Distributional Dynamics in the Hawaiian Vegetation[1]

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ABSTRACT: Vegetation ecology is usually divided into two broad research areas, floristic/environmental gradient analysis and studies of vegetation dynamics. The early influential American ecologist Clements combined the two areas into a dynamic system for classifying vegetation. His succession and climax theory, however, was later severely criticized. A new approach to the study of distributional dynamics, called "landscape ecology," focuses on the dynamics of spatial vegetation patterns. There is a spatial hierarchy rule, which implies greater stability of species and community patterns when one considers larger area units versus smaller ones. It is argued that this rule is frequently transgressed in biotically impoverished areas, like the Hawaiian Islands, where certain dominant plant species have become established over unusually broad areas and habitat spectra. A further point made is that with "species packing" successional patterns change from auto-succession, where the dominant species retains dominance by in situ generation turnover (termed *chronosequential monoculture*), via "normal" succession (i.e., displacement of dominants by other dominants over time [termed *chronosequential polyculture*]), to small-area patch or gap dynamics (termed *chronosequential gap rotation*). Examples of the three spatially different succession paradigms are given for Hawaii, and the point is made that chronosequential monocultures cannot be expected to last, but change to chronosequential gap rotation with the invasion of alien dominants. Before the invasion of alien dominants, certain native dominants seem to have segregated into races or varieties by evolutionary adaptation to successional habitats. Finally, the concept of climax is discussed as having two meanings: (1) permanency of community type, which can only be observed for the aggregate assemblage of smaller communities in a larger space, such as occupied by a biome; (2) the mode of organic production in ecosystem development. The mode seems to occur between 1000 and 3000 yr in the Hawaiian rainforest biome on volcanic soils. Thereafter, productivity declines with acidification and soil nutrient impoverishment over a million years and more. This amounts to a retrogression in the course of primary succession.

RESEARCH IN VEGETATION ecology is usually divided into two broad areas, the study of distribution of species and communities and the study of plant succession and vegetation dynamics. Distribution is a spatial/geographic concept. It relates to the classification and mapping of species and plant communities and, particularly when done in relation to environmental gradients, implies some stability in terms of plant distribution patterns.

Succession is traditionally defined as any time-related change of vegetation in the same area except those recognizable as phenological or evolutionary changes. In a more restricted sense, therefore, plant succession relates to any chronosequential change in species distribution in a given area, site, or habitat. Clements (1916, 1928) tried to combine the two concepts by recognizing any spatially defined community also in a successional and dynamic context. He did this by

analyzing the spatial side-by-side differences of communities in a macro-climatic region and arranging them into hypothetical chronosequences. Clements's dynamic classification ran into trouble because he assumed that all physiographically constrained communities of a region or biome converge into a uniform climatic climax community, given enough time. This proved to be unrealistic (see Mueller-Dombois and Ellenberg 1974).

Another dynamic concept with a spatial implication is the "pattern and process" concept, perhaps most effectively introduced by Watt (1947). This concept postulates what is sometimes referred to as "cyclic" succession (Krebs 1985) by contrasting it to the so-called "directional" succession of Clements. This "cyclic" succession infers a rotation of smaller community patterns within larger community units; the larger units can be formations or biomes. The primary mechanism in cyclic successions may be the demographic behavior of the component species, which grow, mature, and die in an otherwise relatively permanent or stable community. In tropical forest biomes this concept is now often interpreted as "gap dynamics."

For the purpose of integrating the concept of gap dynamics with that of succession, Pickett and White (1986) proposed the term "patch dynamics." This liberates the cyclic succession concept from a preconceived spatial definition. This may be useful for understanding the relationship between the primarily "temperate fire-succession" dynamics and the primarily "tropical gap-rotation" dynamics. However, the two often occur at quite different spatial scales and are associated with different disturbance regimes.

Spatial scales and configurations of dynamic phenomena are an important area of research, now often referred to as "landscape ecology" (Forman 1986, Urban et al. 1987). Such focus should be particularly important to the vegetation ecology of islands, because spatial/dynamic shifts of vegetation patterns are often dramatic in island ecosystems. These spatial/dynamic shifts need attention for an appropriate interpretation in conservation biology, land-use policy, and vegetation management.

In this paper, I emphasize a few concepts that emerged from observing spatial/dynamic patterns in the Hawaiian Islands. They are summarized under three subheadings dealing with (1) dynamics in the hierarchy of vegetation units, (2) changing patterns of plant succession, and (3) the concept of climax in an island context.

