CARIBBEAN LANDSCAPES AND THEIR BIODIVERSITY

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SUMMARY

Both the biodiversity and the landscapes of the Caribbean have been greatly modified as a consequence of human activity. In this essay we provide an overview of the natural landscapes and biodiversity of the Caribbean and discuss how human activity has affected both. Our Caribbean geographic focus is on the insular Caribbean and the biodiversity focus is on the flora, forests, and built up land. Recent land cover changes from agricultural to urban cover have allowed for the proliferation of novel forests, where introduced plant species have naturalized and play important ecological roles that appear compatible with native and endemic flora.

PAISAJES CARIBEÑOS Y SU DIODIVERSIDAD

Ariel E. Lugo, Eileen H. Helmer y Eugenio Santiago Valentín

RESUMEN

Tanto la biodiversidad como los paisajes del Caribe han sido extensamente modificados como consecuencia de la actividad humana. En este ensayo se presenta una visión global de los paisajes naturales y la biodiversidad del Caribe y se discute cómo la actividad humana ha modificado a ambos. Nuestro enfoque caribeño es en el Caribe insular y el foco sobre la diversidad es la flora, bosques y tierras construidas. Cambios recientes en la cobertura de las tierras, de cobertura agrícola a urbana, han permitido la proliferación de nuevos bosques, donde las especies de plantas introducidas se han naturalizado y juegan importantes papeles ecológicos que parecen compatibles con la flora nativa y endémica.

Introduction

The Caribbean, a region with over one thousand islands and continental landmasses, is defined in a variety of ways. Geographically, the area known as the Greater Caribbean includes all the islands plus those continental watersheds draining into the Caribbean Sea and the Gulf of Mexico. The Caribbean Islands belong to three different archipelagoes: the Greater Antilles, the Lesser Antilles, and the Bahamas. The Lesser Antilles date back to about 45my, while portions of the Greater Antil-

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PAISAGENS DO CARIBE E SUA BIODIVERSIDADE

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RESUMO

Tanto a biodiversidade como as paisagens do Caribe têm sido extensamente modificadas como consequência da atividade humana. Neste ensaio se apresenta uma visão global das paisagens naturais e a biodiversidade do Caribe e se discute como a atividade humana tem modificado ambos. Nosso enfoque caribenho é no Caribe insular e o foco sobre a diversidade é a flora, bosques e terras construídas. Mudanças recentes da cobertura das terras, de cobertura agrícola a urbana, têm permitido a proliferação de novos bosques, onde as espécies de plantas introduzidas têm se naturalizado e desempenham importantes papéis ecológicos que parecem compatíveis com a flora nativa e endêmica.

les (e.g., Cuba) contain fragments that date back as far as 1000my and the Bahamian Islands date back about 200my (Acevedo Rodríguez and Strong, 2008). As a group, the Caribbean Islands are also known as the West Indies or Antilles. The Lesser Antilles, separated from the Greater Antilles by the Anegada Passage, extend from Sombrero Island on the north to Grenada on the South. None of the Caribbean Islands is in contact with surrounding continental landmasses. Our emphasis will be on the terrestrial biodiversity of Caribbean Islands with the objective of highlighting the effects of land cover change on the flora.

The Caribbean Biodiversity Hotspot

The Caribbean Islands (Myers *et al*., 2000) and adjacent marine waters (Roberts *et al*., 2000) are global biodiversity hotspots. A hotspot is a region with exceptional concentration of endemic species and experiencing exceptional habitat loss. The Caribbean Islands contain at least 2% of the world's endemic plant and vertebrate species on only 0.4% of the Earth's land surface (Myers *et al*., 2000).

