BIOLOGICAL INVASION AND FIRE
IN TROPICAL BIOMES

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ABSTRACT

Biological invasion and fire-caused disturbances are both natural processes in tropical–subtropical ecosystems. The 2 processes are often interrelated in a complex manner. This will be discussed in relation to the major zonal and intra-zonal tropical biomes, which adjoin each other along climatic and edaphic gradients. Atmospheric change and weather disturbances can promote fire via biological invasion associated with fuel loading. Stand-level demography may also play a major role. In the tropics, pyrophytic C_4 grasses are quick to invade following logging and slash-burning, even in wet rain forests. This appears to be an important difference compared with temperate zone forest biomes. Human activity has contributed to biological invasion in a profound way, particularly in formerly isolated tropical environments with underutilized resource capacities. This has often led to environmental degradation. However, improved understanding of natural processes of vegetation dynamics can help to counteract environmental degradation through appropriate restoration measures.

keywords: aggravated disturbance regimes, biodiversity, climate–fire relationships, forest decline, island vs. continental tropics, natural vs. human-induced invasion, succession and fire, testable hypotheses, vegetation processes.

INTRODUCTION

Because of human intervention, biological invasion and fire are now considered major disturbances that threaten the integrity and sustainability of terrestrial ecosystems (Van Wilgen et al. 1990, D'Antonio and Vitousek 1992, Jaffré et al. 1998). Moreover, both factors have begun to degrade the human environment and quality of life. This has not always been so.

In the theory of island biogeography, biological invasion is considered the fundamental natural process that builds the biological component in ecosystems (MacArthur and Wilson 1967). In terrestrial ecosystems, this principal component is made up of the primary producers, i.e., the green plants that form the vegetation.

In the warm regions of the world—the tropical–subtropical belts north and south of the equator—vegetation is known to be more diverse in species (Raven 1988, Barthlott 1996), and depending on moisture, growing seasons can be longer, and vegetation turnover can be more rapid than in temperate and colder regions (Mueller-Dombois 1992*a,* Phillips and Gentry 1994). Consequently, fire can also be a more aggravating force in species extinction and weed invasion.
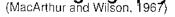
Fire is considered to be one of the principal agents of vegetation turnover in most terrestrial ecosystems (Mooney et al. 1981). Fire as a consumer of vegetation can thus be considered the opposite of biological invasion, resulting in the destruction of biota and species extinction. But the relationship of fire and biological invasion is far more complex. Under the new perspectives of global and regional changes promoted by hu-man activities, biological invasion and fire have become powerful new disturbance factors. A consideration of these broader relationships in more detail may help in mitigating their negative effects.

BIOLOGICAL INVASION AS NATURAL AND HUMAN-INDUCED PROCESSES
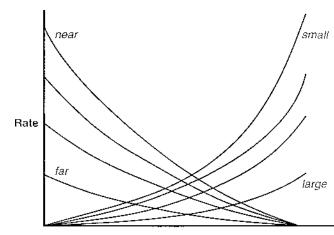
In denuded areas, biological invasion is a natural process in the formation of vegetation and ecosystems. This fact has been incorporated into the island biogeography model (Figure 1) by MacArthur and Wilson (1967). Here, biological invasion is shown as a series of curves that slope downwards from left to right over an axis of increasing species richness. The curves indicate that the rate of invasion declines when the denuded area or island becomes occupied by species. They also show that the rate of invasion declines when the denuded areas or islands are farther removed from a biological source area. Depending on habitat resources, biological invasion may eventually reach a saturation point in terms of species diversity.

However, rates of biological invasion are compensated in the MacArthur and Wilson model by rates of extinction or species displacement. These are shown by a series of curves sloping upwards from left to right. They predict that large islands have lower rates of extinction than small islands. Large islands, which typically are volcanic mountains surrounded by ocean, contain more habitats than small islands. Large islands, therefore, when subjected to major disturbances, such as broadcast wildfires, may still have refugia with spe-

The Island Biogeography Model
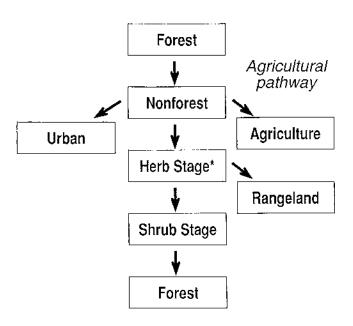### (MacArthur and Wilson, 1967)

Fig. 1.   The model of MacArthur and Wilson (1967) can be used to explain that with globalization current rates of species invasion are predominately in the near-source category (upper left on diagram). Rates of species loss will increase with human-caused habitat fragmentation as indicated by the extinction curves pointing to small islands (upper right on diagram). The overall result is accelerated biodiversity change.