Dynamics in the Spatial Hierarchy

BASIC CONSIDERATIONS. Perhaps one of the better known formalized vegetation hierarchies is the one developed by Braun-Blanquet (1928), which was patterned after the taxonomic system of classifying organisms (Mueller-Dombois and Ellenberg 1974). In this system, the basic unit is the "association," which was treated as analogous to the taxon "species" in the organismic classification system. Egler (1947), when studying Hawaiian vegetation, expressed his dissatisfaction with the association concept and opted instead for Gleason's (1926) "individualistic" concept of the plant community. One reason for Egler's dissatisfaction was the dynamic nature of the Hawaiian vegetation. Changes or shifts in vegetation patterns can easily be expected at the spatial level of relevé analysis. A plot or relevé of 20 m by 20 m, once established in a Hawaiian forest, scrub, or grassland, may have a different species composition in just a few years. By extension, the plant association, a vegetation unit analytically based on a number of floristically similar relevés and used for mapping floristically defined vegetation patterns at large map scales (such as 1 : 10,000 to 1 : 50,000), may require frequent spatial readjustments in such a dynamic environment.

Starting instead from a small-scale map projection, Hawaiian vegetation is relatively stable. For example, the altitudinal boundaries of major vegetation zones have not changed over several decades. Troll's (1959) comparison of the mountain biomes of Hawaii with those on Mt. Kinabalu and other tropical mountains still holds. The distribution of dominant species and plant-life forms can still be used as indicators of climatic gradients unique to oceanic island mountains. Only global warming or cooling may change that.

A STABLE SCHEME FOR DYNAMICS RESEARCH IN HAWAII. A small-scale overview of the Hawaiian Islands provides for a stable framework that may serve for an analysis of dynamic patterns. The very isolated Hawaiian archipelago forms a 300-km stretch of eight high islands, which continues northwest for another 2000 km in a sequence of low leeward islands. The latter are either atolls or rock bluffs. They are also the older islands, ranging in age from 10 to 25 million years, while the high islands are the younger ones. The high islands range in age from the currently building volcanic mountains on the most southern and largest island, Hawaii, to Kauai, with surfaces formed 3 million years ago. All high islands intercept the northeast trade winds and thereby receive orographic rainfall. This is their most reliable moisture source and also provides for a pronounced windward/leeward effect. The two youngest islands, Hawaii and Maui, rise above the prevailing cloud belt and trade-wind inversion (above 2000 m) into a cool-tropical alpine environment.

This three-fold segmentation into leeward, windward, and high-altitude climates provides for an outline of zonal (i.e., primarily climatically controlled) ecosystems. Ten such zonal ecosystems or landscapes were mapped by Ripperton and Hosaka (1942) at an intermediate map scale range of 1 : 100,000 to 1 : 1 million. Because of this relatively small and generalized scale, their map is still mostly valid. Supplied with some modified vegetation designations, this map served well for starting a program of selecting natural areas for biological conservation in Hawaii (Mueller-Dombois and Gagné 1975; see Table 1).

Notice that each of the 10 zones could be characterized by a few dominant species in 1975. Within these 10 zones occur a larger number of smaller-area vegetation types. Fosberg (1972) described about three times as many as "principal Hawaiian ecosystems." The most recent classification, by Gagné and Cuddihy (1990), described 106 community types, most of which can be grouped into this *zonal* and the following *azonal* ecosystem scheme.

In the azonal scheme, physiographic constraints override those of the zonal climates. Moreover, the azonal system includes smaller-area landscape units, which can be projected only on large-scale maps. It incorporates all the strand and coastline communities found on the leeward Hawaiian Islands, the communities on recent lava flows, and the Hawaiian bog vegetation.

TRANSGRESSIONS OF THE HIERARCHY RULE. As presented here, a hierarchy of vegetation units may start with ecological or vegetation zones in the form of zonal and azonal ecosystems. Within these large zonal units, one can recognize smaller-area ecosystems such as those 30 principal terrestrial ecosystems described by Fosberg (1972) for the Hawaiian Islands. These are mostly physiognomic units such as forest, scrub, and grassland, and because of the limited island flora, many of them are species-dominance types (sensu Whittaker 1962). They include, among others, such designations as *Metrosideros* woodland with *Gleichenia* (= *Dicranopteris*), *Acacia koa* forest, *Aleurites* forest, *Psidium cattleianum* forest, *Leucaena* scrub, and *Heteropogon* grassland, to name a few. But the question is, how permanent or dynamic are these units? Can they be considered as climax communities?

