PAPER 9

NOVEL TROPICAL FORESTS: THE NATURAL OUTCOME OF CLIMATE AND LAND COVER CHANGES

ARIEL E. LUGO[1]

[1]International Institute of Tropical Forestry, USDA Forest Service

ABSTRACT: The directional and irreversible change implied in climate and land cover change, modifies the ecological space of the biota and sets it in motion both ecologically and evolutionarily. The result of this change in conditions is the mixing and evolution of species, with consequences to species survival and community assembly. This paper proposes that the natural outcome of ecological end evolutionary changes induced by climate and land cover change is the formation of novel communities that will self-assemble, self-organize, and evolve in response to changing landscapes and prevailing environmental conditions. These communities and landscapes will be as or more diverse than current ones, function as those of today, but will be different in species composition, speed of ecological processes, and landscape structure. Understanding these future scenarios benefits from long-term, holistic, and comprehensive analyses. To solve conundrums, explain paradoxes, and minimize ecological surprises requires integrated consideration of species invasions, natural and anthropogenic disturbances, and ecological and evolutionary change. These events are responsible for sourcing, selecting, and maintaining genetic and ecological novelty in all environments, including urbanized landscapes.

Keywords: climate change, tropical forests, introduced species, novel communities, land cover change

> Previous work has failed to adequately take into account mechanisms of persistence.
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> Botkin et al., 2007, p 228

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> Botkin 2001, p 261[a]

1. Introduction

Recent climate change phenomena and anthropogenic activity involve and/or set in motion directional environmental change, as opposed to assumed cyclic changes in the pre-disturbance era, which modifies the ecological space under which organisms live and function. This directional change induces novel environmental conditions that the biota must adapt to or tolerate to assure survival. The simultaneous changes in biotic and abiotic settings complicate the interpretation of ecological phenomena because cannot predict with certainty

[a]For an alternative view see Lodge and Shrader-Frechette (2003)

the future conditions that the biota will face or the resulting biotic assemblages. However, it is safe to anticipate that continuing changes in environmental conditions will be the only constant for the future, even as the tropical conservation literature views change as generally detrimental to the future of tropical forests. I predict that the natural outcome of climate and land cover change in the tropics is the development of novel forest types within complex and diverse landscapes. I use land cover change as a surrogate for anthropogenic disturbances such as deforestation or urbanization. In support of my proposal I advocate a more holistic and balanced interpretation of the changes now taking place in the tropics and elsewhere on the planet.

To set the stage, I first examine several contemporary issues about tropical biodiversity that divide scientific opinion and prevent a consensus on the future outcome of climate and land cover change. Next, I highlight how current debates about the effects of climate change on biodiversity lead to the realization that we are entering a new era of conundrums, paradoxes, and ecological surprises. To better resolve these complex situations, it is necessary to understand the ecological consequences of disturbances, urbanization, and evolution, which I discuss sequentially. I end with a discussion of the natural outcomes of climate and land cover change.

2. Issues that Divide Scientific Consensus on Biodiversity

The common scenarios about the future of biodiversity in a world under the influence of climate and land cover change involve rampant species invasions, catastrophic levels of species extinction, homogenization of the biota, disruption of ecosystem services, and accelerated rates of tree turnover. How accurate are these predictions? I will discuss three of these in this section and address the other two later.

Tree Turnover in the Amazon

Tree data from long-term plots from throughout the Amazon basin reflect the following trends over a period of about 25 years (Phillips *et al.*, 2005):

- Trees $\geq$ 10 cm dbh recruit and die twice as fast on rich than on poor soils.
- Tree turnover rates have increased throughout the Amazon over the last two decades.
- Tree mortality and recruitment have increased in all regions except for mortality in eastern Amazonia.
- Tree recruitment rates have consistently exceeded tree mortality rates.
- Absolute increases in tree recruitment and mortality rates are greater in western Amazonia.

- Tree mortality appears to be lagging tree recruitment at regional scales.
- Tree biomass is increasing in these forests.

The question that these data raises is whether the observed patterns are, or are not, a reflection of global environmental change. Phillips *et al.* suggest that there are environmental change factors stimulating the growth and productivity of Amazon forests and thus the turnover rate of trees. Two such factors are the global increase in CO_2 concentration and increased nitrogen deposition. The authors might be correct in their suggestion for what these data mean, however, Chambers and Silver (2005) present a different point of view and raise important concerns regarding the mechanisms that would explain such environmental change effects. I believe there are five additional considerations that would limit how much these data can be used to show a global effect on these forests.

1. There is no established base pattern of stand development against which to evaluate these data. Before you can conclude that a temporal pattern represents an acceleration of normal stand dynamics, you need to have a base pattern for comparison. It is unfortunate that such a pattern is not known for Amazonian forests so that the changes over the past two decades can be compared against normal pre-climate change stand development. For Caribbean forests subjected to periodic hurricanes, stand development requires about 60 years and stages in patterns of structural development distinct in time can be detected, that is, period of rapid change (0 to 20 years), period of transition (20 to 45 years) and period of maturity (45 to 60 years). A similar pattern, but extending over 100 years, was documented for New England forests following timber harvesting (Bormann and Likens, 1981). During these distinct periods, mortality, recruitment, turnover, and biomass of trees change in magnitude and may even peak and change direction (Lugo *et al.*, 2000; Lugo, 2008). With long-term data, it is possible to evaluate future changes in stand development dynamics since frequency and intensity of hurricanes change. Is it possible that the tree data from the Amazon are reflecting normal rates of stand development along a temporal gradient that is unknown at this time?
2. The data set is too short. Obviously these data represent the longest record available to Phillips *et al.* (2005), but for forests that live for hundreds of years, 25 years is too short an interval to reach conclusions about long-term responses to subtle climatic change events (actually the mean length of plot monitoring was 10.1 yr). Are the study stands of the same age and stage of development? Do they all have the same history of disturbance?
3. The results appear to be normal values for the parameters being measured. For example, the corrected mean tree mortality rate (in percent per year) for various forest groupings in Phillips *et al.*'s Table 10.2 were 1.58, 1.91, 2.03, 2.59, 1.16,

1.27, 2.12, 2.55, 1.16, 1,41, 2.04, 2.86, 1.48, and 1.70. In a review of tropical forest tree mortality data, Lugo and Scatena (1996) found that normal background mortality for these forests averaged 1.6 percent per year with a few stands reaching 3 percent/yr. In Table 10.1 of Phillips *et al.* (2005), 5 (17 when measured rates are corrected) of 91 plots reach or exceed 3 percent per year turnover. Thus, the tree mortality results show no unusual levels that would lead you to believe there is an acceleration trend in the results.

