Chapter 1
Conundrums, Paradoxes, and Surprises: A Brave New World of Biodiversity Conservation

Ariel E. Lugo

Abstract Anthropogenic activity is altering the global disturbance regime through such processes as urbanization, deforestation, and climate change. These disturbance events alter the environmental conditions under which organisms live and adapt and trigger succession, thus setting the biota in motion in both ecological and evolutionary space. The result is the mixing of species from different biogeographic regions and formation of novel communities of plants and animals. In this essay I present the point of view that this mixing and remixing of species is a natural response to the changing condition of the biophysical environment. The assembly of novel ecological systems reflects a healthy biota changing and adapting to acute and chronic anthropogenic disturbances. These anthropogenic disturbances add uncertainty to the state of the environment by inducing directionality and unpredictability to the disturbance regime, as opposed to the cyclic and predictable patterns of historical natural disturbances. If this view is correct, the paradoxes and surprises that are being recorded in the scientific literature should not surprise us nor appear paradoxical. Rather, they reflect normal responses to the uncertainty and magnitude of change of condition generated by anthropogenic activity. The current conditions under which we must manage tropical resources confront us with conundrums that must be approached with caution. Land managers need to consider their options in terms of cost and opportunities of success when they focus attention and resources on restoring natural conditions that can no longer exist on the planet.

Keywords Novel forests • Introduced species • Species eradication • Anthropogenic disturbances

A.E. Lugo (✉)
International Institute of Tropical Forestry, USDA Forest Service,
Río Piedras, Puerto Rico, PR 00926-1119
e-mail: alugo@fs.fed.us

T. Schlichter and L. Montes (eds.), *Forests in Development: A Vital Balance*,
DOI 10.1007/978-94-007-2576-8_1,

In Shakespeare's The Tempest, when the character Miranda says *O brave new world That has such people in't!,* she is expressing her awe at the beauty and diversity of human characters in the island where she and her father had been banished. Immediately, her father Prospero cautioned her about her enthusiasm by saying: *'Tis new to thee.* We are in a similar situation in the brave new world of biodiversity conservation in that we face a diversity of new combinations of species and community assemblies new to us, but that nevertheless appear beautiful and goodly just as Miranda perceived her new world, (Behrensmeyer et al. 1992). The new angle on the issue is the predominance of human effects on the biota.

Fundamentally, humans are now so dominant on Planet Earth that they are not only changing conditions and creating new habitats at local scales, but are doing so globally and changing the climate of the Earth. The consequences of these anthropogenic changes are reflected in warnings from scientists of impending catastrophic species extinctions, rampant species invasions, homogenization of the world biota, and disruptions of ecosystem services. These warnings are based on changes of the biota that scientists document day to day throughout the world. Sodhi et al. (2007) nicely summarized these effects for tropical ecosystems. Is the world biota at the edge of impending doom or is it adapting and reacting to the new conditions imposed by human activity, in which case the observed changes reflect a healthy biotic system?

I take the view that what we are seeing is adaptation and adjustment to environmental change, and that it behooves us to read the situation correctly to facilitate compliance with our responsibility as forest and land stewards. I base my views on the writings of early ecologists such as Elton (1958), Odum (1962), and Egler (1942) who observed the changes in the biota taking place as a result of human activity but recognized the inevitability of increased human activity and observed order and patterns in the response of the biota to anthropogenic activities. For example, Elton (1958), p 145 wrote: 'Unless one merely thinks man was intended to be an all-conquering and sterilizing power in the world, there must be some general basis for understanding what is best to do. This means looking for some wise principle of co-existence between man and nature, even if it has to be a modified kind of man and a modified kind of nature. This is what I understand by conservation.'

All three authors (C.S. Elton, H.T. Odum, and F. Egler) focused on the self-organization capacity of natural systems as a key element for understanding how new combinations of species might adaptively emerge as a result of increased human activity on Earth. And they expressed no bias against introduced invasive species. For example, Elton (1958), p 155 wrote: 'I believe that conservation should mean the keeping or putting in the landscape of the greatest possible ecological variety-in the world, in every continent or island, and so far as practical in every district. And provided the native species have their place, I see no reason why the reconstruction of communities to make them rich and interesting and stable should not include a careful selection of exotics forms, especially as many of these are in any case going to arrive in due course and occupy some niche.'

