INVESTIGATING SUCCESSIONAL DYNAMICS IN NATURALLY-REGENERATED TROPICAL FORESTS OF PUERTO RICO: TESTING AND LEARNING FROM A CHRONOSEQUENCE APPROACH

by

John D. Souther

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

(Geography)

at the

UNIVERSITY OF WISCONSIN-MADISON

2014

Table of Contents

Acknowledgements

I am deeply thankful to my advisor, Erika Marín-Spiotta, for invaluable guidance and insight throughout the course of this project, as well as for seemingly inexhaustible patience, trust, and support, all of which allowed me freedom to explore and pursue my academic interests. Your commitment to your students was, and is, greatly appreciated.

I am also grateful to Lisa Naughton, who, in addition to providing helpful feedback on drafts of the proposal and thesis, also shared professional wisdom and encouragement. Many thanks also to Don Waller for comments on, and contributions to this project. I am also indebted to official and "honorary" members of the Marín-Spiotta Biogeochemistry Lab: Emily Atkinson, Rosenelsy Marrero Cuebas, Ken Keefover-Ring, Ricardo Rivera, Peyton Smith, Laura Szymanski, Adam von Haden, and various undergrad members for their feedback, support, and ideas to improve this project. My thanks go also to Bil Alverson, Jim Burt, Murray Clayton, Simon Goring, Daijiang Li, and Greg Sonnier for their help with plant ID, computer programs, and statistical analysis.

Finally, I could not have completed this project without the support of my wife, Sara. Your commitment, dedication, and expertise were both inspirational and indispensible throughout this process.

Additional thanks to the Geography Department for financial support from a Trewartha travel grant.

Abstract

Globally, naturally-regenerated secondary forests account for 57% of total forest cover, with most regrowth occurring on former pasture and cropland. These anthropogenic forests may provide important ecosystem goods and services, but are often dominated by novel species assemblages, with unpredictable consequences for ecosystem processes and successional trajectories. Understanding how these forests change with age is a crucial part of efforts to conserve biodiversity, maintain ecosystem functioning, and manage them for services such as carbon sequestration.

In 2012, I collected data from a chronosequence of naturally-regenerated tropical forests on abandoned pastureland in Puerto Rico in order to characterize changes in species composition, structure and aboveground biomass accumulation over 89 years of succession. Then, to test the ability of the chronosequence approach to predict changes through time, I compared my observations from 2012 with predicted changes based on patterns of changes seen across age classes at the same sites in 2003.

Structural characteristics and aboveground biomass generally recovered rapidly to pre-disturbance levels, though changes in biomass with age varied by method of estimation. While species diversity also exhibited rapid recovery to pre-disturbance levels with age, assemblages remained distinct from reference forest communities after 89 years. Though patterns in 2003 data were indicative of some observed changes, they failed to correctly predict many changes in forest structure, biomass and species composition within age classes

General Introduction

The aim of this project was two-fold. The first goal was to characterize successional changes in key tree community attributes in tropical secondary forests in Puerto Rico using data from a chronosequence of sites on abandoned pastureland. The second goal was to use newly collected data to test the validity of chronosequence-based predictions from the same sites in 2003, by comparing predicted changes with changes observed between 2003 and 2012. As primary forests continue to be lost and degraded, the global importance of secondary forests is increasing. In many ecosystems, anthropogenic activities have lead to alterations in historic species assemblages and uncertainty about their long-term function and behavior. This project took advantage of the well-documented land use history of Puerto Rico to study long-term patterns in succession of secondary forests that formed in a human-dominated environment following anthropogenic disturbance, as well as to assess the utility of using chronosequences to study successional dynamics in tropical secondary forests. The results have implications for both the management and study of secondary forests in the tropics.

Background

Though recent decades were marked by extremely high rates of deforestation in the tropics, new data show signs of a reversal of this trend in some areas of the world (FAO, 2010, Aide *et al.*, 2012, Álvarez-Berríos *et al.*, 2013). Across the globe, and especially in the tropics, socioeconomic and political changes are impacting ecosystems through changing land use (Aide and Grau, 2004). Combinations of urbanizing populations, globalization, industrialization of agriculture, and changes in forest management policies have led, in some areas, to agricultural abandonment and subsequent forest regrowth (Grau *et al.*, 2003, Lambin and Meyfroidt, 2010, 2011, Aide *et al.*, 2012, Álvarez-Berríos *et al.*, 2013). Globally, naturally-regenerated secondary forests make up 57% of total forest area, and despite the variety of underlying and proximate drivers of land cover change, increases in forest cover mostly occur on land formerly under agriculture (Chazdon *et al.*, 2007, Barbier *et al.*, 2010, FAO, 2010). A recent study by Aide *et al.* (2012) highlighted this phenomenon in Latin America and the Caribbean. The authors found a >360.000 km^2 increase in woody vegetation cover between 2001 and 2010, with most regrowth consisting of unassisted forest regeneration on abandoned agricultural land that was undesirable for large-scale industrial agriculture.

Previous studies have shown that tropical secondary forests can provide many of the same functions, goods and services as undisturbed forests (Lugo, 2004, Lugo and Helmer, 2004, Hobbs *et al*., 2006, Poffenberger, 2006, Foley *et al*., 2007, Chazdon, 2008, Chazdon *et al*., 2009). There is significant evidence that naturally-regenerated forests regain many characteristics of undisturbed forests within several decades of establishment (Brown and Lugo, 1990, Aide *et al.*, 1995, Zimmerman *et al.*, 1995, Pascarella *et al.*, 2000, Silver *et al.*, 2001, Chazdon, 2003, Chazdon *et al*., 2007, Marin-Spiotta *et al.*, 2007). Secondary forests on abandoned pastures in Puerto Rico showed high rates of biomass accumulation in the first 15-

20 years since abandonment with recovery of standing biomass to levels comparable to those of primary forests within 20 years of abandonment (Brown and Lugo, 1990; Lugo, 2002; Marin-Spiotta *et al.*, 2007). In Costa Rica, Letcher and Chazdon (2009) found that 21- to 30-year-old forests contained as much aboveground biomass as old-growth, and Guariguata *et al*. (1997) demonstrated recovery of basal area to old-growth levels within 15-20 years following abandonment. In two separate studies of forest regeneration on pastures across Puerto Rico, Aide *et al.* (1996, 2001) found that stem densities and basal areas of secondary forests were comparable to those of mature forests by 40 years after abandonment. Pascarella *et al.* (2000) showed that secondary forests on abandoned pastures and coffee plantations in the Cayey mountains of Puerto Rico recovered basal area values similar to those of mature forests after 25-30 years. Similar results illustrating rapid increases in basal area and aboveground biomass have been reported from Hawaii (Mascaro *et al*., 2012) and from throughout the Amazon basin (Uhl and Jordan, 1984, Uhl *et al*., 1988, Saldarriaga *et al*., 1988, Peña-Claros, 2003). In some cases, naturally-regenerated secondary forests have higher basal areas, accumulate more aboveground biomass, and store more carbon than primary forests. Studies in Costa Rica have shown that basal area and/or biomass of secondary forests reaches or surpasses that of local old-growth stands within 25-42 years (Guariguata *et al*., 1997, Letcher and Chazdon, 2009). Though they indicated a slightly longer duration, results from Panama and Puerto Rico have also shown that basal area and aboveground biomass of older secondary forests exceeded those of mature forests 70-80 years following abandonment (Denslow and Guzman, 2000,

Marin-Spiotta *et al*., 2007).

Recovery of forest structure and biomass is directly related to certain ecosystem functions. For example, the ability of forests to accumulate carbon is determined in large part by their aboveground biomass (Bunker *et al*., 2005). Pan *et al*. (2011) found that, from 1990-2007, post-disturbance regrowth of tropical forests accounted for roughly 40% of global carbon fixed by forests. As they grow, secondary forests can positively affect soil conditions, water quality, and nutrient cycling, and they can foster late successional and native species (Brown and Lugo, 1990). They can also act as corridors and buffers between primary forest patches and disturbed areas in fragmented landscapes (Turner *et al*., 1997). This, in turn, is important to maintenance and conservation of biodiversity (Brown and Lugo, 1990, Chazdon, 2008). Several studies from across the tropics have found that species richness in secondary forests is comparable to, and sometimes higher than, richness of comparable old-growth forests (Saldarriaga *et al*., 1988, Brown and Lugo, 1990, Aide *et al*., 1996, Aide, 2000, Denslow and Guzman, 2000, Guariguata and Ostertag, 2001, Marcano-Vega *et al*., 2002, Lugo and Helmer, 2004, Marin-Spiotta *et al*., 2007, Mascaro *et al*., 2012) and though differences in species assemblages between secondary and primary forests may persist for hundreds of years, secondary forests can still play an important role in conservation of endemics species (Lugo and Helmer, 2004, Chazdon *et al*., 2009).

In situations of unmanaged forest regeneration following agricultural abandonment, anthropogenic influences on the biotic and abiotic environment, especially the introduction of exotic species, may lead to formation of 'novel' secondary forest communities *sensu* Hobbs *et al*., (2006) (Lugo and Helmer, 2004, Lugo, 2009, Mascaro *et al*., 2012). These new forest communities consist of combinations of species not previously known to coexist in their observed configurations (Lugo and Helmer, 2004, Hobbs *et al*., 2006). In Puerto Rico and elsewhere in the tropics, nonnative species have taken on special importance in these novel forests, where they may fulfill roles that native or endemic species are temporarily unable to fill. For example, initial colonization by disturbance-adapted, exotic secondary forest species can create an amenable environment for, and acceleration of, the establishment of sensitive native species (Wadsworth and Birdsey, 1985, Vitousek *et al*., 1987, Parrotta *et al*., 1997, Holl *et al*., 2000, Lugo and Helmer, 2004). These species may also serve as habitat or food sources for native species, or may perform ecosystem fuctions in place of extinct native species (Holl *et al*., 2000, Schlaepfer *et al*., 2011).

Despite their structural comparability to old-growth forests, and their potential to fulfill certain ecological roles, secondary forests, especially if they contain novel species compositions, do not inevitably contribute to increases in regional biodiversity (Turner *et al*., 1997) or ecosystem function (Bunker *et al*., 2005). Literature from the field of invasion biology provides ample evidence that exotic species present in novel systems can disrupt established successional processes and negatively affect long-term outcomes of native species (Aide *et al*., 2000, Simberloff *et al*., 2005, Mascaro *et al*., 2008, Brandeis *et al*., 2009, Schlaepfer *et* *al*., 2011). Studies from forests in Hawaii and elsewhere show that while some native species can persist in canopies dominated by introduces species, their numbers generally decline following introductions of exotics (Hughes and Denslow, 2005; Mascaro *et al.*, 2008; Ostertag *et al.*, 2009; Mascaro, 2011, Mascaro *et al*., 2012). In a study of secondary forests in Puerto Rico, Aide *et al*. (2000) found that the non-native *Syzygium jambos* is capable of invading older forests and inhibiting establishment of native trees.

Study Area and Methods

The land cover history of Puerto Rico exemplifies the changes outlined in forest transition theory and observed in various post-agricultural landscapes across the globe (Mather, 1992, Rudel *et al*., 2005). By 1900, much of the island had been deforested for agricultural purposes, with roughly 78% of land under pasture, or cultivation of sugar cane or coffee (Wadsworth, 1950). In the 1940s, forest cover was reduced to 5-6% of its original extent (Birdsey and Weaver, 1987), but around that time the island underwent a substantial shift away from agriculture towards manufacturing (Dietz, 1986). Following large decreases in rural populations and agricultural land use, forest cover expanded dramatically, reaching approximately 57% of land cover by 2003 (Brandeis *et al*., 2007).

Because the dramatic changes in land cover in Puerto Rico over the last century were so well documented, the island represents an ideal opportunity for studying post-agricultural forest regeneration in the tropics. Expectations of future agricultural abandonment and forest regeneration in other parts of the tropics underscore the increasing importance of novel ecosystems and secondary forests. Corlett (1995) calls secondary forests the "tropical forests of the future" and Lugo (2009) concludes that continuing human modification of landscapes and abiotic conditions are likely to lead to increases in novel species assemblages with concomitant decreases in historic ecological communities. Together with the growing importance of these new communities, comes an increased need to understand how they function, for management and conservation purposes. Due to a dearth of studies that extend beyond the first two decades of succession (Marin-Spiotta and Sharma, 2013), long-term data on novel secondary forests are needed to establish how these communities change through time.

One approach to studying long-term forest recovery is the use of chronosequences. Because they represent a practical and convenient substitution of space for time, chronosequences have been a staple of studies of succession in various ecosystems for over a century (Cowles, 1899, Pickett, 1988). Seminal chronosequence studies shaped early notions of succession, and the method continues to be the backbone of many ecological investigations (Johnson and Miyanishi, 2008). As early as 1962, there were calls for caution when interpreting chronosequence data in the absence of other information, but many studies continue to proceed despite challenges to the assumption that the only factor that varies across classes or plots in a chronosequence is age (Rode, 1962, Johnson and Miyanishi, 2008). Validation of this assumption can be extremely difficult, so many studies, including this one, resort to field replication and careful site selection to minimize heterogeneity in environmental variables (Kashian *et al*., 2013).

Contribution

By combining a chronosequence approach spanning a period of almost 90 years with longitudinal data, this study of emerging forests on abandoned pastureland specifically addresses gaps in our knowledge about the long-term dynamics of structural and compositional changes in these systems. These data also shed light on changes in provision of certain ecosystem services as forests develop with age. In addition, I critically assess the performance of the chronosequence method as a proxy for longitudinal studies of succession of my study system.

References

Aide, T. M. (2000) Clues for tropical forest restoration. *Restoration Ecology,* **8,** 327-327.

Aide, T. M., Zimmerman, J. K., Pascarella, J. B., Rivera, L. & Marcano-Vega, H. (2000) Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restoration Ecology,* **8,** 328-338.

Aide, T. M., Zimmerman, J. K., Rosario, M. & Marcano, H. (1996) Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. *Biotropica***,** 537-548.

Birdsey, R. A. & Weaver, P. L. (1987) *Forest area trends in Puerto Rico.* US Department of Agriculture, Forest Service, Southern Forest Experiment Station New Orleans, LA, USA.

Brandeis, T. J., Helmer, E. H., Marcano-Vega, H. & Lugo, A. E. (2009) Climate shapes the novel plant communities that form after deforestation in Puerto Rico and the US Virgin Islands. *Forest Ecology and Management,* **258,** 1704-1718.

Brandeis, T. J., Helmer, E. H. & Oswalt, S. N. (2007) *The status of Puerto Rico's forests, 2003.* US Department of Agriculture, Forest Service, Southern Research Station.

Brown, S. & Lugo, A. E. (1990) Tropical Secondary Forests. *Journal of Tropical Ecology,* **6,** 1-32.

Bunker, D. E., DeClerck, F., Bradford, J. C., Colwell, R. K., Perfecto, I., Phillips, O. L., Sankaran, M. & Naeem, S. (2005) Species loss and aboveground carbon storage in a tropical forest. *Science,* **310,** 1029-1031.

Chazdon, R. L. (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics,* **6,** 51-71.

Chazdon, R. L. (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science,* **320,** 1458-1460.

Chazdon, R. L., Letcher, S. G., Van Breugel, M., Martínez-Ramos, M., Bongers, F. & Finegan, B. (2007) Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **362,** 273-289.

Chazdon, R. L., Peres, C. A., Dent, D., Sheil, D., Lugo, A. E., Lamb, D., Stork, N. E. & Miller, S. E. (2009) The potential for species conservation in tropical secondary forests. *Conservation biology,* **23,** 1406-1417.

Cowles, H. C. (1899) *The ecological relations of the vegetation on the sand dunes of Lake Michigan.* University of Chicago.

Denslow, J. S. & Guzman, G. (2000) Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. *Journal of Vegetation Science,* **11,** 201-212.

FAO (2010) Global Forest Resources Assessment (FRA) 2010. Food and Agriculture Organization of the United Nations, Rome.

Foley, J. A., Asner, G. P., Costa, M. H., Coe, M. T., DeFries, R., Gibbs, H. K., Howard, E. A., Olson, S., Patz, J. & Ramankutty, N. (2007) Amazonia revealed: forest

degradation and loss of ecosystem goods and services in the Amazon Basin. *Frontiers in Ecology and the Environment,* **5,** 25-32.
Guariguata, M. R., Chazdon, R. L., Denslow, J. S., Dupuy, J. M. & Anderson, L. (1997) Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. *Plant Ecology,* **132,** 107-120.
Guariguata, M. R. & Ostertag, R. (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management,* **148,** 185-206.
Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., Epstein, P. R., Ewel, J. J., Klink, C. A., Lugo, A. E., Norton, D., Ojima, D., Richardson, D. M., Sanderson, E. W., Valladares, F., Vila, M., Zamora, R. & Zobel, M. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography,* **15,** 1-7.
Holl, K. D., Loik, M. E., Lin, E. H. & Samuels, I. A. (2000) Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration Ecology,* **8,** 339-349.
Johnson, E. A. & Miyanishi, K. (2008) Testing the assumptions of chronosequences in succession. *Ecology Letters,* **11,** 419-431.
Kashian, D. M., Romme, W. H., Tinker, D. B., Turner, M. G. & Ryan, M. G. (2013) Postfire changes in forest carbon storage over a 300-year chronosequence of Pinus contorta-dominated forests. *Ecological Monographs,* **83,** 49-66.
Letcher, S. G. & Chazdon, R. L. (2009) Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica,* **41,** 608-617.
Lugo, A. E. (2004) The outcome of alien tree invasions in Puerto Rico. *Frontiers in Ecology and the Environment,* **2,** 265-273.
Lugo, A. E. (2009) The Emerging Era of Novel Tropical Forests. *Biotropica,* **41,** 589-591.
Lugo, A. E. & Helmer, E. (2004) Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management,* **190,** 145-161.
Marcano-Vega, H., Aide, T. M. & Baez, D. (2002) Forest regeneration in abandoned coffee plantations and pastures in the Cordillera Central of Puerto Rico. *Plant Ecology,* **161,** 75-87.
Marin-Spiotta, E., Ostertag, R. & Silver, W. L. (2007) Long-term patterns in tropical reforestation: Plant community composition and aboveground biomass accumulation. *Ecological Applications,* **17,** 828-839.
Mascaro, J., Becklund, K. K., Hughes, R. F. & Schnitzer, S. A. (2008) Limited native plant regeneration in novel, exotic-dominated forests on Hawai'i. *Forest Ecology and Management,* **256,** 593-606.
Mascaro, J., Hughes, R. F. & Schnitzer, S. A. (2012) Novel forests maintain ecosystem processes after the decline of native tree species. *Ecological Monographs,* **82,** 221-228.
Mather, A. S. (1992) The forest transition. *Area***,** 367-379.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L. & Canadell, J. G. (2011) A large and persistent carbon sink in the world's forests. *Science,* **333,** 988-993.

Parrotta, J. A., Turnbull, J. W. & Jones, N. (1997) Catalyzing native forest regeneration on degraded tropical lands. *Forest Ecology and Management,* **99,** 1-7.

Peña-Claros, M. (2003) Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon1. *Biotropica,* **35,** 450-461.

Pickett, S. T. (1988) Space-for-time substitution as an alternative to long-term studies. *Long-term studies in ecology*pp. 110-135. Springer.