4. The same is true of the tree biomass accumulation in Baker *et al.* (2005) who report a mean of 1.22 Mg/ha.yr for 59 sites. These values are lower than similar measurements in mature dry to wet forests in Puerto Rico (Lugo *et al.,* 2002), tropical forests in general (Figure 5 in Brown and Lugo, 1982), and world forests (Jordan, 1971). The values reported by Baker *et al.* (2005) reflect a normal carbon sink in mature tropical forests as predicted by Lugo and Brown (1986). Baker *et al.,* (2005) suggest their biomass accumulation values reflect a trend, when in fact they have a single rate determination for each plot. It is probably premature to predict trends from a single point in time but they base their suggestion on the tree turnover data of Phillips *et al.* (2005). However, there is no *a priori* ecological reasoning to expect a biomass accumulation trend in the same direction and in relation to a tree turnover trend. In fact, irrespective of forest stand dynamics, biomass accumulation in wood is similar worldwide (Jordan, 1971; Brown and Lugo, 1982) and Baker *et al.* (2005) have not shown that their results are different from the global average.
5. Only a few plots reflect the statistical trend reported for the combined number of plots, in fact, most plots show no trend at all through the period of measurement while some sites decrease in tree turnover (their Figure 10.2). Phillips *et al.* actually point this out, as their objective was not to analyze individual plots but to seek a landscape level pattern of change. Nevertheless, such a stance would be more convincing if a reasonable number of sites were actually showing an acceleration pattern of tree turnover. This leads you to wonder if the combination of plots used for the analysis reflected a difference in rates over a 20-year period not because of climate change but because the combined natural history of the plots lead them in a particular direction coincident with their particular histories of disturbance and development as suggested by Chambers and Silver (2005).

If these data were analyzed in the absence of a climate change debate, they would reflect a healthy and productive group of tropical forests behaving normally, growing, accumulating biomass, and showing regional differences, as do many other forests in the tropics and elsewhere. However, the authors are probably correct in the anticipation that biomass turnover rates would be

expected to increase should the disturbance regime change and cause more frequent disruption of ecosystem structure. I predicted such a change in a climate change scenario that would increase the frequency of hurricanes over the Caribbean (Lugo, 2000). However, my prediction was based on increased mechanical disruption of forests by hurricane winds. The explanation of how a fertilization effect by CO_2 or nitrogen deposition can increase the tree turnover rate or biomass turnover is less clear as discussed by Chambers and Silver (2005). As cautioned by Phillips and Malhi (2005), the complexity of tropical forests limits our ability to generalize from small scale or single species experiments to whole ecosystem levels.

Prediction of Species Extinctions

The scientific community is also divided in predictions about the level of species extinctions expected in the tropics due to anthropogenic activity. For example, in the process of forecasting the effects of global warming on biodiversity, Botkin *et al.* (2007) noted what they called the Quaternary Conundrum: "While current empirical and theoretical ecological results suggest that many species could be at risk from global warming, during the recent ice ages surprisingly few species became extinct" (p. 227).

Recently, an article by Wright and Muller Landau (2006) caused a debate about these predictions. Many arguments were raised in an effort to demonstrate that the predictions were too low (Laurence, 2006). In my view, the Wright and Muller Landau paper contains a verifiable analysis of the species extinction issue because the assumptions it makes are explicitly stated and the study is based on empirical data. The paper also recognizes the limitations of the analysis and the uncertainties of the issue, unlike previous estimates by Myers (1979, 1982, 1983), Lovejoy (1981), Ehrlich and Ehrlich (1981), and Simberloff (1986) who made predictions with fewer data and undisclosed methods and/or assumptions. Over 10 years ago, a glossy document from the Smithsonian suggested that in 10 years it would be too late to do anything about the species extinction crisis. The ten years passed and what we have is a new discussion of the issue as if the previous exaggerated predictions were never made. The problem is the adequacy of the methods used to predict species extinction rates, the difficulty of achieving scientific consensus, and the potential loss of credibility given the visibility of the alarming rates forecasted compared to the actual loss and available data.

In spite of the strength of the analysis of Wright and Muller Landau, their work continues to depend on the species/area curve to estimate species extinction

rates. Such a focus leaves out ecological considerations and real-world experience that would further reduce the estimate of the expected extinctions (Botkin *et al.,* 2007). The experience in Puerto Rico supports the assumptions of the model used by Wright and Muller Landau but not the predictions of the model.

The island of Puerto Rico, which lost 99 percent of its primary forests and 93 percent of its forest cover to agricultural activity, and has a high population density (>400 people/km^2) experienced much lower rates of species extinctions than predicted by the species/area method. Specifically, the extinction of species in Puerto Rico was no more than 10 percent of bird species, and 5 percent of plant species (Lugo, 1988). If anything, Puerto Rico shows that the species/area curve method for estimating species extinctions is not adequate for predictions because it ignores all the resilience mechanisms of nature that prevent massive species extinctions as a result of land use change and assumes that all species are lost when a parcel is deforested. The species/area method also ignores the role of humans in mitigating their effects (Lugo *et al.,* 1993; Lugo, 1997). In Puerto Rico, not only have native species been retained in higher-than-expected numbers, but also local species richness is now higher than at any known time because of an influx of new arrivals and their assembly in new plant communities (Lugo and Helmer, 2004) with higher species richness per unit area than the original forests (Lugo and Brandeis, 2005).