This did not mean that humans had no role in managing ecosystems. Elton (1958) p 151 added: 'The world's future has to be managed, but this management would not be like a game of chess –more like steering a boat. We need to learn how to manipulate more wisely the tremendous potential forces of population growth in plants and animals, how to allow sufficient freedom for some of these forces to work amongst themselves, and how to grow environments –for example, certain kinds of cover-that will maintain a permanent balance in each community.' At the same time, Aldo Leopold was publishing similar ideas in the United States (Leopold 1953) and Odum (1962) wrote (p 68): 'Synthetic ecosystems include conditions and combinations of organisms never before in existence. When multiple species seedings are done…a functional ecosystem soon evolves with species-number distributions like those in wholly natural systems…Multiple introductions from throughout the world may permit more diverse combinations to evolve, more closely integrating the habitation of man.'

My point is that in the 1950s to the 1960s, leading ecologists laid a strong scientific rationale for dealing with the alterations of species composition of ecosystems as a consequence of human activity. They advocated conservation paradigms that were inclusive of all species in marked contrast to the ideas of eradication of introduced species that are common with government and non-government organizations today.

Have environmental conditions changed so much, as it is commonly argued, to negate the ideas of these pioneer conservationists? One way to find out is to examine how current ecosystems are reacting to present anthropogenic conditions to see if the responses appear adaptive and exhibit order as suggested by Elton, Egler, Odum, Leopold, and others. Because ecosystems are complex and many times behave counter intuitively, a review of some of the paradoxes, conundrums, and surprises described by modern ecologists should help understand the situation and lead us to alternative approaches to ecosystem management.

A major consideration to our thinking should be the realization that with climate change and anthropogenic disturbances, we are seeing environmental change that is neither cyclic nor reversible. Instead, anthropogenic-induced environmental change is directional but we don't know the direction it might take. Uncertainty is now the rule in terms of the predictability of the environmental conditions faced by organisms. These uncertain conditions act as strong selective forces with the consequence that the world's biota must respond and adjust both ecologically and evolutionarily. Organisms shift distributions as they follow the conditions best suited to their life history requirements and in the process experience new interactions with other organisms and novel environments. These new conditions and interactions are natural forces of selection that lead to evolutionary change. Paradoxes, conundrums, and surprises follow from these considerations.

1.1 Paradoxes

The literature is documenting the turmoil of the world's biota in the form of paradoxes such as the following three examples.

1.1.1 *Inbreeding Paradox*

This paradox addresses the issue of how small populations of introduced species invade territories, thus suffering the effects of inbreeding, and instead of becoming extinct, become successful invaders (Pérez et al. 2006). One explanation for this paradox is that the invasion is repeated many times and the repetitive nature of the process overcomes the inbreeding effect. This explanation although plausible has had exceptions, and thus is not sufficient to explain those exceptions where a single event leads to a successful invasion in spite of the inbreeding. Of relevance to the main thesis of this essay is that the invasion involves modification of the environment by the invader, i.e., novel environmental conditions, and genetic modification of the invading species, e.g., invasions may involve genetic adaptation. Examples of genetic modification would be epigenetic adaptations and adaptive mutations. Pérez et al. (2006), p 545 point out: '…evidence that genes are not immune to environmental influences has been accumulating in the findings of molecular genetics.' Similarly, Travis et al. (2010) found increased rates of hybridization in invading clones of cattail stands in the Great Lakes region of North America. These findings are extremely important for understanding how the biota responds both ecologically and evolutionarily and adapts under the influence of a rapidly changing anthropogenic environment. This allows the maintenance of homeostasis and functioning under novel environmental conditions. In short, evolution might be accelerated under the stressful new conditions of an anthropogenic world.