Poffenberger, M. (2006) People in the forest: community forestry experiences from Southeast Asia. *International Journal of Environment and Sustainable Development,* **5,** 57-69.

Rode, A. A. (1962) The soil-forming process and soil evolution. *Soil Science,* **94,** 274.

Rudel, T. K., Coomes, O. T., Moran, E., Achard, F., Angelsen, A., Xu, J. & Lambin, E. (2005) Forest transitions: towards a global understanding of land use change. *Global Environmental Change,* **15,** 23-31.

Saldarriaga, J. G., West, D. C., Tharp, M. & Uhl, C. (1988) Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. *The Journal of Ecology*, 938-958.

Schlaepfer, M. A., Sax, D. F. & Olden, J. D. (2011) The Potential Conservation Value of Non‐Native Species. *Conservation biology,* **25,** 428-437.

Simberloff, D., Parker, I. M. & Windle, P. N. (2005) Introduced species policy, management, and future research needs. *Frontiers in Ecology and the Environment,* **3,** 12-20.

Turner, I., Wong, Y., Chew, P. & Ibrahim, A. B. (1997) Tree species richness in primary and old secondary tropical forest in Singapore. *Biodiversity and Conservation,* **6,** 537-543.

Uhl, C., Buschbacher, R. & Serrao, E. (1988) Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. *The Journal of Ecology*, 663-681.

Uhl, C. & Jordan, C. F. (1984) Succession and nutrient dynamics following forest cutting and burning in Amazonia. *Ecology,* **65,** 1476-1490.

Vitousek, P. M., Walker, L. R., Whiteaker, L. D., Mueller-Dombois, D. & Matson, P. A. (1987) Biological invasion by Myrica faya alters ecosystem development in Hawaii. *Science,* **238,** 802-804.

Wadsworth, F. & Birdsey, R. (1985) A new look at forests of Puerto Rico. *Turrialba,* **35,** 11-17.

<u>Chapter 1:</u> Long-term successional changes in species composition, structure and aboveground biomass in post-agricultural tropical forests of Puerto Rico

Introduction

Ongoing conversion of forests for agricultural use is resulting in continued losses of forest cover in tropical regions (FAO, 2010, Hansen *et al.*, 2013, Foley *et al.*, 2005, Aide *et al.*, 2012), with consequences for biodiversity (Brooks *et al.*, 2002). Loss of forest cover is associated with declines in ecosystem services such as carbon sequestration, regional water flow and climate regulation, and pest and pathogen mediation (Foley *et al.*, 2005, Schimel, 1995, Foley *et al.*, 2007). While forest loss continues to be the dominant pan-tropical trend (Aide *et al.*, 2012, Hansen *et al.*, 2013, FAO, 2010), urbanizing populations, globalization, industrialization of agriculture, and changes in forest management policies have led, in some areas, to a forest transition with abandonment of marginal and small-scale agricultural land and subsequent forest regrowth (Aide *et al.*, 2012, Álvarez-Berríos *et al.*, 2013, Grau *et al.*, 2003, Lambin and Meyfroidt, 2010, Aide and Grau, 2004, Rudel *et al.*, 2005). These former agricultural lands or old-fields are the setting for the majority of natural forest regeneration in Latin America, the Caribbean, and tropical Asia and Africa (Barbier *et al.*, 2010, Chazdon *et al.*, 2007, Aide *et al.*, 2012, Hansen *et al.*, 2013, FAO, 2010, Meyfroidt and Lambin, 2011) , as well as in regions outside the tropics (Munteanu *et al.*, 2014, Rudel *et al.*, 2005).

For most tropical countries, secondary forests represent increasingly large and important proportions of forested area (Brown and Lugo, 1990, FAO, 2010, Lambin and Meyfroidt, 2011, Chazdon *et al*., 2009, Foley *et al*., 2007). Tropical secondary forests can provide many of the same functions, goods and services of undisturbed forests (Chazdon, 2008a, Hobbs *et al*., 2006, Poffenberger, 2006, Chazdon *et al*., 2009, Foley *et al*., 2007, Lugo and Helmer, 2004, Lugo, 2004). Due to direct and indirect anthropogenic alterations of the biophysical environment in which they occur, naturally-regenerated secondary forests often consist of new species assemblages and may form novel (*sensu* Hobbs *et al*., 2006) or emerging ecosystems (*sensu* Lugo, 2009, Milton, 2003). Because of the novelty of these anthropogenic forests, questions remain about the long-term successional processes that operate in them, as well as their comparability with primary forests (Lugo and Helmer, 2004).

While studies have found that successional changes in post-disturbance secondary forests may follow an equilibrium model of deterministic community assembly (Norden *et al*., 2009, Peña-Claros, 2003) there is substantial evidence that initial colonization and the rate and nature of subsequent changes in species composition are controlled by factors like soil fertility, land use history, the configuration of vegetation on the surrounding landscape, presence of seed dispersing fauna, and disturbance regime (Arroyo-Rodríguez *et al*., 2013, Chazdon, 2003, Chazdon, 2008a, Guariguata, 1990, Holl, 2002, Holl *et al*., 2000, Hooper *et al*., 2004, Kupfer *et al*., 2004, Walker, 1994, Zimmerman *et al*., 2000). Together with the influence of introduced species present in novel ecosystems, these factors may interact in ways that result in unpredictable successional outcomes (Lugo, 2009, Chazdon, 2008b). In cases where novel assemblages exhibit different functional traits than historic communities, these differences in composition may affect overall ecosystem functioning (Mascaro *et al*., 2012).

Land use changes over the past century in Puerto Rico have resulted in natural forest regeneration, including the well-documented formation of novel communities (Aide *et al*., 2000, Brandeis *et al*., 2009, Lugo, 2004, Lugo, 2009, Lugo and Helmer, 2004, Marin-Spiotta *et al*., 2007, Pascarella *et al*., 2000). My investigation takes advantage of the island's unique and well-studied land cover history (Álvarez-Berríos *et al*., 2013, Birdsey and Weaver, 1987, Helmer *et al*., 2002, Brandeis *et al*., 2007) to test some of the assumptions of deterministic succession theory. I used a well-replicated chronosequence of noncontiguous, naturally-regenerated forest plots on abandoned pastures to investigate whether, given sufficient time, secondary forests would develop characteristics of reference forests. Specifically, I asked how time since abandonment affects i)forest structure, as measured by stem density and basal area, ii)aboveground biomass stocks and iii)species composition. My inclusion of secondary forest age classes >60 years old provides this study with a longer-term perspective on successional changes than has often been possible.

Materials and methods

STUDY SITES

Study plots were located in the Sierra de Cayey mountains in southeastern Puerto Rico on private land near the border of the municipalities of Guayama and Patillas.

In 1937 the primary land use in this region was pasture, and forests covered <20% of land area (Pascarella *et al*., 2000). By 1995, due to agricultural abandonment, 62% of the area was forested, resulting in a patchwork landscape of small forest patches, interspersed with dwellings and active agricultural land and pastures (Pascarella *et al*., 2000). Forest types in the study region are classified as lower montane wet evergreen forest, tall cloud forest, and palm brake in the subtropical wet forest Holdridge life zone (Ewel and Whitmore, 1973)(Helmer *et al.*, 2002; Ostertag *et al.*, 2008). Elevations of the sites range from 580 to 700 m above sea level, with mean annual precipitation of approximately 2000 mm (1955-2012) reported from the nearby Jajome Alto weather station (730 m a.s.l.). Mean annual air temperature for the period 1971-2000 was 21.5°C (http://www.sercc.com). Soils across the sites are classified as deep, well-drained, volcanically-derived Inceptic Hapludox soils in the Los Guineos series and show very little variation in texture and soil carbon and nitrogen stocks (Boccheciamp, 1977, Lugo López, 1995, Marin-Spiotta *et al*. 2009).

My plots constitute a chronosequence of naturally regenerated secondary forests on former pastures in the following classes: 19-, 29-, 39-, 69-, and 89-years old in 2012, when this study was conducted. All sites were under use as pasture prior to abandonment. In addition, I also surveyed replicate mature reference forest plots for which there is no evidence of clearing. Each forest age class is represented by three non-contiguous field site replicates, except for the 39-year-old class, which has two replicates due to the recent clearing of one site by its owner after plots were originally established, yielding a total of 17 study plots. For all secondary forest plots, the time of abandonment was determined by time-series aerial photography and interviews with landowners (Marin-Spiotta *et al*., 2007, Pascarella *et al*., 2000). When confirmation by landowners was unavailable, dates of abandonment were estimated as the midpoints between the last photos showing active pasture and first photos indicating regrowth of woody vegetation.

DATA COLLECTION

At each forest site, one 24 x 24 m plot was established for tree measurements in 2003 and all trees, which were at least 1.3 m tall and had diameters ≥10 cm at 1.3 m height (dbh) were permanently tagged (Marin-Spiotta *et al*., 2007). In July 2012, I returned to each plot, verified identification of each tree, and recorded the diameters of all stems of live, rooted trees with tags, and of new trees in the ≥ 10 cm diameter size class which had not been previously tagged. For multi-stemmed trees, all stems meeting the size criteria were measured and recorded. I also collected height estimates for the single monocotyledonous species in my sites, the palm *Prestoea acuminata* var*. montana* (Graham) A.J. Hend. & Galeano*.* Species names follow Little *et al*. (1974) and Little and Wadsworth (1964), with updates from *The Plant List* (2013).

FOREST STRUCTURE AND BIOMASS

I calculated stem density (SD) (# stems/ha), basal area (BA) (m^2/ha) and total aboveground biomass (TAB) (Mg/ha) for each site. My SD, BA and TAB calculations include values for every stem, regardless of whether each represents an individual tree or one of multiple stems. Differences in SD and BA with age were analyzed using one-way ANOVA and post-hoc Tukey-Kramer HSD comparisons in SAS JMP (SAS, 1989-2014). I calculated and compared aboveground biomass estimates for each site using four allometric models (Table 1). As a baseline, I applied Weaver and Gillespie's (1992) allometric equation (WG) developed for the tabonuco forest type in Puerto Rico to all trees, regardless of species. Tabonuco forest is a well-studied, mature forest type also known as the *Dacryodes-Sloanea* association (Beard, 1948), which is dominated by tabonuco (*Dacryodes excelsa* Vahl), *Buchenavia tetraphylla* (Aubl.) R.A. Howard, *Tetragastris balsamifera* (Sw.) Oken, *Guarea Guidonia* (L.) Sleumer, *Manilkara bidentata* (A. DC.) A. Chev., and *Sloanea berteroana* (Choisy ex DC.) and is associated with subtropical wet and subtropical rain forest life zones in Puerto Rico *sensu* Holdridge (1967). The equation yields total aboveground biomass (TAB), including woody and leafy components. To account for high abundances of the palm *Prestoea acuminata var. montana* in older secondary and reference forests (proportion of basal area at each site represented by *P. acuminata:* 2%-84%--Fig. 3), my second approach was to estimate TAB using a combination of WG for all dicots and tree ferns (*Cyathea arborea* (L.) Sm.), and Frangi and Lugo's (1985) equation for palms (FL), which was developed specifically for *P. acuminata* in Puerto Rico. FL requires both diameter and height to estimate TAB of *P. acuminata.* I visually estimated heights for all palms and then verified heights of a subset using heights measured with a 10 m telescopic measuring pole the next season. Using this data, I created a correction factor for height estimation, which I applied to all visually-estimated heights to account for estimation error (see Table 1). I then calculated

TAB estimates at the site level for all dicots and monocots by summing the results from WG and FL (WGFL).

My third approach (CHFL) estimated TAB of dicots using Chave *et al*.'s (2005) pan-tropical Model II allometric model for moist tropical forests (CH). In addition to diameter, this model for dicots incorporates wood specific gravity (ρ, g/cm^3) for each species. Here, I calculated site-level TAB estimates by combining estimates from CH for dicots with estimates for *P. acuminata* and the tree fern *C. arborea* using FL and WG, respectively. My fourth approach (VBFL) estimated TAB using van Breugel *et al*.'s (2011) local multispecies allometric "M2" model (VB), which was developed through destructive sampling in secondary forests in central Panama, applied to dicots, FL applied to *P. acuminata*, and WG applied to tree ferns. The van Breugel equation includes a term for wood specific gravity (ρ, g/cm^3) values of each species. I obtained wood specific gravity values from Zanne *et al*. (2009) and other published sources (Little and Wadsworth, 1964, Longwood, 1961, Reyes *et al*., 1992, Turrell *et al*., 1967, Weaver, 1993) (see Appendix A1). Whenever multiple values for the same species were given, I used average values. For those species for which no values could be found, I used genus-level averages, as recommended by Fayolle *et al*. (2013). To test for differences among age classes, TAB estimation approaches, and their interactions, I analyzed data with the Mixed Model Personality in SAS JMP using a split-plot 2-way ANOVA with age as the whole plot factor (as a randomized complete block) and TAB estimation method as the subplot factor.

SPECIES COMPOSITION AND DIVERSITY

To determine differences in tree communities among age classes, I examined species richness, species diversity, and evenness for each site (Table 3). I included three measures of richness: observed species richness, estimated richness using Abundance-based Coverage Estimator (ACE; (Chao *et al*., 2005)) and estimated richness from coverage-based extrapolation (Colwell *et al*., 2012). I used the R package 'fossil' to calculate ACE and the package 'iNEXT' (Hsieh *et al*., 2014) to extrapolate sample-size-based richness and diversity estimates with 50 bootstrap resamples. According to the recommendations of (Chao *et al*., 2014) I determined a base-sample-size of 101 individuals for extrapolation of richness estimates at the site level and 186 individuals for the age class level. In addition, I calculated Fisher's α diversity, exponential Shannon's diversity, inverse Simpson's diversity and Pielou's evenness statistic (*J*) for the reference samples at each site (Table 3) using the R package 'vegan'. Unless otherwise noted, I analyzed diversity metrics using one-way ANOVA and post-hoc Tukey-Kramer HSD comparisons in SAS JMP.

I also evaluated community similarities among pairs of sites using the complements of two abundance-based similarity indices: Morisita-Horn (MH) and Chao-Jaccard (CJ) (i.e., 1-MH and 1-CJ). The values I report are dissimilarity indices, both of which range from 0 to 1, with 0 indicating maximum similarity and 1 indicating maximum dissimilarity between pairs of assemblages. The MH index is based on the probability that a randomly chosen individual from each site belongs to the same species. This index is robust to undersampling because it tends to be dominated by the most abundant species (Chao *et al*., 2008). In contrast to the MH index, the CJ similarity index is based on the probability that a randomly chosen individual from each site belongs to any of the shared species between the two assemblages. In addition, this unbiased index accounts and corrects for the contributions of unseen shared species to these probabilities, thus retaining sensitivity to rare species and relative abundances (Chao *et al*., 2005, Gotelli and Chao, 2013). For both of these indices, I used vegan to generate matrices of pair-wise site dissimilarities.

To test whether species assemblages of secondary forests become more similar to assemblages in reference forest plots with age, I generated all possible pairwise comparisons with reference forest plots within each age class, including within the reference class itself; i.e., I compared each replicate plot within an age group with each replicate plot of reference forest. I then compared mean dissimilarity with reference forest of each age class. In order to visualize these patterns of changing communities with age I also visually assessed differences among sites using nonmetric multidimensional scaling (NMDS) based on both MH and CJ dissimilarities.

Results

FOREST STRUCTURE AND BIOMASS

Stem density differed among forest age classes ($F_{5,11}$ = 6.062, P=0.006) with the mean SD of the 19-year-old age class being significantly lower than that of 39-, 69- and 89-year-old forests (Fig. 1). Basal area also varied by age class ($F_{5,11}$ = 13.86, P=0.0002) (Fig. 2). Mean basal area peaked in the 89-year-old forests, which had significantly higher BA than reference forests. Nineteen-year-old forests had the lowest mean BA. Among secondary forests, there was a significant increase in BA between the 19- and 29-year-old age classes.

The effect of forest age on TAB varied by the approach used to estimate TAB ($F_{15,33}$ = 2.28, P=0.0236) (Table 4). Within each age class, there was high consistency in the ranking of mean TAB estimates produced by each approach, though post-hoc comparisons showed significant differences among models in 3 age classes. In the 29-year-old class, VBFL TAB was significantly lower than CHFL TAB, and in the 69- and 89-year-old classes, VBFL TAB estimates were lower than both CHFL and WG TAB estimates. CHFL TAB in the 89-year-old class was significantly higher than WGFL TAB. VBFL consistently yielded the lowest mean TAB values within each age class, and except for the 69-year-old class, in which it produced the second-highest mean TAB value, CHFL yielded the highest mean TAB estimates within all age classes. Apart from the 69-year-old age class in which WG yielded the largest mean TAB estimate, the mean TAB estimates of WG and WGFL were consistently between those of CHFL and VBFL. The effect of separating the palms and applying FL to estimate their TAB consistently returned lower plot-level TAB estimates for any plots containing palms, relative to the estimates produced by applying WG to all trees regardless of whether they are monocots or dicots.

SPECIES DIVERSITY

Observed species richness did not differ among age classes (Table 3). However, tests on the ACE richness estimates did reveal differences among age classes ($F_{5,11}$ =

3.6620, P=0.0339), with 39-year-old forests having significantly lower mean ACE richness than reference forests. These results agree with extrapolated richness estimates for each age class, which showed that, at equal sample sizes of 186 individuals, the 39-year-old forests had significantly lower estimated species richness than all other age classes except for the 19-year-old forests (Table 3).

Tests on Fisher's α diversity, exponential Shannon's diversity and inverse Simpson's diversity values of the reference samples at each site showed no significant differences in diversity among age classes. However, extrapolated estimates of exponential Shannon's diversity (Fig. 4) and inverse Simpson's diversity (Fig. 5) indicated significant differences among age classes for augmented sample sizes of 186 individuals .The 39-year-old forest class had lower extrapolated diversity than all other classes for both exponential Shannon's and inverse Simpson's diversity. Extrapolated Shannon's diversity of the 89-year-old forests was higher than that of the 19-, 29- and 39-year-old forest classes. Pielou's evenness (*J*) differed among age classes ($F_{5,11}$ = 3.4988, P=0.0388). Post-hoc Tukey-Kramer HSD tests showed that the 39-year-old forests have significantly less even species distributions than the 19- and 89-year old forests.

COMMUNITY COMPOSITION

Differences in species assemblages also varied by age class. Using PERMANOVA, I tested Morisita-Horn (MH) and Chao-Jaccard (CJ) dissimilarity values for each pair of sites and found significant differences in species assemblages among age classes (999 permutations, MH *r*=0.763, P=0.002; CJ *r*=0.740, P=0.001). Nonmetric

Multidimensional Scaling (NMDS) results based on CJ (stress=0.160, Fig. 6) and MH (stress=0.169, Fig. 7) dissimilarities showed a separation between older secondary and reference forests and younger secondary forests. For both MH and CJ dissimilarities, tree assemblages in the 19-year-old forests were closer to assemblages of reference forests along NMDS Axis 1 than were either 29- or 39-year-old forest assemblages.

Similarities to reference forest varied among age classes of secondary forest (Kruskal-Wallis, $P<0.0001$ for both CJ (Fig. 8) and MH (Fig. 9). Ninety-five percent confidence intervals of mean dissimilarity values of both indices indicated that the tree communities of older secondary forests (69- and 89-year-old age classes) were similar to those of reference forests, whereas younger secondary forests were very dissimilar to reference forests. Younger age classes did not differ from one another in their dissimilarities with reference forests.