Egler (1947) objected not only to using the association concept, but also to using physiognomic criteria for classifying vegetation on Oahu. In his words, the application of physiognomic criteria "does extremely serious injustice to the recognition of natural areas" in Hawaii. Instead, he offered his concept of "land-type" (defined as part of a zone with uniform vegetational potentialities) as an intermediate-level class unit in the vegetation hierarchy above his individualistic community and below the level of vegetation zone.

With this, Egler tried to bring permanency or stability into his classification. His objection to the use of physiognomic criteria was based on the frequently made implication of using vegetation physiognomy as an indicator of climate. Egler (1942, 1947) emphasized that in Hawaii several physiognomic types of vegetation such as grassland, scrub, and forest coexist often side by side in the same climatic zone; and moreover, that the causes of such

TABLE 1

ECOLOGICAL ZONATION SCHEME FOR THE HAWAIIAN ISLANDS*

I. Zonal ecosystems (controlled dominantly through macroclimate)
   1. Xerotropical (leeward lowland to submontane)
      A. Savannah and dry grassland (*Prosopis* savannah and *Heteropogon–Rhynchelytrum* grassland)
      B. Dryland sclerophyll forest (or scrub) (*Metrosideros–Diospyros* open forests; displacement vegetation: *Leucaena* scrub and forest)
      C. Mixed mesophytic forest (woodland or scrub). C1, low phase; C2, high phase. (*Acacia koa* open forests; displacement vegetation: *Psidium guajava*, *Eugenia cumini* forests and woodlands)
   2. Pluviotropical (windward lowland to upper montane)
      D1. Lowland rainforest (*Metrosideros* forests) (largely displaced, few remnants only)
      D2. Montane rainforest (*Metrosideros–Cibotium* and dominantly *Cibotium* forests)
      D3. Upper montane rain- or cloud forest (*Cheirodendron* or *Acacia koa–Metrosideros* mixed forests)
   3. Cool tropical (upper montane to alpine; only on Maui and Hawaii)
      E1. Mountain parkland and savannah (*Acacia koa–Sophora chrysophylla* tree communities, *Deschampsia* tussock grassland)
      E2. Subalpine forest and scrub (*Sophora–Myoporum* tree communities, *Styphelia–Vaccinium–Dodonaea* scrub communities)
      E3. Sparse alpine scrub (*Styphelia*, *Vaccinium*) and moss desert (*Rhacomitrium lanuginosum*)
II. Azonal ecosystems (controlled largely through edaphic factors) (not mapped)
   4. Coastline ecosystems (Richmond and Mueller-Dombois 1972) including leeward Hawaiian Islands (Gagné and Cuddihy 1990)
      • Windward (beach, dune, and rock substrates; *Scaevola* scrub, *Pandanus* and *Hibiscus* forests, marshes, and mangroves
      • Leeward (beach, dune, and rock substrates; mangroves, coastal *Prosopis* forests, *Scaevola* scrub, atolls, and rock islands)
   5. Bogs and swamps
      • Low- and mid-elevation bogs and swamps
      • Montane bogs (dwarf *Metrosideros*)
   6. Geologically recent ecosystems
      • Vegetation on new volcanic surfaces (e.g., *Stereocaulon* lichen–*Nephrolepis* fern–*Metrosideros* seedling and sapling stages, young *Metrosideros* forest with *Machaerina* sedge and *Lycopodium* clubmoss–*Gleichenia* [= *Dicranopteris*] and *Sadleria* ferns)
      • Lava tubes and other recent geological features (Howarth 1981)
   7. Aquatic ecosystems
      • Freshwater lakes
      • Streams
      • Coastal brackish and marine ponds

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*The modified vegetation designations of Mueller-Dombois and Gagné (1975) are here summarized for the 10 zonal ecosystems with the letter symbols as mapped on an intermediate scale map by Ripperton and Hosaka (1942). Information synthesized from earlier works: Hillebrand 1888, Rock 1913, Egler 1939, Ripperton and Hosaka 1942, Krajina 1963, Knapp 1965, Doty and Mueller-Dombois 1966, Mueller-Dombois and Krajina 1968, Fosberg 1972, Mueller-Dombois 1981.

fragmentation and physiognomic/structural differentiation are many. This led him to conclude a "highly dynamic condition" for the Hawaiian vegetation.