1.1.2 *Local Adaptation Paradox*

Introduced species successfully compete and replace native species already established in their local environments, i.e., loss of home-court advantage (Allendorf and Lundquist 2003). The expectation is that native species should prevail within their natural geographic boundary because they evolved under those local conditions and this should give them an edge over an invading species. However, there is already recognition that indigenous genetic material may no longer be adaptive in modified ecosystems that have experienced significant environmental change (Jones and Monaco 2009). With increased site degradation organisms encounter both biotic and abiotic thresholds (ecological thresholds) that have to be overcome if they are to remain adaptive to emerging conditions (Whisenant 2002; Jones and Monaco 2009). Thus, if the native species lacks adaptation to a changed or emerging condition they are unlikely to be successful in competition with an introduced species that is adapted to those conditions.

Ricotta et al. (2009) gave examples of the environmental conditions of urban environments that select for introduced organisms. These were: the heat island effect, which favors species whose distribution is limited by cooler temperatures; high proportion of surface runoff and hard surfaces that increase aridity; high alkalinity or urban soils, which are affected by concrete and other lime-based materials, and select for species adapted to high pH soils. It thus appears that the home-court is no longer what local species adapted to and the paradox is resolved by the disappearance of the home court advantage.

Jones and Monaco (2009) suggested the use of 'assisted evolution' as a strategy for designing native plant material for domesticated landscapes where conditions are extreme and sites have passed both biotic and abiotic thresholds. Assisted evolution requires native species to be selected, genetically manipulated, and used (planted) under the conditions they are likely to experience in anthropogenic environments. Assisted evolution is a controlled way for emulating how wild species might naturally adapt to anthropogenic environments. In fact, this is what is already happening with the natural invasion of introduced species that are pre-adapted to the new conditions created by human activity.

The relevant point to this discussion is that home court advantage applies only where the home court environment has not changed. When the environment changes, there is no reason to expect home court advantage. Thus, it might be folly to expect that only native species are suitable for restoration or that only natives have an exclusive presence in anthropogenic landscapes. Jones and Monaco (2009), p 546 said it best: '…we believe that the tacit assumption that local material will demonstrate optimal performance, adaptation, and fitness despite severe disturbance, is unwarranted.'

The phyloecology of introduced urban floras is a testament to the close relationship between novel urban conditions and dominance of introduced species in urban environments (Ricotta et al. 2009). Ricotta et al. examined 21 urban floras in Europe and eight in the United States and found that the phylogenetic diversity of introduced urban species was lower than that of native species at the city and continental scale. They also found that introduced species in cities are not random assemblages of species, but are more clumped than expected from assemblages randomly compiled from the entire flora (the same is true of aquatic organisms [Karatayev et al. 2009]). Ricotta et al. (2009) suggest that the urban environmental filters are responsible for the decline in phylogenetic diversity in urban floras. The species of urban floras are composed of phylogenetically related species that are well adapted to anthropogenic habitats.

While invading species must overcome the environmental filter of cities to be successful in their establishment as part of the urban biota, the pre-existing native species have a different challenge. Schaefer (2009) expressed the opinion that the effect of anthropogenic modification of habitats is the erasing of the ecological memory of sites. The ecological memory consists of the species of an area and the ecological processes that determine the future trajectory of the ecosystem, including disturbances and management actions. Invasions are facilitated by loss of ecological memory, as native species find it difficult to persist under the changing conditions, resulting in loss of ecological memory and the establishment of new stability domains with introduced species.

Also related to the local adaptation paradox is the common observation that a species performs at higher levels of productivity and growth when it is introduced relative to its performance in its native habitat (Rout and Callaway 2009). Rout and

Callaway (2009) attribute this boost in productivity of introduced plants to their interaction with soil microbes that increase nitrogen cycling and boost production. They also suggest that the introduced species evolve, as might their evolutionary relationship with microbes, which allow higher levels of productivity, nutrient-use, and nutrient recycling.

