Novelty in the tropical forests of the 21st century

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CHAPTER TWO

Novelty in the tropical forests of the 21st century

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Abstract

We review literature relevant to assessing the future of tropical forests and supplement the review with new data from the lowlands of Venezuela. Compared to today, future tropical forests will have a higher level of novelty, defined as the degree of dissimilarity of a system relative to a historical baseline. Processes of succession and evolution generate novelty in forests and have done so for millennia. Under increasing human activity and climate change, the rate of generation of novelty has increased and the resulting forests are termed novel forests to distinguish them from historical forests. Historical forests are less exposed to anthropogenic disturbances and operate at slower levels of novelty generation. Acclimation, adaptation, changes in species composition and dominance, and changes in the proportions of species in communities are the responses of the biota to climate change and anthropogenic disturbances. Therefore, novelty contributes to the persistence of tropical forests in spite of increasing levels of human activity. Novel forests are similar to historical forests in terms of structure but they are younger, they have a faster turnover of mass and chemical elements, and different species composition. Historical species assemblages cannot cope with the altered environments that result from chronic anthropogenic disturbances. The dominant species in novel forests tend to be, and function as, pioneer species. High levels of species dominance in novel forests influence the proportions of chemical elements, which when coupled to species traits and attributes, help explain how novel forests cope with the conditions that result from anthropogenic activities. Novelty is more common in the tropics than in other latitudinal regions, and within the tropics, it is more common in islands where human activity is more intense than in continents. Novel tropical forests in islands have greater representation and dominance of introduced species than novel forests in continents, where native species with wide geographic distributions dominate. Regardless of geography, novel tropical forests share similar attributes and functioning. The adaptability of novel forests to extreme conditions created by human activity signals a future for tropical forests that is different from predictions of constant degradation, homogenization, and loss of biodiversity. Instead, a process of recombination of species (all taxa) into new species assemblages maintains structure, function, physiognomy, species richness, and ecological services. This remixing initially involves loss of large organisms, certain groups of species, and loss of old-growth attributes of forests. Some of these losses can be reversed through succession, assuming there is sufficient time to restore depleted stores such as soil organic matter. Continued environmental change will stimulate continued remixing of species, loss of vulnerable species, gains of less vulnerable ones, and more dissimilarity with historical forests. Novel forests are an answer to the changes induced by climate change and other anthropogenic disturbances, and as such require conservation measures, because as they mature, novel forests usually diversify and help restore lost biodiversity. We also review strategies to conserve biodiversity and optimize ecological services using novel forest succession.

> *It is impossible to have any idea as to which will be the future dominants, but it is clear that plenty of combinations are possible and that the advance towards a climax (if such a thing can be visualized for equatorial formations) is a very indirect one.*
>
> ***(Aubréville, 1938, p. 531).***

1. Introduction

When André Aubréville, a French botanist, faced the complexity of the equatorial closed forest of the Ivory Coast (Aubréville, 1938), he saw and described the paradoxical order and stochasticity displayed by the many tree species that formed the magnificent forest. He also pondered the future of the tropical forest and expressed his point of view summarized in the quote above. At the time, he could not anticipate all the changes that would ensue in the region as a result of human influence and climate change. He did comment about the presence of species associated with humans, noting that anyone experiencing the novelty of running into an oil palm in the middle of the forest was witness to the scarce but irrefutable evidence of past human influence on a forest stand in early 20th century Africa. These days, in highly modified tropical islands such as Puerto Rico, botanists might instead find novelty in encountering a once common, but now rare, old-growth native tree species in a secondary forest site.

As did Aubréville almost a century ago, we take a critical look at the degree of transformation of tropical forests, but this time emphasizing the effects of climate change and other anthropogenic disturbances on these ecosystems. Our aim is to project current trends into the future when we expect that novel tropical forests, which we define later, will be more common than they are today. To establish the structural and compositional characteristics of novel forests in the continental tropics, we present new data from the llands of Venezuela and compare those data with similar information from the montane tropics and Caribbean islands. The Appendix contains the methods and justifications for these analyses. We also explore the ecophysiological characteristics of the successional tree species that predominate under disturbed conditions, the functioning of tropical novel forests, review criteria on how to intervene in novel forests for optimizing their ecological services, and illustrate the implications of varying levels of intervention for the future successional trajectories of novel forests. Finally, we address novel forest conservation as a strategy for assuring the persistence of threatened tropical biodiversity.

2. Novelty in ecosystems

Today, the world is characterized by constant change in almost all of its components, including the location of land masses, the climate, and the biogeography of the biota, to name a few. The magnitude, variety, and longevity of human-induced changes has led to the suggestion that we should refer to the present, not as the Holocene Epoch, but as the Anthropocene Epoch (Lewis and Maslin, 2015; Waters et al., 2016). These changes influence the global environment and promote novelty in ecological systems.

Jackson (2013) reflecting on these changes concluded that ecological novelty is not new. Humans have interacted with tropical forests for at least 100 millennia (Roberts et al., 2017), influenced the global environment, including land surface transformation, and changed the composition of the atmosphere as well (Lewis and Maslin, 2015). While the type and scale of these activities has varied across the world, sometimes leading to significant landscape effects (van der Kaars et al., 2017), the oldest evidence of human occupation in the tropical Americas dates back to 13,000 years BP (Roosevelt et al., 2002). Montoya et al. (2020) hypothesized that early scattered human populations, even in low densities, may have been responsible for some of the current patterns of forest biodiversity and structure in Amazonia. What has changed is the scale of human activity, which increasingly exerts greater influence over ecosystems and the environmental conditions of the world. This explains why when Hobbs et al. (2009) defined novel ecosystems, they included ‘human agency’ as one of the necessary components of the definition. There are three foundational principles that support the establishment of novelty in ecosystems (Mascaro et al., 2013). These are: (1) the individualistic concept of H. Gleason, which states that the flora and fauna move independently of one another in response to the environment. (2) The notion that the biotic and abiotic characteristics of an ecosystem are tethered; they interact and influence each other. (3) The fact that humans cause changes in ecosystems that are directional and permanent.

Mascaro et al. (2013) defined a novel ecosystem (p. 55) as: … *one of abiotic, biotic, and social components (and their interactions) that, by virtue of human* *influence, differ from those that prevailed historically, having a tendency to self-organize and manifest novel qualities without intensive human management.*

This definition restricts novelty to that generated through human influence. As we discuss below, novelty can also be generated by ecological processes in the absence of human intervention, but at this historic moment, human influence is accelerating the generation of novelty in ecosystems. This definition also requires a base of comparison, which Radeloff et al. (2015) addressed and we discuss below. Finally, this definition does not make a distinction on the geographic origin of the species that become part of novel ecosystems and is consonant with the Anthropocene Epoch that we live under today. We anticipate that novel ecosystems will continue to increase in abundance into the future as human control over the world reaches a peak, and it behoves scientists to study and understand their structuring and functioning to assure proper conservation policies and activities. Radeloff et al. (2015) developed a formal and quantifiable definition of abiotic and biotic novelty in ecosystems and mapped global novelty, finding that the tropics emerged as the region with the greatest level of novelty in the world.

The definition of novelty proposed by Radeloff et al. (2015) was (p. 2052): *the degree of dissimilarity of a system measured in one or more dimensions relative to a reference baseline, usually defined either as the present or a time window to the past*. The definition requires a baseline of comparison, results in a continuum of novelty, both in time and space, and allows for the comparison of multiple dimensions, both abiotic and biotic. Novelty can develop in almost all abiotic and biotic parameters or ecosystem attributes. Those used by Radeloff et al. (2015) included climate change, atmospheric nitrogen deposition, and changes associated with human population density. Equally important to the biota and the environment is the carbon dioxide concentration in the atmosphere. The concentration of this gas has oscillated over millennia but has recently increased at a fast rate powered by human activity. Because there is a limitation of tropical data availability to conduct the kinds of analyses in Radeloff et al. (2015), we will use a biotic criterion to assess novelty in tropical forests. Specifically, we focus on the species composition, which changes in response to climatic and other environmental disturbances. The tropics have been sufficiently explored taxonomically to allow the exploration of biotic novelty under the influence of human agency, even if we lack sufficient details on the abiotic changes associated with biotic novelty. Our review of tropical forests emphasizes biotic novelty with inferences about abiotic causes, when those causes are not quantified.

Novelty in the form of new species, new species assemblages within communities, rapid turnover of species, or new abiotic conditions is a natural product of species evolution and forest succession. Novelty has existed and will continue to exist as long as evolution and succession occur on the planet. Novelty is a measure of the degree of adaptation to changing conditions under which species evolve and species assemblages change over time. However, the pace of novelty generation has increased in the Anthropocene due to increased human activity and the heterogeneity in environmental conditions that it creates (Lugo et al., 2018). Novelty is revealed in the changes of the relative importance of species within species assemblages, the gains and losses of species from assemblages, and by the remixing of species into different rank order of species irrespective of geographic origin.

3. Change in tropical climates

No one questions the importance of climate to vegetation functioning and physical appearance, and one can safely assume that if the climate changes, the vegetation will respond. The unanswered question at this historic moment is: What is the projected magnitude of climate change into the near future, and what level of persistence can we expect of historical ecological systems given the projected level of climate change? We also do not know the relative roles in the generation of novelty in ecosystems played by climate change and other human disturbances.

A review by Bailey (2009) suggested that tropical rain and dry climates would increase in geographic area while boreal and snow climates would decrease (see also Belda et al., 2014). These predictions are based on global climate models that have a poor performance when dealing with tropical latitudes. For example, the range in the level of the 2000–06 trend in net ecosystem productivity predicted by seven climate models of the Coupled Model Intercomparison Project Phase 5 was about $80\,\mathrm{g\,C\,m^{-2}\,year^{-1}}$ for most latitudes except the tropics. For the tropics, the range of the output among the models was greater than $220\,\mathrm{g\,C\,m^{-2}\,year^{-1}}$ or almost three times more uncertain than for temperate and boreal latitudes (Cavaleri et al., 2015). Worse yet, in terms of the prediction for tropical latitudes, some models describe the region as a net source of carbon, while others do so as a net sink. Global climate models do not recognize the diversity of climatic conditions in the tropics as revealed by the Holdridge Life Zone System (Holdridge, 1947). The Holdridge system depicts climate in general, and that of the tropics and subtropics in particular, with greater geographic precision and repeatability than the Köppen-Trewartha system (Lugo et al., 1999a). The application of the system is limited by the availability of empirical climate data, which the Köppen-Trewartha system was designed to overcome (Bailey, 2009).

We define the tropics and subtropics as those geographic locations without frost in the lowlands (0–500 m elevation; Holdridge, 1967). If climate change reduces the frost occurrence in the lowlands of continents and islands, it is possible that the geographic extent of areas defined as tropical and subtropical will expand. A faster atmospheric warming rate at the higher northern latitudes of the tropics and subtropics, i.e., the Tropic of Cancer at 23.5° north latitude, can have an effect on the northern distributions of tropical and subtropical species. Low temperature sensitive species in tropical, subtropical, and warm temperate life zones can expand their northern range if the frequency of frost declines and if they can overcome other ecological barriers associated with latitudinal changes and migration. The same is true, but in the opposite direction, at the southern limits of the Tropic of Capricorn.

The depiction of the geographic distribution of tropical and subtropical forests by life zone has been used to illustrate the effects on those forests of the accelerating climate change (e.g. Cramer and Leemans, 1993; Emanuel et al., 1985; Smith et al., 1992). One would expect that climate change shifts the geographic influence of life zone conditions. Some areas will shift to warmer and drier life zones while others will shift to wetter and cooler ones, and some might not change. A shift in life zone distribution, coupled with the effects of human activity and extreme events, are likely to induce changes in the composition and the proportions of species in species assemblages. Moreover, the relative importance of a life zone shift and level of anthropogenic disturbances may not be homogeneous geographically. One could expect that some geographic regions may be more vulnerable to a given force of change, or there might be locations where both forces of change (climatic and anthropogenic) converge. An example is the Amazon forests where anthropogenic changes such as deforestation are not distributed homogeneously within climatic life zones (Laurance et al., 2006; Phillips et al., 2008).

A problem when anticipating climate change over specific locations is the resolution of global climate change models. For example, when addressing climate change over montane tropical areas, Helmer et al. (2019) observed that the grid size of global climate change models was too coarse (0.5°) to assume that any of those projections would reflect the conditions that local vegetation would face. Moreover, they indicated that within one grid cell of a global climate model, *climate changes with elevation over distances shorter than each cell* (p. 4/34). Thus, the predicted ecophysiological effects of climate change based on global climate models must be interpreted with caution and with consideration to the difficulties in downscaling global models to local scales, and the ecological and environmental variation within local geographic and ecological scales.

In a study that overcomes the resolution limitations of global climate models, Helmer et al. (2019) predicted that the climatic conditions that lead to the familiar tropical montane cloud forests and *páramo* vegetation in the Caribbean and throughout the Neotropics, will mostly disappear in 25–45 years under a worst-case scenario that projects the Earth-atmosphere energy balance change as a result of continuing increases in greenhouse gas emissions and land use changes. As discussed by Helmer et al. (2019), the implications to the persistence of the unique biodiversity of this rich and extensive region of the Neotropics are dire.

