selection which vague, because hardly definable term, could only apply to closed communities. It is therefore understandable that similar forms which could never develop or maintain themselves in closed high forest conditions are not only found in volcanic islands as the Galapagos, Juan Fernandez, Hawaii, Macaronesia, Madeira. St. Helena, etc., but also in the Andean and East African volcanoes.

In the closed forest communities such forms would not likely evolve *even if they would possess the potential capacity of such development*. The closed tropical and subtropical forests do not offer the opportunity for this development except for the cycadoid life form which is developed in quite a few species. The forest community offers in turn opportunity for the development of other life forms, such as lianes, epiphytes, cauliflory, etc., not through competition but by *opportunity* to evolve in other suitable lianes of morphological development.