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Opinion Article

Novel tropical forests: Nature's response to global change

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Abstract
We now live in a world dominated by humans (the Anthropocene), whose activities on Earth are resulting in new habitats and new environmental conditions, including climate change. To many, the Anthropocene is an era of environmental doom that unless reversed, will result in catastrophic reductions in biodiversity. An alternate view is that the biota will adjust to the new environmental conditions and through processes of species mixing and self-organization will form sustainable novel communities of organisms. Using examples from Puerto Rico, I discuss the conditions that lead to novel forest formation and the characteristics of these forests, including their species composition. Novel forests include native tree and animal species as well as significant numbers of introduced and naturalized species. These introduced species dominate forest stands, and their dominance is not incompatible with the regeneration of native species. I propose that these types of ecosystems might represent the natural response of the biota to the Anthropocene.

Keywords: Puerto Rico, introduced species, tropical succession, Anthropocene, Homogeocene

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"It's tough to make predictions, especially about the future."
Attributed to Yogi Berra

Introduction

Tropical biologists have had a hard time predicting the future of tropical forests. Such predictions usually focus on worst-case scenarios such as the Goodland and Irwin [1] mixed metaphor: "Amazon jungle: from green hell to red desert." Similarly, the first effort for an integrated focus on tropical ecosystem studies had in its title the assumption of "fragile ecosystems" [2]. In fact, the list of myths associated with tropical forests is long and continues to cause disagreements (Table 1). By myth I mean generalizations encompassing all tropical forests that are unproved or false, or which could apply to particular situations but cannot be generalized to all tropical forests. More recently, the predictions of species extinctions have become controversial, particularly in light of early expectations that have proven to be overestimates of extinction rates based on overestimates of deforestation rates and population growth [7-18].

Table 1. Popular tropical forestry myths. See [3] for a longer list.

<table>
<tr><th>Myth</th><th>Observations</th></tr>
<tr><td>The nutrient capital of a forest is mostly stored in the vegetation.</td><td>Studies of extreme environments, shallow soil sampling, and weak chemical extractions led to this myth. Sampling to root depth and analyzing for total nutrients resulted in the following percentages of the forest's total nutrient pool stored in the soil [4]:
<table>
<tr><th>Nutrient</th><th>Dry Forest</th><th>Wet Forest</th></tr>
<tr><td>N</td><td>95</td><td>95</td></tr>
<tr><td>P</td><td>99</td><td>99</td></tr>
<tr><td>K</td><td>97</td><td>98</td></tr>
</table>
More examples in [5].</td></tr>
<tr><td>Rates of tropical deforestation exceed 1 percent per year [6].</td><td>Comprehensive analyses show that tropical deforestation rates are less than 1 percent per year [7] and are likely to decline in the future, thus reducing the expected rates of species extinctions [8]. Early estimates were not based on verifiable empirical data, while recent data confirm the lower estimates [9, 10].</td></tr>
<tr><td>Tropical forests are carbon sources</td><td>Previously, only the carbon flux from lands being deforested was considered when reaching this conclusion [11]. Otherwise, most tropical forests were assumed to be neutral with the atmosphere in terms of their carbon cycles [12]. Critical analysis of this assumption showed that it was not correct [13, 14]. Tropical forests can be sources, sinks, or be in carbon balance with the atmosphere depending on disturbance history and intensity, and age of forest stands.</td></tr>
<tr><td>Tropical forests cannot regenerate after deforestation.</td><td>Abandoned deforested lands recover to forests when given time i.e., there is succession in the tropics. When succession is arrested, management intervention is required to re-establish forest cover [15]. Today the Forest Transition model applies globally and pantropically, and increases in tropical forest cover following deforestation are recognized [16].</td></tr>
<tr><td>Secondary forests have no conservation value.</td><td>This myth is based on comparing mature forests with secondary forests in terms of ecological parameters such as the presence of endemic species. The age difference between these two forests states (i.e., hundreds of years of succession), often accounts for these ecological differences [5, 17].</td></tr>
</table>

Nevertheless, in spite of efforts to reduce the level of uncertainty, the debates about tropical forests rage on and are bound to become more contentious as we try to anticipate the effects of global change on tropical forests. Moreover, the study of the resiliency and adaptive capacities of tropical forests remains in its infancy. For example, a volume edited by A. Markham [19] contains an excellent analysis of the potential negative effects of climate change on tropical forests, but none of the 23 articles considered the capacity of tropical forests to adjust to climate change through the emergence of communities of plants and animals with novel species combinations that maintain familiar ecosystem functions and services [20]. Here I elaborate on this possibility, but first address the reasons why myths about tropical forests develop. Further studies focused on how tropical forests function in the context of anthropogenic effects are required to overcome some of these misconceptions.