Some of the most obvious dynamic transgressions of the spatial hierarchy rule are in the Hawaiian zonation scheme itself. Four of the 10 zones (A, B, C, and D1) are largely characterized by displacement vegetation dominated by alien species in the xerotropical and pluviotropical lowland to submontane environments. Among Fosberg's (1972) principal terrestrial ecosystems, one-third are clearly dominated by alien species.

Is this trend foreshadowing the doom of all native vegetation? Many botanists thought so at Egler's time and continue to think so today. But Egler himself was more optimistic based on his ecological insights.

Changing Patterns of Plant Succession

Disturbance regimes have changed in the Hawaiian Islands and they are continuing to

change. The lowland to submontane environments have been actively converted to other uses, and the remnant natural areas were first subjected to frequent fires by the Hawaiians and later to heavy grazing and browsing from a variety of feral ungulates introduced by Europeans (Cuddihy and Stone 1990). As of late, significant success in controlling the spread and impact of feral ungulates has been accomplished even in remote areas (Stone and Scott 1985).

However, by no means are human-related disturbances, such as the introduction of ungulates and their uncontrolled spread into Hawaii's natural vegetation, logging, burning, land-use conversion, and land-abandoning, the only drastic disturbances. Drastic natural disturbances, such as volcanic activity, drought, extremely wet periods, infrequent hurricanes, naturally caused fires, and landslides, are equally important. These natural disturbances have shaped the evolution of the original Hawaiian vegetation. Because of the archipelago's historical isolation, this original vegetation can be characterized as biogeographically impoverished but secondarily enriched by evolution.

In addition to the taxonomic enrichment by evolution resulting in endemism, "species packing" has occurred and continues to occur by the introduction of alien species to the Hawaiian Islands. The biogeographic theory of MacArthur and Wilson (1967) predicts a one-to-one species extinction through species invasion to oceanic islands after reaching a certain equilibrium. This theory greatly oversimplifies the spatial distribution dynamics of vegetation.

Egler (1947) in his island vegetation studies preferred the term *vegetation change* over the term *plant succession*, because he felt that knowledge was insufficient to predict whether a change in island vegetation was progressive or retrogressive. Although this still holds with regard to alien species invasion, it is nevertheless possible now to predict some general trends in the spatial dynamics of succession patterns.

CHRONOSEQUENTIAL MONOCULTURES. Successful plant invaders often become dominant

species that determine the vegetational structure of island ecosystems. Two of the best Hawaiian examples are the indigenous tree species *Metrosideros polymorpha* and *Acacia koa*. On the youngest Hawaiian mountain, Mauna Loa, *Metrosideros polymorpha* is distributed from sea level to 2500 m elevation, where it forms the tree line ecosystem. It thereby traverses a mean annual temperature range from 23° to 8°C and rainfall regimes from subhumid to wet and then dry. On Mauna Kea and Haleakala, *Metrosideros* does not extend its range quite as high, but it still is the dominant forest tree species on their wet, windward slopes. On the older islands (Lanai, Molokai, Oahu, and Kauai), *Metrosideros polymorpha* is also still the dominant tree of the montane rainforest. The species accomplished this enormous ecological success by its ability to undergo *auto-succession* (i.e., the turnover of many generations of its own kind). Bog pollen analysis has shown that it has accomplished auto-succession for at least the past 10,000 yr (Selling 1948). Stand structure and ecosystem dynamics research led to the conclusion (Mueller-Dombois 1986, 1987) that a process of synchronized mortality of cohort stands and subsequent rejuvenation was responsible for *Metrosideros*'s successional persistence.

Acacia koa likewise has maintained its dominance on all high islands by auto-succession. Exceptions are where stands have been logged and habitats actively converted to alien tree plantations or ranchland. On the latter, *Acacia koa* stands are still present today, but many are senescing and dying, because their reproductive cycle has been interrupted by cattle feeding preferentially on *Acacia koa* seedlings and young suckers.