Discussion

RAPID RECOVERY OF FOREST STRUCTURE

I found rapid post-disturbance recovery of forest structural components, confirming previous findings of other studies from across the tropics (Aide *et al*., 1995, Aide *et al*., 2000, Aide *et al*., 1996, Brown and Lugo, 1990, Chazdon, 2003, Chazdon *et al*., 2007, Guariguata *et al*., 1997, Guariguata and Ostertag, 2001, Letcher and Chazdon, 2009, Lugo, 2002, Marin-Spiotta *et al*., 2007, Mascaro *et al*., 2012, Pascarella *et al*., 2000, Peña-Claros, 2003, Saldarriaga *et al*., 1988, Silver *et al*., 2001, Uhl *et al*., 1988, Uhl and Jordan, 1984, Zimmerman *et al*., 1995). Stem density recovered to levels of reference forests within 19 years and BA within 29 years of abandonment, even for trees ≥ 10cm dbh. The recovery of forest structure in this size class indicates both high recruitment and high incremental growth rates among individuals in young forests. Changes in SD across age classes followed an expected pattern, with increases in the first 39 years, followed by decreases back towards levels of reference forests. This pattern is consistent with traditional models of succession in which early stages are marked by establishment of high numbers of individuals, which then decrease following canopy closure and increased competition from shade tolerant species (Denslow and Guzman, 2000). In contrast to SD, BA of secondary forests continued to increase with age, surpassing the basal area of reference forests within 89 years of abandonment.

The low BA values for reference forest sites are likely due to the high proportion of stems represented by the palm *P. acuminata*. On average, *P. acuminata* accounted for 49% (range 30%-81%) of the stems in reference forests, 33% (range 7%-49%) of the stems in 89 year old forests and 39% (range 22%-54%) of the stems in 69 year old forests. There were no palms present in 19-year-old sites, and palms accounted for less than 5% of stems in 29 and 39 year old forests. In contrast to dicot tree species, which exhibit continuous secondary growth, the lateral stem growth of *P. acuminata* ceases or slows drastically after reaching its mature diameter (maximum palm diameter recorded in this census: 25.4 cm dbh in an 89-year-old site) (Lugo and Batlle, 1987, Waterhouse and Quinn, 1978). Due to their shade tolerance and distribution among my sites, it is likely that palms will continue to increase in proportion in my secondary forest plots. The dominance of palms could lead eventually to decreases in the basal areas of these older secondary forests as large dicot trees die and are replaced by young palms growing in the understory. My results demonstrate the important role of species composition in shaping forest structure.

MIXED PATTERNS IN DIVERSITY AND SPECIES COMPOSITION

Observed species richness and diversity across the secondary forest chronosequence showed rapid recovery following abandonment of pastures and forest regrowth, consistent with forest structural characteristics. With the exception of the ACE richness estimator and Pielou's evenness statistic, all diversity metrics calculated using solely observed, i.e., not augmented, data indicated that richness and diversity recovered to, and remained at, levels found in the reference forests within 19 years following abandonment. Nonparametric ACE richness estimates showed that the 39-year-old forests had lower richness than the reference forests. The ACE estimator incorporates frequencies of rare species, which appear only a few times in a sample, and it uses this information to adjust observed richness based on the likelihood of there being 'unseen' species in the larger community that was sampled, but that were not present in the sample itself (Chao *et al*., 2005). Therefore, the ACE richness of a sample containing many rare species, which occur at low frequencies, will be higher than the observed richness, and when there are few of these rare species, ACE richness will be closer to observed richness. Higher numbers of rare species in the reference forests and lower numbers of them in the 39-year-old forests resulted in the significant difference in their ACE richnesses.

The lower values of Pielou's evenness evident in 39-year-old forests reflects the fact that the 2 remaining plots were dominated by the native colonizer *Tabebuia heterophylla* (DC.) Britton (93% of total stems at both sites).

Because richness and diversity vary by area or number of trees sampled, comparisons across samples of different sizes can result in false conclusions. I generated extrapolated estimates of richness and diversity based on an equal sample size for all classes, thus avoiding problems inherent in assessing them based only on reference samples of differing sizes (Colwell *et al.*, 2012). My extrapolated richness estimates revealed that, at equal sample sizes, 39-year-old forests would be expected to contain fewer species than all but the youngest secondary forests. Due to the sensitivity of species richness to rare species, I included the Hill numbers ^1D (Shannon's exponential entropy) and ^2D (the inverse of Simpson's diversity index) (Hill, 1973). These two metrics put increasing weight on common species and can be thought of as representing the number of "typical species" and "very abundant species" in an assemblage, respectively (Chao *et al.*, 2010, Chao *et al.*, 2014, Gotelli and Chao, 2013). Using augmented and equal sample sizes, extrapolated estimates of both indices returned significantly lower expected diversity for 39-year-old forests relative to all other classes. Shannon's exponential index also resulted in higher extrapolated diversity in the 89-year-old forests than in the 19-, 29-, and 39-year-old forests.

The consistency among estimates indicating low richness and diversity of the 39-year-old forests suggests that these forests differ from the other age classes. A likely reason for the apparent difference is that I only had two replicate plots for this age class. Indeed, Marin-Spiotta *et al*. (2007) reported higher mean richness across these plots in 2003. What is clear is that the 2, 39-year-old plots surveyed for this study, despite having the highest mean stem density of all classes, are actually the least diverse assemblages, dominated almost exclusively by *T. heterophylla*.

The pattern of decreasing species evenness seen across the 3 youngest forest classes is contrary to the findings of Capers *et al*. (2005), who found increases in evenness in tree communities during first 30 years following abandonment in Costa Rican forests. While not as high as in the 39-year-old plots, the proportion of *T. heterophylla* in 29-year-old sites was still 52% of all stems, indicating that it could have been responsible for the lower-than-expected evenness relative to the 19-year-forests. Taken together, the low diversity and evenness of the 39-year-old forests suggest that their use as pastures may have been long enough to deplete the seed bank of mature forests species, or that mature forest remnants were too far to allow for easy propagule dispersal to the plots at the time of abandonment. (Guariguata and Ostertag, 2001, Zimmerman *et al*., 2000) This would have allowed for the establishment of the prolific, wind-dispersed *T. heterophylla.* The extreme dominance of *T. heterophylla* in 39-year-old sites may indicate that is has an inhibitory effect on the establishment and growth of other species in these sites (Mesquita *et al*., 2001, Arroyo-Rodríguez *et al*., 2013). My results, based on both reference and augmented samples, indicate a full recovery of species richness and diversity to reference forest levels within 19 years after abandonment. This is in line with the findings of Marin-Spiotta *et al*. (2007), and is supported by results of rapid recovery of richness and diversity from several other studies and reviews (Brown and Lugo, 1990, Chazdon, 2003, Chazdon, 2008b, Chazdon *et al*., 2007, Guariguata and Ostertag, 2001).

Ordination analyses of Morisita-Horn (MH) and Chao-Jaccard (CJ) dissimilarities did not indicate a clear linear successional trajectory across all age classes, but both analyses grouped the 69- and 89-year-old forests more closely to reference forests than to younger secondary forests. Morisita-Horn- and CJ-based comparisons of dissimilarity to reference forests also clearly separated the age classes into 2 groups. Older secondary and reference forests were similar to each other and very different from younger secondary forests, which were more similar to each other. The CJ-based NMDS and the CJ-based dissimilarity with reference forest comparison both revealed a pattern of increasing similarity to reference forest assemblages with age in the oldest two secondary forest classes. Among the three youngest classes, age did not result in obvious directional change in tree community compositions.

The consistent pattern of similarity seen among the three oldest classes in the NMDS and dissimilarity-compared-with-reference-forest-plots is suggestive of an equilibrium model, with a deterministic pathway towards recovery of forest communities to pre-disturbance configurations, similar to results found in Costa Rica by Norden *et al*. (2009). In contrast, community changes among the three youngest classes do not reveal such a clear trajectory. The loss of the third replicate in the 39-year-old class at least partly explains its low diversity, and may lead to this class obscuring a weak, but present pattern of deterministic changes in my younger forest classes. Nonetheless, the extremely uneven and non-diverse species compositions at the 2 remaining 39-year-old sites, indicate that factors other than age may explain observed differences across my plots. Duration and intensity of previous land use, the proximity and species composition of remnant vegetation in the landscape surrounding sites at abandonment, the presence or absence of seed-dispersing fauna, interspecific interactions, and local scale disturbances are just a few of the important factors widely acknowledged to affect initial colonization and succession following disturbance (Chazdon, 2003, Holl *et al*., 2000, Hooper *et al*., 2005, Kupfer *et al*., 2004, Zimmerman *et al*., 2000, Guariguata, 1990, Walker, 1994, Arroyo-Rodríguez *et al*., 2013). It is possible that a combination of these factors has led to assembly of unique communities in my younger age classes. Therefore, the assumption of eventual convergence with communities in reference forests, barring major disturbances, may not hold in these younger forests, and they may follow novel successional trajectories with age (Chazdon, 2008b, Lugo, 2009). Alternatively, it is possible that, given sufficient time, the younger secondary forest communities will converge towards those of the reference forests. Given that changes in forest structure and species communities can happen very quickly in tropical forests (Marin-Spiotta *et al*., 2007, Brown and Lugo, 1990, Guariguata and Ostertag, 2001, Letcher and Chazdon, 2009), the intermediate steps that might bridge the observed differences in species assemblages in younger and older secondary forests may fall in the 30-year time gap between 39- and 69-year-old age classes.

CHANGES IN BIOMASS WITH AGE VARY BY ALLOMETRIC METHOD

The effect of forest age on total aboveground biomass (TAB) varied by allometric method, highlighting the importance of model choice when estimating TAB for the purpose of comparing differences among forest plots. Estimating TAB of trees is an important part of quantifying the carbon stored within a forest's vegetation, as well as a valuable metric for assessing post-disturbance recovery (Brown, 2002, Chazdon, 2003). Challenges to obtaining accurate estimates of TAB include small plot sizes, diverse tree assemblages, variation in growth form and density within single species, and a large range of trunk diameters and heights (Mascaro *et al*., 2012, Brown, 2002, van Breugel *et al*., 2011, Baker *et al*., 2004). The four allometric models that I tested in different combinations occupy a continuum of specificity and offer different advantages and disadvantages in estimating TAB. Because Weaver and Gillespie's (1992) model calculates TAB solely as a function of diameter, it is a very easy and efficient way to estimate TAB. However, it does not incorporate any species-specific or other size data, so it may lead to inaccurate estimates of TAB where species compositions and/or tree morphologies differ greatly from those in the specific tabonuco forests where the model was developed.

The Chave *et al*. (2005) and van Breugel *et al*. (2011) models are both more global in their geographic applicability, since they can be applied to forests with any species assemblages occurring in the climate types for which they were developed. The incorporation of species-specific wood density values into allometric biomass equations accounts for more variation in tree community composition among forest plots but requires accurate identification of tree species and wood density values, which are not always available. Intra-specific variation in wood specific gravity can also add an additional level of uncertainty to these models (Baker *et al*., 2004). The three multi-species allometric models I used were all developed to be applied at the forest plot level (Weaver and Gillespie, 1992, Chave *et al*., 2005, van Breugel *et al*., 2011), whereas Frangi and Lugo's (1985) single-species palm model was designed to calculate TAB of a single individual or a pure stand of *P. acuminata* (Frangi and Lugo, 1985). We can assume that, with accurate dbh and height measurements as input, the TAB estimate of any single individual of *P. acuminata* will be highly accurate. This should be true of any single-species allometric model, yet it is often impractical, if not impossible, to find single-species TAB models for all species in a forest. The high relative abundance of *P. acuminata* in the older secondary and reference forest sites and the major differences in morphology between monocots and dicots justified the incorporation of this single-species model into my TAB calculations. The consistent differences between TAB estimates of WG and WGFL for sites with palms indicate that general allometric equations that ignore differences in species assemblages may produce misleading results when applied across heterogeneous communities.

My results show the importance of allometric model choice not only for detecting differences among forest plots that may differ in species composition, but also for detecting changes within plots through time. As species compositions within forests change with age, so may the suitability of a particular allometric model. The inconsistencies across models that I demonstrated, highlight the importance of consistency for comparability across studies and could be especially relevant to payment for ecosystem services initiatives such as REDD and the Carbon Fund of the Forest Carbon Partnership Facility, which include forest carbon stocks as a factor in their payment schemes (Kinzig *et al*., 2011).

CONCLUSIONS AND IMPLICATIONS

Overall, these findings support those of previous studies indicating rapid recovery of forest structure, aboveground biomass stocks and species diversity in tropical secondary forests. The apparent effect of age on accumulation of aboveground biomass depended on the allometric models used to calculate estimates. This underscores the need for consistency in estimating and reporting biomass and carbon stocks. The long time span represented in my chronosequence allowed me to discern 2 possible successional patterns among species communities across different forest age classes. Though remaining structurally and compositionally distinct from them, older secondary forests showed evidence of deterministic reassembly of communities similar to those of reference forests with age. However, patterns of change with age in younger secondary forest communities suggest that other factors such as previous land use, distance from mature forests, or interspecific interactions, may result in alternative successional trajectories in these forests. Further research is needed to reveal the long-term outcomes in my younger secondary forest plots. While not equivalent to them, my study shows that naturally-regenerated tropical forests have the potential to rapidly regain many characteristics of primary forests. Faced with global changes in the environment, ongoing decreases in primary forest cover, and increases in agricultural abandonment and natural regeneration in some areas, I expect secondary forests to play increasingly important roles in providing ecosystem services and functioning.

References

Aide, T. M., Clark, M. L., Grau, H. R., López ‐ Carr, D., Levy, M. A., Redo, D., Bonilla ‐ Moheno, M., Riner, G., Andrade ‐ Núñez, M. J. & Muñiz, M. (2012) Deforestation and reforestation of Latin America and the Caribbean (2001–2010). *Biotropica*.

Aide, T. M. & Grau, H. R. (2004) Ecology - Globalization, migration, and Latin American ecosystems. *Science,* **305,** 1915-1916.

Aide, T. M., Zimmerman, J. K., Herrera, L., Rosario, M. & Serrano, M. (1995) Forest recovery in abandoned tropical pastures in Puerto Rico. *Forest Ecology and Management,* **77,** 77-86.

Aide, T. M., Zimmerman, J. K., Pascarella, J. B., Rivera, L. & Marcano ‐ Vega, H. (2000) Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restoration Ecology,* **8,** 328-338.

Aide, T. M., Zimmerman, J. K., Rosario, M. & Marcano, H. (1996) Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. *Biotropica***,** 537-548.

Álvarez-Berríos, N. L., Redo, D. J., Aide, T. M., Clark, M. L. & Grau, R. (2013) Land Change in the Greater Antilles between 2001 and 2010. *Land,* **2,** 81-107.

Arroyo-Rodríguez, V., Rös, M., Escobar, F., Melo, F. P. L., Santos, B. A., Tabarelli, M. & Chazdon, R. (2013) Plant β-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. *Journal of Ecology,* **101,** 1449-1458.

Baker, T. R., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T. J., Laurance, S. G. & Laurance, W. F. (2004) Variation in wood density determines spatial patterns inAmazonian forest biomass. *Global Change Biology,* **10,** 545-562.

Barbier, E. B., Burgess, J. C. & Grainger, A. (2010) The forest transition: Towards a more comprehensive theoretical framework. *Land Use Policy,* **27,** 98-107.

Beard, J. S. (1948) The natural vegetation of the Windward and Leeward Island. *Ox. For. Mem.*

Birdsey, R. A. & Weaver, P. L. (1987) *Forest area trends in Puerto Rico.* US Department of Agriculture, Forest Service, Southern Forest Experiment Station New Orleans, LA, USA.

Boccheciamp, R. A. (1977) Soil survey of the Humacao area of eastern Puerto Rico. *United States Department of Agriculture Soil Conservation Service, San Juan, PR, USA*.

Brandeis, T. J., Helmer, E. H., Marcano-Vega, H. & Lugo, A. E. (2009) Climate shapes the novel plant communities that form after deforestation in Puerto Rico and the US Virgin Islands. *Forest Ecology and Management,* **258,** 1704-1718.

Brandeis, T. J., Helmer, E. H. & Oswalt, S. N. (2007) *The status of Puerto Rico's forests, 2003.* US Department of Agriculture, Forest Service, Southern Research Station.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. & Hilton-Taylor, C. (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation biology,* **16,** 909-923.

Brown, S. (2002) Measuring carbon in forests: current status and future challenges. *Environmental pollution,* **116,** 363-372.

Brown, S. & Lugo, A. E. (1990) Tropical Secondary Forests. *Journal of Tropical Ecology,* **6,** 1-32.

Capers, R. S., Chazdon, R. L., Brenes, A. R. & Alvarado, B. V. (2005) Successional dynamics of woody seedling communities in wet tropical secondary forests. *Journal of Ecology,* **93,** 1071-1084.

Chao, A., Chazdon, R. L., Colwell, R. K. & Shen, T. J. (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters,* **8,** 148-159.

Chao, A., Chiu, C.-H. & Jost, L. (2010) Phylogenetic diversity measures based on Hill numbers. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **365,** 3599-3609.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K. & Ellison, A. M. (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs,* **84,** 45-67.

Chao, A., Jost, L., Chiang, S., Jiang, Y. H. & Chazdon, R. L. (2008) A Two‐Stage Probabilistic Approach to Multiple‐Community Similarity Indices. *Biometrics,* **64,** 1178-1186.

Chave, J., Andalo, C., Brown, S., Cairns, M., Chambers, J., Eamus, D., Fölster, H., Fromard, F., Higuchi, N. & Kira, T. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia,* **145,** 87-99.

Chazdon, R. L. (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics,* **6,** 51-71.

Chazdon, R. L. (2008a) Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science,* **320,** 1458-1460.

Chazdon, R. L. (2008b) Chance and determinism in tropical forest succession. *Tropical forest community ecology***,** 384-408.

Chazdon, R. L., Letcher, S. G., Van Breugel, M., Martínez-Ramos, M., Bongers, F. & Finegan, B. (2007) Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **362,** 273-289.

Chazdon, R. L., Peres, C. A., Dent, D., Sheil, D., Lugo, A. E., Lamb, D., Stork, N. E. & Miller, S. E. (2009) The potential for species conservation in tropical secondary forests. *Conservation biology,* **23,** 1406-1417.