Botanical biodiversity

The West Indian flora is a subset of the Neotropical flora (Acevedo Rodríguez and Strong, 2008). Borhidi (1991) identified two phytogeographical units in the Caribbean region: the Central American and the Antillean sub-regions. The Antillean sub-region (our focus) is subdivided into three island groups: the Bahamas, the Greater Antilles, and the Lesser Antilles. Only 28% of the native seed plant flora in the Caribbean is shared with other geographic regions of the world, as the remaining 72% is endemic to the West Indies (Acevedo Rodríguez and Strong, 2008). The vascular plant flora for the Caribbean Islands including introduced and cultivated plants is estimated at 12847 species in about 231 families (Acevedo Rodríguez and Strong, 2008), of which 7868 species, or about 2.3% of the world's total, are endemic to the region.

Of the 231 seed plant families in the West Indies, 205 are indigenous. None of these families is endemic to the Caribbean, most are shared with other regions of the Neotropics, and 17 are endemic to the Neotropics. These 17 families represent about 49% of the endemic seed plant families in the Neotropics. Francisco Ortega *et al*. (2007) and Acevedo Rodríguez and Strong (2008) listed 181 seed plant genera endemic to Caribbean Islands, *sensu stricto*. These genera belong to 47 families. Francisco Ortega *et al*. (2007) reported 8000 endemic vascular plant species in the Caribbean and 727 species in the endemic genera. Fifty one percent of the endemic genera are unispecific (Francisco Ortega *et al*., 2007). The geographic area that these authors analyzed excludes south Florida but it includes the Netherlands Antilles and the Venezuelan Antilles north of Venezuela. Among the islands, Cuba has the largest number of species and highest number and proportion of endemic plants. Acevedo Rodríguez and Strong (2008) found that 105 of the 181 endemic plant genera occur on a single island, this and the fact that 80% are unispecific, make the genera vulnerable to land cover change. In the Lesser Antilles, a third of the endemic seed plant taxa are single-island taxa, a third occur on two to three islands, and the rest are distributed on four or more islands (Acevedo Rodríguez and Strong, 2008). Torres Santana *et al*. (2010) estimated that there were 156 single-island endemic pteridophyte species in the Caribbean. Kairo *et al*. (2003) reported that 40% of Caribbean butterflies are known only from a single island, which further highlights the vulnerability of endemic taxa in these islands.

TABLE I
ESTIMATES OF THE NUMBER OF INTRODUCED TAXA TO THE CARIBBEAN ISLANDS

Taxon	Native	Introduced
Families of seed plants	205	26
Genera of seed plants	1447	500
Species of seed plants	10948	1899
Floating or submerged plants		4
Cattails		1
Climber/vines		17
Ferns		5
Grasses		28
Herbs		35
Sedges		1
Shrubs		16
Trees		220
Crustaceans		2
Earthworms		1
Insect		90
Jellyfishes		1
Mites		8
Mollusks		17
Solifuguds		1
Tunicates		1
Amphibians		8
Birds		20
Fish		37
Mammals		20
Reptiles		15
Fungi		2
Diseases		2

The first three rows are from Acevedo Rodríguez and Strong (2008) and the rest are from Kairo *et al.* (2003). Empty cells mean the information is not available in the publications cited. However, information for some of the seed plant taxa is available in the following website: http://botany.si.edu/antilles/WestIndies/query.cfm
And also in www.sil.si.edu/smithsoniancontributions/Botany/
The numbers from Kairo *et al.* add up to 552 species (327 plants, 121 invertebrates, 100 vertebrates, and 4 fungi and diseases). Kairo *et al.* also combined the species according to habitat: 479 terrestrial, 55 freshwater, and 18 marine.

TABLE II
NUMBER OF INTRODUCED PLANT AND ANIMAL SPECIES TO VARIOUS ISLANDS OF THE CARIBBEAN

Island	Number of Species
Dominican Republic	186
Puerto Rico	182
Bahamas	159
Jamaica	102
Bermuda	73
Haiti	63
Trinidad & Tobago	61
Barbados	60
Cuba	60
Antigua-Barbuda	45
US Virgin Islands	42
Curacao	41
Grenada	37
Martinique	37
St. Lucia	37
Dominica	34
St. Vincent	32
Guadeloupe	31
Montserrat	26
Anguilla	9
British Virgin Islands	9
Turks-Caicos Islands	8
Cayman Islands	7
St. Kitts-Nevis	5
Aruba	5
Bonaire	4
St. Martin	2
Aves	0
Netherlands Leeward Islands	0
Navassa	0

All data are from Kairo *et al.* (2003). Kairo *et al.* caution that the list is incomplete. Islands are arranged in descending order of introductions.