Several alien invaders have also become dominant species forming naturalized monocultures. One of the earlier tree invaders introduced by the Hawaiians is *Aleurites moluccana*. This species became naturalized by invading most of the steep gulches on the older high islands from near sea level to 500 m elevation. From here it did not spread into other habitats most likely because the characteristics that make it a superior competitor in the ravine bottoms are ineffective in

other habitats with different disturbance regimes. The infrequent, but periodically recurring torrential stream activity must allow this species to maintain a closed canopy in gulches by episodic reproduction and fast growth of saplings into the canopy. This trait, however, did not allow this species to invade forest stands on ridges and spurs, which are often occupied by *Acacia koa*, or those on the slopes next to the gulches, now often occupied by *Psidium guajava* and other introduced tree species.

Another example of a naturalized alien monoculture is the *Leucaena leucocephala* scrub, which ranked so high in spatial dominance that it became an indicator of a zonal ecosystem (zone B, Table 1). During the mid 1980s this species was subject to a severe and widespread dieback (Ikagawa 1987), but it remained in the area.

According to Wester (in press), *Leucaena leucocephala* was introduced before 1837, but it did not become spatialy dominant until the 1920s. Egler (1947) pointed out that the botanist Forbes did not mention the species as a prevailing element of the lowland plant associations in a survey done just after 1919, but that it was actively spreading into dry grassland communities in the 1940s. Thus, although giving the impression of a self-perpetuating monoculture, *Leucaena* scrub probably only dominated as first-generation stands. The dieback was probably the result of a chain reaction of causes involving predisposition from stand senescence (Mueller-Dombois 1983), drought during the last giant El Niño of 1982–1983 as a dieback trigger (Mueller-Dombois 1986), and the introduction of a psyllid (*Heteropsylla cubana*) in April–June 1984 (Nakahara and Lai 1984) as an aggravator and hastening cause of dieback. Although seedlings were observed under the mature *Leucaena* canopy (Egler 1947), the succession now seems to lead to different species becoming dominant after *Leucaena* dieback (Ikagawa 1987).

CHRONOSEQUENTIAL POLYCULTURES. The concept of plant succession arose from the study of temperate zone vegetation, first in North America (Cowles 1899, Cooper 1913,

Clements 1916) and then in Europe (Tansley 1929, Lüdi 1930). Both these continental areas are depauperate of tree species, Europe even more so than North America, relative to the continental tropics. Yet, progressive forest successions involve typically a chronosequence of dominant tree species (e.g., first commonly stands of pine, which then become invaded by hardwoods, such as poplar and birch, which in turn become invaded by spruces and firs). Egler (1954) contributed to this picture of "relay floristics" his concept of "initial floristic composition" implying that later successional dominants may already be present in a latent stage at the beginning of a secondary succession. Each of these stages may form tree associations, in which one or the other species is dominant (Curtis and McIntosh 1951, Daubenmire 1968). Thus, the typical temperate forest succession can be described as a chronosequential polyculture. It is analogous to the long-standing European practice of crop rotation, an empirically established agro-biological principle that promotes agricultural sustainability.

Because of the initial biotic simplicity in geographically isolated ecosystems, such as islands and mountains, auto-successions are rather persistent in such isolated environments, leading to chronosequential monocultures. With the evolution of endemic species or, much more rapidly, with invasion of alien species, new successionally functional species are added. This may lead to the development of chronosequential polycultures. Whether or not this will be so with *Leucaena leucocephala*, now that it has lost its dominance, is still open to question. More likely, the dieback stands will become a patch mosaic of locally more restricted successional species. In the moister segments of *Leucaena* habitat, another alien tree, *Schinus terebinthifolius*, seems to assert a new dominance, while in drier habitat segments the tall bunchgrass *Panicum maximum* has invaded. In some localities the native woody plants *Sida fallax* and *Dodonaea viscosa* have reasserted a certain successional dominance in *Leucaena* dieback stands on Waialae Iki Ridge (Honolulu).

Chronosequential polycultures along a gradient of soil aging have developed in Hawaii

in the subalpine environment. Indirect evidence comes from comparing the subalpine ecosystems on the high Hawaiian mountains. *Metrosideros polymorpha* prevails in the subalpine environment of Mauna Loa, but *Sophora chrysophylla* is slowly increasing in density. *Sophora chrysophylla* is the distinct dominant of the tree line ecosystem on the geologically older Mauna Kea, where *Metrosideros* has long since disappeared. Similar observations can be made in seasonal submontane environments, but not in the rainforest biome, where *Metrosideros* has persisted but appears to have evolved into successional races (Stemmermann 1983, 1986).