Why So Many Myths?

A shortage of scientific knowledge limits the ability to predict the future of tropical forests. In part this is due to the low level of scientific activity in the most complex and extensive of all forest regions of the world [21]. Disagreement among scientists is partially due to the challenges faced by scientific activity in the tropics. These include: complex ecosystems and complex environmental situations, shortage of empirical information and understanding, and unrestrained generalizations across temporal and spatial scales, which many times also involve crossing disciplines without proper precautions. An example of the danger of crossing scales and disciplines would be the extrapolation of laboratory leaf- or plant-level physiological work to whole ecosystem-level ecological processes. At the ecosystem level of functioning, leaves and individual plants are subject to nutrient, light, and water limitations and conditions that are difficult to reproduce in the laboratory, which limits the validity of extrapolating results from the laboratory to the whole system. Also, there are problems of scale when extrapolating from small-scale, short-term studies to large-scale, long-term phenomena (Table 2). Moreover, much of the ecological research since the publication of *Fragile Ecosystems* [2] focused on mature native forests, and less attention was paid to secondary forests responding to anthropogenic disturbances, and even less to forests on degraded lands. Yet today the area of secondary forests is greater than the area of mature forests and we are entering an era of novel forests [27], which developed on degraded lands with combinations of species that are different from those of historic native forests [28].

We Need More Attention to Mechanisms of Persistence

One key shortcoming among scientific debates about the tropics is the low level of attention given to persistence mechanisms that continually undermine predictions of worst-case scenarios, particularly of extinction rates related to climate change [29]. For example, tropical forests are often considered ecologically fragile, yet these same forests also have been known to overcome large-scale intensive disturbances and recover after deforestation [4]. Tropical forests, though vulnerable to human activity, particularly deforestation and urbanization, are also resilient and capable of adjusting to environmental change through self-organization and other mechanisms of persistence, which allow populations and communities to overcome disturbances. The following examples of mechanisms of persistence are pantropical.

- The processes of vegetation and animal succession after abandonment of agricultural lands.
- Biodiversity legacies on degraded landscapes or after catastrophic disturbances, which facilitate the re-seeding of recovering landscapes.
- Dispersal and regeneration capacities of species.
- Adaptation or evolution capacity of populations.
- Self-organization at community scales, which allows community assembly at any location based on naturally mediated biotic interactions following the apparently chaotic dispersal of propagules.

The tropical ecology literature is now expanding in all these areas of research (see review [30]) and collectively they suggest the emergence of new paradigms of tropical forest persistence in the Anthropocene [27], also known as the Homogeocene.

Table 2. Problematic fallacies about tropical forests.

Fallacy	Comment
Not recognizing the diversity of tropical forests types.	Tropical forests are usually viewed in textbooks [22, 23] as one, two, or three biomes that usually include dry or rain forests, or evergreen seasonal or montane forests. In reality, the tropics have more Holdridge [24] life zones than the rest of the world combined [25]. Thus the complexity of the tropical forest is grossly underestimated by most classification systems.
Assuming all tropical forests are under the same level of threat.	The perception that all tropical forests are under critical levels of threat is also related to the failure to differentiate between different forest types. Some tropical forests, such as dry and moist forests, are under greater threat than others such as rain forests *sensu stricto* [7] Moreover, the probability of development is related to multiple factors that include topography, adjacent land covers, climate, and level of protection [26].
Extrapolating from small-scale and short-term observations to larger spatial and temporal scales.	Academic studies tend to generalize or express the relevance of a local finding to general situations. Most tropical ecology research is short-term and small-scale in practice. Generalizing these studies in time and space may create confusion when the complexity of temporal and spatial scales in the tropics is ignored.
Ignoring conservation countermeasures.	Conservation activity worldwide has had significant positive effects in terms of protection, restoration, and rehabilitation of forests as documented in State of the World's Forests publications of the Food and Agriculture Organization (FAO) of the United Nations.[1]

The Anthropocene is Again Dividing Scientific Opinion

There is no question that humans are now a dominant factor influencing the world's environment. Figure 1 illustrates the level of anthropogenic effects on critical global geochemical cycles. These altered geochemical cycles in turn affect ecosystem functioning and global climate. Two opposite points of view have developed regarding future scenarios for global biota in light of human effects on climate and the environment in general. The pessimistic scenario is summarized in Table 3 and is well documented [21, 19] This scenario anticipates rampant species invasions, catastrophic levels of species extinctions, homogenization of the biota, and disruptions of ecosystem services. The alternative scenario is that the biota will adapt and adjust to the Anthropocene and will do so by remixing species into novel ecosystems with familiar functions and ecological services.