Henareh et al. (2016) used a different approach than used by Helmer et al. (2019) to project into the future climate change conditions in Puerto Rico. They downscaled the output of 12 general circulation climate models to assess the distribution of the Holdridge life zones of Puerto Rico from 1960–90 to 2071–99. Life zones shifted from wetter to drier life zones and they projected the loss of the wettest life zone in the island, the subtropical rain forest life zone. In their worse case scenarios, the island loses its subtropical wet, and rain forest life zones, and gains five life zones, including four tropical ones (tropical wet forest, tropical moist forest, tropical dry forest, and tropical very dry forest), and a subtropical thorn woodland. The predicted trend is for warmer and drier life zone conditions. In all scenarios, the model predicts a shift in the most geographically extensive life zone of Puerto Rico from subtropical moist forest to tropical dry forest within 100 years. The application of similar methods yielded similar results for continental Central America; a decrease in the extent of cloud forests at high elevations and an extension of drier climates into higher elevations (Kamalkar et al., 2008). The heterogeneous topography of insular montane landscapes, combined with anthropogenic barriers to dispersal and migration, including abandoned fields and urban development, are likely to affect the expected movement of organisms in response to climate change, more so than in continental areas where dispersal and migration of vegetation may be more feasible.

Cloud forests and other life zones at high elevations may be more likely to be affected by climate change than lowland life zones given the differences in areal extent of the life zones. A lowland life zone is more likely to cover a larger area than a montane one given the steepness of the climatic gradients in mountains relative to lowlands. Therefore, climate change is more likely to affect montane forests much quicker than lowland forests (but see Esquivel-Muelbert et al. (2018) and Edwards et al. (2019), for examples, where the synergy between climate change and other anthropogenic disturbances create greater effects on lowland Amazonian forests). As an insular example, Campos Cerqueira et al. (2017) found bird populations expanding their home ranges in the Luquillo Mountains of Puerto Rico. They found that of 29 bird species in these mountains, eight species, or 28%, showed significant shifts in their range limits, mostly towards higher elevation, between 1998 and 2015. A continental example is Morueta Holme et al. (2015) study of 210 years of vegetation change on the Chimborazo volcano in Ecuador. They compared today's vegetation with the description of von Humboldt and Bonpland (1807). They found an upward shift in the distribution of vegetation zones as well as increases of >500 m in the maximum elevation limits of individual plant taxa. These range shifts are consistent with increased temperatures and glacier retreat on Chimborazo since Humboldt's visit.

The expected climatic changes can fundamentally shift the moisture and temperature conditions under which most organisms live today. This can lead to shifts in the dominance of species within species assemblages to those with ecological response strategies associated to faster rates of processes and smaller size organisms. Corresponding spatial-temporal lags in dispersal and migration-mediated responses may also become more evident with time. A single or a small subset of species from the total species pool already dominates primary and secondary tropical forests in some regions of the tropics (Hubbell, 2001; Kazmierczak et al., 2016; ter Steege et al., 2013). We anticipate that species dominance in novel forests will shift to a subset of those species with favoured traits such as faster growth, larger leaves, fistulose branches, and significant amount of seeds (Gómez-Pompa, 1971; Ramos Prado et al., 1982; Vázquez Yánez, 1980). The shift involves responses to both climatic and edaphic (soil condition) changes. A shift to higher species abundance is implicit in the notion of hyperdominance observed in the trees of the Amazon by ter Steege et al. (2019). They assessed 10,071 tree species and found that over half the stems belong to just 227 species.

A similar imbalance was also observed in species to genus ratios. Over half of all Amazonian tree species belong to genera with 100 or more species, while 52% of the genera have 10 or fewer species (Dexter and Chave, 2016). Some of these hyper dominants are tree species with some evidence of domestication that dominate large forest areas, especially in those locations near archaeological sites (Levis et al., 2017).

4. Three case studies regarding novelty in tropical forests

Novelty in the tropics is revealed in changes in the composition of floras. We reviewed tropical floras from 28 continental and 33 insular locations (Appendix) and found that the percentage of naturalized species in the published floras averaged 9.9 (SE 0.1) and 17.5 (SE 0.1), respectively. The level of species naturalization is more obvious in islands where species from other geographic locations are easier to record. Moreover, synanthropic taxa, i.e., taxa associated with humans, were introduced since the colonial and exploration times, due the Europeanization of their colonies (Correoso Rodríguez, 2005). In Puerto Rico, the species richness of most taxonomic groups has increased as a result of species introductions and naturalization being greater than species extinctions (Lugo et al., 2012a,b; Torres and Snelling, 1997). All these increases in faunal and floral composition strongly suggest that the species assemblages in these tropical locations contain novel combinations of species different from historical combinations of species.

Novel tropical forests appear to be more abundant in the insular tropics than the continental tropics (Ewel et al., 2013) because human population and activity are concentrated in islands compared to continental regions. As a result, a greater fraction of insular territory is affected by human activity when compared to continental territory. This means that the insular biota faces more environmental challenges and anthropogenic disturbances than continental biota, thus generating more novelty. Thus, while islands may appear different when compared to continents because of the intensity of change in their species assemblages, they are reflecting particular circumstances while following the same ecological principles that govern continental systems. Our review of the tropical literature shows that novel forests occur on the montane and lowland continental tropics and are beginning to be recognized as such (Aymard, 2017; Aymard and González, 2014). Nevertheless, we need to examine the outcomes of novelty generation in islands vs. continents to firmly establish what they have in common and where they diverge.

In this section we compare novel forests in Caribbean islands with those in the South American continent. We use Puerto Rico as representative of Caribbean islands, and the Venezuelan Andes (from now on *los Andes*) and Venezuelan Llanos (from now on, *los Llanos*) as representatives of montane and lowland continental areas, respectively. Like in the forests of Caribbean islands, the floras of *los Andes* and *los Llanos* have experienced intense human activity, which has led to changes in the species composition and structural complexity of its vegetation (Aymard, 2017; Aymard and González, 2014; Sarmiento and Llambí, 2011). By comparing continental vegetation with Puerto Rican novel forests, we can advance the understanding of the emergence of novelty in tropical forests and gain insights about the potential future species composition, structuring, and functioning of tropical forests. We start by summarizing the current understanding of novel forests in Puerto Rico, followed by information about vegetation in *los Andes* and *los Llanos*.

4.1 Island novel forests: A case study from the Caribbean

The vegetation survey of Puerto Rico and the US Virgin Islands of Gleason and Cook (1926) documented the importance of native species in the locations that they visited. Detailed succession studies, such the one by Smith (1970) following ionizing radiation and experimental cutting of forests in the Luquillo Mountains, also established a succession of primary and secondary native species with no obvious deviation in terms of species composition from what was expected in the absence of human intervention, even if the experiment themselves (ionizing radiation and clearcutting) were human-induced. The expression of novelty in this succession involved the substitution of the floristic composition of the primary forest with secondary forest ones, and changes in the proportions of species in seedling populations. Four individuals of *Phytolacca icosandra* colonized and expanded on the radiation and the cut sites in locations subjected to heavy trampling. Over the next 23 years the radiation site generated high levels of novelty through a high turnover of herbs, vines, ferns, saplings, seedlings, and graminoids. This succession led to a closed canopy forest with the same species described by Smith (Taylor et al., 1995) but assembled with a different proportion of importance measured by the species Importance Values, i.e., the sum of a species relative density and relative basal area, expressed in percent (Appendix). Notably, all taxa involved in this study were native species. The generation of novelty in this succession was low from the point of view of floristic composition, but the rate of biomass accumulation in this radiation-stressed system was different from similar forest stands responding to hurricane effects (fig. 19.5 in Lugo and Heartsill Scalley, 2014). In this review we use the term 'historical succession' and 'historical secondary forests' to designate successions and their outcomes (respectively) where the native species composition involved deviates very little from what is normally expected in the absence of anthropogenic effects.

Studies of succession on abandoned pastures in northeastern Puerto Rico revealed a higher level of novelty generation than observed in the experimental succession studied by Smith (1970) and Taylor et al. (1995). The findings of these studies (Aide et al., 1995, 1996; Lugo, 1992; Zimmerman et al., 1995, 2000) included: the initial failure of native pioneer tree species to colonize the pasture; over one decade of high levels of dominance by a group of shrubs and treelets, including high elevation sites with a single species (*Miconia prasina*) with 100% Importance Value; the eventual establishment of native tree species; and the emergence of introduced species in the succession (10 of 112 woody species). Aide et al. (1996) noted that the original species composition had not developed after 40 years of succession and that these secondary forests could not be distinguished from undisturbed sites in terms of tree density, basal area, number of species, species diversity, or physiognomy, i.e., the shape, height, and physical appearance of vegetation. A statistical analysis of the succession trajectories resulted in the expected importance of age, elevation, and time as correlates with stand characteristics and species composition. However, those analyses and canonical ordinations could not explain the observed high degree of floristic variation. We argue that this floristic variation is a measure of the high degree of novelty generated by the successions under study. We term this type of succession novel succession and its outcome novel secondary forests (or just novel forests), because both the path and the outcome of succession deviate significantly from historical successions. In Puerto Rico, the deviation includes the presence of introduced species, but as we will see in the example from Venezuela, the deviation from historical patterns may or not involve introduced species.

Aide et al. (1995, 1996) and Zimmerman et al. (2000), still working in northeastern Puerto Rico, explored the causes that prevented native pioneer species from colonizing abandoned pasture sites. They identified biotic and abiotic barriers that impeded forest regeneration and seedling establishment, including depleted seed banks, lack of advanced regeneration, the composition and abundance of seed in seed rain, distance to seed sources, loss of seed dispersers, and species traits. Soil compaction, loss of soil structure, and erosion were identified as abiotic factors that gave advantages to introduced tree species over native ones. Silander (1979) found that the pioneer *Cecropia schreberiana*, a Caribbean endemic element, could not colonize pastures because insects reduced seed viability to 1 or 2 months, and high and fluctuating soil temperatures and/or low and fluctuating soil moisture reduced germination rates. Clearly there is a strong selection at the point of tree establishment (ecesis) that can regulate the species composition of developing forests.

Aide et al. (2000) studied the succession of 71 abandoned pastures in four geographic locations within Puerto Rico, and confirmed the results discussed above while adding an additional level of novelty to the ecological outcome of their observations. They found more introduced tree and shrub species present in the successional trajectories of abandoned pastures compared to sites previously subject to other forms of agriculture, such as shade coffee and subsistence farming. The presence of introduced species, coupled to a predominance of native tree species regenerating in the understory, resulted in forests with species composition that contrasted with the species composition of old forest sites in the vicinity of the emerging forests on abandoned pastures. The differences were sufficient to lead the authors to conclude (p. 333) that: ...*it will take many years for the species composition to converge with that of the old forests*. Alternatively, what if the species composition does not converge? Or better yet, why should it be presumed that it has to converge? Aubréville (1938) made this point clear in his seminal paper: there can be as many successional trajectories as there are biotic, abiotic, and historical (i.e. anthropogenic) contexts.

The repetitive inventory of Puerto Rico's forests, which began in 1982 (Birdsey and Weaver, 1982), and continues today (Marcano Vega, 2019), provided sufficient information at the insular scale to show that 75% of the forest area of Puerto Rico were novel forests (Lugo and Helmer, 2004; Martinuzzi et al., 2013). These novel forests are shaped by the climate (Brandeis et al., 2009) as is the other 25% of the forest area with historical forest cover. An extensive literature documents the structural and species composition of these novel forests (e.g. Abelleira Martínez and Lugo, 2008; Abelleira Martínez et al., 2010; Lugo et al., 2011a, 2012a), the novel animal communities associated with them (e.g. Abelleira Martínez, 2008; Lugo et al., 2012b) and other associated plants (e.g. Pérez et al., 2012), and temporal and spatial structural variation in dry climates (e.g. Molina Colón and Lugo, 2006; Molina Colón et al., 2011; Ramjohn et al., 2012).

These novel forests do not show evidence of homogenization of the biota because the very high dominance of canopy species early in the succession decreases over time and also decreases vertically within stands with increasing species richness in the lower forest strata (Abelleira Martínez, 2010). In fact, fig. 20.3 in Lugo and Brandeis (2005) shows that a hectare of novel forest has a greater number of tree species than a hectare of mature historical forests dominated by native species.

4.2 Montane continental novel communities: A case study from the Andes

The mountaintops in *los Andes* comprise ecosystems known as the *páramos* (Vareschi, 1970). Their vegetation includes a considerable number of endemic species with a particular physiognomy. Standing out is the Espeletiinae group, with a remarkable degree of morphological diversity, including trees with profusely branched, dichotomous or unbranched stems, shrubs, and rosettes that can be sessile, short-branched or, notably, giant caulescent rosettes (Cuatrecasas, 2013). The *páramo* vegetation also comprises numerous representatives of Poaceae, Asteraceae (*Espeletia* sensu *lato*), and Ericaceae (Jiménez Rivillas et al., 2018).