As the first quote at the beginning of this paper states, the problem with the predictions of extinctions of species is that we neglected aspects dealing with the persistence of species, focusing most of our attention on the negative aspects of the biodiversity equation. By doing so, we miss better than half of the biodiversity issue, which involves nature's response to anthropogenic activity and climate change and which contains the elements of potential solutions to the conservation issue. More balance is called for in the analysis of biodiversity issues. As we will see throughout this paper, the narrow focus on aspects of an issue rather than on its totality is a theme that repeats itself in many conservation issues. Sax and Gaines (2003) concluded that the loss of species at the global level exceeds the rate of species addition through evolution but evolution is responsible for species additions at rates faster than previously thought (below). Moreover, on islands worldwide, species invasions exceed species extinctions by a large margin, for example, doubling of plant species (Sax *et al.,* 2002). Therefore, while scientific attention is given to the implications of species loss, a greater challenge is to understand the implications of gains of species at local and regional scales.

Species Invasions

There is no debate about the pervasiveness of species invasions throughout the world and the biotic and abiotic change associated with such invasions. There is debate, however, on who is responsible for what when a species invades. Also, there is no question that when an introduced species becomes dominant in an ecosystem, rate processes, direction of succession, and interactions among populations change (examples in Gordon, 1998; Denslow and Hughes, 2004). However, there is debate on the implications of these changes to ecosystem function and the naturalness of the invasions (see second Botkin quote at the beginning of this paper). Moreover, the role of species invasions as causes of widespread extinctions is unproven, and evidence for supporting a general and primary role for invasive aliens in extinction remains limited (Gurevitch and Padilla, 2004). Vermeij (1996) called attention to evidence that led to the conclusion that invasions on oceanic islands and in lakes can cause extinction of species but rarely in the sea or on large landmasses. Nevertheless, Lodge and Shrader-Frechette (2003) believe there is no question of the fact that introduced species cause extinction of native species without consideration of the conditions under which the statement might apply. The three sources they use in support of their view provide no significant evidence that would lead one to believe their unqualified position (see Lugo and Brandeis, 2005). The assumption that introduced species are agents of change has been questioned experimentally (MacDougal and Turkington, 2005), who concluded invasive species were "passengers" of environmental change and noted that they have suppressive as well as facilitative effects on ecosystems (see also Didham *et al.*, 2005, 2007). However, there is strong evidence that under certain conditions introduced species change rates of ecosystem processes (such as productivity, nutrient cycling, biomass storage) (Vitousek *et al.*, 1987; Denslow and Hughes, 2004).

Mack *et al.* (2000) contains a more restrained assessment of biotic invasions, recognizing that not all invasive species are equally effective in the alteration of environmental conditions or in their effects on other species. Ricciardi and Cohen (2007) examined the literature and suggested that the term "invasive" should not be used to connote negative environmental impact. Paradoxically, invasive introduced species are proposed candidates to solve the energy crisis through biofuel biomass production (Raghu *et al.*, 2006). These plants have characteristics that make them successful invaders as well as excellent biomass producers. The same paradox applies to organisms introduced to control introduced organisms (Simberloff and Stiling, 1996), which essentially act to further homogenize ecosystems rather than maintain their differences.

Strayer *et al.* (2006) noted that the effects of invasive species such as evolution, shifts in species composition, accumulation of materials, and interactions with abiotic variables, all change over time when they can increase, decrease, or qualitatively change the impact of an invader through time. They thus require long-term study. However, most studies of species invasions are brief and they found that 40 percent of recent studies did not even state the time that had passed since the invasion. The short-term study of long-term phenomena is an important obstacle to scientific understanding and consensus on critical conservation issues. There is a need to focus research on a comprehensive and systematic approach to invasion biology (Vermeij, 1996).

A result of inadequate research on species invasions is the ease with which the invading species are held accountable for changes that those species had no part in promoting. Two examples illustrate the point. Amphibian decline in western North America was related to habitat changes that promoted the invasion of introduced species (*Rana catesbeiana*), but it was the habitat change (more permanent vs. ephemeral wetlands) that caused the decline in the native species (*Rana aurora*) and not the invasive species (Adams, 1999). Case (1996) reviewed the global bird literature and his analysis showed that: "Beginning in aboriginal times, the conversion of native habitats, particularly at lower elevations, to disturbed habitats simultaneously enhanced the success and persistence of introduced species, while decreasing population sizes and increasing extinction rates of native species. Thus habitat conversion and deterioration alone could produce a correlation between the number of extinct natives and the number of introduced species even without any direct cause or effect between birds in these two groups" (p. 85).

By not assessing the ecological situation properly, a "shoot first, ask questions later" approach to control of introduced species develops, but such an approach may have unintended ecological consequences as happened for decades in agricultural systems that used the same approach to control agricultural pests (Smith *et al.,* 2006). It turns out that indiscriminate eradication of weeds has negative as well as positive effects on crops and that through management, instead of eradication, crop production, as well as agroecosystem functioning, can be optimized. Zavaleta *et al.* (2001) suggested that because of the unforeseen aspects of invasive species removal, such activities should be coupled to ecosystem restoration goals and accompanied with sufficient monitoring to assure that the desired results are attained.

3. The Debate Turns Subjective

Laurance (2006) suggested that because results such as those in Wright and Muller Landau (2006) could be misused by sectors of society, scientists should be careful with what they conclude. Lewis *et al*. (2006), in response to Wright (2005) when he questioned the tree turnover data discussed above, suggested that Wright's approach "sends a worryingly ambivalent message about the future of tropical forests to students, scientists, policy makers and civil society as a whole" (p 174). Both of the arguments above are inappropriate in a scientific debate and deny the role of independent science in informing policy. The critiques aim to limit scientific freedom or at least force it to serve a particular point of view (advocacy science). The comments also ignore that scientific progress is made by falsifying assumptions and cannot be limited by fear of what others will do with the new information. In an essay entitled "What is wrong with exotic species?" Sagoff (1999) argued against ecology becoming a normative science, and pointed out the pitfalls of such an approach. Moreover, conservation is best served by scientific discovery and well-documented analysis.

In short, the lack of consensus on biodiversity conservation issues is partly due to lack of information, to the absence of a balanced approach, and the subjectivity of some arguments, which on the whole lead to a failure to address and resolve conundrums, paradoxes, and ecological surprises.