TABLE III
PERCENT URBAN, FOREST, AND VEGETATION COVER OF VARIOUS CARIBBEAN ISLANDS IN 2000

Island	Urban	Forest	Vegetation	Island area (ha)	Source
Anegada	2.8	64.8	67.0	3990	Kennaway *et al*., 2008
Barbados†	20.9	17.1	42.8	43431	Helmer *et al*., 2008
British Virgin Islands†	7.0	75.2	80.6	15412	Kennaway *et al*., 2008
Dominican Republic*†	1.5	49	99.2	4797317	Hernández and Pérez., 2005
Grenada†	8.8	51.1	58.0	31341	Helmer *et al*., 2008
Jost Van Dyke	3.2	82.7	89.1	1036	Kennaway *et al*., 2008
Nevis	7.2	49.2	88.9	9311	Helmer *et al*., 2008
NPCG **	1.4	70.2	80.4	1077	Kennaway *et al*., 2008
Puerto Rico†	15.4	44.8	82.4	886951	Kennaway and Helmer., 2007
St. Croix	14.4	56.7	80.7	21795	Kennaway *et al*., 2008
St. Eustatius	7.0	45.1	83.2	2029	Helmer *et al*., 2008
St. Johns	5.9	89.0	90.4	5090	Kennaway *et al*., 2008
St. Kitts†	7.0	46.2	61.3	16695	Helmer *et al*., 2008
St. Thomas	22.5	69.0	72.9	8170	Kennaway *et al*., 2008
Tortola	10.6	79.8	85.6	6847	Kennaway *et al*., 2008
Trinidad	8.2	70.9	90.7	483186	Helmer *et al*., 2012
Tobago	7.9	83.6	90.7	30102	Helmer *et al*., 2012
Trinidad & Tobago†	8.2	71.6	90.6	513288	Helmer *et al*., 2012
US Virgin Islands†	15.9	69.8	87.1	35055	Kennaway *et al*., 2008
Virgin Gorda	7.9	78.2	85.3	2462	Kennaway *et al*., 2008

* Urban includes only high density urban.
** Norman, Peter, Cooper, Ginger Islands.
Agriculture and golf course covers are excluded from the vegetation cover data. For islands with a '†' Kairo *et al.* (2003) gives the number of naturalized introduced species.

Anthropogenic Effects on the Caribbean Biota

Humans have lived in the Caribbean for millennia causing considerable modification to the landscape and its biota. The early people in the Caribbean affected land cover and introduced human settlements to the region, but their main effect on the biota was not due to extensive deforestation and land cover changes. Instead, before their contact with Europeans, the people of the Caribbean had an important effect on the species composition of the biota. They did so by causing the extinction of organisms and moving plant and animal species from one place to another (Francis and Liogier, 1991; Whittaker, 1998; Kairo *et al*., 2003).

The magnitude of these changes due to extinctions, extirpation, or introduction of species is difficult to assess for the region as a whole. However, the changes are evident for particular places or groups of organisms studied by scientists. One example is the extinction and extirpation events in the bird and mammal fauna of Puerto Rico (Brash, 1987; Woods, 1996). Documenting extinction and extirpation of species is harder to do than documenting introductions of species, because the introduced species that survive are in plain sight, which is not the case for those that disappeared before a scientific record of their presence on the Islands existed.