For about 400 years, the *páramos* of the state of Mérida have been dedicated to wheat farming with no apparent efforts to conserve soil. When fields are abandoned, the historical vegetation is slow to return. Sarmiento and Smith (2011) studied the vegetation of this region in relation to past and present land use and found four community variants with different combinations of species: *páramo* (assumed to be undisturbed, but less developed than *páramos* under more favourable conditions), degraded shrublands, transitional vegetation, and degraded communities dominated by a matrix of Poaceae elements called *pajonales* in Peru. They found that after 40 years of abandonment, there is no evidence to show that the combination of plant species that constituted the *páramo* was returning to the abandoned lands. The results of a linearized correspondence analysis (their figure 7), showed that the vegetation aligned along a soil degradation axis with the *páramo* on one extreme and the degraded shrublands in the other. Transitional vegetation overlapped the *páramo* and degraded shrublands but was closer to the *páramo* than to the degraded shrublands.

The *pajonales* separated from the other three vegetation types and fell outside the main disturbance gradient. *Pajonales* exhibited a dramatic change in species composition including the dominance of a taxon that ranges from Argentina to the state of Utah in North America; the grass *Jarava ichu*.

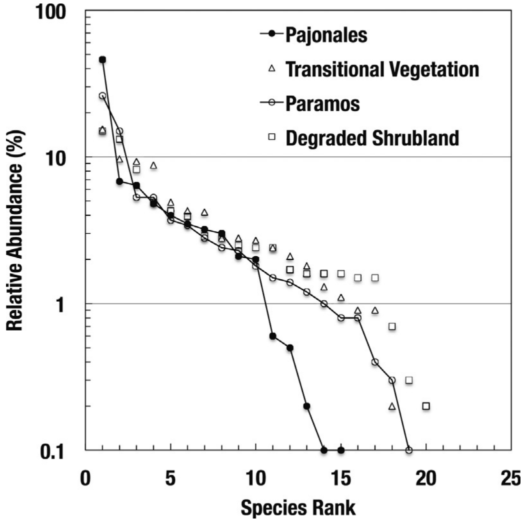

Fig. 1 Ranked-abundance curves for four vegetation types in the wheat-growing region of the Venezuelan Andes. *Data are from Sarmiento, L., and J. K. Smith. 2011. Degradación de laderas durante el ciclo triguero en los Andes venezolanos y factores que limitan su restauración. 17-34 in F. Herrera and I. Herrera, Eds. La restauración ecológica en Venezuela: fundamentos y experiencias. Ediciones IVIC, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela.*

When all the species in all four communities were ranked by abundance (Fig. 1), the graph shows lower number of species and higher abundance for the top ranked species of the *pajonales* compared to *páramo*. The community attributes of the *pajonal* compared with those of the historical *páramo* (increased abundance, lower number of species, different common species, and different mix of species) deviate considerably from the historical vegetation, reflecting a high degree of novelty.

As discussed above for Puerto Rico, the shift in community structure and composition is associated with deteriorating soil conditions due to anthropogenic disturbance. Sarmiento and Smith (2011) found that *pajonales* were associated with significant change in soil texture (more sand and less clay), over 60% reduction in soil organic matter, and lower soil nitrogen relative to the *páramos*. As in Puerto Rico, soil erosion changed the path of succession. The biotic response involved changes in species composition and dominance that led to a biological capability that could deal with the novel conditions of anthropogenic disturbance. The main difference was that in Puerto Rico, introduced species prevailed through all the succession but in *los Andes*, native species prevailed and a grass with a wider geographic distribution emerged as the dominant species. Moreover, the remixing of species through succession in Puerto Rico included both native and non-native species, but in *los Andes*, the emergence of introduced species was only observed for the first 2 years, and from there on, succession was dominated by native species (Sarmiento and Llambí, 2011).

4.3 Lowland Continental Novel Forests: A case study from the Venezuelan Llanos

The 90 0.1 ha-plots (100 by 10 m) from *los Llanos* that we analysed (Fig. 2) had a total of 872 taxonomically resolved morphospecies from at least 96 plant families. However, only 52 plant families (226 species) were contributing more than 50% dominance as measured by the species Importance Value. Further, only 169 species were represented in the grouping of the top three species of each plot arranged by Importance Value. When we focused on the 15 plots with the highest values of Importance Value observed among their dominant species, we found 44 species, and from those then selected the 15 species with the highest Importance Value among them (Table 1). These species are represented by only ten families and are all native species, including trees, palms, and bamboo. Only two of the tree species

Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Fig. 2 Map of Venezuela showing the location of 90 vegetation plots in the Llanos. *Data are from G. Aymard and the cartography is by Olga Ramos González.*

Table 1 Species with the highest importance values (based on stem density and basal area) in novel forests of *los Llanos* of Venezuela.

Species	Family	Importance value (%)
Inga oerstediana	Fabaceae	64.29
Guazuma ulmifolia	Malvaceae	62.57
Cochlospermum vitifolium	Bixaceae	56.51
Virola elongata	Myristicaceae	51.04
Tapirira guianensis	Anacardiaceae	46.39
Guarea guidonia	Meliaceae	45.88
*Attalea maripa**	Arecaceae	44.92
Protium tenuifolium	Burseraceae	43.46
*Guadua angustifolia**	Poaceae	39.91
Anacardium excelsum	Anacardiaceae	39.59
Inga nobilis	Fabaceae	39.51
Senegalia polyphylla	Fabaceae	37.39
Rudgea crassiloba	Rubiaceae	37.12
Ceiba pentandra	Malvaceae	35.69
Protium stevensonii	Burseraceae	34.75

The list includes woody (tree, shrub, liana), and non-woody (*) standing (bamboo and palm).

(*Ceiba pentandra* and *Guazuma ulmifolia*) appear in the list of 29 pioneer species of the Neotropics published by Chazdon (2014), which is a list influenced by forests with greater rainfall than those in *los Llanos*.

High dominance in forests, measured by the sum of the Importance Value of the top three species in a plot, was associated with lower species per plot and lower complexity index (Fig. 3). The complexity index of the community tended to increase with a reduction in dominance, but this relationship was not statistically significant at $P < 0.05$. It appears that the structural attributes of communities (height, basal area, stem density) upon which the complexity index is based are not dependent on the floristic composition of the community, as was described by Aide et al. (1995, 1996, 2000) in Puerto Rico. In other words, communities are seldom novel from the point of view of stand structural parameters. The source of novelty emerges from floristic composition and the effects of species on ecosystem functioning that we discuss below.

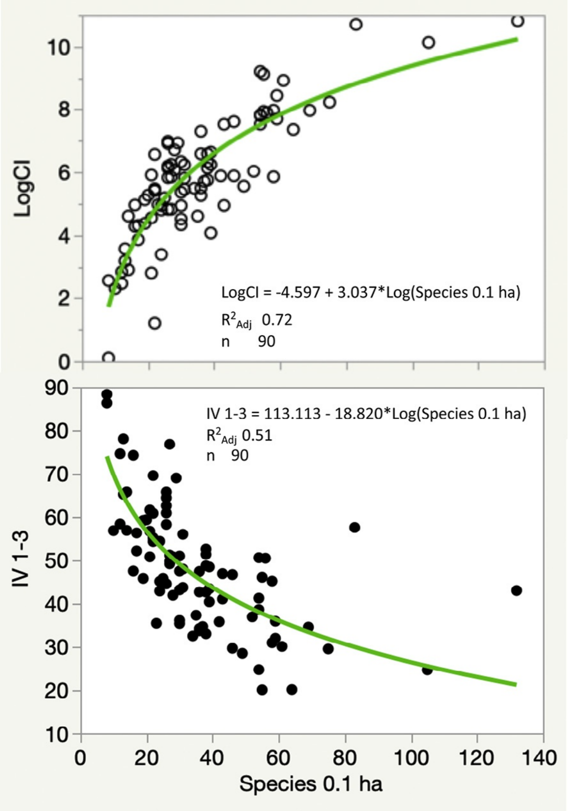

Fig. 3 Non-linear relationship between the number of species per 0.1 ha with the Complexity Index of vegetation (open circles) and sum of the Importance Value of the three-most dominant species in 90 plots in the Venezuelan Llanos (filled black circles). *Data are from G. Aymard.*

The dominant species in the 90 plots have in common a wide geographic distribution throughout the Neotropics, including from Argentina to Mexico, or from Brazil through Colombia to Panama, and also from the Caribbean islands. They all function as pioneer species but have different traits. For example, some are shade intolerant with rapid growth (*Senegalia, Handroanthus, Tabebuia, Hura*), some have seeds dispersed by animals (*Inga, Guazuma*), or by wind (*Ceiba, Heliocarpus, Cochlospermum*). The genera *Inga, Spondias*, and *Erythrina* are examples of taxa that can grow in mature forests favoured by human activity because of their dispersal by animals, and human use for their products or for shade. Species of the genera *Virola*, *Tapirira, Guarea, Anacadium, Protium, Annona*, and *Ficus* have fleshy seeds dispersed by animals and generally occur in later stages of succession where shade tolerance favours them. *Heliocarpus americanus* grows in pre-montane forests above 400 m elevation. Palms form mature forests on sites with soils with poor drainage as is also the case with *Anacardium, Guarea,* and *Zygia.* Leguminosae (sensu *lato*) and species of *Inga* and *Pterocarpus* have associations with nitrogen-fixing bacteria.

The analysis of secondary forests in *los Llanos* established that these forests had high levels of species dominance, with a few species accounting for over 50% of the Importance Value of the communities. Moreover, these dominant species were native species with wide geographic distributions throughout the Neotropics. We now ask: How different are these communities from those described by Veillon in the 1950s to the 1970s?

Jean Pierre Veillon made an extraordinary effort to describe what he designated the natural forests of Venezuela (Veillon, 1995, 1997), which we identify as historical forests. Between 1953 and 1978 he set up 62 large plots (>1 ha) in undisturbed forested areas or in areas in the process of being altered by logging activities. He focused on trees larger than 10 cm diameter at breast height and described in detail the structure and floristic composition of forests throughout nine states in Venezuela, including those of *los Llanos*. Because he was interested in the primary vegetation under various climatic, edaphic, and geomorphological conditions, he also collected information on the level of human activity and intervention within the forests that he sampled. Veillon studied six locations (Table 2) in *los Llanos* where, in his view, the primary and secondary vegetation could be compared because of their similar climate and close proximity. His main findings were that human intervention changed the floristical composition and structure of the stands. Stands with notable human influence were considered secondary vegetation. He also found that these secondary forest stands had not recovered their original species composition when compared with stands that he defined as primary forest stands. We compared species dominance in those same six stands using indices of species relative Importance Value measured by species Importance Values, and also compared them with those studied by Aymard as discussed above (Table 1).

As suggested by Veillon, there was little overlap in the top three dominant species of primary and secondary forests in *los Llanos* (Table 2). Moreover, the Importance Value of individual species and the sum of the Importance Value indices of the top three species did not differ between the two groups. The Importance Value in Veillon's plots were generally low, with the exception

Table 2 Species with the highest importance values in mature, climax, and secondary forests of *los Llanos* of Venezuela sampled by Veillon (1997).

Site and location	Dominant species (IV)	Importance value
Primary forests		
Alto Tucupido (24.7)	***Bombacopsis quinata*** (***Pochota fendleri***)	10.6
230 m elevation. Guanare, Portuguesa	*Unknown*	7.6
	Chrysophyllum caracasanum (*Pradosia caracasana*)	6.8
Ticoporo Aereopuerto (44.2)	***Symmeria paniculata***	16.1
120 m elevation. Pedraza, Barinas	***Bombacopsis quinata (Pochota fendleri)***	15.4
	Pouteria anibaefolia (Pouteria reticulata)	12.7
Mijagual (47.7)	*Anacardium excelsum*	26.5
150 m elevation. Pedraza, Barinas	***Pouteria anibaefolia (Pouteria reticulata)***	16.1
	Sorocea sprucei	5.1
Secondary forests		
Caimital (33.5)	***Symmeria paniculata***	13.7
150 m elevation. Obispos, Barinas	***Maquira coriacea***	10.5
	Bombacopsis quinata (Pochota fendleri)	9.2
Hato Sansun (28.21)	*Bravaisia integerrima*	13.0
100 m elevation. Guanare, Portuguesa	*Spondias mobin*	9.4
	Maquira coriacea	5.8
La Ricaldera (41.9)	*Piptadenia peregrina* (*Anadenanthera peregrina*)	18.8
200 m elevation, Obispos, Barinas	*Cochlospermum vitifolium*	12.6
	Protium heptaphyllum	10.5

All sites are in the tropical dry forest life zone sensu Veillon (1974). Importance Value (IV) is in percent, based on tree density and basal area. The IV for three dominant species is in parenthesis next to the site location. Species in bold appear in more than one site. Scientific names are updated in parenthesis.