4. The Biotic Age of Conundrums, Paradoxes, and Ecological Surprises

Changes in the ecological space of organisms set them in motion both in ecological and evolutionary terms (below). Because the level of environmental change due to human activity is so pervasive at all scales of biotic organization (from cells to global), the magnitude of biotic response is also dramatic and unprecedented. The initial reaction of reasonable observers to this new level of biotic change is to consider all changes as detrimental to the established biotic order. Over time however, evidence accumulates to suggest that the observed changes in the biota are neither negative nor positive. Instead, they are adaptive. Carroll and Dingle (1996) postulated "...that invaders most likely to integrate successfully are those on which high levels of additive genetic variation are expressed in traits most likely to be adaptive in the new environment" (p 207).

The accumulation of examples of novel biotic interactions and species assemblages will be best described as paradoxes or ecological surprises (many

leading to conundrums) for as long as biotic change to negative consequences. This is particularly plausible because for the past 100 years the study of biota from the point of view of a balanced system with predictable environmental conditions. Against that backdrop, the biotic turmoil induced by intense anthropogenic activity and directional climate change certainly appears paradoxical. I now present a few illustrative examples from different parts of the world.

A conundrum faced by the readers of the scientific literature is that on the one hand, introduced species can be held responsible for enormous changes in the environment and cost the human economy billions of dollars. On the other hand, introduced species are a natural component of the response of the biota to the massive changes taking place in the environment and they help sustain environmental services through periods of environmental turmoil. The economic cost of introduced species is greatest in agricultural systems and other intensively managed systems where a change in the biota represents potential losses or gains of money (Westbrooks, 1998). Ecologically, the same critical situation occurs in isolated oceanic islands such as the Hawaiian or Galapagos islands, where the native biota is recognized for its endemism and biotic value or perhaps in stream channels or other similarly confined environments such as lakes, where an unchecked introduced species can create ecological havoc with native species. These well-understood situations, and others that I don't mention, require dedicated management to assure the survival of the natural biotic values involved. However, in most of the landscape where the vastness of the scale constrains what can realistically be accomplished by management, it behooves ecologists to understand the processes at play before promoting expensive and many times unrealistic solutions for the suppression of change, particularly if it turns out that the species invasions are adaptive to new climatic and environmental conditions.

Fridley *et al.* (2007) described the invasion paradox based on observations at small scales (< 10 m^2) of a negative relation between the number of native species and the number of species or success of introduced species. However, at larger scales (> 1 km^2) there is a positive relationship between the number of native species and the number of introduced species. This paradox cannot be explained by a single theory, as it requires the consideration of as many as eight processes, or a pluralistic framework to explain the observed relationships.

The inbreeding paradox raises the question of how invaders of new territories with low numbers (inbreeding) become successful invaders. Pérez *et al.* (2006)

proposed new possibilities for explaining the paradox such as epigenetic adaptations (inheritable modification of gene function without changes in the base sequences of DNA) and adaptive (non-random) mutations, two types of genetic response that suggest that evolution might be hastened under stress. Roman and Darling (2007) resolved the paradox for aquatic plants through the effect of numerous introductions, which promote range expansion through genetic and demographic mechanisms. Other solutions to this paradox are described later.

If local adaptation is common and important, then why are introduced species so successful at outcompeting and replacing native species? This paradox has many explanations. Allendorf and Lundquist (2003) suggested that a lag time after the invasion was necessary for the invading species to develop adaptations to the novel habitat. Alternatively, if the novel habitat is also new to the native species, the competition between the invasive and the native takes place under conditions where either species could gain "a home" advantage. In this case, the outcome depends on a species' capacity to deal with the novel environment. In the long-term, large and infrequent disturbances (LIDS *sensu* Dale *et al.*, 1998) determine which species attain permanence on sites, as the LID might require a particular set of adaptations such as tolerance to wind, drought, fire, flood, etc. Thus, there is a short-term/long-term aspect to the success of invasions (Lugo, 2004b).

The literature is becoming replete with reports of new mutualistic relationships between native and introduced species as well as between introduced species. For example:

- In Hawaii, introduced birds have replaced the native seed-dispersing avian species because nearly all the native seed-dispersing species have been lost. These introduced frugivore birds disperse both native and introduced plant species and they contribute to the regeneration of native plants in the understory of forests dominated by introduced trees (Foster and Robinson, 2007). In their study, Foster and Robinson found that of the total seed dispersal work by introduced birds, 85 percent were native plant species. Most Hawaiian understory plants depend on introduced bird species for their dispersal.
- The introduced black spiny-tailed iguana (*Ctenosaura similis*), native to Mexico, and the introduced Brazilian pepper (*Schinus terebinthifolius*) established a mutualism in south Florida (Jackson and Jackson, 2007). Another example is the importance of the introduced Chinese privet (*Ligustrum sinense*) for sustaining the white tailed deer (*Odocoileus virginianus*) in the Fall and Winter in southeastern United States (Stromayer *et al.*, 1998).

- Gutiérrez *et al.* (2007) describes the conundrum of the spotted (*Strix occidentalis*) and barred (*S. varia*) owls where a native replaces another native perhaps mediated by natural or anthropogenic factors.
- The urban fire ant paradox involves native fire ants (*Solenopsis geminata*), which persist in an urban refuge, while invasive fire ants (*S. invicta*) dominate natural habitats (Plowes *et al.*, 2007). Old residential areas with low landscape disturbance in Austin, Texas, provided refuge to the native fire ant inside the city.
- Apparent competition (Meiners, 2007). The presence of an introduced shrub that shares seed predators with native trees increases predation of native tree seeds and reduces its regeneration.
- Facilitated pollination (Bjerknes *et al.*, 2007). Invasion by introduced plant species do not necessarily reduce pollination success in native plant species. Instead they may facilitate pollination by increasing the density of pollinators. The fact is that the interaction is complex, and requires longer and broader types of studies to unravel the outcome of the interaction.
- The germination requirements for the annual plant *Cardamine hirsuta* were different in its native range (Europe) than in Japan, where it was introduced and naturalized (Kudoh *et al.*, 2007). This shows that not all populations or strains of a species are equally invasive and that adaptive change is sometimes required for an invasive species to be successful in the new environment.
- Ashton *et al.* (2005) found that in mixed deciduous forests in Long Island, New York, the rate of litter decomposition and N release was accelerated both by invasive species relative to native ones and in invaded sites relative to sites not invaded.
- Forys and Allen (1999) were unable to anticipate the expected changes in vertebrate fauna in south Florida using current organisms, body mass data, species distribution and niche classification. Although it is clear that the fauna of the future will be different from that of today, it was impossible to anticipate the nature of the future fauna given the profound ecosystem changes taking place.
- The stoichiometry of a floodplain in New Zealand was affected by the phosphorus accumulation due to early dominance of an introduced shrub (*Buddleja davidii*), but this dominance was short-lived as the native shrub (*Coriaria arborea*) dominated the later stages of succession (Bellingham *et al.*, 2005). There was no immediate impact on forest species composition.