Generalized Secondary Succession

*Tropical/subtropical biomes invaded typically by C4 grasses.

Fig. 2.   Generalized secondary succession patterns. Flammability is greatest at the herb stage in tropical–subtropical habitats when invaded by grasses. Fires are thus likely to occur even in rain forest environments. In contrast, in primary succession, a prolonged cryptogam stage of sparse vegetation cover follows nudation. Thereafter, fire hazards develop when the mat-forming fern *Dicranopteris* spp. invades, as is typical in volcanic successions of Oceania.

cies pools for re-invasion. Small islands, when similarly disturbed, are more vulnerable to species extinction. Examples are the small Fijian high islands Nairai (28 km²) and Batik (9 km²), which lost their original rain forest due to repeated fires and are now covered with *talasiqa* fern grassland (Mueller-Dombois and Fosberg 1998:136). Small forest patches on continents are similarly vulnerable after severe habitat fragmentation (Burgess and Sharpe 1981).

We can easily visualize what happens when humans become the agents of biological dispersal. The rate of invasion will not depend on long-distance dispersal by natural agents. The biological source instead has become very near. It has been moved into the area of impact, which formerly was isolated or non-reachable by natural dispersal.

Biological invasion and extinction are in themselves more complicated processes. Biological invasion begins with transfer of disseminules. This process is not slowed down by any increase in established species. After being transferred, the disseminules must find a suitable environment for development to maturity and reproduction. To become biological invaders, species after transfer must be able to disperse locally to become successful populations. In this follow-up process, the native communities and habitats play a major role. They may favor or exclude a newly transferred organism.

Biological invasion in the context of the island biogeography theory can be compared to the processes in primary succession. In the classical sense, these were stipulated by Clements (1916) in sequence as (1) nudation, (2) migration (transfer of disseminules), (3)

ecesis (population establishment by reproduction in the new habitat), (4) competition, (5) reaction (habitat change through biological invasion), and (6) final stabilization (a dynamic equilibrium stage, called climax by Clements [1916]).

The climax or final equilibrium stage, corresponds to the points of intersection of the species invasion and extinction curves in the island biogeography model. In Figure 1, these intersecting points imply, for example, that a large archipelago near a biological source area contains more species at equilibrium than an equally large archipelago far removed from a continent. This is debatable, however; ultimately it is the resource availability of the habitats and the adaptive and competitive capacity of the organisms that will set the limit.

Structurally and physiognomically, one can visualize the above 6 processes in a broadly simplified form by the successive assembly of dominating plant life-form stages (Figure 2). A primary succession begins with a new substrate. Instead of an herb stage, one would expect a cryptogam stage consisting primarily of algae, mosses, lichens, and ferns (Smathers and Mueller-Dombois 1974). Woody colonizers also may enter early in the cryptogam stage, but overall, cover would remain sparse for a long time. Vegetation development would exclude fire at this stage. A fire hazard develops only when the cohesive mat-forming

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Factors of Vegetation Development

$$v = f\ (g,\ cl,\ d,\ fl,\ ac,\ e)$$

g = geoposition   **fl** = flora
cl = climate   **ac** = access potential
d = disturbance   **e** = ecological properties

*time and spacial scale are overriding
dimensions*

disturbances aggravated by human activity:

d1 = biological invasion

d2 = CO_2 and other chemical changes
     in the atmosphere

d3 = climate variability and/or change

d4 = fire in space and time

d5 = habitat fragmentation

Fig. 3.   An ecosystem-based formula used by Mueller-Dombois and Fosberg (1998) to characterize the vegetation of the tropical Pacific islands. The 5 human-aggravated disturbance factors are elements of global environmental change that presently affect both ecosystem and vegetation development.

fern *Dicranopteris linearis* invades at a later stage. This applies especially to tropical rain forests in Oceania.