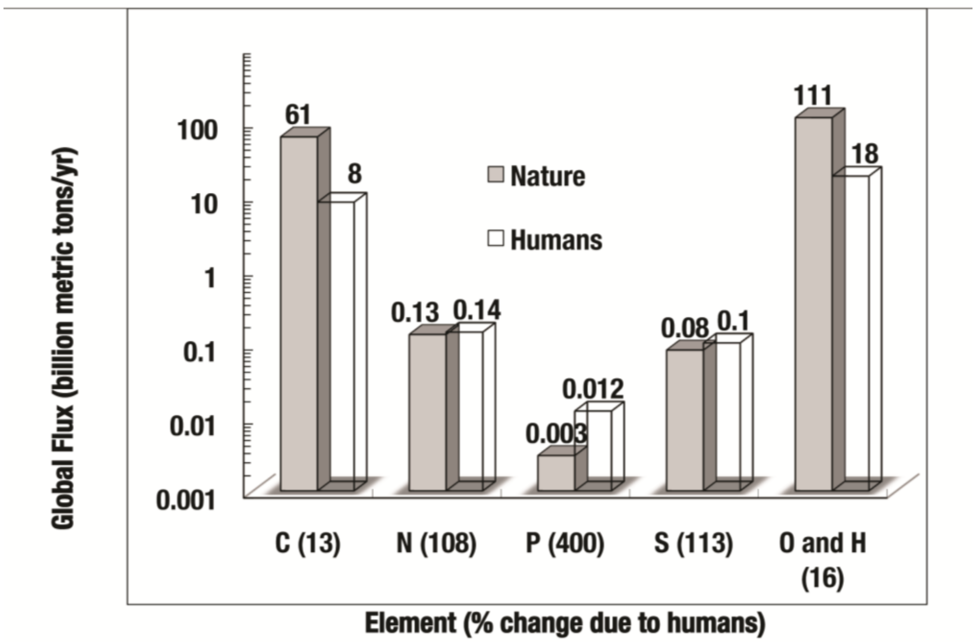

Fig. 1. Level of anthropogenic effects on critical global geochemical cycles. Data are from Sterner and Elser [31].

Here I present the alternative scenario using the island of Puerto Rico as a case study [36]. Although this discussion mainly focuses on the emergence of novel forests from an ecological perspective, I briefly review the socioeconomic and political forces, explored thoroughly elsewhere [37], that allow for this emergence. The influence of socioeconomic phenomena on forest cover has often been discussed within the context of the Forest Transition model, which describes the tendency for forest cover to decrease due to colonization and population growth, but then subsequently rebound as societies undergo economic development, industrialization and urbanization [38]. Therefore, under the right circumstances, economic development can have positive feedback relationships with forest cover, at regional scales. The Forest Transition model has global applicability [29, 40], having been documented in tropical countries as varied as Costa Rica, Cuba, Dominican Republic, The Gambia, Morocco, and Rwanda, and suggesting that the events in Puerto Rico are not unique. We now know that understanding the fate of natural systems requires incorporation of the influence of human systems. Moreover, the combination of diverse disciplines to address these questions challenges the mythology of individual disciplines and broadens such understanding.

Table 3. The Anthropocene: the era of human domination of the biosphere when the world's biota will be homogenized. Each "Predicted Scenario" is drawn from McKinney and Lockwood [32]. Comments are by the author.