The few examples listed above show that the mixing of species now in progress worldwide involves much more than plant and animal species sharing geographic

or ecological space. Instead, the newly mixed biota is reacting, changing, interacting, adjusting, and adapting to the new biotic and abiotic conditions (more on this below). This results in the assembly of novel communities with novel species to species and species to environment relationships that surprise many or appear paradoxical in the context of a non-changing world. Moyle and Light (1996) assumed the *Frankenstein Effect* as a firm rule for anticipating the community assembly rules due to species invasions: "New invasions are likely to have unexpected consequences" (p. 159).

Botkin (2001) summarized this new circumstance by describing a new conundrum. He stated that "one can either preserve a "natural" condition or one can preserve natural processes, but not both" (p. 261). This is so because the preservation of natural processes requires change in environmental conditions and the biota. By focusing on a particular natural condition, Botkin says, one would have to stop environmental and biotic change at a great cost to humans. This conundrum is at the crux of the issue facing us in the world of climate and land cover change. These two processes of environmental change appear irreversible and it is very difficult, if not impossible, to reverse them.

5. The Role of Disturbances

One of the most important advances in modern ecology is establishing how natural and anthropogenic disturbances influence ecosystem composition, structuring, and functioning. Because disturbances alter conditions in forests, they set in motion responses that last for a long time, well after the event, as will be shown below. Ecologists have made significant advances in understanding the role of natural disturbances on ecosystems and are now focusing attention on anthropogenic disturbances, which appear to have novel effects on the composition, structuring, and functioning of ecosystems. In this section I review literature that shows how anthropogenic disturbances determine the species composition of forests. This is a particularly important subject for our understanding of how forests might respond to climate and land cover change and it also integrates a large literature on invasion biology into the debate of the future of biodiversity in the tropics.

Many studies show that land use has a long-lasting influence on the species composition of forests established on deforested lands (for example, Foster and Aber, 2004; Balée and Erickson, 2006). In Puerto Rico, Thompson *et al.* (2002) found that land cover in 1936 influenced the contemporary forest species composition in spite of decades of forest succession and numerous passages of storms and hurricanes over the site. In France, Dambrine *et al.* (2007) showed

that the effect of land use remains on the landscape over millennia after abandonment. Species richness patterns follow soil alteration and human activity some 1500 years ago, and they believe part of the explanation is the human effect on the biogeochemistry of sites. Dupouey *et al.* (2002) observed that species richness and plant communities vary according to the intensity of former agriculture. These variations are linked to long-term changes of chemical and structural properties of soils. The effects are historically irreversible. Vellend *et al.* (2007a) found legacies of human land use on species composition of forests in North America and Europe that last for centuries. Cramer and Hobbs (2007) assembled examples from throughout the world that show the long-term legacy of vegetation change after abandonment of agricultural activity.

Aplet *et al.* (1998) used a chronosequence approach on the lava flows of Mauna Loa, Hawaii, to study primary succession of vegetation on wet and dry sites along precipitation, substrate texture, time, and temperature gradients. Of the 124 species they encountered, 27 species were introduced and they mostly occurred on lowland dry sites. Although introduced species were found in 27 of 42 sites, their dominance in terms of biomass contribution (> 20 percent of the total biomass) was significant in eight sites. They also found that the presence of introduced species reflected past disturbances rather than primary succession. Repeated burning on dry sites appears to facilitate the presence of introduced grasses such as *Pennisetum setaceum*. Otherwise, the primary succession gradient was dominated by native species. Disturbance mediation is apparently required for the invasion and dominance of introduced species in Hawaii.

This was also the result of an analysis of the 180-year history of *Syzygium jambos* in the Luquillo Experimental Forest (Brown *et al.*, 2006). This tree was most abundant in locations that had been deforested or heavily impacted by human activity. However, its density in mature or primary forests was very low (Brown *et al.*, 2006; Thompson *et al.*, 2007). The tree has remained dominant on previously altered riparian areas, where it forms a novel forest type *sensu* Lugo and Helmer (2004).

The synergy between habitat fragmentation, grazing, and species invasions explains resulting communities with better insight than by classic fragment area approaches (Hobbs, 1991). Laurance and Williamson (2001) described a synergy or positive feedback between forest fragmentation, drought, and climate change in the Amazon. This feedback involved fire disturbances, deforestation, and logging as forcing functions that accelerated forest response to climate change. Hobbs and Mooney (1998) argued and provided illustrative examples showing

that the effects of humans on biodiversity was much more than implied by the extinction of species debate. In fact humans add more species to landscapes than become extinct (Hobbs, 2001), but they also cause the local extinction of populations, reduce species ranges, greatly modify the habitats, promote species invasions, and thus the structure, functioning, and species composition of ecosystems. Hobbs (1991) examined the circumstances that favored the invasion of the most serious environmental weeds in Australia. In all cases, weed invasion was enhanced by anthropogenic disturbance. While all disturbances do not lead to invasions, invasions increased if the disturbance increased the availability of limiting resources and propagules were available. Natural disturbances maintained native species, but anthropogenic disturbances added new conditions to the disturbance regime that favored the invasion of introduced species. Combinations of disturbances act synergistically and make invasions more certain.