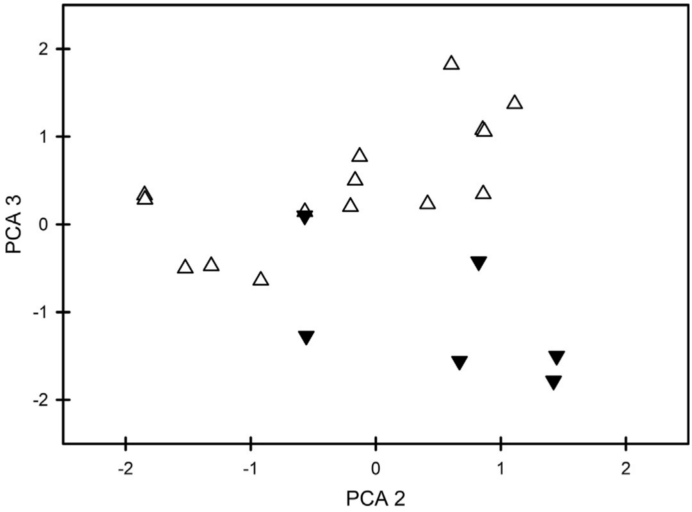

Fig. 4 Relationship between the number of species per 0.1 ha (X axis) and the annual basal area growth in m^2 ha^{-1} in 90 vegetation plots in the Venezuelan Llanos. *Data for plots from G. Aymard are symbolized with open triangles and from Veillon, J. P. 1997. Los bosques naturales de Venezuela. Parte III. Los bosques tropóficos o veraneros de la zona de vida de bosque seco tropical. Universidad de Los Andes- Consejo de Publicaciones, Instituto Forestal Latinoamericano, Facultad de Ciencias Forestales y Ambientales, Mérida, Venezuela, p. 127 with filled inverted triangles.*

of *Anacardium excelsum* with an Importance Value of 26.5. This was due to the large size of these trees (high basal area), which are among the largest trees in *los Llanos*. Although the stands were different floristically, they were not different in terms of species dominance; the level of novelty in the successional forests was low compared to the historical primary forest stands. In contrast, species dominance in the subsequent Aymard inventory in Table 1 was higher than all six Veillon stands by a factor of 2. This is illustrated in the distribution of plots in ordination space as defined by the Importance Value contribution of individual species (Fig. 4), which has shifted from the proportions observed in the Veillon plots to those in the Aymard plot inventory. The horizontal axis separates plots by their second highest Importance Value species ($r^2 = 0.705$), while the vertical axis separates plots based on their highest Importance Value ($r^2 = 0.987$).

The secondary species in Veillon plots, like those in Aymard plots, had wide geographic distribution. The range of *Symmeria paniculata*, *Maquira coriacea*, and *Protium heptaphyllum* extended from Bolivia to Venezuela. *Spondias mombin* extended from Bolivia to Mexico and the Caribbean, while the distribution of *Anadenanthera peregrina* is accelerated by humans because its seeds are the source of a powerful hallucinogenic snuff called *yopo*. Currently, the distribution of this species ranges from Argentina to Venezuela, the Guianas, Brazil and the Caribbean. *Cochlospermum vitifolium* extends from South America, Central America, Mexico, and the Caribbean, and *Bravaisia integerrima* from Colombia, Venezuela, the Caribbean, Central America, and Mexico.

The suite of species dominating the historical forests of *los Llanos* had little overlap with those dominating Aymard plots, i.e., 4 species in Veillon plots appeared among the list of the top 15 dominant species in Aymard plots. Notably, one species that dominated secondary forests in Veillon plots was among the top dominants in Aymard's plots (e.g. *Cochlospermum vitifolium*), which raises questions about the level of disturbance in Veillon's primary forest plots. These comparisons reflect a high level of novelty in the forests that now prevail in *los Llanos* compared to historical forests studied by Veillon.

5. The functioning of novel tropical forests

In the preceding text we have argued that some anthropogenic disturbances, such as soil erosion, can affect the conditions of plant establishment (ecesis) for a long time, essentially acting as chronic events. The novel conditions for ecesis that result from these anthropogenic disturbances can lead to novel successional trajectories and novel forests that are different from those associated with the historical forests that they replace. In this section we focus attention on functional comparisons between novel and historical forests. Such comparisons are affected by the age of stands, particularly when dealing with successional trajectories. Lugo et al. (2018) took age into consideration when comparing the functioning and related ecological attributes of novel and historical forests (their table 1). They compared young novel with young historical, and mature novel with mature historical forests, and found that mature novel forests were more similar to young novel forests than they were to mature historical forests. The age range of available stands limited comparisons because the age difference between mature historical and mature novel was high. The oldest novel forests available for comparison were less than 100 years old, while mature historical stands can be twice that age.

Age also has an influence on other comparisons that involve species and system attributes. At the species level, Grime and Pierce (2012) analysed the role of species within ecosystems by what they called the CSR strategies. These involved the maximization of resource acquisition (C), maintenance of metabolic performance in variable and unpredictable conditions (S), and regeneration or the rapid completion of the life cycle (R). Lugo et al. (2018) compared novel with historical forests in the subtropical moist forest life zone of Puerto Rico using the CSR strategy as the measure of comparison. They found that historical forests were consistently S-selected, while novel forests had both C-selected and R-selected traits. In no comparison did novel forest species fall on the S-selected strategies.

At the ecosystem-level novel and historical forests differentiate by what Walker and Salt (2006) defined as slow variables. In any system, a slow variable is a storage or compartment, such as soil or wood in forests, with a slow turnover rate. The turnover rate is calculated by dividing a flux (mass per area and time) into the compartment by the storage (mass per area), resulting in X turnovers per time. In a forest, for example, state variables can be arranged by decreasing turnover rate: leaves < roots < aboveground wood < soil organic matter. In this example, soil organic matter, with the slowest turnover rate is a slow variable. Slow variables are important for ecosystem function because their turnover is associated with resilience. Slow variables take more time to develop, but they provide buffering to disturbances. Conversely, fast variables recover quickly but are less resistant to change. When comparing novel with historical forests, Lugo et al. (2018) found that slow variables had larger storages in historical forests than in novel forests, where fast variables predominate over slow ones.

The three case studies that we presented above have shown that novel forests, in contrast to historical forests, have higher species dominance and novel species assemblages with introduced and/or native species with wide geographic distribution. The question that we address next is: What are the implications of high species dominance and novel species composition to ecosystem-level functional attributes of forests?

We do not expect to find novel ecophysiological characteristics at the species level when comparing novel and historical secondary forests. The reason is that the types of species in secondary novel forests are mostly pioneer species with similar ecophysiological traits as those in historical secondary forests. The common ecophysiological traits of pioneer species occur regardless of whether they are part of a novel or a historical forest. However, the ecophysiological traits of pioneer species contrast with those of species classified as non-pioneer or late-succession species (Table 3). Exceptional cases emerge from remnant agricultural or ornamental trees that have

Table 3 Properties of secondary forests and the dynamics of ecosystem reconstruction (Bazzaz, 1979).

Attribute	**Early successional plants**	**Late-successional plants**
Seeds		
Dispersal in time	Long	Short
Wind dispersed or animal dispersed?	Wind	Animal
Seed germination enhanced by:		
Light	Yes	No
Fluctuating temperatures	Yes	No
High NO_3^- concentrations	Yes	No?
Inhibited by far-red light	Yes	No
High CO_2 concentrations	Yes	No?
Photosynthesis		
Light saturation intensity	High	Low
Light compensation point	High	Low
Efficiency at low light	Low	High
Photosynthetic rates	High	Low
Respiration rates	High	Low
Transpiration rates	High	Low
Stomatal and mesophyll resistances	Low	High
Resistance to water transport	Low	High
Acclimation potential	High	Low
Recovery from resource limitation	Fast	Slow
Physiological response breadth	Broad	Narrow
Resource acquisition rates	Fast	Slow?
Material allocation flexibility	Fast	Slow?

naturalized and do not necessarily conform entirely to an early-successional set of plant traits as are the cases of *Delonix regia* and *Mangifera indica*. Nevertheless, these differences are expected to hold in most examples of species belonging to these two groupings, regardless of whether they are growing in novel or historical forests. Similarly, the ecophysiological response of tropical tree species and communities to the environmental challenges associated with climate change and deforestation are beginning to be understood (Table 4), and it is unlikely that the ecophysiological responses to those challenges will be different in novel vs. historical forests. The same would apply to systems level comparisons of mass and nutrient fluxes between those two types secondary forests (but see table 1 in Lugo et al., 2018).

We do expect that individual species traits could influence the comparison of novel vs. historical secondary forests, if the species in question through its dominance in the community could influence the behaviour of the whole forest. Given the differences in the degree of species dominance

Table 4 Likely ecophysiological challenges to tropical plants and other predicted changes that can affect tropical forests as a result of environmental changes associated with the Anthropocene Epoch.

Environmental challenge	Effects on plants or forests	Plant or forest responses	References
At the plant population level			
Increased in atmospheric carbon dioxide concentration	Response is species-specific; transient increase in photosynthesis rates of C-3 plants. Decrease of stomatal conductance	Increased nitrogen use efficiency, non-structural carbohydrates, and water use efficiency. Frequency of lianas related to CO_2 and wind dispersed seeds	Körner (2003), Long et al. (2004), Cernusak et al. (2013), Phillips et al. (2002), Wright et al. (2004), and Schnitzer and Bongers (2011)
Increase in air temperature	Respiration rates increase faster than photosynthesis rates	Acclimation, hot nights increase carbon loss. Woody lianas can acclimate to nighttime warming. Leaves can acclimate to gradual warming	Lloyd and Farquhar (2008), Clark (2004), Slot and Kitajima (2015), and Slot and Winter (2017)

Continued

Table 4 Likely ecophysiological challenges to tropical plants and other predicted changes that can affect tropical forests as a result of environmental changes associated with the Anthropocene Epoch.—cont'd

Environmental challenge	Effects on plants or forests	Plant or forest responses	References
Changes in rainfall	Recurrent severe drought, uncertainty on local amounts and distribution. Water stress and loss of local species	Migration to less water stressed locations. Expansion of water stress resistant species into drier locations. Selection of wind dispersed over animal dispersed seeds	Huang et al. (2013) and Zhang et al. (2018)
At the community and forest level			
Loss of forest area	Potential loss of species, loss of biotic connectivity, productivity, and level of biogeochemical cycles	Fragmentation of forests and their functions	Hansen et al. (2013) and Austin et al. (2017)
Increased in atmospheric carbon dioxide concentration	Some forests increase growth rates, others do not as they are not limited by carbon	Increase in growth might be temporary, average minimum temperature might drive growth	Clark et al. (2003) and Körner (2003)
Increase in air temperature	Increase plant and soil respiration Increased decomposition. Increased demand for water	Faster mineralization of elements, unclear effect on net productivity, possibility of an unknown threshold from carbon sink to source	Doughty and Goulden (2008) and Wood et al. (2012)
Changes in rainfall	Increased drought frequency Stronger effects of seasonal fires Reduction in carbon sequestration	Changes in species composition Increase in fast growing, short leaved tree species	Lewis (2006) and Huang et al. (2013)

between novel and historical secondary forests, it may be reasonable to expect differences when comparisons involve high levels of dominance of species whose attributes or traits are sufficiently unique to influence the comparison. For example, due to relatively small leaf size and short leaf longevity (deciduousness) of leguminous trees, novel stands dominated by these species allow for higher inputs of solar radiation, throughfall, and litterfall to the forest floor compared with stands dominated by large-leaved evergreen species with a larger Leaf Area Index (Abelleira Martínez, 2011). A difficulty with this expectation is the absence of sufficient ecophysiological and functional data to allow for valid statistical differences to surface. Also, we know that forest structure and physiognomy are similar in novel and historical forests (Aide et al., 2000), and it is also possible that systems dynamics such as mass and nutrient turnovers might also be similar. Therefore, the following review on functioning is exploratory and preliminary rather than conclusive.

5.1 Organic matter dynamics

Novel forests in the subtropical moist forest life zone of Puerto Rico have a high turnover of wood mass and volume as expected of young secondary forests (Table 5). The low standing biomass and volume in these forests' turnover twice and five times a year, respectively. Tree mortality is low (1.6% year^{-1}). Most of the volume turnover (3.7% year^{-1}) is due to tree growth.

Novel forests in *los Llanos* also exhibited rapid growth rates. The rate of basal area accumulation (growth) in the *los Llanos* averaged 1.6 m^2 ha^{-1} year^{-1} with a wide range of variation (0.01–8.5). On average, the annual turnover of basal area in *los Llanos* was 3.5% (range of 2.2–6.7), a value similar to the turnover of wood volume in Puerto Rican forests (Table 5). This average rate of growth is high and was not related to the age of stands (range of 15–45 years). Values are higher than those in Aide et al. (2000) for novel forests on abandoned pastures in Puerto Rico. Species density explained 30% of the variation in basal area growth at *los Llanos* (Fig. 5). The variation in growth can be attributed to contrasting environmental conditions and levels of disturbance as was reported in Puerto Rico by Aide et al. (1996) when they also encountered differences in the rates of biomass accumulation among different successional sequences.

Erickson et al. (2014) found a low leaf litter mass on the forest floor of secondary forests (both novel and historical) of the subtropical moist forest life zone in Puerto Rico. This low accumulation of leaf litter, coupled to high leaf litterfall rates, results in high leaf mass turnover on the forest floor (Table 5). The turnover of leaf litter mass was 100 times faster than the turnover of wood mass.