Today, Caribbean island floras contain more taxa than they did before humans arrived to the region. The increase is due to the large number of species introductions and naturalizations. For the West Indies as a whole, Acevedo Rodríguez and Strong (2008) report that the percent of the total number of seed plant taxa represented by introduced taxa was 11, 26 and 15% for families, genera, and species, respectively (Table I). For Puerto Rico, which has benefited from intensive taxonomic activity, the present number of taxa for trees (Little *et al*., 1974), monocotyledonous plants (Acevedo Rodríguez and Strong, 2005), vines and climbing plants (Acevedo Rodríguez, 2005), ferns (Proctor, 1989), orchids (Ackerman, 1996), aquatic invertebrates (Williams *et al*., 2001), fish (Kwak *et al*., 2007), birds (Raffaele, 1989; Biaggi, 1997), ants (Torres and Snelling, 1997), amphibians and reptiles (Rivero, 1998), and earthworms (Borges, 1996), are higher than before humans arrived. Kairo *et al*. (2003) compiled data for a variety of taxa (Table I) and found that the number of introduced species varied with the size and location of the island. The larger islands of the Greater Antilles had more introduced species than those of the smaller Bahamas and the Lesser Antilles (Table II). The species-area relationship between both introduced and naturalized species and island area for ten Caribbean Islands was significant ($p = 0.003$ and 0.001, respectively) for log-transformed data.

Available information on the richness of Caribbean biota shows that the flora and fauna of the islands is today richer than it was before they experienced significant human activity. As we will see below, the success of introduced species in the Caribbean may be related to land cover changes, particularly the increase in built-up and degraded lands. These land cover changes create new environmental conditions to which native species are poorly adapted to, thus giving a competitive edge to introduced taxa (Francis and Liogier, 1991; Hobbs *et al*., 2006).