Simulation models for New England forests underscore the importance of disturbance to the outcomes of climate change or introduction of species scenarios (Loehle, 2003). Without disturbance, but a reduction in growth rate due to climate change, shade tolerant species or species with long life spans persist longer than light-adapted or short life span species. This slows down the invasion by introduced species. Disturbance events speed up displacement of species by allowing quicker turnover of species, thus facilitating the dominance of introduced species.

Corbin and D'Antonio (2004) found that unless land use, climate, or both changed, the conversion of native perennial grasses to annual introduced grasses was unlikely to occur by simply introducing propagules of the invasive grasses. However, if land use or climate or both changed, then propagules of introduced annual species have a greater opportunity to become established and slowly replace native perennial species in a California coastal prairie. After Hurricane Hugo in Puerto Rico, Chinea Rivera (1992) found that as the native forest recovered, the only sites available for regeneration of the introduced *Albizia procera* were roadsides and other anthropogenic-impacted areas.

The above Puerto Rican and Australian examples focused on the influence on species composition of disturbances. The Hawaii examples illustrated that introduced species gain a foothold because of anthropogenic disturbances, a principle confirmed through experiments in California (Corbin and D'Antonio, 2004), modeling in New England (Loehle, 2003), and experience in Australia and Puerto Rico. The effects of anthropogenic activity on species composition

persist for a long time, perhaps influenced by the high level of synergy that occurs between natural and anthropogenic disturbances and the novel environments they create. However, not all anthropogenic disturbances have the same effects on ecosystems. Molina Colón and Lugo (2006) found that those disturbances that opened the forest canopy but left the soil intact had milder effects on subsequent forest succession than disturbances that both opened the canopy and altered soil conditions. Similarly, some anthropogenic disturbances associated with climate change such as increasing temperatures and CO_2 concentrations affect ecosystems physiologically, which involves a different set of ecosystem response mechanisms than those associated with agricultural activities. Urbanization is a general term for many types of anthropogenic activities that involve an equally diverse range of disturbance types. These vary from total conversion and replacement of forests to ecophysiological disturbances such as air or soil pollution. As we will see next, ecosystem responses to urbanization are also diverse.

6. The Role of Urbanization

Of all anthropogenic disturbances none is more dramatic than the urbanization process. This process transforms the land to a greater level than agricultural activity and it is a process whose intensity is on the rise, given the global movement of people to urban settings. Because of the increasing rate of expansion of cities, urbanization is believed to be one of the leading causes of species extinctions, as natural populations become fragmented, habitats are converted to other uses or degraded, and the biota is extirpated or homogenized (McKinney, 2006). Cities also contain new environments to which many native organisms are not adapted to colonize. Some of these environments are usually colonized by introduced species (Kühn and Klotz, 2006).

McKinney (2006) suggested that urbanization was a major cause of biotic homogenization. Cities homogenize the physical environment, are maintained for centuries under conditions different from the natural ones surrounding them, and they promote the same kinds of species adapted to city conditions. Thus, the expansion of cities promotes the expansion in numbers and area of these same kinds of species. Cities also can act as refugia for plant species that then expand their ranges into rural areas (Kühn and Klutz, 2006). As there are local disturbance gradients within cities, these induce gradients of homogenization from the core, where the global homogenizers are found, to the suburban and urban fringe where native species occur (McKinney, 2006). Paradoxically, the species richness of cities is higher than that of natural systems in the vicinity (McKinney, 2006; Kühn and Klotz, 2006).

Issues of comparability (area sampled, taxa included, life zone conditions included) and availability of data complicate the comparison of species richness or similarity data such that the predictions of homogenization do not always lead to the same conclusion. On a regional scale in Germany, urbanization is not unequivocally related to homogenization (Kühn and Klotz, 2006). Native species and introduced species before 1500 show signs of homogenization due to urbanization but all species and those species introduced after 1500 do not show a homogenization effect. McKinney (2006) found that introduced species have lower similarity among cities than native species, suggesting differentiation of the introduced flora instead of homogenizing it.The Jaccard Similarity Index is used to demonstrate homogenization among cities (McKinney, 2006). Generally, the index shows more similarity among cities than among natural areas. However, the pattern applies to cities such as New York, Boston, Philadelphia, Minneapolis, Washington DC, Detroit, and Saint Louis in similar latitudes and life zones *sensu* Holdridge (1967) compared with natural areas that span into western United States, where the life zones are considerably different (Lugo *et al.,* 1999). The Jaccard Similarity Index compares the species composition of different floras and indicates how similar the floras are based on the number of species they have in common. However, the Index does not include the relative quantitative presence of the species (Mueller Dombois and Ellenberg, 1974). The Jaccard Similarity Index weights all species equally and ignores the effects that the mixing of species has on the structuring and functioning of ecosystems. Two floras could be very similar floristically and, thus assumed to be homogenized, but they might not be similar ecologically because the distribution of species within each flora assembles into different types of communities.

There is no argument that a homogenized environment, be it in a city or under natural conditions, leads to a few species and high species dominance. And there is no argument that some species associated with human dwellings have global distributions and can occur in most cities or that the world is experiencing a loss of endemic taxa. Olden *et al.* (2004) discussed the ecological and evolutionary effects of homogenization, and like others raised important consequences of the process to displaced and vulnerable organisms. However, all their analysis is focused on the assumption of extinction and that the ecological and evolutionary change would lead to reductions in diversity. They do not consider the other side of the equation, namely the possibility of evolutionary and ecological change within the urbanized area that would lead to genetic diversity and ecological novelty in light of new environmental conditions. Cities are not globally homogeneous in their biota, as anyone who travels across latitudes or across life zones, instead of within latitudes or life zones, can attest. The San Juan Metropolitan Area has a flora much different from that of

Washington DC. The point is that cities do have an ecological cost as they displace natural ecosystems and local populations but they also diversify the landscape, are collectively diverse, and contribute to the formation of novel communities.