In secondary successions, which follow removal of forest, the substrate is already developed soil containing soil microorganisms, organic matter, and a seed bank. The herb stage may thus form rapidly. In temperate forests of the Pacific Northwest, Central Canada, and Europe, I have seen this herb stage often represented predominantly by fireweed (*Epilobium angustifolium*). In tropical forests, however, this herb stage is often dominated by caespitose C_4 grasses, which invite fires and spread readily after slash burns (Mueller-Dombois 1981*a,* Mueller-Dombois and Goldammer 1990). Fire exclusion at this critical early stage in succession, allows woody plants to regenerate where forest was the dominant cover prior to forest removal (Fearnside 1990, Gill et al. 1990, Kaufman and Uhl 1990). Shifting agriculture with bush fallow (Mueller-Dombois and Fosberg 1998), including spontaneous establishment of secondary fast-growing tropical forest trees, is based on this biological principle.

GLOBAL VEGETATION PROCESSES AND FIRE

Vegetation, the object of wildfires, can be understood as the plant cover of an area. More fundamentally, vegetation is a function of 6 formation factors (Mueller-Dombois and Fosberg 1998). These can be characterized in a formula as shown in Figure 3. Here, the 'g' factor, geoposition, includes geographic location, geology, geomorphology with topographic position, and ground condition, the soil. The 'cl' factor, climate, includes macro-, meso-, and micro-climate, as well as any significant aspect of the atmospheric environment. The 'd' factor, disturbance, includes any significant disruption in vegetation development, such as fire, extreme weather events, or accelerated biological invasion. If the 'd' factor shows a pattern, it can be characterized as a disturbance regime. For example, the El Niño Southern Oscillation (ENSO) events are a climatic disturbance regime that impacts the forests in the western and central Pacific area periodically with fire hazards as a consequence. The 'fl' factor, flora, refers to the regional flora or floristic province. From this flora, plant species become assembled in specific locations, habitats, or sites. For this to happen, species must have an access potential, the 'ac' factor, to get to the specific locality. Finally, the 'e' factor, relates to the ecological properties, or the ecological role of a species in the species assemblage that forms the plant community. The latter can be considered a subdivision of the vegetation cover as defined by species composition.

Time in vegetation development is extremely important and should be considered an overriding dimension that shapes all vegetation formation factors. Space is also an overriding dimension, which refers to vegetation over a range of spatial scales from biomes to small-area floristic groupings.
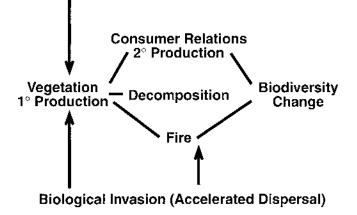
The formula in Figure 3 can be applied at any geographic scale, and it treats vegetation in an ecosystem context as proposed originally by Tansley (1935). However, disturbance as a vegetation formation factor has only recently received much attention with the conceptual advent of global change. Under this more recent aspect, we may now list several new anthropogenically aggravated disturbance regimes of particular application to the topic (see Figure 3 d1–d5).

A simple model of global vegetation processes (Figure 4) may help to clarify the relationship of biological invasion and fire. Chemical and physical changes in the atmospheric environment and biological invasion from accelerated dispersal are now impacting vegetation on a global scale. These new, human-induced, stress–disturbance patterns are overlaid on the normal processes of vegetation development and turnover. Fire is one of the natural turnover processes of vegetation in fire-prone ecosystems. It complements decomposition and herbivory where these 2 processes are less active or disrupted. At the same time, fire facilitates biological invasion through destruction of existing vegetation. Depending on their ecological roles, the invaders in turn may exclude or invite fire, thereby changing the fire regime and the trajectory of ecosystem development. The overall outcome of the new human-induced stress–disturbance patterns will be a changed biodiversity, i.e., global homogenization combined with locally increased species packing. It takes regionally integrated efforts of conservation scientists,

Global Vegetation Processes

Enhanced CO$_2$, N, Radiation (Climate Change)

Consumer Relations
2° Production

Vegetation
1° Production — Decomposition

Biodiversity
Change

Fire

Biological Invasion (Accelerated Dispersal)

(A question of balance vs. disruption)

Fig. 4. A simple model of vegetation build-up and breakdown processes. Overriding are the global change factors as accelerated by human activity, which cause shifts in biodiversity. It is not yet known how these changes affect ecosystem resilience.

managers, and policy makers to mitigate this trend of biological degradation.