Anthropogenic Effects on Caribbean Landscapes

Large-scale land cover changes in the Caribbean were the legacy of European

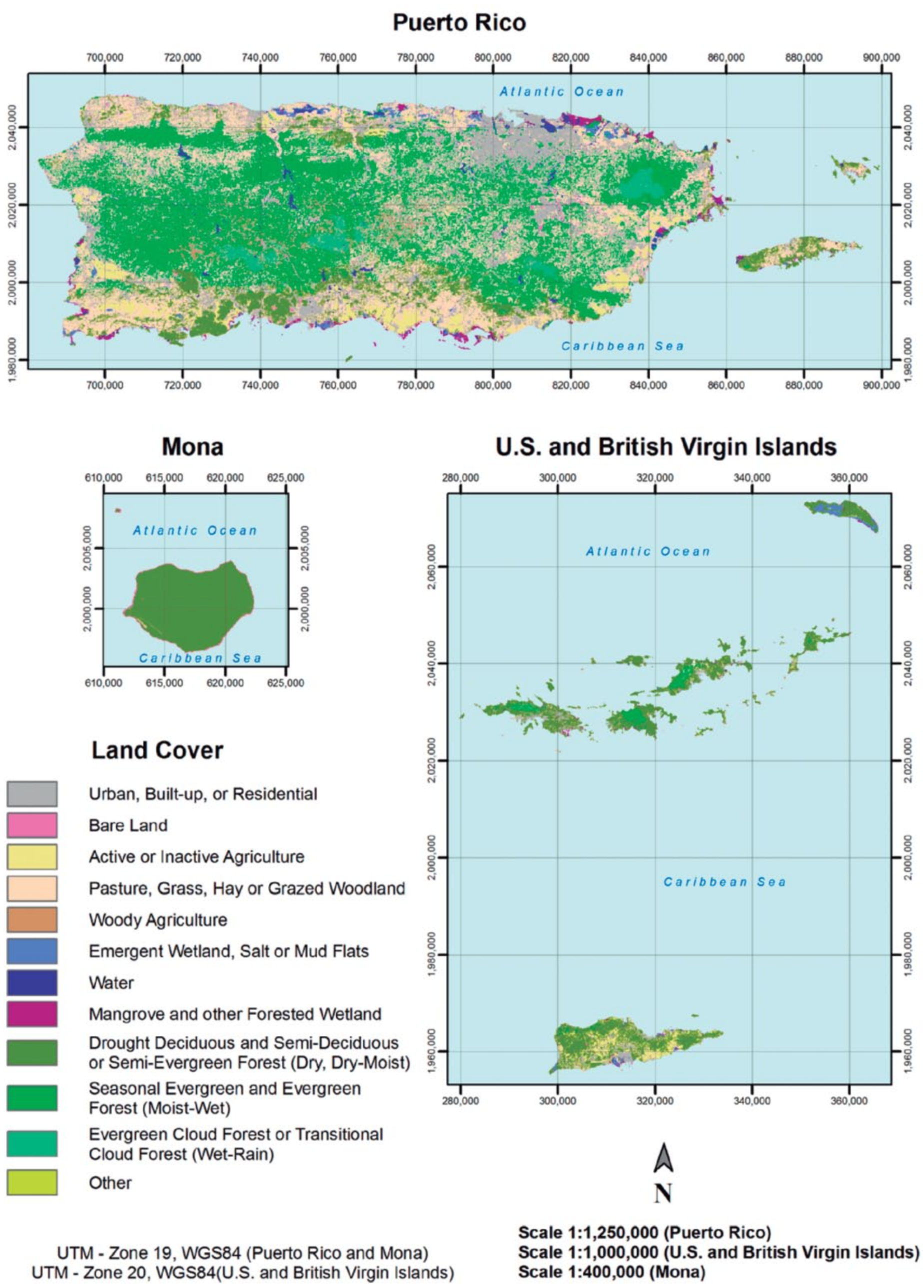

Figure 1a. Land cover maps of several Caribbean Islands (Kennaway and Helmer 2007; Helmer *et al*., 2008; Kennaway *et al*., 2008).

settlers. They did so to exploit forest resources, for mining activities, and for agriculture. At the turn of the 20th century it was difficult to identify pristine forest cover anywhere in the Caribbean (Zon and Sparhawk, 1923; Gill, 1931). In fact, Gill asserted that Trinidad, Haiti, Puerto Rico, and most of Cuba were 'almost forest-less lands'. Gill (1931, p. 66) wrote: "The woodlands of Porto Rico are only a memory". He attributed much of the anthropogenic effects as high grading of forests, i.e., to the repetitive and selective removal of the best timbers, with dramatic effects on forest composition and structure. Outright deforestation for agricultural purposes was the other major anthropogenic effect on Caribbean forests.

Any objective analysis of Caribbean landscapes leads to two fundamental observations: 1. The landscapes of the Caribbean, like any other landscape in the world, reflect the intensity and types of human activity prevailing on them (Lugo, 1996); the land covers in the Caribbean during the early to mid 20th century reflected the prevailing agricultural activities of humans, and these activities coupled to charcoal production resulted in reductions in forest areas (Lugo *et al*., 1981). 2. Because human activities change over time, land cover and land uses change, and thus it is possible for landscapes to change dramatically in a period of decades; this happened in Puerto Rico with the decline of agriculture and the expansion of urban built-up land (Lugo, 2002; Kennaway and Helmer, 2007). Helmer *et al.* (2008) showed that this pattern of land cover change from agricultural to urban and forests also happened in other Caribbean Islands.

Recent Land Cover in the Caribbean

By the end of the 20th century, Caribbean Island landscapes had experienced a dramatic change in land cover as a result of declining agricultural activity and increasing urbanization. These changes are reflected in the land cover data in Table III and Figure 1. Although the data cover a small fraction of the Caribbean Islands and mostly those of the Lesser Antilles, the general pattern is clear: forest cover and vegetation account for a large fraction of the land, and urban cover is proportionally high in comparison with countries in the continents.