1.1.3 Forest Fragmentation Genetics Paradox

Contrary to theory, forest fragmentation does not appear to reduce the genetic diversity of tree populations (Kramer et al. 2008). The incorrect notion that fragmentation would reduce genetic diversity was based on four assumptions that proved wrong: (1.) That fragment edges delimit populations. (2.) That genetic declines manifest, and are detectable, quickly. (3.) That different tree species respond the same way to fragmentation. (4.) That genetic declines supersede ecological consequences. Kramer et al. (2008) conclude that neither the ecological or genetic issues affecting how trees respond to fragmentation have been addressed broadly enough with respect to each other to allow definitive conclusions about how relatively important ecological and genetic factors are.

1.2 Conundrums

Conundrums reveal the difficulty that we find ourselves in when attempting to predict future biodiversity scenarios under the assumption that past conditions will somehow repeat themselves. A classic example is our effort to restore ecosystems to historical conditions that will not be present in the future. Thus, a fundamental conundrum facing forest managers is: 'One can either preserve "a natural" condition, or one can preserve natural processes, but not both' (Botkin 2001). This is a problem because if we elect to preserve 'a natural condition' (and thus suppress natural processes) the cost might be so high as to be practically impossible to achieve, particularly at large spatial scales. Yet, many resource management policies lead us to preserve 'a natural condition' and commit to overcoming natural processes.

Species eradication is a technique commonly utilized by land managers hoping to restore a natural condition to particular ecosystems. The idea is to remove introduced or invasive species in the hope that the native species will recover and restore ecosystems to natural conditions deemed superior to existing ones. This effort to restore a natural condition through the eradication of unwanted species has consequences, both at the population and ecosystem levels that are increasingly being assessed by ecologists. Zipkin et al. (2009) assessed the issue at the population level with plant and animal population examples, and simulation of a general population model. They found that demographic structure and density-dependent processes can

confound removal efforts and lead to undesirable consequences such as increases rather than decreases of target organisms or population cycling chaos. Species with high per capita fecundity, short juvenile stages, and fairly constant survivorship rates are more likely to respond undesirably to harvest.

At the level of the ecosystem, the example of the sub-Antarctic World Heritage Macquarie Island has stimulated considerable debate (Bergstrom et al. 2009a; Dowding et al. 2009). Like many such types of islands, Macquarie Island contained a compliment of introduced species deemed detrimental to its naturalness. In this case the undesirable species were rabbits and cats. A virus (Myxoma) was introduced to control the rabbits, and cats were shot to extirpation. These two actions occurred over a period of several years between 1978, when the virus was introduced, and 2000, when the last cat was shot. By 2008 the rabbit population had grown out of control in spite of the virus, and the vegetation of the island was devastated. Bergstrom et al. (2009a, b) attribute the unexpected result to a trophic cascade, caused by the extermination of cats. The effects of the conservation action were thus island-wide. Dowding et al. (2009) point out that there were positive effects as well from the eradication program. Notably, sea bird populations recovered rapidly due to the absence of cats. They also suggested that the vegetation of the island has been devastated before, and thus likely to recover when rabbits again decrease in numbers. The important lesson from the example, however, is the system-level ramifications of single species management actions, and the unpredictability of the effects. Moreover, the example illustrates the high cost and complexity of resolving the Botkin conundrum by attempting to restore 'a natural condition' against the directions of 'natural processes'.

Conversely, if we elect to allow natural processes to take over the biota without any control, we may face outcomes that are not beneficial to humans or to sustaining human activities. In these cases we may have to steer natural processes towards desired outcomes as suggested in the above quotes from Elton (1958). Clearly we need to recognize that sustaining human activity will require a balance between the two extremes of Botkin's conundrum and that we depend on science to help us identify where that balance might reside.

1.3 Surprises

Paradoxes and conundrums reflect the many surprises that biologists are observing as they study the mixing of species and assembly of new communities of organisms in novel environments. These observations are particularly surprising or appear paradoxical if they are evaluated within the norms and rules of a cyclic natural world. However, in the context of a human-dominated world many of these paradoxes and surprises are not so, or have clear explanations.