Thirty years ago, during the International Biological Program years, the central theme for multidisciplinary team research was the biological basis of productivity and human welfare. The U.S. biome studies were organized into study groups on primary production, decomposition, and consumer relations with an overall modeling component. Little attention was given to fire as the other main turn-over process in vegetation. This was subsequently remedied, in part by the ''Fire Regimes and Ecosystem Properties'' symposium during 1978 (Mooney et al. 1981).

The following decade saw an emphasis on acid rain and air pollution as a major problem with regard to forest decline or *Waldsterben,* as it was called in Germany (Vogelmann 1982, Schütt and Cowling 1985, Hinrichson 1987). This was followed by a little known book by Spiecker et al. (1996), revealing that during the same ''forest decline period,'' European spruce forests displayed about 40% gain in diameter increments. Many of the curves of incremental gain in wood production showed a close correlation to the CO$_2$ enhancement trend recorded at the Mauna Loa climate station (Keeling 1984, Fosberg et al. 1990). However, the causes of this apparent contradiction or turn-around from decline to growth increase, are not yet established. Elevated levels of nitrogen deposition over Central Europe have been suggested as a contributing factor (Kreutzer 1993).

From studies of elevated CO$_2$ in artificial tropical ecosystems, Körner (Körner and Arnone 1992, Körner

1998) concluded that there will be no increase in the biomass of tropical forests. The only increase would be in the form of non-structural starch in the tops of canopies and fine root production. In view of the well documented growth increase in temperate zone spruce forests, Körner's prediction for tropical forests seems contradictory. But the difference could be that the European spruce forests are mostly even-aged cohort forests that have been managed with thinning regimes to avoid intra-specific competition as well as fire, while the moist tropical forests are mostly unmanaged natural forests where the canopy species compete for soil nutrient resources.

THREE HYPOTHESES AND A CASE-EXAMPLE FROM HAWAI'I

Three consequences of the enhanced CO$_2$ environment on the acceleration of biological invasion and fire in tropical biomes may be stated here as testable hypotheses:

(1) The enhanced CO$_2$ environment increases the rate of plant metabolism, resulting in shorter life-spans of leaf tissue and whole plants. This would be revealed in increasing forest canopy dieback and accumulation of senescing or dead plant tissue. See Mueller-Dombois (1992*a*) and Phillips and Gentry (1994) for support for this hypothesis.

(2) Among life forms of woody plants, vines in particular, will benefit from enhanced CO$_2$ because of their carbon allocation programs. These genetic programs encourage rapid growth into forest canopies without much carbon investment into stems and roots. There is also some support for this hypothesis from observations reported by the above authors. Dukes and Mooney (1999) consider 2 invasive vines in N. America—kudzu (*Pueraria lobata*) and Japanese honeysuckle (*Lonicera japonica*)—to be driven into aggressiveness by accelerated CO$_2$ and N deposition. Vines, when senescing, can easily serve as transfer ladders of ground (litter and/or grass) fires to crown fires in forests, thereby causing high intensity fires.

(3) Enhanced CO$_2$ will promote the grass life form. In temperate and tropical mountain environments C$_3$ grasses are directly favored, such as the European cheatgrass (*Bromus erectus*) in the western United States (Duke and Mooney 1999). In the tropics, C$_4$ grasses prevail. Enhanced CO$_2$ has been shown to increase their water-use efficiency (Jackson et al. 1994). Thus, elevated CO$_2$ compensates for reduced water or soil drought. This may in part explain the aggressiveness of C$_4$ grasses following forest fragmentation.

In Hawai'i, introduced C$_4$ grasses have invaded unburned open forests and shrublands (D'Antonio and Vitousek 1992, Daehler and Carino 1998). Following their invasion without the help of fire, these grasses have invited fire and thereafter have spread rapidly, becoming a dominant life form in a submontane seasonal forest (Tunison et al. 1995). Only 30 years ago,

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this forest was almost devoid of grasses (Doty and Mueller-Dombois 1966).