Table 5 Standing volume, total biomass (above and below ground), volume growth, volume mortality, volume removals, mass accumulation, and mass and volume turnover of novel forests of the subtropical forest life zone of Puerto Rico.

Parameter and units	Mass or volume	Annual rates	Annual turnover (%)
Standing volume ($m^3\ ha^{-1}$) and rate of volume growth ($m^3\ ha^{-1}\ year^{-1}$)	78.8	2.95 (growth)	3.7
		1.25 (mortality)	1.6
		0.25 (removals)	0.3
		4.45 (total)	5.6
Total mass ($Mg\,ha^{-1}$) and rate of mass production ($Mg\,ha^{-1}\ year^{-1}$)	94.6	2.0	2.1
Leaf litter mass ($Mg\,ha^{-1}$) and leaf fall rate ($Mg\,ha^{-1}\ year^{-1}$)	2.3	6.8	296

Data covers 230,985 ha of forests or 49% of insular forests. Data for stand volume and mass are from Marcano Vega (2019) and apply to trees with a diameter at breast height ≥ 12.5 cm. Data for leaf litter mass are from Erickson et al. (2014) and for leaf fall rate we used the mean of six annual measurements in Lugo et al. (2011b), Abelleira Martínez (2011), and Fonseca da Silva (2011).

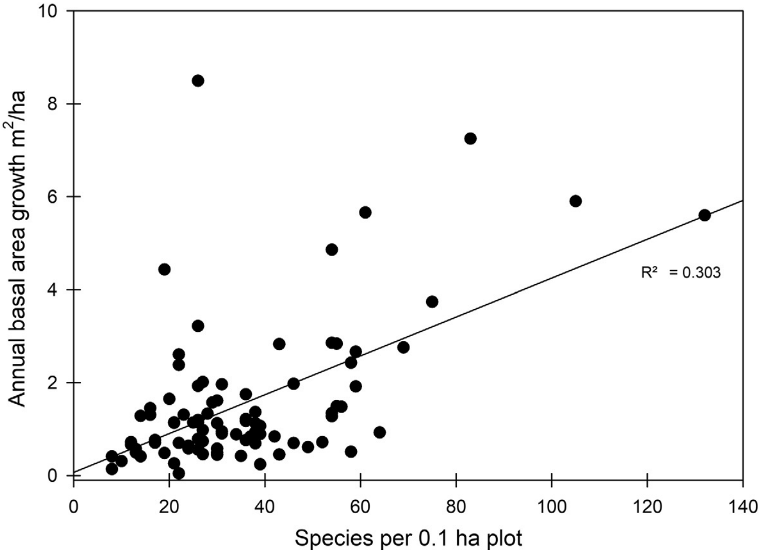

Fig. 5 Principal Components Analyses ordination based on Importance Values of species per plot. *Data are from G. Aymard.*

Novel forests, like most secondary forests, are carbon sinks given their high accumulation of mass and basal area over periods that exceed 40 years. At the insular scale, for which we have robust data, forests are accumulating 1 Mg C ha^{-1} $year^{-1}$ (Marcano Vega, 2019). The carbon sink function of these novel forests is confirmed at the stand level, when detailed ecophysiological measurements are conducted in tandem with stand structural ones (Lugo et al., 2008), or when isotopes are used to trace the accumulation of soil organic matter through succession, coupled with long-term tree growth data (Silver et al., 2004).

5.2 Cycling of elements

The high turnover of wood mass and wood volume in novel forests is accompanied by an even faster turnover of chemical elements in the leaf litter (Fig. 6). Element return via leaf litterfall was larger than element accumulation in leaf litter (Table 6). Novel forest stands had faster turnover than historical secondary forests with the exception of iron (Fig. 6). The flux and turnover of elements through leaf litter is not uniform but varies with the element, with potassium and manganese being the most mobile followed by nitrogen and magnesium. Aluminium is particularly immobile in the

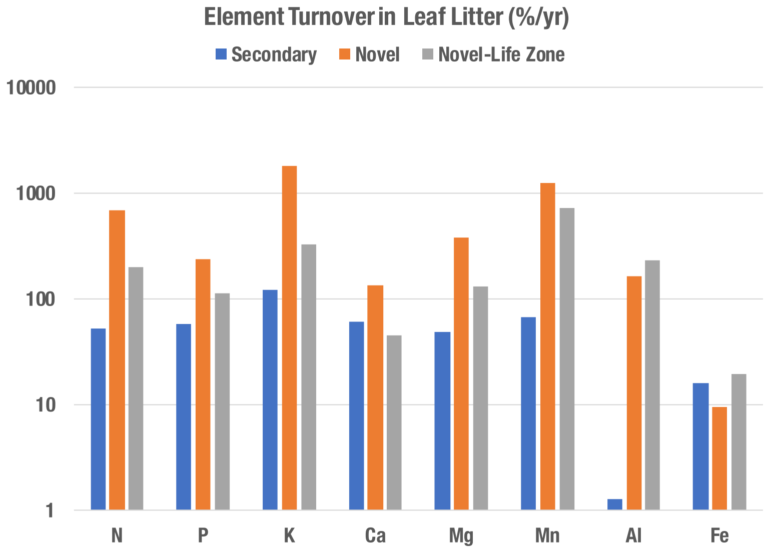

Fig. 6 Annual element turnover in leaf litter of a historical secondary forest and a novel secondary forest in the subtropical moist forest life zone of Puerto Rico. Estimates of turnover rate are based on data in Table 6. For the estimate of novel element flux-life zone element storage, we used the chemical storage data for the life zone in Erickson et al. (2014).

Table 6 Elemental mass accumulated in leaf litter and element return in leaf fall of novel and historical secondary forests in the subtropical moist forest life zones.

Forest type	N	P	K	Ca	Mg	Mn	Al	Fe	S
Storage (kg ha^{-1})									
Moist Forest Life Zone	71	3	9	104	12	1	8	8	14
Novel on Alluvial	17	2	2	44	5	1	15	22	2
Novel on Alluvial	8	1	1	13	2	0	4	6	1
Novel on Alluvial	37	2	3	48	6	1	14	20	5
Secondary on Volcanic 1	145	5	25	121	31	2	63	48	
Secondary on Volcanic 2	168	6	22	125	29	2	35	35	
Flux (kg ha^{-1} year^{-1})									
Novel on Volcanic 98–99	181	4	33	55	19	6	24	2	27
Novel on Volcanic 99–00	105	3	29	38	13	4	11	1	15
Secondary on Volcanic 1	93	3	28	77	17	2	1	4	
Secondary on Volcanic 1	77	3	27	80	12	1	1	11	
Secondary on Volcanic 2	87	3	29	71	15	2	1	4	
Secondary on Volcanic 2	72	3	28	74	14	1	1	9	

Data for the life zone as a whole are from Erickson et al. (2014). Data for the historical secondary forest on volcanic substrate are from Lugo et al. (1999b) and data for novel forests on alluvial and volcanic substrate are, respectively, from Abelleira Martínez and Lugo et al. (2008) and Lugo et al. (2011b). In this comparison, the difference between novel and historical is the presence of introduced species in novel and not in historical forests. Values are rounded to the nearest kg, and empty cells mean there are no data.

historical secondary forest. For discussion of the role of litterfall in nutrient cycling in historical forests, see chapter "Revisiting nutrient cycling by litterfall—Insights from 15 years of litter manipulation in old-growth lowland tropical forest" by Sayer et al., this issue.

The analysis of Erickson et al. (2014) of 11 elements in fallen leaf litter and 143 historical and novel secondary forest stands systematically located across Puerto Rico, revealed that the stoichiometry of leaf litter was influenced by climate (life zone), geologic substrate (karst vs. non-karst), stand age (up to 60 years), and species composition. They found that leaf litter chemistry on the island was spatially heterogeneous and that elements behaved independently, i.e., responding differentially to various control factors or to tree species. For example, the basal area of leguminous trees correlated with leaf litter nitrogen concentration. Erickson et al. (2014) suggested that the availability of nitrogen and phosphorus on insular forest floors was greater than before deforestation, because nutrient availability increased with decreasing forest stand age and novel species composition. Litter with higher nitrogen and phosphorus concentration, i.e., more chemically labile, would favour the rapid chemical turnover and support faster uptake and productivity.

The contribution of the introduced *Spathodea campanulata* to rapid element turnover in leaf litter was confirmed in a decomposition experiment in three geologic formations in the subtropical moist forest life zone (Lugo and Abelleira Martínez, 2018). They found the fastest leaf decomposition rates in the Neotropics, and faster decomposition rates for leaves from novel forests compared to leaves from historical forests. These differences may be reflecting species differences in terms of the species-specific chemical quality of leaf litter, rather than the novelty or lack of it of forests.

Lugo and Erickson (2017) related nutrient concentration anomalies in fallen leaf litter in the subtropical dry forest life zone to species dominance, both native and non-native (introduced). Species groups, such as nitrogen-fixing species and other naturalized species that dominate novel dry forests, have a disproportional influence on forest element stoichiometry. For example, historical stands dominated by *Citharexylum fruticosum* had significantly lower carbon concentration anomalies than other species assemblages. Novel dry forests, compared to the mean of all forest species assemblages island-wide, tend to have fallen leaf litter with lower than average manganese and sodium concentrations and lower than average C/N and C/P ratios. After accounting for significant differences in stand age, geology, and or precipitation, novel dry forests compared to historical dry forests have higher carbon anomalies, lower calcium and sodium anomalies, and lower C/N ratio anomalies. Nitrogen, sulphur, phosphorus, magnesium, potassium, manganese, aluminium, and iron concentration anomalies did not differ among the forest assemblages or between novel dry and historical dry forests. The overarching pattern in the comparisons of element concentration anomalies between novel and historical dry forests and with island-wide forests is the absence of a consistent pattern among elements (Lugo and Erickson, 2017).

The stoichiometric characteristics of species assemblages can influence forest functioning through the speed of recycling and accumulation of nutrients, not only in leaf litter dynamics as discussed above, but also at

Table 7 Traits of introduced tree species that dominate novel forests in the moist life zones of north and western Puerto Rico (Little et al., 1974; Little and Wadsworth, 1964).

	Leaf		Fruit		Nitrogen
Species	Phenology	Size	Flesh	Size	Fixer
Albizia procera[a]	D	S	No	L	Yes
Castilla ellastica	D	L	Yes	S	No
Delonix regia[a]	D	S	No	L	No
Mangifera indica	E	L	Yes	L	No
Peltophorum pterocarpum[a]	SD[b]	S	No	S	Yes
Senna siamea[a]	SD[b]	S	No	L	No
Spathodea campanulata	D	L	No	L	No
Terminalia catappa	SD	L	Yes	S	No

[a] Leguminous tree species (i.e. Fabaceae).
[b] Species classified as evergreen by Little and Wadsworth (1964) but that exhibit deciduous behaviour in some areas of moist Puerto Rico (Abelleira Martínez, personal observation).
For phenology: D is deciduous, SD is semi-deciduous, and E is evergreen. For size, small is S, large is L, and medium is M. For leaves, size corresponds to leaflet size.

the level of whole stands (Lugo et al., 2011a, 2012a). In addition, different leaf chemistry traits can affect species composition, diversity, and food web dynamics of organisms in litter and soil as was shown by Barberena Arias (2008). She related biotic responses at the animal species level to the leaf litter stoichiometry of individual tree species.

The traits of species exhibiting high dominance (Tables 7 and 8) make a difference not only on biotic interactions among organisms as shown in those tables, but also in the flux and turnover of nutrients through the forest compartments that they dominate, be they novel or historical. Dominant species not only capture the resources of sites, but they have the capacity to modify site conditions through their cover, differential use of resources, and regulating nutrient storages and fluxes. Moreover, each dominant species has a particular stoichiometry requirement and capability that allows it to function and influence site conditions. The best examples are those associated with nitrogen fixation, which clearly influence the nitrogen cycle of stands. But their varied ecological traits allow each species to optimize functioning under the conditions that match their traits (Vitousek, 1990; Vitousek and Walker, 1989). Such functioning has implications to management in terms of matching species to site conditions and using species to restore degraded sites.

Table 8 Structural and functional attributes of large ($\geq$10 cm diameter at breast height [DBH]) trees in 250 m^2 plots and small ($\geq$2.5 < 10 cm DBH) trees in concentric 100 m^2 plots established on novel forest sites in the subtropical moist forest life zone of Puerto Rico.