Colwell, R. K., Chao, A., Gotelli, N. J., Lin, S.-Y., Mao, C. X., Chazdon, R. L. & Longino, J. T. (2012) Models and estimators linking individual-based and sample-based

rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology,* **5,** 3-21.
Denslow, J. S. & Guzman, G. (2000) Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. *Journal of Vegetation Science,* **11,** 201-212.
Ewel, J. J. & Whitmore, J. L. (1973) Ecological life zones of Puerto Rico and US Virgin Islands.
FAO (2010) Global Forest Resources Assessment (FRA) 2010. Food and Agriculture Organization of the United Nations, Rome.
Fayolle, A., Doucet, J.-L., Gillet, J.-F., Bourland, N. & Lejeune, P. (2013) Tree allometry in Central Africa: Testing the validity of pantropical multi-species allometric equations for estimating biomass and carbon stocks. *Forest Ecology and Management,* **305,** 29-37.
Foley, J. A., Asner, G. P., Costa, M. H., Coe, M. T., DeFries, R., Gibbs, H. K., Howard, E. A., Olson, S., Patz, J. & Ramankutty, N. (2007) Amazonia revealed: forest degradation and loss of ecosystem goods and services in the Amazon Basin. *Frontiers in Ecology and the Environment,* **5,** 25-32.
Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C. & Gibbs, H. K. (2005) Global consequences of land use. *Science,* **309,** 570-574.
Frangi, J. L. & Lugo, A. E. (1985) Ecosystem dynamics of a subtropical floodplain forest. *Ecological Monographs***,** 351-369.
Gotelli, N. J. & Chao, A. (2013) Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. *Encylopedia of Biodiversity* (ed S. Levin), pp. 195-211. Academic Press, Waltham, MA.
Grau, H. R., Aide, T. M., Zimmerman, J. K., Thomlinson, J. R., Helmer, E. & Zou, X. M. (2003) The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. *Bioscience,* **53,** 1159-1168.
Guariguata, M. R. (1990) Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. *The Journal of Ecology***,** 814-832.
Guariguata, M. R., Chazdon, R. L., Denslow, J. S., Dupuy, J. M. & Anderson, L. (1997) Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. *Plant Ecology,* **132,** 107-120.
Guariguata, M. R. & Ostertag, R. (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management,* **148,** 185-206.
Hansen, M., Potapov, P., Moore, R., Hancher, M., Turubanova, S., Tyukavina, A., Thau, D., Stehman, S., Goetz, S. & Loveland, T. (2013) High-resolution global maps of 21st-century forest cover change. *Science,* **342,** 850-853.
Helmer, E., Ramos, O., del MLópez, T., Quiñónez, M. & Diaz, W. (2002) Mapping the forest type and land cover of Puerto Rico, a component of the Caribbean biodiversity hotspot. *Caribbean Journal of Science,* **38,** 165-183.
Hill, M. O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology,* **54,** 427-432.

Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., Epstein, P. R., Ewel, J. J., Klink, C. A., Lugo, A. E., Norton, D., Ojima, D., Richardson, D. M., Sanderson, E. W., Valladares, F., Vila, M., Zamora, R. & Zobel, M. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography,* **15,** 1-7.
Holdridge, L. R. (1967) *Life zone ecology.* Tropical Science Center, San Jose, Costa Rica.
Holl, K. D. (2002) Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. *Journal of Ecology,* **90,** 179-187.
Holl, K. D., Loik, M. E., Lin, E. H. & Samuels, I. A. (2000) Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration Ecology,* **8,** 339-349.
Hooper, E., Legendre, P. & Condit, R. (2005) Barriers to forest regeneration of deforested and abandoned land in Panama. *Journal of applied Ecology,* **42,** 1165-1174.
Hooper, E. R., Legendre, P. & Condit, R. (2004) Factors affecting community composition of forest regeneration in deforested, abandoned land in Panama. *Ecology,* **85,** 3313-3326.
Hsieh, T. C., Ma, K. H. & Chao, A. (2014) iNEXT: An R package for interpolation and extrapolation in measuring species diversity. Unpublished manuscript.
Kinzig, A., Perrings, C., Chapin, F., Polasky, S., Smith, V., Tilman, D. & Turner, B. (2011) Paying for ecosystem services—promise and peril. *Science,* **334,** 603-604.
Kupfer, J. A., Webbeking, A. L. & Franklin, S. B. (2004) Forest fragmentation affects early successional patterns on shifting cultivation fields near Indian Church, Belize. *Agriculture, ecosystems & environment,* **103,** 509-518.
Lambin, E. F. & Meyfroidt, P. (2010) Land use transitions: Socio-ecological feedback versus socio-economic change. *Land Use Policy,* **27,** 108-118.
Lambin, E. F. & Meyfroidt, P. (2011) Global land use change, economic globalization, and the looming land scarcity. *Proceedings of the National Academy of Sciences,* **108,** 3465-3472.
Letcher, S. G. & Chazdon, R. L. (2009) Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica,* **41,** 608-617.
Little, E., Woodbury, R. & Wadsworth, F. (1974) Trees of Puerto Rico and the Virgin Islands. Second volume. Agriculture Handbook, US Department of Agriculture.
Little, E. L. & Wadsworth, F. H. (1964) Common trees of Puerto Rico and the Virgin Islands. Agriculture Handbook, US Department of Agriculture.
Longwood, F. R. (1961) Puerto Rican woods; their machining, seasoning and related characteristics. USDA Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA, USA.
Lugo, A. E. (2002) Can we manage tropical landscapes? - an answer from the Caribbean perspective. *Landscape Ecology,* **17,** 601-615.

Lugo, A. E. (2004) The outcome of alien tree invasions in Puerto Rico. *Frontiers in Ecology and the Environment,* **2,** 265-273.
Lugo, A. E. (2009) The Emerging Era of Novel Tropical Forests. *Biotropica,* **41,** 589-591.
Lugo, A. E. & Batlle, C. T. R. (1987) Leaf production, growth rate, and age of the palm Prestoea montana in the Luquillo Experimental Forest, Puerto Rico. *Journal of Tropical Ecology***,** 151-161.
Lugo, A. E. & Helmer, E. (2004) Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management,* **190,** 145-161.
Lugo López, M. A. (1995) Updated taxonomic classification of the soils of Puerto Rico, 1994.
Marin-Spiotta, E., Ostertag, R. & Silver, W. L. (2007) Long-term patterns in tropical reforestation: Plant community composition and aboveground biomass accumulation. *Ecological Applications,* **17,** 828-839.
Mascaro, J., Asner, G. P., Dent, D. H., DeWalt, S. J. & Denslow, J. S. (2012) Scale-dependence of aboveground carbon accumulation in secondary forests of Panama: A test of the intermediate peak hypothesis. *Forest Ecology and Management,* **276,** 62-70.
Mascaro, J., Hughes, R. F. & Schnitzer, S. A. (2012) Novel forests maintain ecosystem processes after the decline of native tree species. *Ecological Monographs,* **82,** 221-228.
Mesquita, R. C., Ickes, K., Ganade, G. & Williamson, G. B. (2001) Alternative successional pathways in the Amazon Basin. *Journal of Ecology,* **89,** 528-537.
Meyfroidt, P. & Lambin, E. F. (2011) Global forest transition: prospects for an end to deforestation.
Milton, S. J. (2003) 'Emerging ecosystems' - a washing-stone for ecologists, economists and sociologists? *South African Journal of Science,* **99,** 404-406.
Munteanu, C., Kuemmerle, T., Boltiziar, M., Butsic, V., Gimmi, U., Halada, L., Kaim, D., Király, G., Konkoly-Gyuró, É. & Kozak, J. (2014) Forest and agricultural land change in the Carpathian region—A meta-analysis of long-term patterns and drivers of change. *Land Use Policy,* **38,** 685-697.
Norden, N., Chazdon, R. L., Chao, A., Jiang, Y. H. & Vílchez ‐ Alvarado, B. (2009) Resilience of tropical rain forests: tree community reassembly in secondary forests. *Ecology Letters,* **12,** 385-394.
Pascarella, J. B., Aide, T. M., Serrano, M. I. & Zimmerman, J. K. (2000) Land-use history and forest regeneration in the Cayey Mountains, Puerto Rico. *Ecosystems,* **3,** 217-228.
Peña ‐ Claros, M. (2003) Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon1. *Biotropica,* **35,** 450-461.
Poffenberger, M. (2006) People in the forest: community forestry experiences from Southeast Asia. *International Journal of Environment and Sustainable Development,* **5,** 57-69.

Reyes, G., Brown, S., Chapman, J. & Lugo, A. E. (1992) Wood densities of tropical tree species. USDA Forest Service, Southern Forest Experiment Station, Institute of Tropical Forestry, New Orleans, LA, USA.

Rudel, T. K., Coomes, O. T., Moran, E., Achard, F., Angelsen, A., Xu, J. & Lambin, E. (2005) Forest transitions: towards a global understanding of land use change. *Global Environmental Change,* **15,** 23-31.

Saldarriaga, J. G., West, D. C., Tharp, M. & Uhl, C. (1988) Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. *The Journal of Ecology***,** 938-958.

SAS (1989-2014) JMP Pro, Version 11. SAS Institute Inc., Cary, NC.

Schimel, D. S. (1995) Terrestrial Ecosystems and the Carbon-Cycle. *Global Change Biology,* **1,** 77-91.

Silver, W., Ostertag, R. & Lugo, A. (2001) The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. *Restoration Ecology,* **8,** 394-407.

The Plant List (2013) The Plant List. http://www.theplantlist.org.

Turrell, F., Austin, S., McNee, D. & Park, W. (1967) Thermal conductivity of functional citrus tree wood. *Plant physiology,* **42,** 1025-1034.

Uhl, C., Buschbacher, R. & Serrao, E. (1988) Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. *The Journal of Ecology***,** 663-681.

Uhl, C. & Jordan, C. F. (1984) Succession and nutrient dynamics following forest cutting and burning in Amazonia. *Ecology,* **65,** 1476-1490.

van Breugel, M., Ransijn, J., Craven, D., Bongers, F. & Hall, J. S. (2011) Estimating carbon stock in secondary forests: decisions and uncertainties associated with allometric biomass models. *Forest Ecology and Management,* **262,** 1648-1657.

Walker, L. R. (1994) Effects of fern thickets on woodland development on landslides in Puerto Rico. *Journal of Vegetation Science,* **5,** 525-532.

Waterhouse, J. T. & Quinn, C. J. (1978) Growth patterns in the stem of the palm Archontophoenix cunninghamiana. *Botanical Journal of the Linnean Society,* **77,** 73-93.

Weaver, P. L. (1993) Micropholis chrysophylloides Pierre Caimitillo. USDA Forest Service, Southern Forest Experiment Station, New Orleans, LA, USA.

Weaver, P. L. & Gillespie, A. J. R. (1992) Tree biomass equations for the forests of the Luquillo Mountains, Puerto Rico. *Commonwealth Forestry Review,* **71,** 35-39.

Zanne, A., Lopez-Gonzalez, G., Coomes, D., Ilic, J., Jansen, S., Lewis, S., Miller, R., Swenson, N., Wiemann, M. & Chave, J. (2009) Global wood density database. *Dryad. Identifier:* http://hdl.handle.net/10255/dryad.

Zimmerman, J. K., Aide, T. M., Rosario, M., Serrano, M. & Herrera, L. (1995) Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. *Forest Ecology and Management,* **77,** 65-76.

Zimmerman, J. K., Pascarella, J. B. & Aide, T. M. (2000) Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology,* **8,** 350-360.

Chapter 1 Tables and Figures

Table 1. Allometric models used to estimate total aboveground biomass

Model	Equation	Application	Source
WG	TAB = 4.7306 - 2.8566 x (dbh) + 0.5832 x (dbh^2)	Tabonuco forest (all trees)	Weaver & Gillespie, 1992
FL	TAB = 6.4 x (total ht) - 10.0	*Prestoea acuminata var. montana*	Frangi & Lugo, 1985
CH*	TAB = ρ x exp(-1.499 + 2.148ln(dbh) + $0.207(\ln(dbh))^2 - 0.0281(\ln(dbh))^3$)	Model II for moist forest stands	Chave, et al. 2005
VB§	ln(TAB) = -1.130 + 2.267 x ln(dbh) + 1.186 x ln(ρ)	Model 2 (M2) for multiple species	van Breugel, et al. 2011

Palm height correction based on verification of heights of 63 palms	**r^2**	**p-value**
Corrected Ht = -1.119051 + 1.2615696 * Estimated Ht	0.90543	p<0.0001

*includes correction factor: CF = $\exp(RSE^2/2)$

§ includes correction factor: CF = $e^{0.5xMSE}$

Table 2. Total aboveground biomass (Mg/ha)

Forest Age (yrs)	Site	WG	WGFL	CHFL	VBFL
19	8	64.10	64.10	69.77	54.18
19	67	40.74	40.74	53.28	39.36
19	68	18.73	18.73	18.72	14.81
19 Mean+se		41 ± 13	41 ± 13	47 ± 15	36 ± 11
29	26	187.62	185.03	283.59	165.41
29	78	209.05	209.05	181.42	111.63
29	79	137.31	137.31	171.91	120.42
29 Mean+se		178 ± 21	177 ± 21	212 ± 36	132 ± 17
39	50	187.90	187.90	242.62	164.69
39	77	149.68	135.11	169.61	118.63
39 Mean+se		169 ± 19	162 ± 26	206 ± 37	142 ± 23
69	32	260.19	183.39	248.40	157.66
69	33	256.97	190.10	225.57	143.42
69	38	186.26	160.13	201.75	143.58
69 Mean+se		234 ± 24	178 ± 9	225 ± 13	148 ± 5
89	5	241.85	233.91	351.28	236.51
89	23	326.71	270.19	333.70	230.25
89	28	377.84	323.09	395.87	313.65
89 Mean+se		315 ± 40	276 ± 26	360 ± 19	260 ± 27
Reference	88	244.87	215.58	283.35	173.27
Reference	89	161.33	78.39	82.04	73.14
Reference	90	174.06	151.34	229.54	148.14
Reference Mean+se		193 ± 26	148 ± 40	198 ± 60	132 ± 30

Table 3. Sample size, richness, diversity and evenness metrics by site with age class means. Values in parentheses represent means ± se. *Extrapolated richness values in parentheses are 95% confidence intervals

Age (yrs)	Site	Number of individuals	Observed richness	Extrapolated richness*	Fisher's α	ACE estimated richness	Exponential Shannon's diversity (^{1}D)	Inverse Simpson's diversity (^{2}D)	Pielou's evenness (J)
19	8	30	5	5 (3-7)	1.71	5.36	3.21	2.43	0.73
19	67	30	4	4 (3-6)	1.24	4.67	2.4	2.03	0.63
19	68	12	5	6 (0-13)	3.22	6	4.15	3.6	0.88
19-yr means		24 (18-30)	4.67 (4.34-5)	11 (5-17)	2.06 (1.46-2.66)	5.34 (4.96-5.72)	3.25 (2.74-3.76)	2.69 (2.22-3.16)	0.75 (0.68-0.82)
29	26	33	8	14 (5-23)	3.36	13.78	3.57	2.29	0.61
29	78	36	10	11 (5-17)	4.59	11.69	6.01	3.83	0.78
29	79	74	2	2 (2-2)	0.38	2	1.45	1.27	0.53
29-yr means		47.67 (34.47-60.87)	6.67 (4.27-9.07)	17 (14-20)	2.78 (1.53-4.03)	9.16 (5.53-12.79)	3.68 (2.36-5)	2.46 (1.72-3.2)	0.64 (0.57-0.71)
39	50	101	3	3 (2-3)	0.58	4	1.12	1.04	0.1
39	77	84	3	3 (2-3)	0.61	3.29	1.42	1.21	0.32
39-yr means		92.5 (84-101)	3 (3-3)	5 (3-6)	0.6 (0.58-0.62)	3.65 (3.29-4.01)	1.27 (1.12-1.42)	1.13 (1.04-1.22)	0.21 (0.1-0.32)
69	32	58	11	13 (8-18)	4.02	14.33	3.96	2.24	0.57
69	33	79	11	12 (7-16)	3.47	12.64	5.24	3.4	0.69
69	38	42	8	10 (7-13)	2.93	9.38	5.37	4.37	0.81
69-yr means		59.67 (48.96-70.38)	10 (9-11)	18 (13-22)	3.47 (3.16-3.78)	12.12 (10.67-13.57)	4.86 (4.41-5.31)	3.34 (2.72-3.96)	0.69 (0.62-0.76)
89	5	49	15	19 (11-27)	7.37	16.7	12.01	10.3	0.92
89	23	52	6	6 (4-7)	1.75	6	3.6	2.53	0.71
89	28	59	10	12 (8-17)	3.45	12.5	4.16	2.51	0.62
89-yr means		53.33 (50.37-56.29)	10.33 (7.73-12.93)	18 (13-23)	4.19 (2.53-5.85)	11.73 (8.62-14.84)	6.59 (3.88-9.3)	5.11 (2.52-7.7)	0.75 (0.66-0.84)
Reference	88	51	10	13 (6-19)	3.72	12.91	5.29	3.76	0.72
Reference	89	65	8	10 (5-15)	2.4	20.56	2.04	1.39	0.34
Reference	90	41	12	20 (10-29)	5.71	16.28	7.16	4.87	0.79
Reference means		52.33 (45.37-59.29)	10 (8.85-11.15)	20 (16-25)	3.94 (2.98-4.9)	16.58 (14.37-18.79)	4.83 (3.33-6.33)	3.34 (2.31-4.37)	0.62 (0.48-0.76)

Table 4. Results of a 2-way, split-plot ANOVA showing the significance of forest age, TAB estimation method and their interaction

	Factor					
	Forest age		TAB estimation approach		Forest age x TAB estimation approach	
	F	*P*	*F*	*P*	*F*	*P*
Total aboveground biomass (Mg/ha)	12.816	0.0003	30.7108	<0.0001	2.2842	0.0236

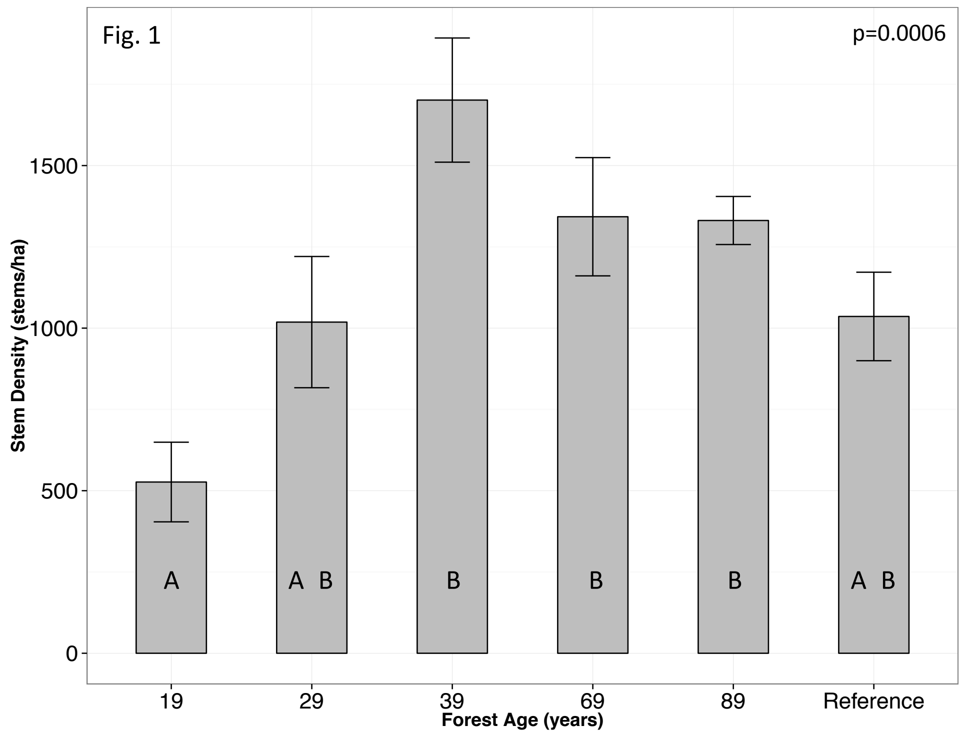

Fig. 1: Stem density per hectare
Bars not connected by the same letter are significantly different