In the above example from Macquarie Island, managers were surprised by the results of their interventions with cat and rabbit populations because they failed to consider that many protected islands of the world have had similar types of introduced animal populations for centuries and their flora and fauna exists in balanced states that have led to their recognition and selection for protection. However, the managers of this island decided to return the communities to historical conditions by eradicating the introduced species and creating transitional ecological systems whose management costs are now prohibitive. The surprise should not have been so if managers had realized that the biota of the island system had self-organized to include the introduced species. Species-by-species eradication actions based on notions of pristine communities are ineffective because they ignore the overall system's self-adjustment to current conditions and also ignore basic population ecology principles (Zipkin et al. 2009). In the context of the novel system with introduced rabbits, cats, and rats, the disruption of vegetation as a consequence of the eradication of populations is not surprising.

Another set of surprises revolves around the notion of unintended consequences of species invasion, also known as the Frankenstein Effect because many of these consequences are deemed detrimental to the biota (Moyle and Light 1996). Here I draw attention to unexpected symbiotic relations as a result of mixing species in novel environments. These unintended consequences or surprises need not be judged as positive or negative to organisms, but evaluated for their adaptive value to environmental conditions. An example would be the new food web that developed in the United Kingdom as a result of the introduction of turkey oak and gail wasps (Hobbs et al. 2009). These introduced species interacted with native species of oak, gail wasps, and Blue tit birds to form a new food web that included historical as well as new trophic links, and which appears stable.

In northeastern forests of the United States, *Alliaria petiolata* (garlic mustard) is a successful introduced ground covering plant. Rodgers et al. (2008) found that the presence of this species improves nutrient availability in soils and increases their pH. The nutrient-rich plant parts of this species also stimulated fungal and microbial activity and resulted in positive feedbacks into the growth of the plant. Dassonville et al. (2008) examined the phenomena of soil nutrient enrichment by introduced species by analyzing data from 36 sites with widely divergent edaphic and biotic conditions in NW Europe. They found that all species-invaded plots had increased aboveground biomass and nutrient stocks compared to uninvaded sites. The magnitude of the effect was site-specific, but the stronger effects were measured in sites with low initial nutrient concentration in topsoil, while negative effects were generally found in the opposite conditions.

The examples given above show that adding introduced species to sites has wide ranging ecological effects both in the trophic structure as in site fertility. These changes in turn affect many organisms within the community. These new symbiotic relationships point to the biotic mechanisms of self-organization during natural succession. They lead directly to the establishment of novel communities of plants, animals, and microbes.

1.4 Novel Forests: The Natural Response to Human-Induced Environmental Change

The formation of the novel forests has its genesis in a variety of circumstances, one of the most important being the establishment of introduced species in sites altered by human activity (Hobbs et al. 2006). Here I emphasize the development of novel food webs by the presence of mixtures of animal and plant species. As the example above from the United Kingdom shows, when organisms that previously had not shared the same ecological space come in contact and interact, new trophic relationships and novel food webs develop. Another example describes how native predators capable of feeding on an abundant introduced prey have a fitness advantage over a predator that cannot (Carlsson et al. 2009). They can do so rapidly via existing phenotypic plasticity or slowly via natural selection. Carlsson et al. (2009) discuss numerous examples of native predators switching to introduced prey such as the Lake Erie water snake (*Nerodia sipedon insularum*) feeding on Eurasian round goby (*Neogobius melanostomus*). Unfortunately, long-term data are not available in sufficient quantity to establish how prevalent these mechanisms are under natural conditions.

Hobbs et al. (2009) recognized that the degree of novelty of ecological systems developing in altered conditions could vary from slight to completely novel. They used a two dimensional graphic to depict alternatives for management and conservation of these ecosystems with abiotic conditions ranging from historical to altered on the X-axis and biotic composition also ranging from historic to altered in the Y-axis (their Fig. 1). Within these axes they classified systems from historic to hybrid to novel depending on how far their respective abiotic and biotic attributes deviated from the historical condition. Novel ecological systems were located in both X and Y axes at the most distant states from historical systems. Hobbs et al. (2009) suggested the following criteria to evaluate if a particular novel ecosystem was suitable for conservation or a candidate for restoration: its capacity to mature along a stable trajectory, its resistance and resilience to disturbances, its thermodynamic efficiency, its production of goods and services, and its capacity for providing opportunities for individual or community engagement.