7. The Role of Evolution

The modern biological invasion is an unprecedented form of global change (Ricciardi, 2007). This is so in terms of temporal and spatial scales, novel species combinations, novel evolutionary pressures, and potential evolutionary consequences. Ecological and evolutionary insights can be gained from the study of species invasions (Sax *et al.,* 2007; Yoshida *et al.,* 2007). Vellend *et al.* (2007b) pointed out that invasions have positive values in terms of promoting evolutionary diversification such as establishing allopatric populations in new environments, altered ecological opportunities for native species, and new opportunities for hybridization between previously allopatric taxa. Cryptic species invasions, phenotypic plasticity, general-purpose genotype, non-additive genetic variation, hybridization, introgression, polyploidy, and trait genetic variation are examples of the evolutionary considerations with implications to invasion ecology (Yoshida *et al.,* 2007). Of these evolutionary events, introgression or genetic "swamping" is the focus of conservation concerns because of its negative consequences to the genetic purity of endemic and endangered species (Cox, 2004). This is a legitimate concern, but only one aspect of the evolutionary changes in progress today.

Hoffmeister *et al.* (2005) recognized the importance of evolutionary change as a result of the combined effects of species invasions, habitat fragmentation, and isolation. They argued that both ecological and evolutionary change require consideration if we are to understand the full effects of environmental change. Lambrinos (2004) showed with examples that invasion dynamics can be influenced by the interaction of ecological and evolutionary processes acting over similar time scales and at any stage of the invasion process (his Figure 1). Parker *et al.* (2003) recognized and discussed the relevance of evolutionary biology to the study and control of invasions.

Interspecific hybridization between a native and introduced species following plant invasions may sometimes lead to the rapid evolution of new plant taxa (Abbott, 1992). In Germany, 134 hybrids between 109 native and 81 introduced species have been anticipated, although 75 have been found (Bleeker *et al.,* 2007). Thirty-seven threatened native plant species hybridize with introduced

species, of which 17 may suffer outbreeding depression when hybridizing with a more common introduced species. Introgression of alien genes may affect 8 of these threatened species. In the case of *Fallopia japonica*, a highly invasive species that was introduced in the 19th century to Europe, Bailey *et al.* (2007) documented how a single female plant that greatly spread by vegetative means, overcame its lack of genetic variability through hybridization and polyploidy. Some of the hybrids possessed novel genotypes with higher fitness than parents. These plants can switch from clonal dispersal to a home-produced hybrid and backcrosses, honed by natural selection that fits the particular ecological niches in which they happen to find themselves.

Dacus tryoni, the Queensland fruit fly dramatically increased its range over a hundred years not because there were more resources to support the expansion but because it overcame a physiological limitation to extreme temperature. Through adaptation by the mechanism of hybridization and introgression of genes from other fruit flies, the species acquired this physiological capability. Hybridization is an effective mechanism towards rapid evolution of organisms (Lewontin and Birch, 1966).

Invasions represent a novel selection process (Carroll, 2007). Contemporary evolution in response to anthropogenic change appears increasingly common. Native phytophagous insects in North America and Australia evolved substantially after colonizing introduced hosts. Evolving natives and introduced species may reconfigure contemporary and future communities. Adaptive evolution may also enhance native communities' capacity to control invasive populations. In support, Carroll gives examples of evolution in native prey to invasive predators in a few generations. Maron *et al.* (2004) conducted experiments with *Hypericum perforatum* (St. John's wort) to test the relative effects of contemporary evolution, phenotypic plasticity, and founder effects in affecting phenotypic variation among introduced plants. Multiple introductions add considerable genetic variation to the invading populations. Some genotypes were pre-adapted to conditions faced in the new range. Some genotypes were not, and these are the ones evolving to the new conditions they are facing. The rate is fast, as the plant has only undergone 12 to 15 generations over 150 years. The results suggest that introduced plants are evolving adaptations to broad-scale environmental conditions in their introduced range.

In short, evolutionary change is at play in novel environments created by anthropogenic activity. Much of this change appears critical to the maintenance of species and communities in rapidly changing conditions. When the genome

of species keeps pace with environmental change, the likelihood of maintaining environmental services in novel environments is enhanced.

8. Novel Tropical Forests and Diverse Landscapes

At the outset I advocated a more holistic and balanced interpretation of the changes now taking place in the tropics and elsewhere on the planet and highlighted the problems with an excessive focus on the negative aspects of the effects of environmental change on biodiversity. To avoid the pitfalls of negativism (see the exchange between Orr, 2007; Nugent, 2007; and Knight, 2007), a holistic approach on biodiversity will:

- Focus research on the long-term behavior of complex tropical forests and the synergy within and between ecosystems and external disturbance forces;
- Be transparent in the analysis by stating assumptions;
- Focus on both the resilience, including the adaptability, and vulnerabilities of the biota;
- Distinguish between short and long-term system responses;
- Recognize the emerging system properties with changing levels of biotic organization, that is, the whole is greater than the sum of the parts;
- Practice inter- and trans-disciplinary approaches to the analysis of complex socioecologic problems; and
- Focus on all species and all environments.

Given the magnitude of anthropogenic activity on the world and the consequences of this activity, the biota is on the move, both ecologically and evolutionarily, as it has done over millennia as conditions on Earth change (Behrensmeyer *et al.,* 1992). Rich and Woodruff (1996) describe large-scale temporal changes in the vascular flora of England (1930 to 1988) that reflect changes in land use and human activity (that is, loss of species in converted habitats and gains of introduced species throughout). What will the eventual outcome of this large-scale biotic change be?

Allan (1936) argued that introduced and native plant species in New Zealand co-existed in different types of plant assemblages characterized by different levels of human intervention. Egler (1942) agreed from the point of view of Hawaii vegetation and underscored that the issue is to "...consider the ecological status of each species of the available flora, quite independently of whether the species has been introduced during recent years or arose there by evolution from pre-existing forms" (p. 15). Hatheway (1952) confirmed Egler's observations and both recognized the role of the introduced tree *Leucaena glauca* as a nurse crop for native vegetation.

Future scenarios under the influence of climate change have been described as "new species, new biotic communities, new ecosystems" p. 271 (Cox, 2004). Moreover, he explains that given climate and land cover change the question of what species are truly alien becomes nebulous because the range expansion within continental areas by many species involves hundreds of kilometers. The ecological and evolutionary adjustments by both introduced and native species mean that maintaining or restoring the original community composition of many areas is impossible, thus providing a clue to the solution of the conundrum of Botkin (2001, p. 261).