	Large trees					Small trees		
Dominant introduced tree species	**Sites (N)**	**Tree density (trees/ha)**	**Basal area (m^2 ha^{-1})**	**Dominant species importance value (%)**	**Leaf Area Index**	**Introduced species importance value (%)**	**Bat-dispersed species importance value (%)**	**Community-weighed mean of fruit size (cm)**
Albizia procera	6[a]	670	21.6	64.2	2.6	50.0	0.9	9.6
Castilla elastica	3	613	43.6	68.3	4.8	38.1	26.7	3.4
Delonix regia	2	520	31.3	59.6	N/A	67.3	0	30.8
Mangifera indica	2	520	42.2	43.9	4.2	1.7	0	2.3
Peltophorum pterocarpum	2	540	26.8	75.7	4.0	48.0	3.4	6.1
Senna siamea	4[a]	873	27.7	51.6	4.4	42.4	5.6	9.8
Spathodea campanulata	5	888	38.0	67.2	5.2	30.4	0.8	7.3
Terminalia catappa	3[a]	329	46.2	65.4	3.8	13.1	51.6	6.7

[a] Large and small trees were sampled in 250 and 100 m^2 plots except in sites denoted with an asterisk where 5–9 quarter points per size class were used at 1–2 sites. Relative frequency was also considered when estimating species Importance Values on sites sampled with quarter points (Cottam and Curtis, 1956).

Tree density, basal area, and dominant species Importance Values correspond to the mean estimated across the sites sampled. Species Importance Values were based on relative tree density and basal area. Leaf Area Index corresponds to the mean of a subset of sites (1–4) sampled during March–May 2017. Importance Values of introduced species and bat-dispersed tree species for small trees are based on pooled values for introduced species (Little and Wadsworth, 1964; Little et al., 1974) and for six species typically dispersed by bats in Puerto Rico: *Andira inermis*, *Calophyllum calaba*, *Melicoccus bijugatus*, *Terminalia catappa*, *Thespesia grandiflora,* and *Syzigium jambos* (Rodríguez Durán, 2005). *Andira inermis* and *C. calaba* are native, *T. grandiflora* is endemic, and *M. bijugatus*, *T. catappa* and *S. jambos* are introduced. The community weighted mean of fruit size was estimated according to maximum fruit length.

6. Tropical forests of the future

Viewed from the point of view of biodiversity and conservation biology, the future of tropical forests depends on what conservationists can accomplish before current forests collapse or are converted to other cover (Sodhi et al., 2007). Sodhi et al. (2007) stated (p. ix): *Habitat loss and fragmentation, overexploitation of species and environmental degradation are operating on a massive scale worldwide, and these are the processes fueling the current extinction crisis. These human impacts on the biosphere predict a grim future for global biodiversity, especially considering that in many regions the rates of destruction and modification are accelerating….the present-day and future biodiversity crisis loom largest in the tropics.* The future of tropical forests, although dire, is not as grim as expressed from the perspective of a particular academic point of view. For example, Wright and Muller Landau (2006) examined future scenarios of population growth and deforestation in the tropics and found that as those processes slow down, the area of remaining tropical forests is much larger than most studies suggest. Any credible discussion of the future of tropical forests has to consider scale and temporal effects on the predictions; small scale, short-term phenomena are difficult if not impossible to extrapolate to global and long-term scales. The global generalization in Sodhi et al. (2007) may be true at smaller geographic scales but not necessarily at the global scale. As an example, the future condition of forests is associated with their area. Forest area is related to the number of species and the exchange and accumulation of matter, which influence biogeochemical cycles. All modelling, regardless of scale, requires knowledge of the area involved to estimate extinctions rates, potential carbon loss or accumulation, or importance of fragmentation. Small changes in area greatly affect model outputs.

For the tropics, reliable knowledge about the area of tropical forests at global and even national scales is illusive. Since the first global inventory by Zon and Sparhawk (1923), the perception of tropical forest area increased until 1990, when the Food and Agriculture Organization (FAO, 1993) began standardized estimates of global forest areas. Since 1990 the perception of the area of tropical forests has decreased until 2015, but at rates that have been adjusted downward from earlier estimates by the FAO (see fig. 1 in Keenan et al., 2015). Satellite technology also results in variable estimates, depending on the definition of 'forest' and the resolution of images. Due to high uncertainty in the basic information available, the larger the temporal or spatial scale used for predictions or estimates, the greater the uncertainty of the outcome.

The problem is that anticipating the future of tropical forests is a lot more complex than generally realized, particularly if the reality of the

Anthropocene Epoch and the creativity of humans and of evolutionary and successional processes are ignored. As an example, Keenan et al. (2015) identify 19 countries (mostly tropical) that have transitioned from forest loss to forest gain between 1990 and 2015. Forest and landscape fragmentation are also reversible processes as is species endangerment. Only extinction is irreversible, but the current and future rates of the process are subject of debate (Briggs, 2017), whose outcome does not affect the problem of predicting the future. Therefore, the future of tropical forests can at best be imagined or inferred given the temporal and spatial complexity of landscapes and the uncertainty of the Anthropocene environment. For Chazdon (2014), the secondary forests of today will be tropical forests of the future. We agree, but ask: Will they conform to historical species combinations or will the mixing of species lead to novel secondary forests? Will they function at similar rates as historical secondary forests do? We believe that the answers to these questions require the contributions of many disciplines because of the complexity introduced by human activities and the ever-changing environmental conditions.

The documented Holocene history of human activity on the Neotropical lowlands was the subject of analysis by scientists representing many disciplines who came together to address the historical ecology of the region (Balée and Erickson, 2006). They concluded after comprehensive analysis of historical trajectories that human nature per se is not the culprit of the calamities described by conservation biologists. Moreover, they describe cases where human activity results in situations favourable to biodiversity and abiotic conditions. In the view of Balée and Erickson (2006, p. 9) *…causality can be addressed to historically defined configurations of interrelationships over time between specific societies and their economies, on the one hand, and given environments, on the other.*

Our perspective is cemented on Anthropocene conditions, which are more variable and less predictable than those of the Holocene. These conditions select for ecological systems and organisms with fast metabolic rates, low biomass, and shorter-lived and small-sized organisms (Brown, 1995; Enquist et al., 1998; West et al., 1999), a process that is already in motion (Galetti and Dirzo, 2013; Wilkie et al., 2011; Wright et al., 2007). Thus, the novel forests of the future may lack large, long-lived organisms unless humans intervene, through conservation-oriented management, to prevent so. Some taxa will be missing or be more affected than others, particularly those with large sized organisms. These reductions in the numbers of large organisms reflect intense human use and require and equally intense or greater effort to overcome it.

If we limit the prediction to the ecological point of view and to current trends of environmental change, we anticipate that tropical forest ecosystems will continue to change towards high turnover of nutrients, mass, and species. Greater levels of disturbances (anthropogenic and non-anthropogenic) and constantly changing environmental conditions power the increases in turnover. Those conditions also favour a change in forest physiognomy from tree to shrub or shrublands. Shrublands are best suited for coping with extreme environmental conditions given their physiognomy, plant traits, and ecophysiological characteristics (Lugo et al., 2019). The structure of these future forests and shrublands and their plant species richness (not their species composition) will be similar to the forests and shrublands of today as will be the range of speeds of their processes. We base this prediction on the case studies presented above, which showed that after 30–100 years of succession, those parameters did not change even though the species composition did. Species composition and the ecological services associated to particular species are obvious differences between novel and historical forests. Also, the secondary forests of *los Llanos* studied so far do not harbour naturalized species like the Puerto Rican ones. This difference reinforces the notion that as time proceeds, species will mix regardless of geographic origin. It is possible that introduced species have a greater potential to dominate when the local flora is less diverse as it happens in Puerto Rico relative to *los Llanos*. Forest fragmentation should continue to vary temporally in response to human activity with particular effects to particular taxa that are favoured or not by fragmentation. Moreover, the expansion of agricultural, mining, and urban areas will likely continue to reduce the area under forest cover.

6.1 Conservation of novel tropical forests and interventions for ecological services

The conservation of novel forests is important to the conservation of biodiversity as they represent natural responses to prevailing environmental conditions (Ellis, 2015; Radeloff et al., 2015). We reject the notion that only the primary forests, as important as they are, are irreplaceable for sustaining tropical biodiversity (Gibson et al., 2011). Novel forests can provide sites where active conservation interventions are implemented for the sake of native, primary, threatened, or endangered species (see chapter "Protecting environmental and socio-economic values of selectively logged tropical forests in the Anthropocene" by Bousfield et al., this issue). Novel forests are further advanced in successional time compared to non-forest land cover under environmental conditions that can support forests, which means they can be more effectively managed for a variety of purposes that require time to develop. These purposes include increased levels of biodiversity, rehabilitating soil, replenishment of slow variables that provide resilience, for food and wood production, for restoring lost species, and for watershed protection (Table 9; Chapin et al., 2009; Light et al., 2013).

In this section, we review the literature and work in progress in Puerto Rico on passive and active interventions in novel tropical forests. These terms (passive and active) reflect the range in the intensity level of human intervention required to conserve forests of all types. Passive interventions are at the lower range of human intervention, while active interventions are at the upper level of human intervention. The actions that we discuss, even the active ones, strive to minimize human interventions while

Table 9 Potential tradeoffs in supporting, regulating, provision, and cultural ecosystem services (*sensu* Chapin et al., 2009) in novel forests undergoing hands-off conservation (i.e. status quo), and agroforestry and silviculture conservation interventions.

Ecosystem service	Status quo	Agroforestry	Silviculture
Supporting			
Carbon storage	0/+	+	++
Biodiversity	−/0	+	++
Regulating			
Microclimate	0/+	0/+	+
Soil rehabilitation	0/+	0/+	+
Provision			
Food	+	++	0
Wood	0/+	+	++
Cultural			
Identity	−/0	+	+
Recreation	0/+	+	+

Positive (+), negative (−) and neutral (0) effects indicate potential changes in ecosystem services capacity relative to historical forests in the case of novel forests under status quo, and relative to novel forests under status quo for agroforestry and silviculture interventions. Double signs (++) indicate superior effects by intervention. For some ecosystem service and conservation strategy combinations, the potential range in relative changes is separated by a backslash.

maximizing the ecological work of forest organisms. We address the successional trajectories and faunal composition of novel forests passively managed for biodiversity conservation in comparison with those under active conservation interventions. In doing so, we report on on-going experiments aimed at designing and testing active interventions that couple food and wood production with the conservation of biodiversity and the restoration of native species into novel forests through agroforestry and silvicultural practises (Table 9 and Fig. 7).

6.2 Passive interventions

Insular novel forests are depleted in late-successional species, possibly due to their restricted distribution, lack of dispersers, or failure to regenerate and grow with competing secondary vegetation (Abelleira Martínez, 2010; Ewel et al., 2013; Mascaro et al., 2008; Zimmerman et al., 2000). Humans can unknowingly alter the ecological situation and favour the conservation of late-successional species. For example, the tree species *Guaiacum officinale* is native to the dry forests of the Caribbean and Mesoamerica, and its prized wood has resulted in it being currently listed as threatened by IUCN. Nevertheless, this species is planted in urban areas in Puerto Rico for its ornamental value. Within 30 years of its urban planting and without human assistance, seeds of *Guaiacum* had dispersed, germinated, and became

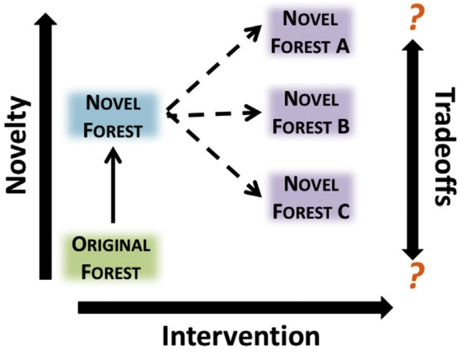

Fig. 7 Deforestation, agricultural land use, land abandonment, and species introductions have converted most original native forest cover into novel forests in Puerto Rico. Interventions can result in novel forests that (A) increase, (B) remain the same, or (C) decrease in novelty due to positive, neutral, or negative feedbacks between traits of introduced species (i.e. flora and fauna) and disturbance levels associated to agroforestry or silviculture. Identifying interventions that help reduce ecosystem service tradeoffs in novel forests can contribute towards a resilient social-ecological-technological system.

established on a novel forest at a site with greater humidity than found in its native environment (Abelleira Martínez et al., 2015). Although this is a highly contextual local-scale example, it nevertheless illustrates that when given the opportunity, species forming novel forests contribute to the ex situ conservation of late-successional species without direct human assistance.

Humans do set the initial conditions under which novelty develops and sustains diverse species assemblages. This is done by influencing the functional trait composition of novel forests by virtue of the traits of introduced or domesticated species that are favoured by anthropogenic activities such as agriculture, landscaping, and trade (Tables 7 and 8). Regardless of the factors influencing the functional traits in novel forests at the time of their establishment (ecesis), it is the successional processes operating outside of human influence what shapes the structure and functioning of communities over subsequent temporal scales.

Social factors that mediate succession of traits include the use of introduced species in agroforestry combined with the myriad of environmental conditions that can be the outcome of site-level management practises. Although species that colonize abandoned agricultural fields are typically wind dispersed, small seeded species; animals may also be the agents of colonization. An example is that of *Terminalia catappa*, a species introduced for ornamental purposes throughout the tropics and that is typically dispersed by bats in Puerto Rico (Rodríguez Durán, 2005). These animals may be attracted to coconut palms and dispersing *Terminalia* in the process, shaping succession and adding novelty. On the other hand, the dominant species may also be remnant fruit trees planted by humans, such as *Mangifera indica*, akin to remnant late-successional trees present in continental secondary forests following deforestation and fragmentation (Guevara et al., 2005). Given the variety of traits of dominant tree species in insular novel forests, the ecological services that are potentially provided by these forests, such as carbon storage, biodiversity conservation, microclimatic regulation and soil rehabilitation, are likely to vary as well (Table 9).