Chronosequential polycultures have not yet been described for secondary successions in Hawaii, although the current invasion of the alien *Myrica faya* in Hawaii Volcanoes National Park may represent such a case. The N-fixer *Myrica* is explosively invading an open *Metrosideros* forest in the seasonal submontane ecosystem (Vitousek and Walker 1989), where it appears to become the new dominant. *Myrica* has already formed a monodominant stand of about 1 ha, approximating 1% of the area of the seasonal submontane ecosystem. In the adjacent subhumid segment of closed *Metrosideros–Cibotium* rainforest, *Myrica* has become a significant canopy associate. In this subhumid rainforest environment and the seasonal submontane ecosystem, only a new lava flow may permit *Metrosideros polymorpha* to reassume pioneer dominance, while lesser disturbances may provide *Myrica* with a further advantage to dominate in secondary succession.

CHRONOSEQUENTIAL GAP ROTATION. This concept relates to the successional turnover of tree species in multispecies tropical forests, which typically occurs in single tree-fall gaps (Brockaw 1985).

This form of small-area successional rotation appears to have evolved in native Hawaiian forests containing several canopy species, such as Fosberg's (1972) mixed mesophytic forest. Canopy trees include at least six evergreen species, such as *Diospyros ferrea, Acacia koa, Eugenia malaccensis* (another Hawaiian introduction), *Osmanthus sandwicensis, Myr-*

sine lessertiana, and *Metrosideros polymorpha,* and occasionally two deciduous species, *Reynoldsia sandwicensis* and *Erythrina sandwicensis.* These forests have been described in more detail by Hatheway (1952) and Wirawan (1974). Wirawan found them to have remained stable 20 yr after Hatheway's first detailed analysis, but alien tree species such as *Schinus terebinthifolius* had also remained in the absence of further disturbance.

Fosberg's mixed lowland forest belongs to the same dynamic category. He wrote (Fosberg 1972:32) that "At present this forest presents an irregular aspect more a mosaic of small patches of other forests than an integrated entity. However, *Pandanus, Eugenia malaccensis, Eugenia cumini,* and *Hibiscus tiliaceus* and others" (including *Eugenia jambosa, Psidium guajava, P. cattleianum, Persea americana, Samanea saman, Terminalia catappa, Calophyllum inophyllum*) "reproduce themselves effectively and with their associates do form a recognizable forest belt." This mixed forest belt has largely displaced the former *Psidium guajava*–dominated forest belt (or zone). Notice that this displacement of one dominant by several associates resulted from "species packing," mostly with alien tree species.

Climax in an Island Context

The concept of climax has been much debated in the literature. Egler (1947), from his experience with island vegetation, rejected the concept as totally misleading. However, in the most recent treatment of Hawaiian vegetation by Gagné and Cuddihy (1990), the climax concept has been resurrected. In the conceptual statement of their classifying philosophy, these authors stated (Gagné and Cuddihy 1990:51), "Distinguishing between climax communities and successional communities can be difficult. Indeed, one might argue that *all* of our vegetation is successional, in that our islands are either growing volcanically or eroding back to sea level, with profound ecological and vegetational consequences in either case." This shows that a powerful concept cannot simply be dismissed, and that instead, clarification is needed.

CLIMAX AS A PATCH MOSAIC. Whittaker (1953) emphasized the need to separate the concept of climax from its physiographic connotation and to treat it as a pattern of population structures. By that he meant that to be considered climax a vegetation must display a species assemblage that perpetuates itself in the same area. The geographic site of the area must therefore be large enough to allow for the complete growth cycle of all its component species. If tree species reproduce and grow under their own canopy or in small gaps as is the case in most multispecies tropical forests, community permanency may be maintained over a few tens of hectares under protection and with allowance of a generous buffer zone. However, if communities form a patch mosaic consisting of different successional stages, for example those developing after disturbances, such as fire or hurricanes, the climax concept must include these successional stages, and the frequency and scale of such disturbances must be taken into consideration. In this case the disturbance regime would set the spatial limit for what may be considered the climax community. Thus, a climax community may be considered a patch mosaic of different dynamic stages that only become constant or stable at a larger level of the spatial hierarchy, that of a vegetation zone or biome.