Subsequently, Smathers (1970) reported an explosive spreading of the nonnative broomsedge (*Andropogon virginicus*; a C_4 grass) following a 1968 lava flow that ignited indigenous, dried-up *Dicranopteris* fern mats in a small part of this area. Beginning during the early 1970s, the same forest experienced an explosive invasion of firetree (*Myrica faya*), an introduced tree from the Macaronesian Islands. This nitrogen-fixing evergreen, dispersed by alien birds, threatened to out-compete the dominant native tree species 'ohi'a lehua (*Metrosideros polymorpha*; Vitousek et al. 1987). However, during the late 1980s, firetree was attacked by the two-spotted leafhopper (*Sophonia rufofascia*), an accidentally introduced leaf-sap sucking insect, which caused firetree dieback in a drought-prone area of its invasion range. 'Ohi'a lehua trees also died in this area (Tunison et al. 1993).

The dead trees, together with the introduced grasses, now form a fire hazard that has become especially serious due to the large volume of dead stem wood and branches present. Biological invasion and fire, in this case, have severely disrupted the balance of this native seasonal woodland whose natural turn-over processes were originally restricted to decomposition of senescing leaf tissue and some minor damage of green leaf tissue by native insects. The latter were clearly non-disruptive. The overall result now is a mixed native–alien community whose ecosystem processes have been changed completely by 2 introduced plant life forms, caespitose and mat-forming pyrophilous grasses and an alien N-fixing tree, whose dispersal was facilitated by introduced birds (Vitousek and Walker 1989, Woodward et al. 1990).
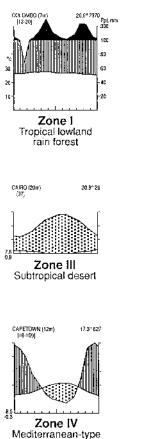
TROPICAL–SUBTROPICAL CLIMATE RELATIONSHIPS

The increasingly widespread occurrence of fire in tropical–subtropical biomes of the developing countries is well known (Goldammer and Price 1998). Its contribution to the release of carbon dioxide and potential effects on climate variability and warming has been a topic of discussion in the book edited by Goldammer (1990). Part of the increasingly widespread use of fire is due to population pressures that result in the conversion of tropical rain forest to cropland and pastures by slash burning. Another part is due to savannization, a more complex process. Savannization is likely to involve a combination of causes, such as invasion of pyrophytic grasses and trees through forest fragmentation and human-induced transfer or dissemination of such plant types, as well as climate change and variability.

Figure 5 presents some tropical and subtropical climate types. The climate-diagram maps (after Walter et al. 1975) are well known as ecologically useful portrayals of zonal biome types. Such diagrams are increasingly used in the ecological literature and they

Tropical/Subtropical Climate Diagrams
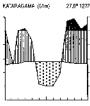(Walter *et al.,* 1975 and Mueller-Dombois, 1968)

Fig. 5. Six climate diagrams representative of 4 tropical–subtropical zones. Zone II and Zone IV have predictable fire regimes.

give a good projection of fire regimes (Van Wilgen 1990).

The temperature curve in each diagram depicts the climate as either tropical or subtropical. Tropical temperatures remain relatively even from month to month, thus displaying a more or less horizontal line, parallel to the *X*-axis, which shows the calendar months. On Figure 5, this applies to Colombo and Kataragama in Sri Lanka, and to Calabozo in Venezuela. The other 3 diagrams represent subtropical climates (Cairo, Egypt; Johannesburg and Cape Town, South Africa). They display greater differences between warmer and cooler seasons, but monthly mean temperatures remain above freezing even during the cool season. In tropical and subtropical mountains, respectively, the temperature curves retain the same shape, but they drop down according to the lapse rate. They can be partly below the bottom axis, which represents the frost line. For places in the southern Hemisphere, the calendar months begin with July, so that on the diagrams the warmer season is always in the center.

The typically uneven curve on each diagram

shows mean monthly precipitation values. A black field at the top indicates a wet period with rainfall averages above 100 mm per month. Here, the scale on the right-hand ordinate is changed. While the intervals below 100 mm represent 20 mm each, the same intervals above 100 mm represent 200 mm each. Whenever the precipitation curve undercuts the temperature curve, a drought period is indicated. This is shown by the dotted fields on the diagrams. The relationship of 1:2 in the plotting of these 2 curves has been found to provide for a useful drought index. This ratio is obtained by matching the 2 Y-ordinates in such a way that 10 °C on the left is at the same level as 20 mm on the right ordinate.

