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COMMENTARY

The Emerging Era of Novel Tropical Forests

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ABSTRACT

In 1966 Eugene P. Odum delivered a speech before the Ecological Society of America that transformed the way ecologists looked at succession. His comparison of mature and successional systems lead ecologists to place secondary forests in an inferior position relative to mature ones to the point that today, prominent tropical biologists argue for and against the conservation value of secondary forests. Nevertheless, we live in the era of secondary forests that is rapidly giving way to a new era of novel tropical forests. Research in Puerto Rico documents the emergence of novel forests, which are different in terms of species composition, dominance, and relative importance of species from forests that were present before the island was deforested. These novel forests emerged without assistance. They are a natural response to the new environmental conditions created by human activity. Natural processes have remixed or reassembled native and introduced plant and animal species into novel communities adapted to anthropogenic environmental conditions. Novel forests are expected to protect soils, cycle nutrients, support wildlife, store carbon, maintain watershed functions, and mitigate species extinctions. The dawn of the age of tropical novel forests is upon us and must not be ignored.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: homogeocene; introduced species; invasive species; novel forests; secondary forests; tropical forests; tropical succession.

PLANT SUCCESSION AFTER ANTHROPOGENIC DISTURBANCES often results in novel combinations of species and novel forests. I focus on this phenomenon through the lens of my experience in the tropics. In 1966, I had the opportunity to listen to Eugene P. Odum deliver the Presidential Address before the annual meeting of the Ecological Society of America at the University of Maryland (Odum 1969). It was an inspiring speech on the strategy of ecosystem development that would transform the way ecologists looked at succession from then on. As ecosystem science developed in the 1970s and 1980s, ecologists focused attention on mature forests and generally ignored secondary ones. After all, mature systems maximized complexity, diversity, and stability, while secondary ones were deemed simple, unstable, and poorly organized. An attribute of secondary forests that always trumps mature forests is their high net productivity, but that productivity was depicted merely as a 'quantity' as opposed to the high 'quality' of mature forests. Thus, when conservation objectives had to be prioritized, ecologists placed mature forests at the top of the list. I did so also even though it always bothered me that the comparison was flawed because it compared the hundreds of years of growth and development of mature forests with the few decades of development of a secondary forest.

As ecologists focused on mature forest vegetation, Gómez-Pompa and Vázquez Yanes (1974) called for more attention to secondary forests and their species and argued that we were living in the era of secondary forests. In response to Gómez-Pompa and Vázquez Yanes, Sandra Brown and Lugo (1990) reviewed the tropical secondary forest literature to explore a number of ecological attributes of tropical secondary forests such as the rate at which they accumulated biomass and species. In so doing, we could not escape the paradigm that most of the ecological attributes achieved their zenith at maturity. I should have known better.

H. T. Odum's Systems Ecology course at Chapel Hill had taught us that the successional sequence highlighted by E. P. Odum was one scenario in a matrix that involved four alternative successional pathways and that depending on initial conditions and conditions at steady state, natural systems with different balance of production and consumption could emerge (Odum 1971, Fig. 9.7). Thus, it was possible to have attributes typically associated with successional systems at maturity. My own work with mangroves exemplified this plethora of successions (Lugo 1980). Jack Ewel (1980) explained it best by reasoning that the high species richness in the tropics plus the many tropical environments, meant that tropical succession could take many paths to maturity, progressed at different rates depending on conditions, and could maintain high production and low species richness at maturity if conditions allowed. Views like those of Odum and Ewel allowed a fresh look at secondary forests. Moreover, the International Tropical Timber Organization documented the foresight of Gómez-Pompa and Vázquez Yanes by reporting that 850 million ha or 'roughly 60 percent of the area that is statistically classified as forest in the tropics' was secondary forest (ITTO 2002).

As I listened to the 1966 speech, I could not imagine that Odum's brilliant comparison of mature and successional systems would lead ecologists to place secondary forests in an inferior position relative to mature ones. Today, prominent tropical biologists argue on the pages of the *New York Times* (29 January 2009) for and against the conservation value of secondary forests. In the legitimate effort to conserve tropical forests, some ecologists ignore the fact that secondary forests are on the path to maturity and without them, mature systems could not develop in modified landscapes. Moreover, many colleagues are oblivious to the era of secondary forests and what it means in terms of the prevailing types

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of forests on the tropical landscape. Worse yet, they don't realize that the era of secondary forests is rapidly giving way to a new era of novel tropical forests. Ecologists are on the verge of repeating history by devaluating novel tropical forests just as they devaluated secondary forests in the past.