I have argued that novel forest ecosystems are a natural response to the novel environmental conditions created by human activity (Lugo 2009). Because human activity is so prevalent today, novel forest and other types of novel ecosystems are increasing in area and importance (Marris 2009). What distinguishes a novel ecosystem from a native or historical one is its species composition, which includes introduced species and combinations of native and introduced species not seen before (Lugo and Helmer 2004; Hobbs et al. 2006). The current debate about species eradication may become moot in the future as the pace of species mixing accelerates with climate change (Walther et al. 2009). Species viewed as undesirable today, could be acceptable tomorrow because of their capacity to cope with, and function in, new climates. As a result, novel ecosystems will be even more prevalent. There is a strong justification to understand the mechanisms that lead to novel forest assembly (e.g., Brandeis et al. 2009) and the functioning of these systems relative to human needs and sustainability of human activity.

1.5 Conclusion

There is no longer any question about the state of turmoil of the world's biota. The biota is on the move in both ecological and evolutionary space, as it normally does when subject to natural disturbances (discussed for hurricanes in Lugo 2008) or after anthropogenic disturbances (Lugo and Brandeis 2005). Today's global movement of the biota is due to the insidious changes to the global environment by anthropogenic activity. In this essay I have presented the point of view that this mixing and remixing of species is a natural response to the changing condition of the biophysical environment. The assembly of novel ecological systems reflects a healthy biota changing and adapting to acute and chronic anthropogenic disturbances. These anthropogenic disturbances add uncertainty to the state of the environment by inducing directionality to the disturbance regime, as opposed to the cyclic patterns of natural disturbances. The anthropogenic disturbance regime also adds trends and gradients to the biophysical world to which organisms adapt. If this view is correct, the paradoxes and surprises that are being recorded in the scientific literature should not surprise us nor appear paradoxical. Rather, they reflect normal responses to the uncertainty and magnitude of change of environmental conditions when driven by anthropogenic forces. Land managers need to consider their options in terms of cost and opportunities of success when they focus attention and resources on restoring natural conditions that can no longer exist on the planet.

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Chapter 2
Understanding the Role of Resource Use Efficiency in Determining the Growth of Trees and Forests

Dan Binkley

Abstract In the twentieth century, silviculturists commonly thought about the growth of trees and stands in terms of "growing space." Trees and stands grew faster when they obtained more growing space. Unfortunately, growing space is intangible and not quantifiable, limiting the opportunities for quantification and hypothesis testing. Patterns of tree and stand growth can be evaluated quantitatively with a production-ecology perspective, testing hypotheses about factors that influence growth. The growth of trees and forests depends on the acquisition of resources (light, water, nutrients), on the efficiency of using these resources for photosynthesis, and on the partitioning of photosynthate to wood growth. Trees and stands with high rates of resource use might be expected to show lower efficiency of resource use as a result of some sort of declining marginal return; however, empirical patterns show that increasing resource use is generally accompanied by sustained or increased efficiency of use. For example, in fast-growing Eucalyptus plantations, large trees may intercept twice as much light as smaller trees, and use the light twice as efficiently to provide a fourfold greater rate of stem growth than smaller trees. At the stand level, increases in water supply (across geographic gradients or from irrigation) often show 50% increases in water uptake by trees, and constant or increasing efficiency of water use leads to large increases in stem growth. These insights are valuable for forest management, including understanding why subordinate trees contribute so little to stand growth, why uniform stands grow better than stands with greater variety of tree sizes, and why some species mixtures grow better than others. The production-ecology approach offers a powerful framework for how to think about the growth of trees and forests.

Keywords Forest productivity • Light use • Water use • Production ecology equation

D. Binkley (✉)
Department of Ecosystem Science and Sustainability, Warner College of Natural Resources, Colorado State University, Fort Collins, CO 80521, USA
e-mail: dan@warnercnr.colostate.edu

T. Schlichter and L. Montes (eds.), *Forests in Development: A Vital Balance*,
DOI 10.1007/978-94-007-2576-8_2,