Predicted Scenario	Comment
Massive species extinctions.	Usually these scenarios use extinction rates that are higher than those observed empirically [7, 29].
Species extinctions affect rare and endemic species to a greater degree than other species groups.	This may or may not be true. Certainly some endemic species are more vulnerable to extinction than other species, but neither abundance or biogeography by itself is a harbinger of probability of extinction. Moreover, some rare and endemic species are capable of growing in anthropogenic environments, i.e., synanthropic species [33, 34]. However, we must do all in our power to conserve endemic species.
Environmental change favors introduced and invasive species.	This is generally true, but a rare native species can become weedy when environmental conditions are appropriate. For example, in the Caribbean and Central America, *Delonix regia*, an endangered tree species in Madagascar, is naturalized and very common. Similarly, the Blue-and yellow Macaw (*Ara ararauna*) is endangered in Trinidad but thrives in Miami-Dade County, Florida and San Juan Puerto Rico as an introduced naturalized species.
There are fewer introduced species that are successful than rare and endemic species that go extinct, leading to species homogenization.	This is not necessarily true, although there are no empirical data to support either side of the argument. However, any species can become a successful introduced species, if the conditions are right. Thus the pool of potential successful invasive species is large. Nevertheless, of greater relevance to the issue of species homogenization is the fact that the Sørensen index used to assess homogenization is based on a simple comparison of presence/absence of species and ignores the relative abundance of species in communities. When abundance data are used with the Motyka variation of the index [35], similarities decrease and species homogenization becomes less clear.
Some taxa (e.g., parrots) or habitats (e.g., streams) are particularly hit hard by anthropogenic activity.	True, some species and habitats are more vulnerable to human activity than others. They deserve greater conservation attention.

Puerto Rican Case Study

In Puerto Rico, deforestation, agricultural development, and land degradation occurred over several centuries after the 17th century [41]. By the mid-20th century 93 percent of all forest cover and 99 percent of primary forest had been converted to agriculture, mostly for the cultivation of sugar cane, tobacco, and coffee. In the 1990s, the landscape was extremely fragmented, with about six miles of road per square mile of land, splitting the landscape into 20,000 forest fragments, such that the predominant patch size was 1 ha or less [42]. How has the biota responded to such an extreme record of human manipulation?

Surprisingly, documented extinction rates of both plants and animals have been well below those expected from species-area analysis [43]. Moreover, following land abandonment due to economic development, industrialization and urbanization, forest cover has increased from less than 5 percent in mid-20th century to over 50 percent today [44]. In the process, forest patch sizes increased in area while decreasing in numbers. Today, forested watersheds in private lands supply water, support wildlife, and deliver other ecological services to a highly urbanized human population. The Puerto Rican example does not conform to the worst-case scenarios of the Anthropocene, and one could ask if there are lessons from this case study that might apply to other tropical locations. The unique species composition and species diversity of the emerging forests of Puerto Rico, termed novel forests [28] and described below, may represent the future of tropical forests [45].

Puerto Rico's Novel Forests

Results from island-wide forest inventories in Puerto Rico have demonstrated that 75 percent of forests on the island are novel forests [44, 46, 47] and have maintained a steady increase in area converted from abandoned agricultural lands [48]. Their species composition possesses several attributes that distinguish them from undisturbed forests [46, 33, 48]. Canopy species are dominated mostly by introduced species associated with past human activity, while forest understories remain dominated by native species [49-51], [52]. Additionally, the number of tree species per hectare is higher in these forests than in mature native forests. Between 1982 and 2002, the abundance and importance value (measured by the relative tree density and basal area of each species) of individual species changed, but overall the importance value of introduced and naturalized tree species increased. For example, one species, the African tulip tree (*Spathodea campanulata*), has become the most common tree species on the island.

Over time, the resurgent forest canopy has diversified into a mix of introduced and native species that have survived hurricanes. Survival of hurricanes is a key element in the naturalization of introduced species, as those that cannot cope with natural disturbances would not prevail in the future forests of the island. Native species, including primary, secondary, and endemic forest species, have persisted alongside introduced species [49-51], [52], and species homogenization has not been observed at the local or landscape scale [50]. These novel forests have structural attributes such as basal area, canopy height, tree density, and wood volume that are similar to those of native forests. Moreover, their net primary productivity, biomass accumulation, and nutrient fluxes are greater than those of the native forests they replaced [53, 54]. Animal communities in these novel forests consist of mostly native (e.g., birds, amphibians, and reptiles) and combinations of native and introduced species (e.g., earthworms) [55, 56], [34].

Analysis of the island's tree flora has shown that introduced and naturalized species now comprise 23 percent of the flora, and that these species are becoming permanent components of the island's forests [57]. The novel species composition of these forests concurs with observations elsewhere in the world, where the species composition of emerging forests on degraded lands includes combinations of species not recorded before in those locations [28, 58, 59].