Changes in the functional trait composition of forest cover can modify ecosystem function and the capacity to provide ecological services (Finegan et al., 2015; Lavorel et al., 2011). For example, the difference in the community-weighed mean traits (Grime, 1998) of insular novel forests relative to historical forests may be larger than in continents due to higher monodominance in insular forests (i.e. Importance Value of dominant species in continental forests of 35–64% vs. 44–76% in insular forests based on Tables 1 and 8).

Given the above, one can expect that the traits of dominant introduced species can influence the species and trait composition of juvenile trees that get established and grow in the understory of novel forests. They do so by attracting particular seed dispersal agents or by creating microclimatic conditions that favour the growth and establishment of species with particular traits or trait values. Therefore, passive interventions benefit from an understanding of species traits and their influence on community development. Application of this understanding allows better alignment between conservation objectives and favoured forest species composition.

6.3 Active interventions

Some sectors of society place higher value on native and endemic species, and historical species assemblages than they do for introduced species or taxa with high abundance. This normative gives social licence for active interventions with novel forests (Davis et al., 2011; Hobbs et al., 2014; Hulvey et al., 2013). These interventions can be designed and implemented in tandem with activities that generate socio-economic benefits, such as the establishment of agroforestry systems in existing novel forests. Interventions can also be aimed towards the restoration and assisted migration of rare native species that were previously common or present in historical forests, but that were decimated due to deforestation, wood exploitation, and agricultural expansion (Jackson and Hobbs, 2009; Wadsworth, 1950; Wright and Muller Landau, 2006).

The relatively greater extent of novel forests in islands, coupled with scarce land area, places greater demand for innovative conservation strategies that favour ecological services (Brauman et al., 2007; Ewel et al., 2013; Gould et al., 2017).

Gould et al. (2017) suggest devising and incentivizing interventions that use existing forest cover for agroforestry production of shade crops and for silvicultural stand enrichment with late-successional hardwoods in a way that existing forest cover can be conserved in tandem with increased food and, perhaps, wood production. Ecosystem service tradeoffs (*sensu* Foley et al., 2005) need to be assessed in the design and implementation of interventions such that tradeoffs are minimized, and interventions act to synergistically increase societal benefits and value of novel forests across multiple management objectives (Table 9). For example, agroforestry interventions aimed at the enrichment of novel forest stands with fruit trees that are also late-successional or native, such as *Genipa americana* and *Pouteria multiflora*, can couple food production with increased capacity for carbon storage (e.g. dense wood and recalcitrant leaves), native species conservation, cultural identity, and recreation. The same strategy applies to stand enrichment with late-successional native or endemic tree species.

Agroforestry systems are as diverse as environmental conditions and the evolution of cultures and peoples and are considered a feasible alternative to agricultural intensification for supplying food while conserving forests (Cernansky, 2018; Jose, 2009; Weaver, 1979). Agroforestry practises are ancient and have moulded the composition of forests that were once considered primary and pristine, such as the Mayan forests of the Yucatán peninsula, *terra preta* forests in the Amazon, the *taungya* systems of tropical Asia, and the ancient terrace systems of Sri Lanka and Indonesia (Diemont and Martin, 2009; Weaver, 1979; Willis et al., 2004). The social-ecological-technological context and cultural value of agroforestry also plays a role in species selection and local practises in agroforestry systems. For example, breadfruit (*Arthocarpus atillis*) is planted in subsistence farms and commercial mono-cultures in Puerto Rico and is rarely used as a shade tree, whereas in Pacific islands, from where breadfruit originates, it is used for shade of introduced cacao, coffee, bananas, and other shade crops (Elevicht and Ragone, 2018). The species assemblages that result from agroforestry practises are novel within the timeframe in which they are implemented, but as intervention ceases and time elapses, these systems change through self-organization and become so wild and complex as to elicit pristine attributes by those that describe them (Jackson and Hobbs, 2009; Willis et al., 2004).

Some elements of novelty generated by past agricultural practises in Puerto Rico's forests, such as dominance and presence of *Mangifera indica*, could be reduced with time and ecological succession, especially if these species lack adequate seed dispersal agents. The novelty that has been added by the addition of introduced species with large fruits and no analogue native seed dispersal agents will eventually be reduced unless introduced fauna begin to disperse these fruits, which may be already happening (below). Novelty can also be reduced by active conservation interventions (e.g. Gbètoho et al., 2017). However, we focus on experimental conservation interventions designed to increase the capacity of novel forests to provide ecosystem services while reducing tradeoffs (Table 9). Although interventions for ecosystem services has certainly occurred in the past and contemporary times in other areas, we focus on experimental interventions that explicitly consider novelty as an aspect of the system to be conserved in Puerto Rico.

6.4 Experiments

Experiments in progress in Puerto Rico are based on the results of studies of novel forests and they aim to match the structural and functional characteristics of novel forests with the requirements of forest understory crops or trees deemed important to conservation objectives such as maintaining forest cover and native canopy species. The high nutrient concentration and decomposition rates of leaf litter in novel forests can act to increase nutrient turnover rates and productivity of crops planted in these sites (Erickson et al., 2014; Lugo and Abelleira Martínez, 2018). Plant traits such as leaf longevity and recalcitrance, canopy leaf area, and the capacity to fix nitrogen can also influence microclimate (i.e. incoming light levels, relative humidity, and temperature; Abelleira Martínez, 2011), soil conditions (i.e. organic matter and nutrient availability; Lugo and Abelleira Martínez, 2018), and regulate understory tree growth. Forest stands dominated by different species, functional groups, or trait values, may favour growth and productivity of one or another crop tree planted in their understory (Abelleira Martínez, 2019). In *Spathodea campanulata* forests, for example, full deciduousness and high leaf nutrient content coupled with fast decomposition rates act to make stoichiometric relationships (i.e. C/N and C/P) in standing litter and soil more favourable for plant growth (Abelleira Martínez, 2011; Lugo and Abelleira Martínez, 2018; Lugo et al., 2011a, b). Experiments can also test for the effect of dominance of any one of the most common introduced tree species in Puerto Rico's novel forests, particularly the effect of their species traits, on the growth, survival and, eventually, fruit production of crop trees planted in the understory (Tables 7 and 8).

One experiment aimed at incorporating agroforestry production of shade crops, commercial fruit trees, and native yet relatively rare edible fruit trees, into existing novel forests in the subtropical moist forest life zone of Puerto Rico (Abelleira Martínez, 2019; Túa Ayala and Abelleira Martínez, 2019). The planted crop trees consisted of deep shade tolerant cacao (*Theobroma cacao*), mid-shade tolerant coffee (*Coffea arabica* var. bourbon), the native mid-shade tolerant forest species jagua (*Genipa americana*) and jácana (*Pouteria multiflora*), and light-demanding commercial fruit species avocado (*Persea americana*) and breadfruit (*Artocarpus altilis*).

The unexpected passage of hurricane María over the 31 research sites, allowed for testing survivability of crops after such an event (see also chapter "Soil biogeochemical responses of a tropical forest to warming and hurricane disturbance" by Reed et al. (this issue) for discussion of the effects of hurricane María on an experimentally warmed tropical forest). The event caused an unplanned thinning and pruning of trees and branches across the vertical strata of the canopy except for the low understory that was protected from winds and falling limbs due to low stature and high flexibility

Fig. 8 Juvenile tree of *Pouteria multiflora* planted 2 weeks before hurricane María on a volcanic novel forest site dominated by *Albizia procera* in western Puerto Rico (A), and juvenile trees regenerating naturally in the understory of a novel forest karst site dominated by *Spathodea campanulata* in northern Puerto Rico (B). On both sites, canopy trees of dominant introduced species were heavily affected, resulting in high amounts of coarse woody debris and litter on the forest floor among juvenile trees that survived and that were and fully foliated in some cases. Both photos were taken a month or so after the hurricane's passage.

of juvenile trees (Fig. 8). Virtually all fruit trees planted before the hurricane survived the disturbance (Túa Ayala and Abelleira Martínez, 2019). A year and a half after planting at 10 of the sites established before the hurricane, high (>70%) survival was observed for all planted species except for avocado, breadfruit, and coffee on sites dominated by *Albizia procera* and

Delonix regia. On the other hand, cacao and coffee were setting flower in some sites, and some breadfruit, jacana, and jagua trees reached more than twice the initial (1 m) height; in the case of breadfruit reaching up to 3 m. The success of these plantings in withstanding a category 4 hurricane and reaching reproductive maturity in times equalling those of traditional agroforestry shade crop systems (i.e. cacao and coffee; Haggar et al., 2011; Somarriba and Beer, 2011) illustrate the potential of novel forests to harbour productive agroforestry systems in Puerto Rico and the potential of agroforestry systems to be resilient to future stressors (Fig. 7).

A second experiment had the objective of restoring a late-succession wetland tree species to the understory of novel forests on riparian floodplain sites. The experiment was established in 2010 on novel forests dominated by *Spathodea campanulata* on abandoned sugar cane fields in riparian wetlands (Abelleira Martínez and Lugo, 2008). Initial results show higher (>50%) survival of *Pterocarpus officinalis* trees planted in floodplain areas away from levees, where they are more susceptible to flood waters and debris (Cruz and Abelleira Martínez, personal communication, 2019). The plantings were protected by the forest canopy during hurricane María, and canopy opening may eventually accelerate species turnover.

In a third experiment, the rare late-succession tree species *Dacryodes excelsa* and *Manilkara bidentata*, and the endangered *Coccoloba pubescens* and *Stahlia monosperma* were planted in a line arrangement in novel forests dominated by leguminous and non-leguminous species across the subtropical moist forest life zone. The traits of leguminous vs. non-leguminous species often contrast, with the former group typically capable of fixing nitrogen and possessing deciduous leaves of low laminar leaf size (Tables 7 and 8). These traits, when combined, may favour the growth of species with early-successional traits (i.e. light and resource demanders) in novel forests dominated by legumes, and make non-legume dominated novel forests better sites for late-successional species establishment. Some of these rare native tree species are typical of historical forests in wetter (i.e. *Dacryodes excelsa* and *Coccoloba pubescens*) and drier (i.e. *Stahlia monosperma*) life zones, and their successful establishment can help populations expand and migrate. Due to anthropogenic barriers, dispersal of some species that lack effective natural seed dispersal mechanisms in contemporary times benefit from human-mediated dispersal to keep up with land conversion and climate change. The establishment of these species in novel forests can increase their value for biodiversity conservation, cultural identity and aesthetics, and improve the capacity of novel forests to support socio-economic activities, such as ecotourism, outdoor education, and recreation, that benefit neighbouring communities (Tavárez and Elbakidze, 2019). Coupled with agroforestry production and silviculture (Table 9; Lugo, 2012), these activities can empower communities in tandem with increasing their perspective and appreciation towards novel and historical ecosystems.

The three examples of experimental interventions that are being implemented in novel forests of Puerto Rico can help other island nations cope with expanding novel forest cover. In Fiji, for example, novel forests dominated by *Spathodea campanulata* seem to result in negative effects to socio-economic activities such as agricultural production and tourism, affecting the capacity of these systems to provide ecological services (Brown and Daigneault, 2014). Alternatively, Fijian institutions and stakeholders may be compelled to accept that these systems are a natural, inevitable response of forests to human intervention, and turn their attention towards the design and implementation of interventions to conserve these forests in the way they deem more valuable; be that accelerating species turnover towards more historical states or incorporating agroforestry crops. After all, Polynesian islands conserve agroforestry systems dominated by breadfruit, which was originally introduced from one island to others for a variety of purposes, making these agroforestry systems, although culturally engrained, also highly novel. The same reasoning in ecosystem service tradeoffs may be applied to the conservation of novel forests dominated by *Swietenia* spp. in islands as far apart as Dominica in the Caribbean and the Philliphine Archipelago (Cernansky, 2018; Norghauer et al., 2011).

The realization that novel forests are not 'invasive', 'thrash', or 'weed-dominated' homogenized forests but that they are heterogeneous and diverse forests intricately related to human activities is important for the understanding of tropical landscapes. Such realization can help island communities adopt a perspective that can facilitate the inclusion of novel forests into conservation strategies aimed at better adapting to increased number of disturbances and lowering vulnerability to extreme events (Hobbs et al., 2014). Although the examples from Puerto Rico can be illustrative, interventions should be context-specific and designed for taking into consideration the needs of peoples, communities, societies, and cultures.