These droughts are the normal periods of fire hazards in the respective tropical–subtropical biomes. Of course, in Zone III, which indicates a year-round fire hazard, wildfires will not have a chance. Extreme deserts, such as the Sahara, have little or no vegetation to burn. Zone I, representing tropical rain forest, also is not a fire climate, because of almost year-round wetness. However, in the Colombo climate, with a short dry period during February each year, plantation rubber trees are known to shed their leaves synchronously (Mueller-Dombois 1968). This could bring about a certain fire hazard in this biome. Moreover, a February dry period is normal for the Sinharadja rain forest near Colombo. Early succession stages with invasion of grasses and/or the mat-forming fern (*Dicranopteris linearis*) could carry fire into the rain forest.

That tropical rain forests have burned in the past has been well documented by Goldammer and Seibert (1990) for Southeast Asia, and by Kauffman and Uhl (1990) for Amazonia. However, the recent fires in Southeast Asia, such as the enormous rain forest fire in Kalimantan during the 1982–1983 El Niño events, are new phenomena related to accumulation of debris after logging, forest fragmentation, and invasion of pyrophilic grasses and vines (Wirawan 1993).

One only has to imagine what consequences climate variability, in terms of extending drought periods, will have on the accumulation of senescing tissue in the form of litter and woody debris. Drought periods are times when the activity of decomposers is at a minimum.

An interesting departure from the fire hazard of tropical seasonal climates occurred in the dry zone of Sri Lanka, here represented by the climate diagram of Kataragama (Figure 5). When I studied and mapped the vegetation there, in Ruhuna National Park (Mueller-Dombois 1969), the natural pastures among the secondary thorn scrub and monsoon (evergreen, mixed, deciduous) forests were close-cropped like garden lawns. There was no recent historical record of any fire in this area. The explanation was the intense grazing and biomass removal by the large herbivores in this National Park. This was caused by the activity of native herbivores (primarily axis deer [*Cervus axis*] and water buffalo [*Bubalus bubalis*]). Elephants (*Elephas maximus*) using these pastures could not grab the grasses directly with their trunks. Instead, they had to churn the grass-sod into piles with their feet and then

use their trunks to grab a mouthful of grassy diet. They also thinned the scrub and removed the lower branches of their favored trees up to a browse height of 5 m (Mueller-Dombois 1972). In this monsoon vegetation, the native animal community shaped ecosystem function by reducing the likelihood of fire.
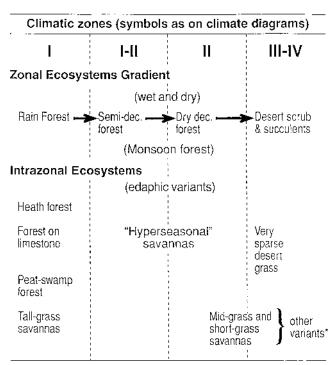
This function is to remove "the stress of stored fuel" Schüle (1990:285). Schüle (1990:285) stated that "undergrazing is just as disastrous as overgrazing." He considered undergrazing to result in fuel loading, which thereafter is followed by high-intensity fires. Schüle's hypothesis can be stated as follows: during prehistoric eras (Pleistocene, Holocene), fire frequency and intensity were kept low because large herbivores roamed throughout continental vegetation consuming large amounts of biomass. There was no excessive buildup—only when humans succeeded in hunting and eradicating these herbivores—fire became the alternative consumer, and fire intensity as well as frequency increased dramatically. Thus, Schüle's hypothesis emphasizes "biological extinction" as the principal cause of fire increase. In his view, "human invasion," a form of biological invasion, in prehistoric eras, is the ultimate cause of interaction. Thus, fire intensity increased due to excess biomass and fire frequency increased because fire became an effective hunting tool.

ISLAND VERSUS CONTINENTAL TROPICS

Unlike islands, continental biomes were continuous over large areas in prehistoric eras. They followed in their vegetation structure and life form composition spatially uninterrupted gradients determined by climate, provided they occurred on non-extreme substrates, i.e., the Zonal Biomes on Figure 6 (Zone I Tropical rain forest, Zone II Tropical dry (seasonal) forest, Zone III Tropical–subtropical desert, Zone IV subtropical Mediterranean biome or tropical monsoon forest). Another group can be called Intrazonal Ecosystems or Pedobiomes (Walter et al. 1975), implying occurrence on extreme substrates in the same climatic zone. They include forests on limestone, forests on sandy substrates, peat swamp forests, etc. On these extreme substrates the soil microorganisms are less active. Thus, organic matter decomposes slowly and may accumulate as, for example, in peat swamp forests. Such intrazonal forest biomes have a higher fuel load above ground level and thus are more prone to fire. The same applies to tropical–subtropical upland forests. They have a certain build up of organic matter on top of the mineral soil, which presents a fire hazard during droughts.