Kennaway and Helmer (2007) aged the forests of Puerto Rico and found that between 1991 and 2000 most of the forests cleared for development (55%) were 1 to 13 years old, reflecting the recent abandonment and colonization of agricultural lands. Only 13% of the forests cleared for development were older than 41 years old. They found that the tendency for urban development was on flat lands or lands with easy access, regardless of land cover (forest or agricultural). Helmer (2004) found that the likelihood of urban development in Puerto Rico was positively related to proximity to urban areas, size of urban area, proximity to roads and surrounding proportion of pasture. It was negatively related to elevation, percent slope, alluvial substrate relative to other substrates, and surrounding proportion of shrubs plus low canopy density forests. Helmer (2004) also found that pasture is more likely to undergo development than shrubland plus forest with low canopy density, and that most land development occurs in the least protected ecological zones.

By the end of the 20th century, built-up land due to urbanization had become a determinant factor in the outcome of land cover change. Like topography, built-up land became a correlate of forest clearing and landscape fragmentation, much like road access to forestlands was at the turn of the 20th century. This pattern of land conversion is only possible in an energy-rich society whose machines allow conversion of lands that before were topographically inaccessible. This new reality is what makes the endemic biota of the Caribbean vulnerable to urbanization and other land cover changes. However, the land-cover data of Helmer *et al*. (2008) show recovery of vegetation, including forests, on abandoned agricultural lands such that there is more vegetation and forest cover in the Caribbean today than during the first half of the 20th century. This reversal of land cover and forest area will likely have important ecological consequences for the future.