Clearly the tactics for the conservation of biodiversity need to account for new species combinations in small fragments of fragmented landscapes as argued by Kellman (1996). In addition to addressing the specialization aspect of species, more attention is needed on the ecological flexibility of species. In these new combinations of species never seen before, species will have to perform roles that may appear unnatural in a continuum of communities, but not in fragments. The number of small and different fragments is bound to increase in the future and they offer new scientific challenges.

Williams and Jackson (2007) discussed the concept of no-analogous communities and novel climates to refer to communities that are compositionally unlike those of today, but which occurred frequently in the past and will develop in the greenhouse world of the future. A no-analog community "consists of species that are extant today, but in combinations not found at present" (p. 477). Williams and Jackson assumed that species will move along gradients of ecological space in accordance to their tolerance and adaptations, because the species niche might only be partially described by modern climate. They were referring to climates that in modeling exercises appear in 2100 in tropical and subtropical regions. They see these climates as warmer than any present climate and see them globally with spatial variable shifts in precipitation and increased risk of species reshuffling into no-analog communities and ecological surprises.

The analysis of Sax *et al.* (2007) suggests that the notion of species migrating geographically in response to climate migration assumes that today's species distributions in relation to climate variability will enable predictions of future distributions. Consult Iverson *et al.* (1999) for an Atlas of how tree species distributions will change due to climate change in northeastern United States. However, assuming that today's species distributions enable predictions of tomorrow's species distributions might not always be true. Species with small native ranges but large naturalized distributions and species with large native ranges, but growing in naturalized ranges outside their predicted climate

envelope, do not fit the models as they cause a climate envelop mismatch. What this means is that the experience with introduced species appears to change the rules of the game. Moreover, it is possible that the predictions for the next century of species movement in climatic space based on modeling exercises are already in progress in the world. These actual species movements are greatly accelerated by the movement of introduced species by anthropogenic vectors and the acceleration of novel climate formation by human activity.

Well before Williams and Jackson (2007), Allan (1936) recognized the formation of novel plant communities with combinations of introduced and native species. Also, Lugo and Helmer (2004) had already proposed the identical definition of no-analog communities when they described the new forests of Puerto Rico, whose parameters of anthropogenic activity place the island well into the Homogeocene (Lugo, 2004a). Similarly, Hobbs *et al.* (2006) used the same definition and provided examples from all over the world to illustrate the emergence of novel communities in response to the anthropogenic alteration of the biotic and abiotic environment. Thus, there is increasing support for recognizing the formation of novel communities in response to climate and land cover change. The process is already well underway in regions with heavy anthropogenic activity, which leaves three questions to complete the description of the potential outcome of climate and land cover change in the tropics.

1. **How will the novel communities develop?** The novel communities will self-assemble, self-organize, and evolve in response to prevailing environmental conditions. Self-organization is called upon to explain the non-random distribution of earthworms under novel environments (Barot *et al.,* 2007) and to explain the emergence of the novel communities and ecosystems (Odum, 1988). Egler (1942) described self-organization, but did not use these words when describing the emerging novel communities of Hawaii: "Out of chaos emerges a new order, and plant succession…, though novel, is beautifully orderly and comprehensible" (p 17).

   Because we are dealing with living entities, the introduction of species to the environment activates a plethora of biotic responses in the short- medium- and long-term both in the introduced species as in the species already in location. The induced responses also involve different sectors of the ecosystem as has been shown by Bohlen (2000) who observed that changes aboveground as a result of the introduction of species have effects on belowground processes and species composition as well, including belowground invasions. The fungal dimension of biological invasions also

changes as a result of changes in the aboveground component of ecosystems (Desprez Loustau *et al.*, 2007).

The theory and experience of naturalists, ecologists, and evolutionary biologists clearly show that for as long as the biota has been scientifically observed natural, systems never remain still in space or time. The biota is forever adjusting to change and adapting to the ever-dynamic physical environment. There is no reason to expect this natural history to be suspended with the emergence of intense human activity. On the contrary, both the evolutionary and ecological literature briefly reviewed here shows that the adjustments of the biota in the face of climate and land cover change have accelerated, just as the extinction rates have also accelerated.

2. **How diverse will the novel forests and landscapes be?** The novel forest and the landscapes will be as diverse as the current forests and landscapes. The main difference will be the species composition and the relative importance of species in communities. The accelerated responses of the biota to human activity do not appear to lead to a homogenized world *sensu* McKinney and Lockwood (1999) because the resulting environments are not as pervasively homogeneous as anticipated. For example, Case (1996) found that the gain in the number of introduced bird species in the world was close to the number of bird species lost to extinction and the resulting new assemblages of bird populations were as diverse as before. Humans may in fact be increasing the diversity of environments in the world by introducing novel environments that the biota had not experienced before. And the human element is also active in the conservation and preservation of familiar natural environments and wilderness because it values such environments.

3. **Will we lose environmental services?** No. Ecological functioning is resilient and is maintained even as species composition changes, particularly if the novel community is adapted to prevailing environmental conditions. Energy, water, nutrients, and organisms will flow, cycle, and/or turnover in response to community development, environmental conditions, and disturbances. Rates can be faster, slower, or the same as those of previous communities as those rates respond to environmental conditions and available resources.

In summary, the literature reviewed here suggests that ecological and evolutionary processes will continue to play important roles in all environments, including anthropogenic-dominated environments. These changing environments will support novel ecosystems with different species assemblages than today but familiar functional attributes. Reviews of studies of ecological functioning of

novel forests do not yield abnormalities in terms of primary productivity and nutrient cycling processes (Lugo, 1992; Silver *et al.*, 1996, 2004; Lugo and Helmer, 2004). In the last analysis, the equation that determines the future of tropical forests will hinge on an allocation of space for humans and wilderness. How much space will people allow for tropical forests and tropical wilderness where the forces of natural selection and self-organization can play out? Such a division of space will also change over time as it has in the past and as the proportion of space changes, so will the composition of the biota.

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