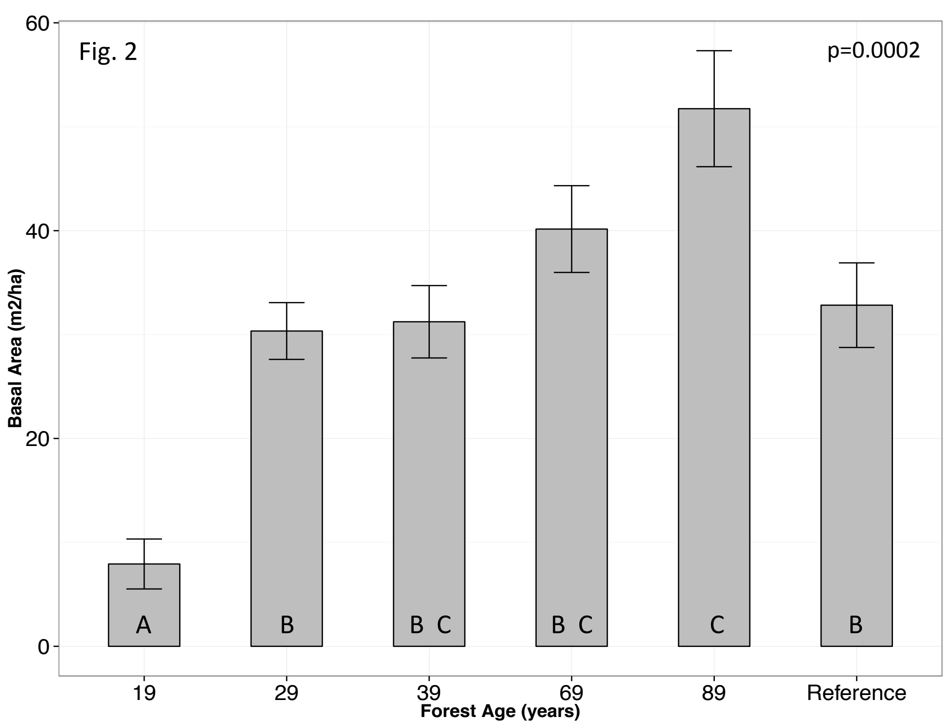

Fig. 2: Basal area (m^2/ha)
Bars not connected by the same letter are significantly different

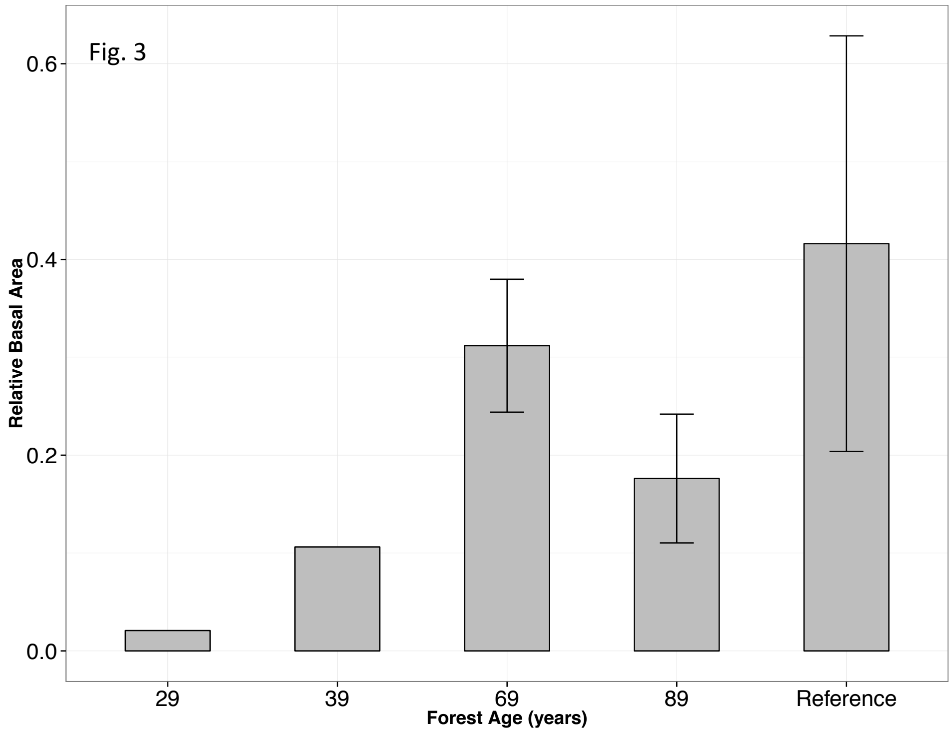

Fig. 3: Mean proportional contribution of the palm *P. acuminata* to the total basal area of each age class. Error bars are shown where palms were present in more than one site per age class. No palms were present in 19-year-old sites.

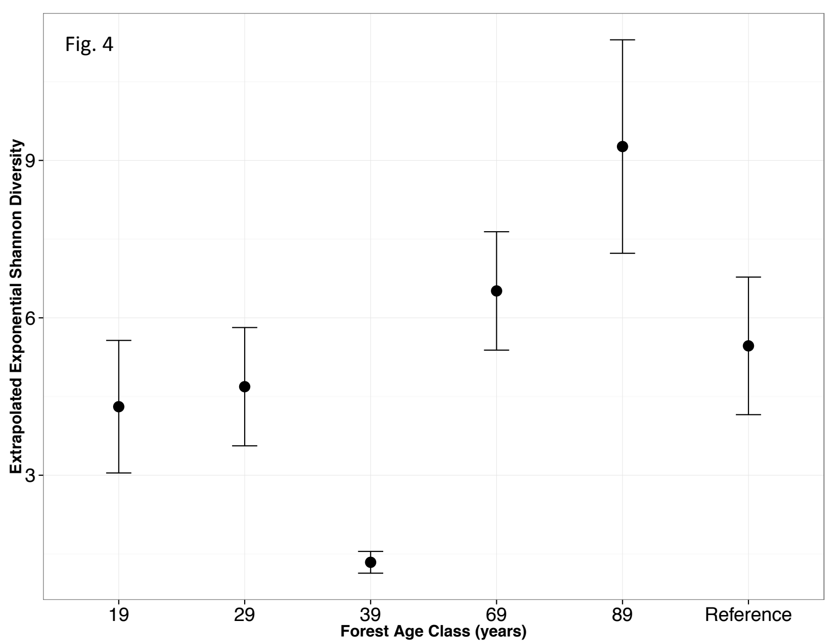

Fig. 4: Extrapolated exponential Shannon's diversity with a base sample size of 186 individuals. Bars represent 95% confidence intervals.

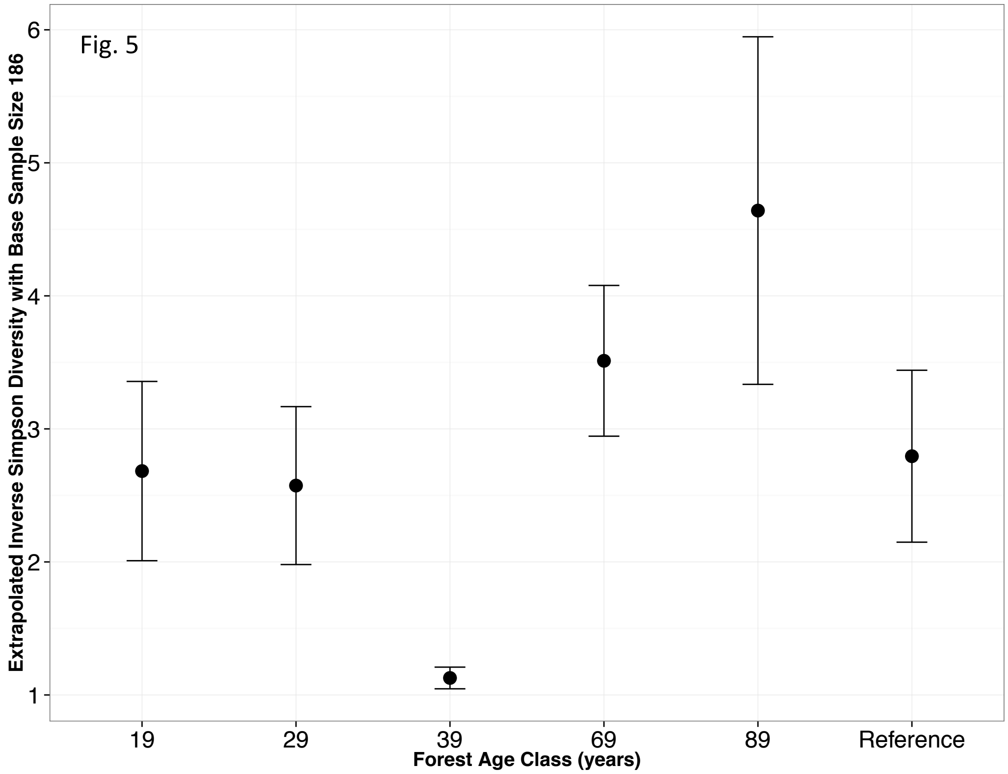

Fig. 5: Extrapolated inverse Simpson's diversity with a base sample size of 186 individuals. Bars represent 95% confidence intervals.

Fig. 6

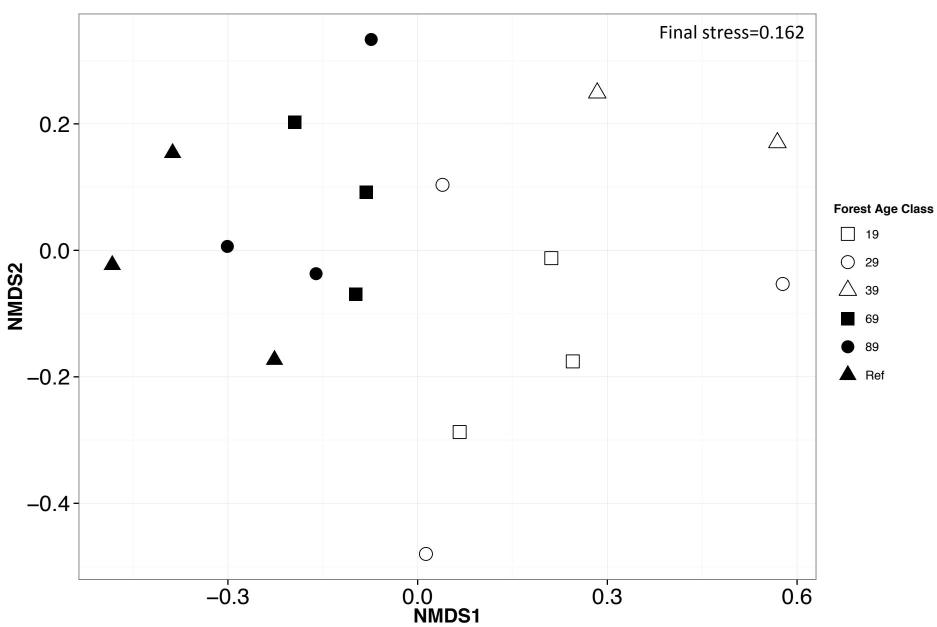

Fig. 6: NMDS analysis of species abundances in each site based on Chao-Jaccard dissimilarity measure scores

Fig. 7

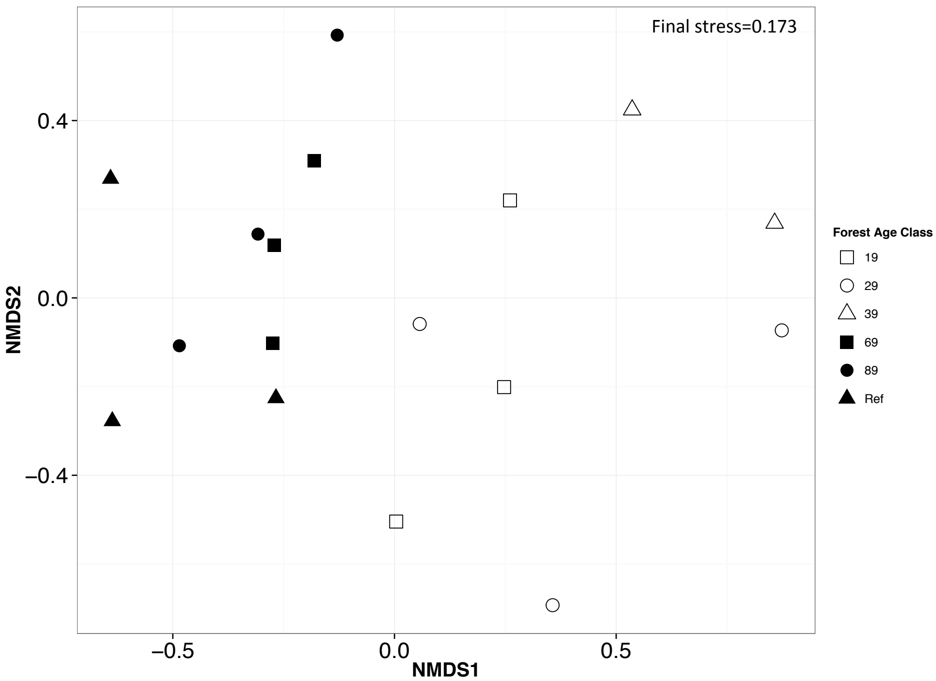

Fig. 7: NMDS analysis of species abundances in each site based on Morisita-Horn dissimilarity measure scores

Fig. 8

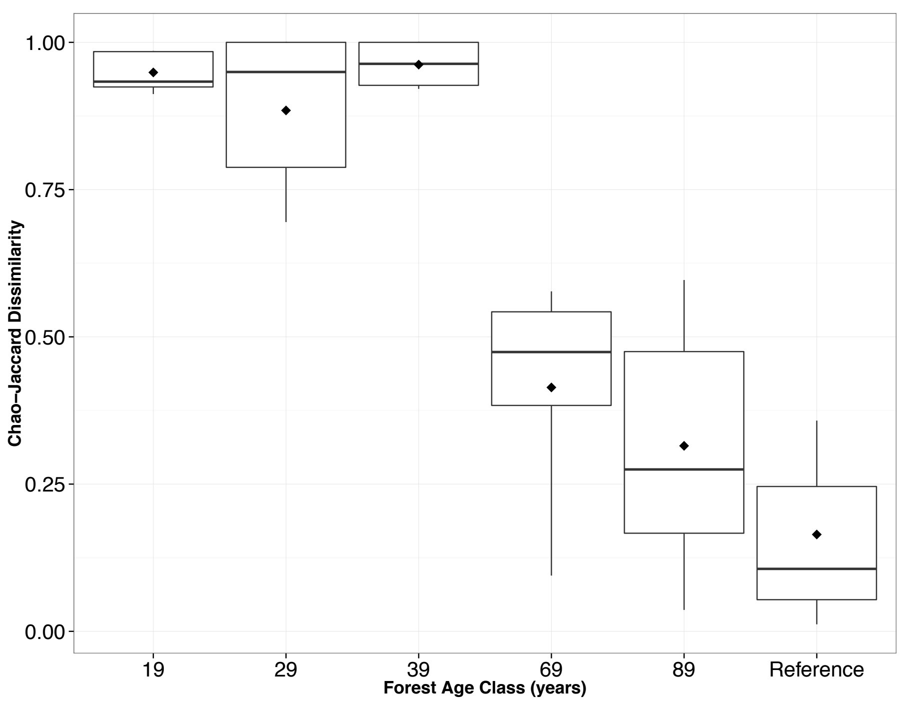

Fig. 8: Chao-Jaccard dissimilarity between tree communities in secondary and reference forests. Dots are means, bold lines are medians. Whiskers extend from 2.5 percentile to 97.5 percentile. 0 is least dissimilar, 1 is most dissimilar.

Fig. 9

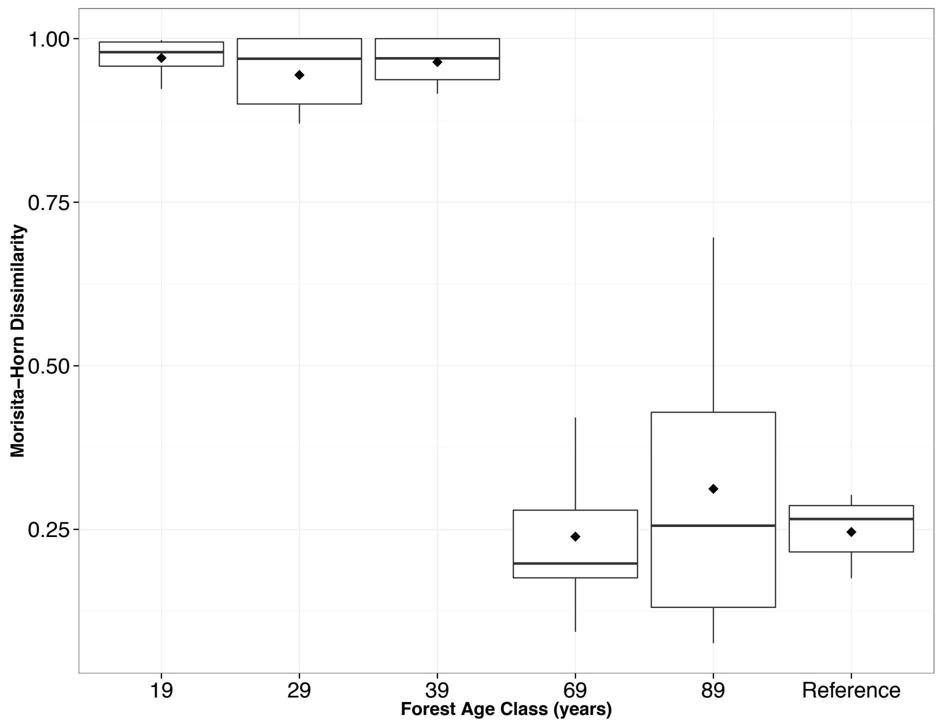

Fig. 9: Morisita-Horn dissimilarity between tree communities in secondary and reference forests. Dots are means, bold lines are medians. Whiskers extend from 2.5 percentile to 97.5 percentile. 0 is least dissimilar, 1 is most dissimilar.

<u>Chapter 2:</u> Testing and learning from a chronosequence: differing successional patterns in forest structure and species composition

INTRODUCTION

Globally, naturally-regenerated secondary forests account for 57% of total forest cover, with most regrowth occurring on former pasture and cropland (Chazdon et al. 2009, FAO 2010, Aide et al. 2012). These forests have the potential to provide important ecosystem goods and services, but because they arise in human-disturbed environments, they are often dominated by novel species assemblages, with unpredictable consequences for ecosystem processes and successional trajectories (Lugo 2004, Lugo and Helmer 2004, Hobbs et al. 2006, Poffenberger 2006, Wright and Muller-Landau 2006, Barlow et al. 2007, Chazdon 2008a, Hobbs et al. 2009, Marin-Spiotta and Sharma 2013). Most attempts to study succession in tropical secondary forests have relied on chronosequences to infer long-term dynamics and processes because of the difficulty in monitoring any single forest stand over decades or longer (Denslow and Guzman 2000, Chazdon et al. 2007, Johnson and Miyanishi 2008).