Forests on limestone, on sandy substrates, on ultramafic substrates, and peat swamp forests are not conducive to invasion of the pyrophytic bunchgrass life form. In this respect, they are less vulnerable to an easily ignited, rapid fire-carrying fuel. An exception are open forests on such substrates that are invaded by bracken fern (*Pteridium* spp.) This fern becomes se-

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The Tropical/Subtropical Ecoregion: Main Lowland Biomes

Fig. 6. The main lowland biomes of the 4 tropical–subtropical zones that correspond to the climate diagrams in Fig. 5. These biomes occur on continents as well as on islands. They are more vulnerable to global change pressures on islands because island biomes are fragmented by intervening ocean and occupy only small land areas.

nescent in annual cycles, and thus can also become a rapid fire-carrying fuel on such extreme soil substrates.

According to Schüle's hypothesis, forests on oceanic islands should be more prone to fire than continental forests because large mammalian herbivores did not occur on oceanic islands. They evolved only with insect herbivores. These do not account for much removal of green biomass, perhaps only 10% per year (M. Lowman, Marie Selby Botanical Gardens, personal communication). Fire has indeed occurred in the Hawaiian Islands prior to human invasion (Mueller-Dombois and Lamoureux 1967, Burney et al. 1995), primarily in seasonal native upland tussock (*Deschampsia nubigena*) grassland or in mountain parklands with such native legume trees as koa (*Acacia koa*) and mamane (*Sophora chrysophylla*). The latter 2 species recover well after fires. However, it is unlikely that the evolution of the Hawaiian rain forest was conditioned by fire as proposed earlier by Vogl (1969). He believed the Hawaiian tree ferns (*Cibotium* spp.) to be a fire-adapted life form and considered the seemingly even-aged stand mosaic of the Hawaiian 'ohi'a lehua rain forest as caused by a long-interval fire cycle.

Because 'ohi'a lehua, the leading canopy species in the Hawaiian rain forest, cannot be aged due to an absence of annual growth rings, we cannot really speak of even-aged stands. However, stands are often even-structured. They represent in such cases generations of trees or cohort stands that developed after catastrophic disturbances such as volcanic explosions with ash blanket deposits, lava flows, or after hurricanes, also after fires and frequently after landslides on the older volcanic mountains and islands.

The phenomenon of stand-level canopy dieback in the Hawaiian rain forest has been the subject of intensive research during the 1970s and 1980s (Hodges et al. 1986, Mueller-Dombois 1986, 1992*b*, Jacobi 1993, Akashi and Mueller-Dombois 1995). The dieback has been identified as a stand-demographic, natural growth cycle, which begins with a major stand-level disturbance. This is followed by a regeneration wave of 'ohi'a lehua seedlings and saplings. These then form a generation stand or cohort stand. After a long period of vigorous growth (estimated to last at least 200 years) such cohort stands enter a post-mature, or senescing, life-stage. At this stage, such stands become predisposed to decline or canopy dieback. This can be triggered by a climatic instability such as a prolonged dry spell. Thus, the dieback causes are at least 2, a predisposing cause and a trigger cause. An additional third, or contributing cause, can be biotic agents that may hasten the dieback process, such as the endemic cerambycid beetle tree borer *Plagithmysus bilineatus,* or the indigenous root fungus *Phytophthora cinnamomi* (Papp et al. 1979).

Under such stand dieback conditions, there is certainly an accumulation of senescent tissue. But it comes down in stages: (1) an accumulation of litter from crown foliage, followed by (2) thin branches, and later (3) larger branches. The snags remain standing for a very long time (>50 years) in the upland rain forest, which, so far, lacks termites. Eventually, they also break down and add to the rotting wood and organic peat.