6.5 Historical and novel fauna

While certain environmental conditions favour small organisms over large ones, humans create conditions, either purposefully or by neglect, which favour large sized organisms and even vulnerable ones that without human intervention would not survive. For example, in Puerto Rico, *Rhesus* monkeys were introduced for medical trials at the medical research facilities of the US Navy base in Sabana Seca, and for experiments in the Magueyes island Experiment Station of the University of Puerto Rico at Lajas. In the dawn of the 21st century, these monkeys extended in range and population size throughout Puerto Rico's coastal lowlands, consuming crops and scaring people. Monkeys have begun to alter the composition of forests by dispersing tree species with large sized fruits and seeds, such as the Caribbean native mammee apple (*Mammea americana)*, and endemic and native cacti (Augusto Carvajal, personal communication; Omar Monsegur, personal communication; S.A. Sloan, personal communication; Watlington, 2009). The persistence of these monkeys in Puerto Rico may eventually modify the functional (i.e. reproductive) trait composition of novel and historical forests (Table 8).

The success and outcomes of assisted migration of endangered native flora and fauna in Puerto Rico, although equally intriguing, is less controversial and has received positive reception and support from the public, government, and private entities. For example, the endangered Puertorrican Parrot (*Amazona vitatta*) and Sapo Concho frog (*Bufo lemur*) have been re-introduced with modest success in areas outside of the 20th century ranges of populations, which was restricted to protected areas in the Luquillo Mountains for the parrot and the Guánica dry forest for the frog. As their populations spread, these species will benefit from resources, such as food and habitat, found in novel forests. For example, the Dominican Parakeet and the Scarlet Macaw are two parrot species (i.e. Psittaciformes) that actively forage pods and consume seeds of *Spathodea campanulata* trees in urban novel forests (Abelleira Martínez, 2008). Moreover, the protected areas where many native and endangered fauna are now found, are delimited and restricted in size and surrounded by a matrix of novel forests. Humans can intervene to make these novel forests better resources for this fauna.

The examples above are just a few among many that illustrate the natural mixing of species and the ensuing assembly of novel communities of plants and animals functioning in response to their traits and life history requirements irrespective of their geographic origin. As discussed in detail in Lugo et al. (2012b), these assemblages self-organize, experience succession, and reach maturity and sustainability in tropical landscapes. They are the harbingers of the future tropical forests.

7. Conclusion

This literature review on the role of climate change in shaping the tropical forests of the future focused its attention on changes already in progress that anticipate the future state of tropical forests. We used three case studies supplemented with new data to enrich information in the literature. Tropical forests will be shaped not only by climate change but also by other anthropogenic disturbances that interact in synergy with a changing climate. We anticipate that tropical forests will continue to change as they have done in the past. They will change and adapt to an increasing level of disturbances through the generation of novelty. Novelty is measured by the degree of dissimilarity of a system measured in one or more dimensions relative to a reference baseline, usually a historical one. Novelty is the product of evolutionary and successional processes; whose rate of emergence increases in proportion to anthropogenic disturbances. In the current Anthropocene Epoch, novelty in ecosystems will increase dramatically because the environment itself is increasingly changing and uncertain. We used a species composition criterion to assess the current level of novelty in tropical forests and to make judgement about the implications to the future of these forests, known as novel forests. In contrast to novel forests, historical forests are exposed to lower anthropogenic stressors, and their generation of novelty through succession and evolution is much lower.

Climate models predict a dire future for tropical forests, particularly those in montane regions. Land use changes also affect tropical forests and in combination with climate change cause greater stress to forests. We found that changes in species composition was a major response of vegetation to disturbances associated with anthropogenic activities. Moreover, that response is usually accompanied by an increased level of dominance by a few species. In Caribbean islands the change in species composition and high dominance favours introduced species but in the continental lowland and montane regions, native species with wide geographic distributions predominate. In both locations (tropical islands and continents) the floras are enriched by the introduction and naturalization of species.

Novel forests behaved as historical forests in terms of many functional attributes such as having high rates of mass, volume, and nutrient turnover. We could not establish differences in ecophysiological and functional traits with historical secondary forests. The importance of dominant species in influencing the behaviour of forest stands was well established, whether the species was introduced or native. The level of dominance is important for establishing differences among stands as was well demonstrated for the nitrogen dynamics in relation to basal area of nitrogen-fixing species. Highly dominant species like *Spathodea campanulata* (an introduced species) or *Citharexylum fruticosum* (a native species) in Puerto Rico were influential in affecting nutrient and carbon dynamics, respectively, in their species assemblages. While much research remains to be done in the functional characteristics of novel forests, the results available suggest their functional behaviour is similar to the behaviour of historical secondary forests, and thus there is no apparent reason to expect novel forests to be somehow abnormal or detrimental to the biogeochemical fluxes of landscapes or the delivery of ecological services.

Given the complexity of the tropical biome and our poor understanding of its functioning, we caution against the extrapolation of local events to global scales. Thus, our prediction of the future of tropical forests focus on the current trend towards smaller organisms, faster rates of turnover of organic mass and chemical elements, greater species dominance, and different combinations of species. Because these emerging novel forests are doing so under the forces of natural selection and self-organization that have always regulated ecosystem functioning and development, they represent adaptive solutions to emerging environmental challenges. These forests support biodiversity and provide services that need conservation, as is normally done with historical forests.

We reviewed different examples of passive and active interventions on novel forests with the objective of providing social and ecological services to people. In so doing the importance of species traits, particularly the traits of highly dominant species, emerged as important for conservation. Knowing species traits and incorporating those traits into conservation schemes reduce the need for active interventions and promote passive interventions, because the ecological work is done by the organisms rather than people. Similarly, tropical forests will have a positive outcome into the future if humans give their organisms the space and time to respond with novelty to the challenges of the Anthropocene.

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Appendix

This appendix contains material developed in support of this literature review. The material is presented in two sections. First, a description of the information collected in *los Llanos* of Venezuela by Gerardo Aymard. This section contains background information about *los Llanos*, its flora, and the methods used to analyse the data collected in the field. Second, a table with the list of tropical locations were we found published flora that itemized introduced and naturalized species. The table includes the data extracted from the published flora.

A.1 Los Llanos of Venezuela

Description of the los Llanos Region. The broad lowland zone that extends from northeastern Colombia to eastern Venezuela, occupies an area of ca. 532,000 km^2 (Huber et al., 2006). *Los Llanos* comprise 26.6% (about 240,000 km^2) of the continental area of Venezuela (Fig. 2). It is the largest savannah area in north-western South America—with rich sedimentary deposits of Quaternary origin (Schargel, 2015). The tropical dry forest life zone covers most of the *los Llanos* geography, but within this climate, vegetation varies depending on edaphic conditions, local climate, periodic flooding, and anthropogenic activity. The region also has smaller areas with other life zones and transitions between life zones such as the transition from tropical dry to very dry thorn forest, and less frequent, from dry semi-deciduous to evergreen forests (Ewel and Madriz, 1968).

The flora of *los Llanos* has a measurable affinity with the Caribbean flora (Takhtajan, 1986, DRYFLOR et al., 2016). About 60% of the *los Llanos* species belong to the Caribbean bioregion (Aymard, 2017). Currently, the vegetation of *los Llanos* is composed of a mosaic of savannahs mixed with pastures, shrubby vegetation, gallery forests; an array of communities composed by thorn dry forest, and a transition of dry semi-deciduous to evergreen forests highly transformed by human activity. The region contains extensive tropical savannahs whose origins are controversial because of the relative influences of anthropogenic activity, fire, seasonal flooding, edaphic factors, and climate. We do not address the extensive literature on the anthropogenic vs. non- anthropogenic origin of savannah vegetation. Instead, we focus on existing forests in *los Llanos*.

Background and Methods. Veillon (1986, 1995, 1997) described the structure, species composition, and dominance of *los Llanos* forests. We used those descriptions as the base of comparison to assess the degree of novelty in the current forest cover of the region. To do so, we also analysed unpublished raw data from one of the authors (G. Aymard). He had systematically sampled vegetation that had been affected by anthropogenic activity with the eventual objective of restoring historical forests. However, the floristic composition of stands, much like the work in the Andes discussed above, did not reflect evidence that the combinations of species of the historical vegetation was present in the developing mature forests in *los Llanos*.

Aymard's data comprises 90 0.1 ha-plots (100 m by 10 m) established in *los Llanos* and the seasonally dry forests of Bolívar, Trujillo and Zulia states, the latter *fide* (Figueroa, 2011; Fig. 2). In these plots, all free-standing stems of woody (trees, shrubs, lianas) vegetation, and non-woody (tree ferns, bamboo, palms) vegetation with a diameter at breast height >2.5 cm were identified to species and their height and diameter measured. From those data, we calculated species Importance Values based on the relative density and relative basal area of each species, and the complexity index for stands sensu Holdridge (1967). The complexity index is calculated by multiplying the height of the three tallest trees (m), number of tree species per 0.1 ha, stand basal area (m^2 per 0.1 ha), stem density per 0.1 ha, and 10^{-3}. We calculated the basal area growth rate ($m^2\ ha^{-1}\ year^{-1}$) of forest stands by dividing their basal area by their age. The basal area growth rate was then expressed as a percent of the standing basal area (% $year^{-1}$). We used stand species composition and structural information to identify the most dominant species by plot, the relationship between stand dominance and complexity index, and the relationship between stand dominance and number of species. We further explored Importance Values with multivariate ordination analyses (principal component analyses, PCA) to illustrate the differences in distribution and proportion of Importance Values by species per plot. The PCA was done on a correlation matrix (PC ORD v 7). Using a subset of the 90 plots inventoried by G. Aymard, we compared the 15 plots with the highest levels of dominance to the six historical forest plots from Veillon to ascertain difference in parameters that could be attributed to the generation of novelty. Geographically, the Veillon plots were between 100 and 650 km from those selected for comparison.

For descriptive statistics and regression analysis we used JMP version 14.2 (SAS Institute Inc., Cary NC, USA).

A.2 Analysis of published floras

This work involved compiling bibliographical references that document absolute numbers of native and naturalized species of vascular plants in tropical floras. Texts of the early 20th century floras seldom recognize introduced (or naturalized) species; those that do often group native and naturalized species together and do not provide separate enumerations. However, in the late 20th century we observed an increasing trend of reporting and quantifying introduced species and naturalizations. This compendium consists mainly of books but includes some online databases and scientific articles of floristic inventories. An annotated bibliography of the flora's covered by this analysis is available from the senior author. The following table contains the countries or regions covered by the survey. Multiple reports for the same country reflect different floras or area coverage.

Country	Native	Naturalized	Sum	Percent naturalized
Angola	304	20	324	6.2
Antioquia, Colombia	8302	612	8914	6.9
Bermuda	165	303	468	64.7
Bolivia	2709	24	2733	0.9
Brazil	580	44	624	7.1
British Guiana	536	65	601	10.8
Cayman Islands	24,030	250	24,280	1.0
Colombia	25,585	168	25,753	0.7
Colombia	33,849	85	33,934	0.3
Cuba	308	117	425	27.5
Cuba	63	1	64	1.6
Cuba	6504	516	7020	7.4
Cuba	75	5	80	6.3
Cuba	67	10	77	13.0
Cuba	12	2	14	14.3
Cuba	94	1	95	1.1
Cuba	15	9	24	37.5

Continued

—cont'd

Country	Native	Naturalized	Sum	Percent naturalized
Cuba	47	2	49	4.1
El Salvador	486	97	583	16.6
El Salvador	205	86	291	29.6
El Salvador	257	75	332	22.6
El Salvador	1757	313	2070	15.1
Ethiopia	309	19	328	5.8
French Guiana	5900	165	6065	2.7
Galapagos Islands	480	264	744	35.5
Galapagos Islands		185	185	100.0
Galapagos Islands	85	1	86	1.2
Guam	402	64	466	13.7
Guatemala	8194	55	8249	0.7
Guiana Shield	13,074	293	13,367	2.2
Hawaii	860	139	999	13.9
Hawaii	60	92	152	60.5
Jawaii	1358	1366	2724	50.1
Hawaii (montane)		349	349	100.0
India	17,212	730	17,942	4.1
India	18,115	471	18,586	2.5
Indonesia		651	651	100.0
Kenya	779	29	808	3.6
Kruger NP, South Africa		159	159	100.0
Fiji Islands	288	128	416	30.8
Margarita Island, Venezuela	642	2	644	0.3
Martinique	1668	1111	2779	40.0
Netherlands Antilles	418	49	467	10.5
Nicaragua	1548	408	1956	20.9

—cont'd

Country	Native	Naturalized	Sum	Percent naturalized
Panama	9140	380	9520	4.0
Philippines	9465	582	10,047	5.8
Puerto Rico	2337	575	2912	19.7
Puerto Rico	2900	300	3200	9.4
Puerto Rico	3126	583	3709	15.7
Puerto Rico and the US Virgin Islands	176	74	250	29.6
Rwanda	486	240	726	33.1
Rwanda	157	25	182	13.7
Somalia	34	7	41	17.1
South Florida		187	187	100.0
South Florida and Virgin Islands	41	28	69	40.6
South Sudan	17	5	22	22.7
St. Bartholomew	367	125	492	25.4
St. Croix	920	26	946	2.7
St. John	642	105	747	14.1
Taiwan	3910	340	4250	8.0
Tanzania	869	41	910	4.5
Trinidad & Tobago	267	56	323	17.3
Uganda	226	24	250	9.6
Virgin Gorda, British Virgin Islands	367	36	403	8.9
Zambia	415	25	440	5.7
Zimbabwe	5533	391	5924	6.6

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