Chronosequence studies represent a practical approach to studying ecosystem development and forest succession. This methodology is underpinned by the assumption that changes seen across the chronosequence are solely due to the effect of age (Johnson and Miyanishi 2008). By substituting spatially distinct plots of different ages for a single forest plot at different temporal stages of succession, we can study changes in structure and composition on time scales that would be impractical, if not impossible to carry out by sequential, longitudinal censusing. For this reason, reliance on chronosequences has been, and remains a predominant approach to studying long-term forest succession. Major criticisms of this approach are that chronosequences may confound variation in environmental variables among sites with changes due to successional processes, and also that they assume conditions at the time of abandonment were equal, and are constant through time, for all sites (Pickett 1988, Yanai et al. 2000, Johnson and Miyanishi 2008). Careful site selection and replication within age classes are both ways to reduce potential attribution error (Norden et al. 2009, Kashian et al. 2013). Critics of chronosequence studies also point out that, though the data collected are from plots of different ages, they are just a ‘snapshot’ in time, and do not accurately represent the dynamic changes that occur during succession (Chazdon et al. 2007). One-time sampling may lead to false attribution of the causes of changes seen across groups to age, when other stochastic processes may be responsible (Chazdon 2008b). However, revisiting chronosequence plots over time can help disentangle deterministic effects of age on successional changes from other stochastic and dynamic processes. In this way, gradual changes can be observed that may challenge assumptions derived from single-visit chronosequence data (Pascarella et al. 2004, Chazdon et al. 2007, Johnson and Miyanishi 2008).

Forest structure and species composition often exhibit differing rates of return to pre-disturbance or reference forest levels (Finegan 1996, Guariguata et al.

1997, Guariguata and Ostertag 2001, Chazdon 2008b). Past chronosequence studies of secondary tropical forests have generally found rapid increases in basal area (BA) and its correlate, total aboveground biomass (TAB), in the first few decades of succession (Chazdon 2003). In an earlier study at my sites in Puerto Rico, Marin-Spiotta et al. (2007) found that BA and TAB both reached levels comparable to those of reference forests within 20 years following abandonment, and BA and TAB of 80-year-old secondary forests were higher than in reference forest plots. In a study of lowland forests in Costa Rica, BA recovered to old-growth levels within 15-20 years (Guariguata et al. 1997). BA values of secondary forests in the Barro Colorado National Monument in Panama, reached and surpassed levels of old-growth within 70 years of agricultural abandonment (Denslow and Guzman 2000). Letcher and Chazdon (2009) found that 21- to 30-year-old forests in Sarapiqui, Costa Rica contained as much standing biomass as nearby old-growth stands, with biomass values of 30-42-year-old forests surpassing those of old-growth.

Though forest structure and TAB may recover within a few decades of abandonment, most chronosequence studies have revealed that changes in tree species composition with age occur over longer time periods and are less predictable (Chazdon 2008b). Species richness of woody plants may reach levels of local old-growth or reference forests at time scales comparable to those of more rapid (i.e., 15-20 years following abandonment) forest structural recovery, or it may take upwards of four decades or longer for recovery of diversity, especially in larger (i.e., ≥10 cm dbh) size classes (Saldarriaga et al. 1988, Brown and Lugo 1990, Aide et al. 2000, Denslow and Guzman 2000, Guariguata and Ostertag 2001, Marin-Spiotta et al. 2007). Owing largely to dispersal limitations of mature forest species, tree communities in post-disturbance forests have generally been found to remain distinct from pre-disturbance or reference forest communities for many decades or even centuries after abandonment (Saldarriaga et al. 1988, Gorchov et al. 1993, Guariguata and Ostertag 2001, Chazdon 2003, Ingle 2003).

The objective of this study was to compare decadal changes in forest structure, biomass and community composition from a long-term secondary forest chronosequence with observed changes over time at individual sites. I re-surveyed a chronosequence of naturally-regenerated forests on abandoned pasture land in Puerto Rico, which were originally surveyed nine years earlier, in 2003 (Marin-Spiotta et al. 2007). By re-surveying the same sites, I introduce a longitudinal component to the traditional chronosequence method to produce a more accurate picture of the dynamic processes that occur throughout succession. This combination also allows for testing of the predictive accuracy of chronosequences, and may inform our interpretation of data from other chronosequence studies. Specifically, I asked: 1) Do observed changes in species compositions, forest structure, and total aboveground biomass between the two surveys deviate from expectations based on across-age comparisons in the original chronosequence? And 2) Does choice of allometric model for estimating biomass affect the result of testing observed versus predicted changes in biomass?

METHODS

Study Area

My study area is located on private land in southeastern Puerto Rico in the Sierra de Cayey mountains near the Carite State Forest and the border between the municipalities of Guayama and Patillas (18°01' N, 66°05' W). Individual plot elevations range from 580 and 700 m a.s.l., and the area experiences a relatively stable intra-annual climate with approximate mean annual precipitation of 2000 mm (1955-2012) and a mean annual air temperature of 21.5°C (1971-2000) as measured at nearby weather stations at Jajome Alto and Carite Dam (Daly et al. 2003, SERCC 2014). The soils at all sites are volcanically-derived, deep, well-drained, silty clay loams classified as fine Inceptic Hapludox soils in the Los Guineos series (Boccheciamp 1977, Lugo López 1995). These plots were selected for earlier studies to control for soil type and parent material, and they show low variability in texture and stocks of soil carbon and nitrogen (Marin-Spiotta et al. 2007, Marin-Spiotta et al. 2009). Forest types in the study area include lower montane wet evergreen forest, tall cloud forest and palm brake (Helmer et al. 2002). The study area falls in the subtropical wet forest Holdridge life zone (Holdridge 1967, Ewel and Whitmore 1973).

As with forest cover across much of Puerto Rico in the 19th and 20th centuries, forests in the study area were largely cleared for agricultural use (Birdsey and Weaver 1987, Brandeis et al. 2007). In 1937, forests covered <20% of the land area in the Sierra de Cayey region, with most land under pasture use. As agricultural activity in the area decreased and land was abandoned, forest cover more than tripled to 62% by 1995 (Pascarella et al. 2000). Patterns of agricultural abandonment across this landscape were driven largely by changes in socioeconomic policies in Puerto Rico and rural to urban migration. In the mountainous interior, this resulted in a landscape mosaic composed of small parcels of intact old-growth forest, surrounded by parcels along a continuum of land cover from active agriculture to regenerating forests of varying ages (Rudel et al. 2000).

Chronosequence establishment and sampling methods

My study plots comprised a replicated chronosequence with 14 secondary and three reference forest plots representing a total of six age classes. The five secondary forest classes ranged in age from 10-80 years post-abandonment at the time of initial survey in 2003 and the sixth age class included reference forest plots for which there was no evidence of direct human disturbance, other than occasional collection of palm fronds by local residents (Marin-Spiotta et al. 2007). In 2003 when the chronosequence was originally established and surveyed by Marin-Spiotta et al. (2007), each age class contained three replicate plots. However, between 2003 and the time of resurvey in 2012, one replicate plot in the 39-year class was cleared, leaving only two replicates in this age class.

Ten of the original 18 plots were first described by Pascarella et al. (2000, 2004) as members of their higher elevation Carite sites, and ages for the remaining 8 plots were determined using a combination of time-series aerial photography

(1936,1951,1967,1977,1988, and 1995) and interviews with landowners. When confirmation by landowners was unavailable, the dates of abandonment were estimated as the midpoints between the last photos showing active pasture and the first photos indicating the presence of woody regrowth (Marin-Spiotta et al. 2007).

In the original survey in 2003, one 24 x 24 m plot was established at each site, in which all stems of live, rooted trees at least 1.3 m tall, with diameters ≥ 10cm at 1.3m height (dbh) were measured, identified, and tagged (Marin-Spiotta et al. 2007). In addition, palm heights were visually estimated and recorded for use in an allometric equation for total aboveground biomass (TAB). For this study, I re-censused the plots following the same protocols, including the tagging of any new stems within the plots that met the above criteria. I also visually estimated heights of all palms and then verified heights of a subset (n=63) using a 10 m telescopic measuring pole the next season. Based on the relationship between estimated and verified heights of my sub-sample, I developed a correction for the height estimates of palms whose heights were not verified (Table 1).

Species composition and diversity

In order to test the ability of the chronosequence to predict successional changes in species compositions, I used a combination of approaches to compare observations from 2012 with what I expected to find based on the 2003 chronosequence. To examine changes by single species, I calculated importance values (IV) for each species in each year at the age-level and across all age classes. IVs were calculated as the sum of each species' relative basal area and relative abundance (maximum possible IV=2). IVs are one indicator of the proportion of the canopy represented by a single species (Curtis 1959). I selected the top 13 species based on overall IVs in each survey year, and then I examined how their IVs changed from 2003 to 2012 within each age class (Table 3). Species names follow Little *et al*. (1974) and Little and Wadsworth (1964), with updates from *The Plant List* (2013).

I also tested the ability of the chronosequence to correctly predict changes in tree communities through time. I used independent sample t-tests to compare observed richness values of age classes in 2012 with observed richness values of the next-oldest class from 2003; e.g., Does richness of 19-year-old forests differ significantly from richness of 20-year-old forests? I also generated extrapolated estimates of species richness for each age class in 2003 based on the guidelines described by Chao et al. (2014) (base sample size = 172) and 2012 (base sample size = 186) using the program iNEXT (Hsieh et al. 2014) in R (R Development Core Team 2013) (Fig. 1). This allowed me to compare richness at more equal sample sizes, thus decreasing the likelihood of confounding differences in actual richness with differences in sample size (Chazdon 2003). To correct for uneven species abundances that can unduly influence richness values, (Jost 2006, Tuomisto 2010) I also compared changes in diversity within and among age classes using estimates of Shannon's exponential diversity. This measure accounts for species' relative abundances within a community without being biased towards either abundant or rare species (Jost 2007), so it can be considered a representation of the number of "typical" species in an assemblage (Chao et al. 2012). Using the same sample sizes used to obtain extrapolated richness values, I used iNEXT to generate extrapolated estimates of Shannon's exponential diversity for each age class in 2003 and 2012 (Fig. 2).

To evaluate expected changes not only in richness and diversity, but also in proportions of species represented over time, I used the SPADE program to generate Morisita multiple community similarity (MMCS) values based on species abundances in each plot (Chao and Shen 2012). MMCS values range from 0 to 1 with larger values indicating higher similarity. Morisita multiple community similarity is an improvement on traditional pairwise similarity comparisons because it captures global similarity among all communities under consideration, though it primarily reflects relationships among more abundant species in each assemblage (Chao et al. 2008). To establish baseline relationships in similarity among the plots in each age class with the plots in the next-oldest class, I first generated MMCS values for all plots in each pair of nearest age classes (e.g., 20- versus 30-year-old plots) using abundance data from the original survey in 2003. I then calculated MMCS values for the same plots in the same age class pairings, but I replaced the 2003 abundance data from plots in the younger classes in each comparison with 2012 abundance data for the same plots (e.g., 29- versus 30-year-old plots) (Fig. 3). I examined similarities between 30- and 60-year-old plots with and without the plot that was lost. Due to small sample sizes in the 10-year-old class, I was unable to compare community similarity with 20-year-old forest communities.

In addition to comparing across-age-class changes in MMCS values from 2003 to 2012, I also used MMCS values to examine how the similarities of sites within each age class changed between surveys (e.g., did species compositions of 20-year-old sites become more or less similar to each other from 2003 to 2012). (Fig. 4). This comparison provides a sense of change in community composition within each age class relative to changes seen within other age classes and it allowed me to infer which forest age class changed most rapidly between surveys. As with my across-age class MMCS comparisons, small sample sizes in the 10-year-old class did not permit me to assess changes through time in this class. In order to visualize changes in communities at the site level, I used the R package 'vegan' to analyze species abundance data for each site and survey using nonmetric multidimensional scaling (NMDS) based on Chao-Jaccard pairwise dissimilarities (R Development Core Team 2013)(Figs. 5a,b).

To assess species' habitat specializations, I used the program CLAM to classify species into one of four categories: early secondary specialists, late secondary specialists, reference forest specialists, or generalists. The program uses species distributions among age classes to classify species into specialization groups. Based on 2003 data, I used an iterative process in which I first tested to see which species were reference forest specialists, secondary forest specialists, or generalists. Then, among the secondary forest specialists, I reclassified species as either as early- or late-secondary specialists (Chao and Lin 2011, Chazdon et al. 2011).

Forest structure and aboveground biomass

I calculated total basal area (BA) and stem density (SD) per hectare of each plot and I used independent sample t-tests to compare expected outcomes from the 2003 chronosequence against observed changes in BA from 2003 to 2012.

I used a combination of allometric models to account for unique species compositions and to determine if model choice affected the predictive power of the chronosequence (Table 1). I calculated two TAB estimates for each plot. The first estimate (WGFL) is based on a combination of two allometric equations, which were both developed in Puerto Rico. For all dicot species and tree ferns (*Cyathea arborea* (L.) Sm.), I applied Weaver and Gillespie's (1992) general allometric equation for the tabonuco forest type. Tabonuco forest is a well-studied, mature forest type also known as the *Dacryodes-Sloanea* association (Beard 1948), which is dominated by tabonuco (*Dacryodes excelsa* Vahl), *Buchenavia tetraphylla* (Aubl.) R.A. Howard, *Tetragastris balsamifera* (Sw.) Oken, *Guarea Guidonia* (L.) Sleumer, *Manilkara bidentata* (A. DC.) A. Chev., and *Sloanea berteroana* (Choisy ex DC.) and is associated with subtropical wet and subtropical rain forest life zones in Puerto Rico *sensu* (Holdridge 1967). For development of their allometric model, Weaver and Gillespie (1992) selected 29 individuals from the tabonuco forest type with stems ≥5 cm dbh for destructive sampling. I used their equation for TAB, which includes woody and leafy aboveground biomass. Due to the abundance of the monocot palm *Prestoea acuminata var. montana* (Graham) A.J. Hend. & Galeano in some plots (up to 83% of stems in one reference forest plot in 2003), and because of significant differences in growth patterns relative to dicots, I separated all stems of *P. acuminata* and calculated their TAB using Frangi and Lugo's (1985) allometric equation for this species. In addition to dbh, this model requires total palm height in order to estimate TAB. For survey 1, I used heights estimated by Marin-Spiotta et al. (2007) and for survey 2 I used corrected heights for all palms whose heights were not verified in 2013 (verification was performed the season following initial data collection for survey 2) using a telescoping pole. In sites with no palms, my first TAB estimate (WGFL) was based solely on Weaver and Gillespie's (1992) tabonuco model, and where palms were present, my estimates consist of the sum of the results of these two models for each plot.

I used a combination of van Breugel et al.'s (2011) multi-species allometric model "M2" and Frangi and Lugo's (1985) palm model as a second approach to estimating TAB. The van Breugel et al. (2011) model more accurately estimates TAB of stems with diameter ≤25 cm dbh (88% of stems in this study for both surveys) than other multispecies models that include a wood density parameter, and has been recommended for use in secondary forests (van Breugel et al. 2011). This model was developed using destructive sampling in young secondary forests within the subtropical moist forest zone *sensu* (Holdridge 1967) near Barro Colorado, Panama. As with WGFL, I separated palm stems and calculated their TAB using Frangi and Lugo's (1985) allometric equation for my second TAB estimate (VBFL). However, for VBFL I applied van Breugel et al.'s (2011) model "M2" to all dicots (see Table 1). In addition to dbh, this model includes a parameter for wood density (ρ, g/cm^3). Wood density values for each species were taken from Zanne et al. (2009) and other published sources (Longwood 1961, Little and Wadsworth 1964, Turrell et al. 1967, Reyes et al. 1992, Weaver 1993) (see Appendix A1). In cases where multiple values were reported for the same species, I calculated and used the average of reported density values, and for species for which no values were found, I used genus-level averages (Fayolle et al. 2013). Because height and specific gravity data were unavailable for the tree fern *C. arborea*, I estimated TAB values for stems of this species using Weaver and Gillespie's (1992) general tabonuco forest equation.

By comparing TAB of plots in 2012 with TAB of the next-oldest plots from 2003 using the same strategy I used for observed richness, BA, and SD, I was able to test whether the chronosequence correctly predicted the changes in TAB I observed from 2003 to 2012, and whether the significance of those changes varied by model choice. In addition to t-tests, I also compared BA, SD, and my two TAB estimates between survey dates using analysis of covariance (ANCOVA) with plot age as the covariate, survey date as fixed factors, and survey date x plot age as the interaction term. Data for all t-tests and ANCOVA analyses were tested for normality and homoscedasticity, and nonparametric analyses were used when appropriate. Except where otherwise noted, data assessment and analysis was carried out in JMP (SAS 1989-2014).

RESULTS

Species composition and diversity

Survey data from 2003 predicted that observed species richness in 30- and 60-year-old forests would increase as they aged, but they showed no significant differences between the richness values of 30- and 60-year-old forests, or between those of 60- and 80-year-old forests (Table 2). Data from 2012 showed that, while their richness had increased since 2003, on average, 39-year-old plots still contained 8.5 fewer species than 60-year-old forests (two-tailed independent sample assuming unequal variances: $t(1)=17$, $p= 0.0374$). Instead of increasing as predicted, richness of 60-year-old forests decreased between surveys with the result that, on average, 69-year-old plots held 3.67 fewer species than 80-year-old forests in 2003 (two-tailed independent sample: $t(4)=3.05$, $p= 0.0380$). Extrapolated richness values in the 10-19-year-old class changed as expected based on values of the 20-year-old forests. 2003 data predicted a decrease in extrapolated richness from 20-30 years, but observed changes showed a slight increase in richness from 20-29 years. Excluding the 30-39-year-old class as an outlier shows that changes in extrapolated richness in 20-29-year-old forests fit the pattern seen between 20- and 60-year-old forests in 2003. (Fig. 1). Extrapolated richness values showed that 30-39-year-old forests had not changed as expected based on values of 60-year-old forests. Extrapolated richness values of 60-69-year-old and 80-89-year-old classes supported expectations based on 2003 data.

Extrapolated estimates and 95% confidence intervals of exponential Shannon's diversity based on 50 bootstrap resamples of 2003 data predicted significant decreases in diversity in the 20- and 80-year-old forests, a significant increase in diversity in the 30-year-old forests, and no change for 60-year-old forests. Extrapolations of data from 2012 indicated divergence from expectations in the 29-, 39-, 69- and 89-year-old classes (Fig. 2). Diversity of 69-year-old plots decreased unexpectedly (11.46 to 6.51), and rather than decreasing as expected, there were no significant changes in diversity of the 29- and 89-year-old plots. Instead of the predicted increase for 39-year-old plots, analysis revealed no significant change in diversity.

Across-age Morisita multiple community similarity (MMCS) comparisons from 2003 and 2012 revealed differing patterns in community change among age groups (Fig. 3). Based on data from 2003, 30- and 60-year-old forest communities were significantly less similar to each other than the communities in all other age-pair comparisons. Inclusion of the lost site in the 30-39-year-old class did not affect results, so it was included. I did not find significant changes in similarities between surveys, though a clear pattern of increasing similarity in species communities over time emerged among the three oldest age classes.