The Homogeocene (the era of human domination over the world) is viewed as the greatest threat to the conservation of forests and biodiversity (McKinney & Lockwood 1999). Humans are dramatically modifying the environment (including the climate) and making things worse with the introduction of species that displace native species. The issue of invasive species is a subject of controversy between those that advocate a 'shoot-first, ask questions later' approach to the management of these species and others who point out that these species have ecological roles that require ecological understanding before the shooting begins. The federal government has joined the war on species by spending millions of dollars in many eradication programs with targets ranging from frogs in Hawaii to trees in the Everglades. However, the recent experience in the World Heritage island of Macquarie is a sobering example of the need for ecological understanding of the role of invasive species before expensive management actions are undertaken (Cadotte 2009). A successful irradiation program for introduced feral cats ultimately compounded human arrogance rather than rectifying it, releasing introduced rabbits from their primary enemy. The assumption that newly formed ecological relationships between native and introduced species either did not exist or were expendable now threatens to exterminate native Macquarie vegetation.

When tropical biologists analyze the consequences of the Homogeocene they tend to focus on the negative aspects of change giving the impression that the biota is incapable of adjusting, adapting, or coping with the new environmental conditions that humans are creating. The argument is made that today's environmental changes are unprecedented in the geologic record because of the short time period over which they occur. This argument is not totally correct because instances of fast, huge disturbances followed by massive species extinctions and reassembly of new communities occur in the geologic record (Donovan 1989). Moreover, we tend to exaggerate future species extinctions (Lugo 1988).

My views on the emergence of novel forests developed slowly as a result of research by colleagues in Puerto Rico (summarized in Lugo & Helmer 2004) that showed that:

(1) The dominant tree species in the forests of Puerto Rico were mostly introduced species used by people for a variety of reasons.
(2) A diverse cohort of native tree species develops underneath the canopy of introduced species.
(3) Abandoned plantations of introduced species behaved like native forests and allowed the establishment of a rich understory of native species, which then mixed with the introduced species to form a different forest type than originally present.
(4) Experimental plantings of introduced species overcame arrested succession and native forest species reestablished below their canopy.
(5) Introduced tree species had the capacity to invade degraded lands while native pioneer species could not.
(6) Introduced tree species gained importance in island forests between 1982 and 2003.
(7) Introduced species were not randomly distributed on the landscape, but reflected past land uses, bioclimate, and substrate.
(8) Emerging forests had higher tree species richness than those that were native, and functioned as did native forests, but at different rates.

I realize that the presence, dominance, and relative importance of tree species in these Puerto Rican forests made them different from the species composition, dominance, and relative importance of species of forests that were present before the island was deforested. I also realize that the species composition of the original forest would never return, and would forever be different because introduced species had become part of the new mix of species. This view is contrary to a common refrain in the tropical conservation literature that assumes that after site degradation and abandonment succession will proceed towards the historic species composition of forests. The reality is that succession can proceed through many paths to maturity and the speed, direction, and species composition is influenced by environmental conditions including the types of species available and capable of competing for site dominance. The result that we see in Puerto Rico is that the forests of today are novel; they contain combinations of species not known to have existed before and the relative abundance of these species is different from those of the past.

I also realize that these novel forests emerged without assistance. They were not planted nor are they the product of the invasion of native forests. The dispersal, establishment, and growth of species in the novel forests took place under natural conditions after people abandoned agricultural or urban lands. They represent a natural response to the Homogeocene—a response to the new environmental conditions created by human activity. Native and introduced animal and plant components have been remixed or reassembled into novel communities by the natural processes in response to novel environmental conditions.

The results from Puerto Rico raise many questions. Is this phenomenon unique to Puerto Rico or is it more generalized? Are we at the onset of a new era, the era of novel forests? What are the ecological consequences of the establishment and expansion of novel forests? Will their presence result in a reduction of ecosystem services? Will species extinctions ensue?

I believe the phenomenon of novel forests is worldwide in scope, although Puerto Rico is an extreme example of the Homogeocene with its high population density, high proportion of urbanized lands, history of total deforestation of the landscape followed by centuries of agricultural use and degradation, and high proportion of introduced species in its flora and fauna (Lugo 2004). Because the bulk of Puerto Rican forests are novel, ecologists there have been able to thoroughly document the phenomenon. However, there are now many examples of novel forests (Richardson *et al.* 1996, Wilkinson 2004, Hobbs *et al.* 2006, Mascaro *et al.* 2008). Yet, in most of the tropics, ecologists have just begun to focus on secondary forests (Chazdon 2008), and continue to ignore forests dominated or 'contaminated' as some argue, by introduced species.

I also believe we are entering an era of novel tropical forests because human activity continues to modify landscapes in ways that are unfavorable to the regeneration of traditional community

assemblages, particularly in the periurban environment and after the cycle of deforestation, agricultural use, and abandonment of lands (Hobbs *et al*. 2006). Novel environmental conditions created by human activity favor the remixing of species and formation of novel forests. I expect novel forests to behave ecologically as native forests do, *i.e*., protect soil, cycle nutrients, support wildlife, store carbon, and maintaining watershed functions. Moreover, novel forests mitigate species extinctions as they, like secondary forests, are in successional paths to maturity and species accumulation. Nature's response to the Homogeocene cannot continue to be ignored or remain undetected by ecologists. The dawn of the age of tropical novel forests is upon us and must not be ignored.

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