Table 4 summarizes some of the characteristics of Puerto Rico's novel forests. The presence and natural development of these forests are relevant to the establishment of vegetation on degraded sites, the colonization of sites where environmental conditions are novel, adaptation to global change, succession after land use change, and aboveground carbon storage. For example, many native primary and secondary forest species are unable to grow on degraded lands, allowing introduced species to prevail [63, 64]. Once forest conditions are restored by the growth of introduced species and the canopy closes, those native species that could not grow on the degraded site establish viable populations in the understory and eventually reach the canopy, thus adding species diversity to the novel forest [63].

Table 4. Some generalizations about the structural and functional attributes of novel forests in Puerto Rico. The citations are illustrative of many additional examples.

Novel Forest Characteristic	Observation
Have similar structural characteristics as native forests.	It is difficult to distinguish their physiognomy from that of native forests, particularly as they mature [60]. Structural parameters such as basal area, tree density, and canopy height are similar to those of native forests [60, 61] although their species density is higher [33].
Are young (<80 years) and lack old growth characteristics.	Recent colonization precludes large trees and endemic species are few in these forests [46, 47] but these attributes develop with age.
Function as carbon sinks.	They have high NPP and high biomass accumulation. For example, 24 to 39 yr-old *Spathodea* forests on abandoned agricultural lands had over bark wood volume that ranged from 163 to 849 m^3/ha and aboveground biomass that ranged from 60 to 296 Mg/ha [54]. They can store more biomass than native and plantation forest stands of similar age and their litterfall reaches 13.8 Mg/ha.yr [53].
Function like native forests, but at different rates.	Their productivity and cycling rates may be faster [53, 62] or slower [61] than those of native forests of similar age, depending on site degradation.
Improve site conditions and foster native species.	They help restore canopy cover, microclimate, and soil organic matter and nutrient content [63, 50].
Occur on fragmented landscapes; many times in places where native species cannot grow.	Native pioneer tree species usually do not germinate and/or grow on degraded pastures [64] but do so in the understory of the introduced species [63] because the conditions on degraded pastures are not suitable for native seed germination, seedling establishment, and growth.

Predictions

From the experience in Puerto Rico and elsewhere [59], it appears that new combinations of introduced and native tree species will persist where humans dominate the environment. It is unlikely that the pre-existing native species combinations will replace the current novel species assemblages because the naturalized introduced species are capable of regeneration under the prevailing environmental conditions of the island, i.e., both natural and anthropogenic disturbance regimes. When anticipating climate change effects, it is important to consider the synergy between any climate change parameter and other anthropogenic disturbances such as urbanization or land degradation. In other words, climate change effects should not be considered in isolation, because in the real world they interact with other anthropogenic disturbances. Hence I focus here on global change, which includes both types of disturbances. Continuous global change favors the persistence of introduced species and formation of novel communities. One could use observations from the Puerto Rican case study to make the following predictions for the future of tropical forests in a world dominated by anthropogenic activity and experiencing global change:

- Novel forest types will emerge after disturbances within complex and diverse landscapes.
- These forests will self-assemble and self-organize and will contain novel combinations and proportions of plant and animal species.
- Novel forests will exhibit a suite of species diversity whose levels will be similar to, lower, or higher than those in current forests depending on the level and frequency of disturbances and site conditions. Increased rates or intensities of disturbance reduce species richness and the stature of forests.
- Novel forests will function similarly to current native forests in their delivery of vital ecological services to people.
- Historically native species communities are unlikely to replace novel communities in the future because the environmental conditions continue to change and the historic conditions that favored traditional native species are not likely to prevail.

These predictions contrast those of worst-case scenarios for the tropics, but they merit research attention given that the experience in places like Puerto Rico shows that if natural systems are allowed space, they expand and adjust to emerging conditions rather than self-destruct. The consequences of either scenario are of importance to the public, governments, and conservationists in general. Each scenario has different costs and requires different levels of effort to address them. For example, restoring natural vegetation on small islands through the eradication of introduced animals can be costly with unpredictable effects and controversy [65], [66-68], while natural processes at no cost to the economy powered the reforestation process that led to increasing the forest area in Puerto Rico from 6 percent to 57 percent. We face a conundrum as articulated by Botkin [69]: “One can either preserve a ‘natural’ condition, or one can preserve natural processes, but not both.” If in the future we need to reverse natural trends to accomplish our conservation goals, the cost will be enormous and probably unattainable. If however, the natural responses of forests to anthropogenic effects are compatible with our goals of sustainable development, the costs associated with conservation might be within our reach. Only in time will we find out.

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