Within-class MMCS comparisons showed that tree assemblages at plots in the 20-29-year-old class were significantly less similar to each other over time than assemblages at plots in all other age classes, while assemblages at plots in the 30-39-year-old class were significantly more similar to each other over time than assemblages at plots in all other age classes (Fig. 4). Intermediate MMCS similarity values of the three oldest age classes indicated that species communities in each of these age classes changed from 2003 to 2012, but not to the degree that 20-29-year-old communities changed.

The NMDS analysis (2 dimensions; final stress = 0.168) of community change in age classes between surveys showed that some age classes responded as expected based on the relationships between groups in 2003, while others deviated from those expectations (Figs. 5a,b). Changes in the 10-19-year-old class showed the communities in these sites had become more similar to 20-year-old communities from 2003 to 2012. Changes in the 20-29-year-old class did not indicate that the communities in these sites had become more similar to communities in 30-year-old sites. Similarly, changes in the 30-39-year-old class did not indicate that the communities in these sites had become more similar to 60-year-old communities. Changes in the 60-69-year-old class and the 80-89-year-old class did suggest that communities in these sites had become more similar to 80-year-old and reference communities, respectively. Not only did the results indicate that communities in older secondary forests became more similar to those of reference forests, but from 2003 to 2012, communities in the reference forest plots became more similar to those in older secondary forests.

The ability of the chronosequence to predict changes in importance values (IV) of the 13 most important species varied by age class. (Table 3) The direction of observed changes (i.e., positive or negative) matched chronosequence-based predictions in 27 of 65 (42%) of cases. In 58% of the cases, observed changes in the IV of species in each age class through time either increased when expected to decrease or vice versa. The early secondary specialist *Tabebuia heterophylla* (DC.) Britton had lower-than-expected importance in the 69-year-old class. The IV of the late secondary specialist *Syzygium jambos* (L.) Alston was lower than expected in 39- and 69-year-old plots. A predicted decrease in importance of *S. jambos* in 80-year-old forests was confirmed by 2012 data, and it also decreased in importance in reference forest plots.

Forest structure

Based on 2003 data, BA was expected to increase significantly from 10-20 years, and begin to decrease in 80-year-old plots . BA of 20-year-old forests was predicted to decline, though not significantly (Table 2). While it increased substantially, the BA in the 19-year-old forest class was, on average,15.76 m^2/ha lower than that of 20-year-old plots (two-tailed independent sample: t(4)=3.72, p= 0.0204). Rather than declining over time as predicted, the BA of the 80-89-year-old class increased and was, on average, 22.83 m^2/ha higher than reference forests in 2003. Similarly, though a decline in BA over time was predicted for 20-year-old forests, I observed an increase, and in 2012, the BA of 29-year-old forests was, on average 13.45 m^2/ha higher than BA of 30-year-old plots (two-tailed independent sample: t(4)=4.53, p= 0.0106). Changes in SD across age classes in 2003 suggested that SD of 80-year-old forests would decline over time. Instead, it increased, with SD of 89-year-old forests higher by an average of 405 stems/ha than mean SD of reference forests in 2003 (two-tailed independent sample: t(4)=3.36, p= 0.0283). ANCOVA analyses of BA and SD found no differential response to age by survey year.

Aboveground biomass stocks

According to data from 2003, TAB as calculated using the WGFL allometric method, was expected to increase significantly from 10-20 years, and begin to decrease in 80-year-old plots. TAB of 20-year-old forests was predicted to decline, though not significantly (Table 4). Though WGFL-based TAB estimates did increase in the 10-19-year-class between surveys, the TAB of 19-year-old plots was, on average, 96.88 Mg/ha lower than that of 20-year-old plots (two-tailed independent sample: $t(4)=3.45$, $p= 0.0262$). While expected to decline, WGFL-based TAB in the 80-89-year-old class increased from 2003 to 2012 and on average, 89-year-old plots contained 153.19 Mg/ha more TAB than reference forests did in 2003 (two-tailed independent sample: $t(4)=4.42$, $p= 0.0115$). Instead of declining, WGFL TAB estimates increased over time in the 20-29-year-old class with the result that mean TAB of 29-year-old forests was 88.01 Mg/ha higher than that of 30-year-old plots (two-tailed independent sample: $t(4)=4.04$, $p= 0.0155$).

Results based on the VBFL allometric method were similar to those based on WGFL for all but one comparison. VBFL-based TAB estimates from 2003 predicted significant increases from 10-20 years, and from 60-80 years. Declines in TAB were also predicted with time in 20- and 80-year-old forests. Though TAB in the 10-19-year-old class did increase over time, TAB in 19-year-old forests was, on average 76.41 Mg/ha (two-tailed independent sample: $t(4)=3.69$, $p= 0.0210$) lower than TAB in 20-year-old sites. While TAB in 60-year-old forests increased, the increase still resulted in 69-year-old forests having 88.42 Mg/ha lower mean TAB than 80-year-old forests (two-tailed independent sample: $t(4)=3.36$, $p= 0.0283$). Though a decline with increasing age was predicted in VBFL-based TAB estimates in the 20-year-old forests, I observed an increase from 2003 to 2012. Mean TAB as calculated with VBFL was 53.46 Mg/ha (two-tailed independent sample: $t(4)=3.11$, $p= 0.0357$) higher in 29- versus 30-year-old forest plots. Plots in the 80-year-class in 2003 were expected to decline in TAB with age, based on the chronosequence. Data from 2012 showed that TAB increased in this class, and that VBFL-based TAB estimates for 89-

year-old forests were an average of 148.87 Mg/ha (two-tailed independent sample: $t(4)=4.57$, $p= 0.0103$) higher than TAB of reference forests in 2003.

With one exception, comparison results using the two allometric approaches concurred, despite the fact that WGFL estimates were higher than VBFL estimates for every age class. WGFL TAB estimates suggested that the 60-69-year-old forests accumulated TAB as expected, while VBFL estimates suggested that 69-year-old forests were not accumulating TAB as quickly as could be expected. ANCOVA analyses of TAB found no differential response to age by survey year using either allometric approach.

DISCUSSION

Deviations from expected changes in species composition vary among age classes

With the exception of an unexpected decease in observed richness and extrapolated exponential Shannon's diversity in 69-year-old sites, observations from 2012 supported expectations of compositional changes in the two oldest secondary forest classes. Extrapolated richness values, however did not reveal a significant decrease in richness in the 60-69-year-old sites over time. Changes in the 60-69-year-old and 80-89-year-old classes seemed to indicate deterministic successional dynamics (Chazdon 2008a, Norden et al. 2009). Across-age MMCS comparisons and the NMDS analysis both revealed especially strong evidence for deterministic community reassembly resulting in increased similarity with reference forest communities from 2003. However, examination of changes in the reference forests themselves from 2003 to 2012 revealed these communities underwent similar changes to those observed in the communities of the 60-69- and 80-89-year-old classes. The NMDS ordination clearly showed changes in reference forest plots leading to more similar communities with the 69- and 89-year-old plots, and all three of these age classes showed a pattern of moderate change through time (Figs. 5a,b) as well as a decline in exponential Shannon's diversity estimates. The changes in reference forest indicating increased similarity with older secondary forests could be interpreted several ways. One possibility is that these plots do not truly represent old growth forest conditions, and are still undergoing late-stage succession. This seems unlikely, as NMDS ordination of species community similarities indicate opposite change from what would be expected if reference forest plots were actually late-successional forests (Figs. 5a,b). A second possibility is that changing environmental conditions such as changes in annual temperatures and rainfall (Peterson et al. 2002), changes in storm events (Bender et al. 2010) or increased levels of atmospheric CO_2 or nitrogen availability are causing directional shifts in these communities by favoring species, which were already present in all three age groups, and are now increasing in dominance (Drake et al. 1997, Dukes and Mooney 1999, Yanai et al. 2000, Neftel et al. 2011). It is also possible that observed changes in the older secondary forest communities indicate an eventual return to reference forest-like conditions, with incipient gap formation allowing for recruitment and growth of species previously only found in reference forests (Denslow 1987), and changes within reference forests caused by ongoing processes of gap-phase dynamics (Dupuy and Chazdon 2006, Chazdon 2008b).

Though I found changes in community similarities within each age class in 2012, none were significant, as indicated by overlap in their confidence intervals. However, because I analyzed change in the same plots over a relatively short interval of nine years, it is not surprising that species assemblages had not changed significantly in any age group, and I do not think that it invalidates the change patterns I observed. It should also be noted that I focused only on larger-diameter trees, and that seedlings and saplings in the understory often have higher diversity and different compositions than larger canopy trees (Denslow and Guzman 2000, Guariguata and Ostertag 2001).

Observed within-class changes in diversity and composition do not always follow chronosequence-based expectations

Perhaps unsurprisingly, differences between age classes in 2003 tended to be preserved as forests changed through time. In many cases, conditions in plots observed in 2003 were more predictive of conditions in the same plots in 2012 than were conditions in plots of the next-oldest age class in 2003. While not true across all metrics and age classes, this result lends credence to the criticism that age is often not the only factor that varies across groups in a chronosequence (Johnson and Miyanishi 2008), and it lends support to stochastic, non-equilibrium models of succession (Chazdon 2008b).

Rather than indicating a failure of the chronosequence to predict changes through time, my results showing lower than expected observed richness in 39- versus 60-year-old forests are due to the loss of the most species-rich site in the 30-

39-year-old class. In 2003, there was no difference in richness between the 30- and 60-year-old age classes. Therefore, only a decrease in richness from 2003 to 2012 could result in a lower-than-expected outcome. Though richness increased by one species at one of the remaining sites (seven individuals of *P. acuminata* had colonized site 77 between 2003 and 2012), it was not enough to offset the loss of the richest plot, which had nine species in 2003. Based on 2003 data, 60- and 80-year-old forests had similar richnesses. The lower-than-expected result in the 69-year-old class resulted from decreases in richness in each plot between surveys (Table 2). Site 38 lost three of 12 species present in 2003: the early secondary specialist, *T. heterophylla,* the late secondary specialist, *Alchornea latifolia* (Sw.), and the late secondary/reference forest specialist, *Buchenavia tetraphylla*. Site 32 lost one of 12 species present in 2003: the generalist *Cecropia schreberiana* Miq., and site 33 also lost one of 12 species observed in 2003: the rare/late secondary specialist, *Cordia alliodora* (Ruiz & Pav.) Oken. The losses of *T. heterophylla and C. schreberiana* were not surprising, as these are early secondary specialists and generalists with only three and two individuals, respectively, that were present in these sites in 2003. In terms of successional process, the loss of the other later secondary and old growth specialist species in 60-69-year-old forests was unexpected. However, in each case, the lost species had been represented by no more than three individuals in 2003, so small plot size, stochastic mortality events, and the fact that I only surveyed trees ≥ 10cm dbh are likely contributors to this unexpected outcome (Guariguata and Ostertag 2001, Chazdon 2008b).

The higher-than-expected value of exponential Shannon diversity in 29-year-old forests was due not to the fact that these plots rapidly accumulated species between 2003 and 2012, but because the extremely low diversity of 30-year-old forests indicated that there would be a decline in diversity over time in the 20-year-old plots. The pattern seen across 20- and 60-year-old plots in my 2003 data suggest an expected increase in diversity as 20-year-old forests age, and though the increase was non-significant, I observed a gain of one species at two sites, with no change in the third site in this age class..

Based on the implied changes in diversity between 30- and 60-years post-abandonment, I expected to find a large increase in diversity in in 30-39-year-old forests between surveys. As with observed richness, the loss of one plot in this age class actually led to a decrease in extrapolated diversity from 2003 to 2012. At the same time, even in 2003 with all three replicates intact, the 30-year-old class had significantly lower extrapolated exponential Shannon's diversity than all but the 10-year-old class. Therefore, even without the loss of the third plot in this age class, because of its originally uneven species abundance distribution in 2003, it would have likely had lower-than-expected extrapolated exponential Shannon's diversity in 2012.

The probable explanation for the unexpected decrease in diversity in the 60-69-year-old class is two-fold. First, as reported above, there was a decrease in observed species richness at each site in this age class. Second, the combination of the particular species lost, together with large increases in other species that were already present in 2003 (i.e., *P. acuminata*) resulted in a more uneven species distribution, and thus a lower-than-expected number of “typical” species for the age class in 2012. Extrapolated estimates of species richness in the 60-69-year-old class bear this out. These also indicate a decline in richness, though the decline is not significant, as it was with exponential Shannon’s diversity.

That species assemblages in 30-39-year-old and 60-year-old forest communities were significantly less similar to each other than communities in other age-pair comparisons was not surprising. This pairing represents the largest age gap between any 2 groups I compared, and it spans a period when I would expect major species turnover based on a deterministic interpretation of my reference samples and of differences in extrapolated exponential Shannon’s diversity (Johnson and Miyanishi 2008). In communities representing 30-39-year-old forests the proportion of stems of *T. heterophylla,* declined from roughly 90% to just 5% of stems present in 60-year-old plots and 3% of stems in 69-year-old plots. Regardless of whether I included or excluded the lost third replicate site in my baseline similarity calculations, I observed only minor changes in tree assemblages of 30-year-old forests between 2003 and 2012. Because other studies have found that *T. heterophylla* germinates best under low-light conditions (Uriarte et al. 2005) and that it may continue dominate secondary forests for at least 60 years following agricultural abandonment (Zimmerman et al. 2000), the deterministic assumption that *T. heterophylla’s* dominance will drastically decline and there will be high turnover in 39-year-old sites in the next 21 years may not prove to be true.

Results of my within-class MMCS comparisons can be interpreted as indicating amount of change in species assemblages of each age class between 2003 and 2012. High similarities as seen in the 30-39-year-old class indicate little change in these species assemblages, while the low values seen in the 20-29-year-old class reveal larger changes in tree communities in this age class between surveys. This implies high rates of species turnover and/or shifting species abundance distributions in 20-year-old forests during the 9-year-interval. My extrapolated values of exponential Shannon's diversity and inverse Simpson's diversity for 20- and 29-year-old forests do not suggest a significant change in evenness in these plots, but extrapolated richness values indicate that richness in this age class increased more than in other classes and observed richness increased more than in all but 10-year-old forests. The extremely high similarity of assemblages at plots in the 30-39-year-old class reflects the fact that the two plots analyzed through time were almost monospecific stands of *T. heterophylla* in both surveys.

My analysis of within-class MMCS showed more change in tree communities at plots in the 80-89-year-old class than in the 60-69-year-old and reference classes. This was driven chiefly by a large decrease in the importance of *T. heterophylla* and a relatively large increase in importance of *P. acuminata* in 80-year-old plots from 2003 to 2012 (Table 3). Changes in 60-69-year-old plots reflect a sizeable decrease in the importance of the late secondary specialist *S. jambos* and a very large increase in the importance of *P. acuminata* over time. Other studies in Puerto Rico showed that the exotic *S. jambos* persists well into succession, and that it may disrupt the establishment of native species (Aide 2000, Aide et al. 2000, Brown et al. 2006).

Though my CLAM analysis of *S. jambos* classified it as a late secondary specialist, it declined in importance through time in every age class in which it occurred.

NMDS results showing a large shift in similarity towards older classes in 10-year-old forest communities between 2003 and 2012 is probably due to two factors. The first is that these communities were so sparsely populated in 2003, that one species (or even one stem) may have disproportionately impacted the NMDS result. The second factor is that this analysis focused on trees ≥ 10cm dbh. Species present in 10-year-old forests as seedlings and saplings would not have appeared in my characterizations of those communities, but by 2012, would likely have grown sufficiently to be surveyed and cause apparent change. The likelihood that this played a role is demonstrated by the increase in censused stems in this age class from 17 in 2003 to 89 in 2012 and supported by other studies, which showed that species richness in small diameter classes increases much more rapidly than does richness in larger-diameter trees (Saldarriaga et al. 1988, Guariguata et al. 1997, Denslow and Guzman 2000).

In contrast to the within-class MMCS analysis, which indicated significant change in species compositions in the 20-29-year-old class, the NMDS analysis did not reveal such a large shift. The directional shift seen in the ordination plot in this age class from 2003 to 2012 did, however, exhibit divergence from expectations based on patterns in older secondary forests in the NMDS and may suggest an alternative successional pathway in these young forest plots (Lugo 2009).

Varied patterns of change in forest structure

Basal area (BA) is correlated with, and can act as an indicator of successional stage (Held and WInstead 1975, Guariguata and Ostertag 2001). Young forests typically have low BA, while older forests have higher BA, though BA values in older stands may show an asymptotic increase with age or may peak at an intermediate stage of succession (Saldarriaga et al. 1988, Peet 1992, Aide et al. 1996, Denslow and Guzman 2000, Mascaro et al. 2012). In general, there is an inverse relationship between BA and stem density (SD). As BA increases with time since abandonment, SD decreases due to the onset of mortality among the cohort of individuals that colonized the site of disturbance. (Brown and Lugo 1990, Kennard 2002).

Patterns across the chronosequence in 2003 predicted significant increases in BA from 10-20 years, and the beginning of a significant decrease in 80-year-old plots . BA of 20-year-old forests was predicted to decline, though not significantly (Table 2). Patterns across age classes in 2003 varied in their ability to predict observed changes in BA. BA of 19-year-old forests was lower than expected, based on the BA of 20-year-old forests in 2003. While it is probable that BA would have increased in year 20 for these plots, the average increase in BA in this age class from 2003 to 2012 was 0.72 $m^2\ ha^{-1}\ yr^{-1}$, which would not likely have changed the outcome if my survey had been done in 2013. The discrepancy in BA is probably due to the fact that 19-year-old forests had a total of 91 stems, whereas 20-year-old forests had 146 stems. In addition, the 20-year-old forests contained 10 stems with larger diameter than the largest diameter stem in 19-year-old plots. Because most trees in the 19-year-old plots are probably from the same cohort that colonized the sites after abandonment, it is likely that a substantial number of saplings will continue to grow "into" the survey over the next few years as their diameters reach 10cm dbh. However, in the absence of disturbance in 20-year-old plots, it is probable that this difference will persist. By contrast, the BA of 29-year-old plots was significantly higher than expected, based on the BA of 30-year-old plots in 2003 (including all 3 sites). Marin-Spiotta et al. (2007) found that, in 2003, though not a significant difference, the BA of 20-year-old plots was, on average, 6.8 m^2/ha higher than for 30-year-old forests. This apparent failure of chronosequence to correctly predict changes observed is due more to the fact that the 30-year-old class is an outlier than by unexpected developments in 20-year-old forests from 2003 to 2012.

Similarly, the higher-than-expected BA values of 89-year-old plots, relative to reference plots in 2003, is a continuance of a trend reported by Marin-Spiotta et al. (2007). Due to higher ratios of dicots to palms in 80-year-old forests than in reference forests, the BA of 80-year-old forests was significantly higher than BA of reference forests. Though the ratio of dicots to palms decreased in 80-year-old plots from 2003 to 2012, the difference in BA between this class and the reference forest class increased slightly in the same period, suggesting that the combination of secondary growth of dicots present in 80-89-year-old forests, together with ingrowth of palms is driving continued increases in BA in these plots. The unexpectedly high SD of 89-year-old forests compared to reference forests was also a continuation of a trend noted by Marin-Spiotta et al. (2007). In 2003, mean SD of 89-year-old forests was 237 stem ha^{-1} higher than mean SD of reference forests. That difference was amplified by changes between survey dates, most likely due to ingrowth of the shade-tolerant *P. acuminata,* under the dicot-dominated canopy in 80-89-year-old plots (Lugo and Batlle 1987). The mean proportion of stems represented by *P. acuminata* increased between surveys from 14% to 24% in these plots, whereas there was just a 2% increase in *P. acuminata* in reference plots. My results run counter to studies showing that SD decreases as BA increases (Brown and Lugo 1990, Guariguata and Ostertag 2001) though I did see indications that the rate of increase in BA of secondary forests is approaching either an asymptote or a peak, so this relationship may change as these forests age.