In the Hawaiian rain forest, young soils are described as histosols. As such, they may be considered to provide a fuel source for ground fires. But, notwithstanding Goldammer and Seibert's (1989) discovery of the burning coal-seams below the soil surface in some locations of the rain forest of Kalimantan, Borneo, fire in tropical rain forests is an unusual event. Instead, microbial decomposition is rapid and usually in balance with the litter fall and deposits of woody detritus.

In fact, the latter provides the substrates for forest regeneration (Santiago 2000). In the Hawaiian rain forest, we found that almost all woody plant species are preferentially established on rotting logs (Mueller-Dombois et al. 1981). After several stand generations, 'ohi'a lehua trees on older soils are often stilt-rooted. This growth form indicates that such stilt-rooted trees germinated on rotting logs or on tree fern trunks often 1–2 m above the mineral soil. Rain forest rejuvenation can be said to be based on the accumulation of decaying wood of pioneer forests.

However, upland rain forests throughout Oceania, where fragmented by landslides or other stand and

landscape-level disturbances, typically show open areas recovered with the mat-forming stoloniferous staghorn fern, *Dicranopteris linearis.* This fern, when senescing, presents a fire hazard. When ignited, fires can spread into surrounding rain forest, thereby favoring further invasion and spread of this fern and other heliophytes.

CONCLUSIONS

Both the island biogeography and ecological succession theories include biological invasion as natural processes. It is only through human interference with these natural processes that biological invasion has become a new disturbance of major consequences.

Fire, likewise, has always been a periodically recurring natural disturbance factor in all tropical–subtropical biomes that are subject to seasonal drought. This includes even the hyperseasonal savannas that are considered to have been caused by wet-season inundation (Mueller-Dombois 1981*a*). The only natural fire curbing, or even fire preventing factor, is the activity of large herbivores. Introduction of goats into islands, the classical form of human-induced biological invasion, certainly resulted in high entropy (i.e., loss of resilience) of certain island ecosystems, such as the ''goat island'' in the Juan Fernandez Archipelago or the coastal lowland zone in Hawai'i Volcanoes National Park (Mueller-Dombois and Fosberg 1998). Prior to goat removal during the early 1970s, this vegetation was reduced to a sparse annual grassland dominated by the pan-tropical lovegrass *Eragrostis tenella* (Mueller-Dombois 1981*b*). Fire was thereby excluded from this area.

Thus, the new type of biological invasion, i.e., the human-aggravated form, can lead to fire exclusion, such as when tropical forests are converted to pastures that are constantly grazed by introduced cattle. Conversely, it can lead to a new fire regime where none before existed.

As explained above, a rather complex example was the succession of invaders in the native seasonal woodland of Hawai'i Volcanoes National Park. The invasion of African C_4 grasses was followed by the invasion of firetree, whose seeds were distributed by alien birds. After about 20 years, a combination of drought and the invasion of an alien insect, resulted in firetree dieback in a large section of woodland. This complex invasion sequence then led to a super-high fire hazard.

The dry–wet seasonal climate can be considered the master factor for fire frequency in tropical–subtropical biomes of islands and continents. Increased variability of climate will further increase the fire hazard.

The relationship of biological invasion and fire depends on the type of invader. Grasses, heliophyte ferns, fire-tolerant shrubs, and trees, will heighten the fire hazard. Such tree invaders in the tropics include pines and eucalypts, the 2 favored plantation trees, but also *Melaleuca, Casuarina, Araucaria,* and other tree spe-

cies whose populations are conditioned to attract fire or can tolerate fire by surviving through subsequent reproduction. The latter include the typical island invaders in Oceania, such as strawberry guava (*Psidium cattleianum*), Christmas-berry tree (*Schinus terebinthifolius*), silk oak (*Grevillea robusta*), and koa haole (*Leucaena leucocephala*), to name a few.

The overall result of the human-aggravated invasion of fire-tolerant plant life forms will be a diminished and simplified biodiversity in natural areas. This trend, further accelerated by human-induced atmospheric changes and climate variability, will be more severe on islands than on continents. The main reason for this is a lesser capacity of island ecosystems to buffer such disturbances. This limited buffering capacity is related to the small area of island habitats and refugia as well as to their limited native biodiversity and population pools. Natural area management under these conditions is a formidable task. Managers must rely on the best scientific knowledge and be prepared for intelligent compromises.

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