Egler (1947) in his rejection of the climax concept went even farther. On the island of Oahu, he considered as relatively permanent only three broad floristic areas, which he called strand, xerotropical, and pluviotropical. He certainly had a point, because alien species may even change the dominance relationships at the most generalized level in the vegetation hierarchy.

THE PHYSIOGRAPHIC CLIMAX. Clements (1916, 1928) had postulated a climatic climax into which all physiographically constrained communities of a climatic zone would converge, given enough time. Ecosystem development in Hawaii emphasizes that this much-criticized, but persuasive concept should be interpreted with caution.

The island of Hawaii displays a series of lava flows and pyroclastic surfaces of different ages in the same rainforest climate. The other high islands, in addition, form a continuing age sequence, which starts with Hawaii at the southeast end of the chain, and continues to Kauai at the northwest end, where rainforest soils exceed 3 million yr of age.

Plotting forest biomass and biophilic nutrient availability over this substrate age sequence (which forms a hypothetical primary successional sequence) reveals that a physiographic/edaphic climax is reached at 1000 to 3000 yr. This time range marks the mode (i.e., the high point or climax) of organic production in the Hawaiian rainforest biome. There is enough evidence to show that a physiographic/edaphic climax in the form of a production mode is followed by a retrogression of forest site capacity. This retrogression is due to the constantly high rainfall regime, which causes cation leaching and, in association with increasing acidity, aluminum toxicity and, under poor drainage, also iron and manganese toxicity (Mueller-Dombois 1990). Such processes of accelerated soil aging are probably typical for most humid tropical environments, although high-stature forest species that could cope with such soil nutrient limitations evolved in the continental but not in the isolated island tropics.

This process of continuous change or development supports those who have seriously critiqued the climatic climax concept. It further clarifies that it is necessary, when speaking of climax in vegetation studies, to distinguish between ecosystem development and persistence of vegetation patterns or communities.

Conclusions

Transgressions of the spatial hierarchy appear to be typical for isolated islands. This is documented by dominant species extending through more than one ecological zone. Good Hawaiian examples are *Metrosideros polymorpha* and *Acacia koa*. Such spatial transgressions also imply larger patterns of vegetation dynamics than occur in floristically richer regions. The maintenance of such larger patterns of monodominance is accomplished through auto-succession.

Evolution, however, works against auto-succession and the maintenance of chronosequential monocultures. This is indicated in Hawaii by different races of *Metrosideros polymorpha* participating in the generation turnover of these forests in successionally older rainforest ecosystems.

Introduction of alien species occasionally results in the biological invasion of new dominant species. These seem to behave in ways similar to the indigenous dominants. Good examples are *Leucaena leucocephala* and *Myrica faya*. However, none of these species, including *Prosopis chilensis*, *Psidium guajava*, and *Psidium cattleianum*, have managed to extend their ranges over such broad habitat spectra as *Metrosideros polymorpha* and *Acacia koa*. Instead, their initial establishment in the form of naturalized monocultures seems to become fragmented, during their generational turnover, by successional species, resulting in mosaics of patches. These successional species are often aliens that have been present in the general area for a long time. They also include indigenous species as long as prior physical disturbances (such as habitat conversion and subsequent abandonment) have not eliminated them totally from such areas. In such cases superior dispersal mechanisms of introduced tree species are often the decisive factor favoring aliens over natives.

Thus, the trends in the distributional dynamics of the Hawaiian vegetation seem to go from large-area chronosequential monocultures to mosaics of patches, which may persist in the form of chronosequential gap rotation involving many canopy species.

Spatial dynamic patterns seem to exclude what was considered to be a typical succession in forest environments of the north temperate zones (i.e., the chronosequential appearance of dominant tree species forming larger-area successional stages). Such chronosequential polycultures provided the basis for Clements's succession theory. Although his climatic climax theory was certainly an exaggeration, large-area uniform successional behavior has been well documented.

Successional patterns are a function of both the ecological properties of the available species and the disturbance regime. Many of the documented temperate forest successions were either successions following fire or successions on abandoned fields. Unfortunately in the humid tropics, forest destruction by fire often encourages invasion of pyrophytic grasses. Where aggressive tropical pioneer trees, fast-growing species of *Cecropia*, *Melochia*, *Trema*, and *Albizia*, are not readily available as secondary pioneers, such areas are converted by frequently recurring fires that arrest forest succession or the redevelopment of a chronosequential polyculture.

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