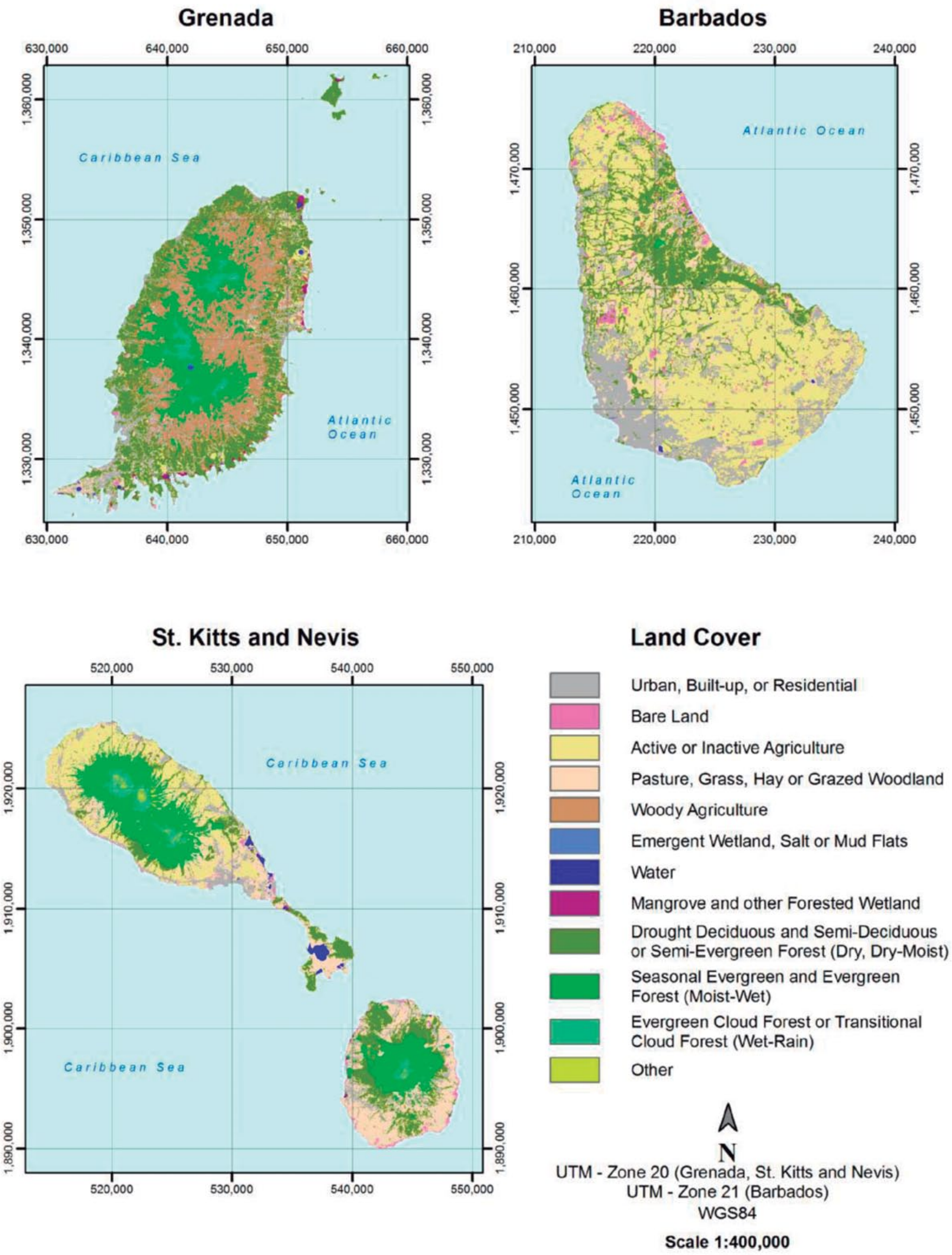

Figure 1b. Land cover maps of several Caribbean Islands (Kennaway and Helmer 2007; Helmer *et al*., 2008; Kennaway *et al*., 2008).

Ecological Consequences and Future Trends

The abandonment of agricultural lands and the natural recovery of vegetation on those lands has not only resulted in the greening of Caribbean Islands, but also has led to a change in species composition in the resulting secondary vegetation (Lugo and Helmer, 2004). Introduced species initially colonize abandoned and degraded lands; they form even age monospecific stands and at first appear to exclude native species. However, over time, these stands are invaded by native tree species and they diversify and increase the number of species per area (Lugo, 2004). These forests are new forest types on the landscape, i.e., novel forests *sensu* Hobbs *et al*. (2006). Their emergence is a global phenomenon (Marris, 2009): a natural response to environmental change triggered by anthropogenic activity. Research on the functioning of novel forests of the Caribbean is just beginning to take shape, but the species diversification of these forests represents a mitigating effect in relation to the effects of deforestation and urbanization. In fact, we found that the percent urban cover in eight Caribbean Islands identified with an '†' in Table III was significantly related to the number of naturalized species per unit land area ($p= 0.016$; adjusted $r^2= 0.59$). The urban cover is a proxy for the level of human activity responsible for diversifying the landscape and increasing the opportunities for the naturalization of species.

In summary, for millennia the Caribbean Islands have been a hot bed of human activity, which has continuously transformed the landscape and its biodiversity. The appearance of the landscape, as measured by changing land covers, has changed significantly several times from landscapes dominated by natural vegetation cover with native species, to fragmented and deforested agricultural landscapes with both native and introduced species, and more recently urbanizing landscapes with a mosaic of small fragments of vegetation cover composed of native, introduced, and naturalized species. In spite of all the changes in land cover, the fundamental original patterns of natural vegetation composition has not changed and the Islands remain a hotspot of terrestrial biodiversity, particularly Cuba and Hispaniola, as are the adjacent marine waters in terms of marine biodiversity. Humans have added complexity to the native biota by introducing species to the Caribbean with mixed results in relation to the expectations of the introductions. However, land cover changes induced by changing Caribbean economies have allowed natural processes of species naturalization, dispersal, growth, and self organization to produce a suite of novel ecosystems such as the extensive *Spathodea campanulata* forests in Puerto Rico, where 75% of the forest area contain novel combinations of tree species (Brandeis *et al*., 2009). These novel forests now appear as natural on the Caribbean landscape as do their predecessor native ecosystems. The net result is that the Caribbean Islands are now richer in species and community types than they were prior to human habitation but the cover of natural ecosystems (including the novel ones) is now less than it was before people. Humans now occupy spaces previously occupied by natural ecosystems. The vulnerability of all Caribbean ecosystems to unwanted anthropogenic effects is now higher than ever and requires judicious conservation measures to assure that the Caribbean continues to function as one of the world's premiere hotspots of biodiversity.

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