Allometric models affect differences in aboveground biomass across age classes and through time

TAB is a function of BA, so except for one case in which species composition differentially affected the two allometric estimates, the results of my cross-age-pair comparisons of TAB revealed the same patterns, and can be explained by the same factors as BA. The primary differences between allometric approaches are the inclusion of wood density of dicots as a factor in the VBFL approach, and the fact that it was developed specifically in secondary forests (van Breugel et al. 2011). Differences in allometric model choice only affected my analysis of expected versus observed changes in TAB in one age class. WGFL TAB estimates suggested that the 60-69-year-old forests accumulated TAB as expected, while VBFL estimates suggested that 69-year-old forests were not accumulating TAB as quickly as could be expected. While the top two most important species were shared between the 69- and 80-year-old forests, the average wood density of the next three most important species is lower for 69-year-old forests (0.565 g/cm^3) than for 80-year-old forests (0.643 g/cm^3). Thus, it is likely that this small difference resulted in an apparent significant difference in TAB using the VBFL approach, whereas the tabonuco forest model (Weaver and Gillespie 1992) was insensitive to differences in TAB based on specific species compositions. Though I did not carry out destructive sampling to test the accuracy of the WGFL and VBFL allometric models at my sites, van Breugel et al. (2011) found that inclusion of wood density decreased uncertainty of TAB estimates at the plot level, suggesting that the VBFL approach is more likely to result in accurate estimates than allometric models that do not include this parameter. At the same time, the two approaches' concurrence on most comparisons reveals that, unless detection of small differences in TAB is necessary, the simplicity of the WGFL approach makes it an attractive option for use in tabonuco forests.

CONCLUSION

As Chazdon (2008b) notes, changes in forest communities and structure with time involve complex interactions between deterministic and stochastic processes. By combining a chronosequence approach with repeated sampling, I showed that changes in forest structure and species composition within age classes through time were not always predicted by changes across age classes at the time of the first survey. Unsurprisingly, structural and compositional properties in plots in 2003 were often more predictive of observed conditions in those plots in 2012 than were differences among age classes in 2003. I found stronger evidence for deterministic changes in older secondary forests than in younger forests, whereas predicted versus observed changes in forests younger than 39 years showed evidence of more stochastic changes through time. Differences in aboveground biomass with age varied by allometric model choice, highlighting the need for consistent methodologies for assessing and comparing aboveground biomass across studies. This study reinforces the necessity of caution when drawing conclusions about successional outcomes based on single-survey chronosequence studies, and emphasizes the importance of longitudinal studies to understanding dynamic successional processes.

LITERATURE CITED

Aide, T. M. 2000. Clues for tropical forest restoration. Restoration Ecology **8**:327-327.

Aide, T. M., M. L. Clark, H. R. Grau, D. López‐Carr, M. A. Levy, D. Redo, M. Bonilla‐Moheno, G. Riner, M. J. Andrade‐Núñez, and M. Muñiz. 2012. Deforestation and reforestation of Latin America and the Caribbean (2001–2010). Biotropica.

Aide, T. M., J. K. Zimmerman, J. B. Pascarella, L. Rivera, and H. Marcano‐Vega. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. Restoration Ecology **8**:328-338.

Aide, T. M., J. K. Zimmerman, M. Rosario, and H. Marcano. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. Biotropica:537-548.

Barlow, J., T. A. Gardner, I. S. Araujo, T. C. Ávila-Pires, A. B. Bonaldo, J. E. Costa, M. C. Esposito, L. V. Ferreira, J. Hawes, M. I. M. Hernandez, M. S. Hoogmoed, R. N. Leite, N. F. Lo-Man-Hung, J. R. Malcolm, M. B. Martins, L. A. M. Mestre, R. Miranda-Santos, A. L. Nunes-Gutjahr, W. L. Overal, L. Parry, S. L. Peters, M. A. Ribeiro-Junior, M. N. F. da Silva, C. da Silva Motta, and C. A. Peres. 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proceedings of the National Academy of Sciences **104**:18555-18560.

Beard, J. S. 1948. The natural vegetation of the Windward and Leeward Island. Ox. For. Mem.

Bender, M. A., T. R. Knutson, R. E. Tuleya, J. J. Sirutis, G. A. Vecchi, S. T. Garner, and I. M. Held. 2010. Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. Science **327**:454-458.

Birdsey, R. A., and P. L. Weaver. 1987. Forest area trends in Puerto Rico. US Department of Agriculture, Forest Service, Southern Forest Experiment Station New Orleans, LA, USA.

Boccheciamp, R. A. 1977. Soil survey of the Humacao area of eastern Puerto Rico. United States Department of Agriculture Soil Conservation Service, San Juan, PR, USA.

Brandeis, T. J., E. H. Helmer, and S. N. Oswalt. 2007. The status of Puerto Rico's forests, 2003. US Department of Agriculture, Forest Service, Southern Research Station.

Brown, K. A., F. Scatena, and J. Gurevitch. 2006. Effects of an invasive tree on community structure and diversity in a tropical forest in Puerto Rico. Forest Ecology and Management **226**:145-152.

Brown, S., and A. E. Lugo. 1990. Tropical Secondary Forests. Journal of Tropical Ecology **6**:1-32.

Chao, A., C.-H. Chiu, and T. Hsieh. 2012. Proposing a resolution to debates on diversity partitioning. Ecology **93**:2037-2051.

Chao, A., N. J. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, and A. M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs **84**:45-67.
Chao, A., L. Jost, S. Chiang, Y. H. Jiang, and R. L. Chazdon. 2008. A Two‐Stage Probabilistic Approach to Multiple‐Community Similarity Indices. Biometrics **64**:1178-1186.
Chao, A., and S.-Y. Lin. 2011. CLAM (Classification Method). http://purl.oclc.org/clam.
Chao, A., and T. J. Shen. 2012. SPADE (Species Prediction and Diversity Estimation). http://chao.stat.nthu.edu.tw.
Chazdon, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. Perspectives in Plant Ecology, Evolution and Systematics **6**:51-71.
Chazdon, R. L. 2008a. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science **320**:1458-1460.
Chazdon, R. L. 2008b. Chance and determinism in tropical forest succession. Tropical forest community ecology:384-408.
Chazdon, R. L., A. Chao, R. K. Colwell, S.-Y. Lin, N. Norden, S. G. Letcher, D. B. Clark, B. Finegan, and J. P. Arroyo. 2011. A novel statistical method for classifying habitat generalists and specialists. Ecology **92**:1332-1343.
Chazdon, R. L., S. G. Letcher, M. Van Breugel, M. Martínez-Ramos, F. Bongers, and B. Finegan. 2007. Rates of change in tree communities of secondary Neotropical forests following major disturbances. Philosophical Transactions of the Royal Society B: Biological Sciences **362**:273-289.
Chazdon, R. L., C. A. Peres, D. Dent, D. Sheil, A. E. Lugo, D. Lamb, N. E. Stork, and S. E. Miller. 2009. The potential for species conservation in tropical secondary forests. Conservation biology **23**:1406-1417.
Curtis, J. T. 1959. The vegetation of Wisconsin: an ordination of plant communities. University of Wisconsin Press.
Daly, C., E. H. Helmer, and M. Quiñones. 2003. Mapping the climate of Puerto Rico, Vieques and Culebra. International Journal of Climatology **23**:1359-1381.
Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. Annual review of ecology and systematics **18**:431-451.
Denslow, J. S., and G. Guzman. 2000. Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. Journal of Vegetation Science **11**:201-212.
Drake, B. G., M. A. Gonzàlez-Meler, and S. P. Long. 1997. More efficient plants: a consequence of rising atmospheric CO2? Annual review of plant biology **48**:609-639.
Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? Trends Ecol Evol **14**:135-139.

Dupuy, J. M., and R. L. Chazdon. 2006. Effects of vegetation cover on seedling and sapling dynamics in secondary tropical wet forests in Costa Rica. Journal of Tropical Ecology **22**:65-76.

Ewel, J. J., and J. L. Whitmore. 1973. Ecological life zones of Puerto Rico and US Virgin Islands. Ecological life zones of Puerto Rico and US Virgin Islands. US Department of Agriculture.

FAO. 2010. Global Forest Resources Assessment (FRA) 2010. Food and Agriculture Organization of the United Nations, Rome.

Fayolle, A., J.-L. Doucet, J.-F. Gillet, N. Bourland, and P. Lejeune. 2013. Tree allometry in Central Africa: Testing the validity of pantropical multi-species allometric equations for estimating biomass and carbon stocks. Forest Ecology and Management **305**:29-37.

Finegan, B. 1996. Pattern and process in neotropical secondary rain forests: the first 100 years of succession. Trends Ecol Evol **11**:119-124.

Frangi, J. L., and A. E. Lugo. 1985. Ecosystem dynamics of a subtropical floodplain forest. Ecological Monographs:351-369.

Gorchov, D. L., F. Cornejo, C. Ascorra, and M. Jaramillo. 1993. The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. Vegetatio **107**:339-349.

Guariguata, M. R., R. L. Chazdon, J. S. Denslow, J. M. Dupuy, and L. Anderson. 1997. Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. Plant Ecology **132**:107-120.

Guariguata, M. R., and R. Ostertag. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. Forest Ecology and Management **148**:185-206.

Held, M. E., and J. E. WInstead. 1975. Basal Area and Climax Status in Mesic Forest Systems. Annals of Botany **39**:1147-1148.

Helmer, E., O. Ramos, T. del MLópez, M. Quiñónez, and W. Diaz. 2002. Mapping the forest type and land cover of Puerto Rico, a component of the Caribbean biodiversity hotspot. Caribbean Journal of Science **38**:165-183.

Hobbs, R. J., S. Arico, J. Aronson, J. S. Baron, P. Bridgewater, V. A. Cramer, P. R. Epstein, J. J. Ewel, C. A. Klink, A. E. Lugo, D. Norton, D. Ojima, D. M. Richardson, E. W. Sanderson, F. Valladares, M. Vila, R. Zamora, and M. Zobel. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography **15**:1-7.

Hobbs, R. J., E. Higgs, and J. A. Harris. 2009. Novel ecosystems: implications for conservation and restoration. Trends Ecol Evol **24**:599-605.

Holdridge, L. R. 1967. Life zone ecology. Rev. edition edition. Tropical Science Center, San Jose, Costa Rica.

Hsieh, T. C., K. H. Ma, and A. Chao. 2014. iNEXT: An R package for interpolation and extrapolation in measuring species diversity., Unpublished manuscript.

Ingle, N. R. 2003. Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation. Oecologia **134**:251-261.

Johnson, E. A., and K. Miyanishi. 2008. Testing the assumptions of chronosequences in succession. Ecology Letters **11**:419-431.

Jost, L. 2006. Entropy and diversity. Oikos **113**:363-375.
Jost, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology **88**:2427-2439.
Kashian, D. M., W. H. Romme, D. B. Tinker, M. G. Turner, and M. G. Ryan. 2013. Postfire changes in forest carbon storage over a 300-year chronosequence of Pinus contorta-dominated forests. Ecological Monographs **83**:49-66.
Kennard, D. K. 2002. Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia. Journal of Tropical Ecology **18**:53-66.
Letcher, S. G., and R. L. Chazdon. 2009. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. Biotropica **41**:608-617.
Little, E., Woodbury, R. & Wadsworth, F. (1974) Trees of Puerto Rico and the Virgin Islands. Second volume. Agriculture Handbook, US Department of Agriculture.
Little, E. L., and F. H. Wadsworth. 1964. Common trees of Puerto Rico and the Virgin Islands. US Department of Agriculture, Agriculture Handbook **249**:428-429.
Longwood, F. R. 1961. Puerto Rican woods; their machining, seasoning and related characteristics. USDA Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA, USA.
Lugo, A. E. 2004. The outcome of alien tree invasions in Puerto Rico. Frontiers in Ecology and the Environment **2**:265-273.
Lugo, A. E. 2009. The Emerging Era of Novel Tropical Forests. Biotropica **41**:589-591.
Lugo, A. E., and C. T. R. Batlle. 1987. Leaf production, growth rate, and age of the palm Prestoea montana in the Luquillo Experimental Forest, Puerto Rico. Journal of Tropical Ecology:151-161.
Lugo, A. E., and E. Helmer. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. Forest Ecology and Management **190**:145-161.
Lugo López, M. A. 1995. Updated taxonomic classification of the soils of Puerto Rico, 1994.
Marin-Spiotta, E., R. Ostertag, and W. L. Silver. 2007. Long-term patterns in tropical reforestation: Plant community composition and aboveground biomass accumulation. Ecological Applications **17**:828-839.
Marin-Spiotta, E., and S. Sharma. 2013. Carbon storage in successional and plantation forest soils: a tropical analysis. Global Ecology and Biogeography **22**:105-117.
Marin-Spiotta, E., W. L. Silver, C. W. Swanston, and R. Ostertag. 2009. Soil organic matter dynamics during 80 years of reforestation of tropical pastures. Global Change Biology **15**:1584-1597.
Mascaro, J., G. P. Asner, D. H. Dent, S. J. DeWalt, and J. S. Denslow. 2012. Scale-dependence of aboveground carbon accumulation in secondary forests of Panama: A test of the intermediate peak hypothesis. Forest Ecology and Management **276**:62-70.

Neftel, A., E. Moor, H. Oeschger, and B. Stauffer. 2011. Evidence from polar ice cores for the increase in atmospheric CO2 in the past two centuries. The Warming Papers:403.

Norden, N., R. L. Chazdon, A. Chao, Y. H. Jiang, and B. Vílchez ‐ Alvarado. 2009. Resilience of tropical rain forests: tree community reassembly in secondary forests. Ecology Letters **12**:385-394.

Pascarella, J. B., T. M. Aide, M. I. Serrano, and J. K. Zimmerman. 2000. Land-use history and forest regeneration in the Cayey Mountains, Puerto Rico. Ecosystems **3**:217-228.

Pascarella, J. B., T. Mitchell Aide, and J. K. Zimmerman. 2004. Short-term response of secondary forests to hurricane disturbance in Puerto Rico, USA. Forest Ecology and Management **199**:379-393.

Peet, R. K. 1992. Community structure and ecosystem function. Pages 103-151 *in* D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. Plant succession: theory and prediction. Chapman & Hall, London,New York.

Peterson, T. C., M. A. Taylor, R. Demeritte, D. L. Duncombe, S. Burton, F. Thompson, A. Porter, M. Mercedes, E. Villegas, and R. Semexant Fils. 2002. Recent changes in climate extremes in the Caribbean region. Journal of Geophysical Research: Atmospheres (1984–2012) **107**:ACL 16-11-ACL 16-19.

Pickett, S. T. 1988. Space-for-time substitution as an alternative to long-term studies. Pages 110-135 Long-term studies in ecology. Springer.

Poffenberger, M. 2006. People in the forest: community forestry experiences from Southeast Asia. International Journal of Environment and Sustainable Development **5**:57-69.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reyes, G., S. Brown, J. Chapman, and A. E. Lugo. 1992. Wood densities of tropical tree species. USDA Forest Service, Southern Forest Experiment Station, Institute of Tropical Forestry, New Orleans, LA, USA.

Rudel, T. K., M. Perez-Lugo, and H. Zichal. 2000. When fields revert to forest: development and spontaneous reforestation in post-war Puerto Rico. The Professional Geographer **52**:386-397.

Saldarriaga, J. G., D. C. West, M. Tharp, and C. Uhl. 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. The Journal of Ecology:938-958.

SAS. 1989-2014. JMP Pro, Version 11. SAS Institute Inc., Cary, NC.

SERCC. 2014. Southeast Regional Climate Center. http://www.sercc.com.

The Plant List (2013) The Plant List. http://www.theplantlist.org.

Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography **33**:2-22.

Turrell, F., S. Austin, D. McNee, and W. Park. 1967. Thermal conductivity of functional citrus tree wood. Plant physiology **42**:1025-1034.

Uriarte, M., C. D. Canham, J. Thompson, J. K. Zimmerman, and N. Brokaw. 2005. Seedling recruitment in a hurricane ‐ driven tropical forest: light limitation, density ‐ dependence and the spatial distribution of parent trees. Journal of Ecology **93**:291-304.
van Breugel, M., J. Ransijn, D. Craven, F. Bongers, and J. S. Hall. 2011. Estimating carbon stock in secondary forests: decisions and uncertainties associated with allometric biomass models. Forest Ecology and Management **262**:1648-1657.
Weaver, P. L. 1993. Micropholis chrysophylloides Pierre Caimitillo. USDA Forest Service, Southern Forest Experiment Station, New Orleans, LA, USA.
Weaver, P. L., and A. J. R. Gillespie. 1992. Tree biomass equations for the forests of the Luquillo Mountains, Puerto Rico. Commonwealth Forestry Review **71**:35-39.
Wright, S. J., and H. C. Muller ‐ Landau. 2006. The Future of Tropical Forest Species. Biotropica **38**:287-301.
Yanai, R. D., M. A. Arthur, T. G. Siccama, and C. A. Federer. 2000. Challenges of measuring forest floor organic matter dynamics:: Repeated measures from a chronosequence. Forest Ecology and Management **138**:273-283.
Zanne, A., G. Lopez-Gonzalez, D. Coomes, J. Ilic, S. Jansen, S. Lewis, R. Miller, N. Swenson, M. Wiemann, and J. Chave. 2009. Global wood density database. Dryad. Identifier: http://hdl.handle.net/10255/dryad.
Zimmerman, J. K., J. B. Pascarella, and T. M. Aide. 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. Restoration Ecology **8**:350-360.

Chapter 2 Tables and Figures

Table 1. Allometric models used to estimate total aboveground biomass

Model	Equation	Application	Source
WG	TAB = 4.7306 - 2.8566 x (dbh) + 0.5832 x (dbh^2)	Tabonuco forest (all trees)	Weaver & Gillespie, 1992
FL	TAB = 6.4 x (total ht) - 10.0	*Prestoea acuminata var. montana*	Frangi & Lugo, 1985
VB§	ln(TAB) = -1.130 + 2.267 x ln(dbh) + 1.186 x ln(ρ)	Model 2 (M2) for multiple species	van Breugel, et al. 2011

Palm height correction based on verification of heights of 63 palms	r2	p-value
Corrected Ht = -1.119051 + 1.2615696 * Estimated Ht	0.90543	p<0.0001

*includes correction factor: CF = exp(RSE^2/2)

§ includes correction factor: CF = $e^{0.5xMSE}$

TABLE 2. Summary data for each site in 2003 and 2012

Site	Age-2003	Age-2012	Nr. Individuals-2003	Nr. Individuals-2012	Nr. Stems-2003	Nr. Stems-2012	Stem density (stems/ha)-2003	Stem density (stems/ha)-2012	Basal area (m2/ha)-2003	Basal area (m2/ha)-2012	Mean stem basal area (m2/ha)-2003	Mean stem basal area (m2/ha)-2012	% Stems represented by palms-2003	% Stems represented by palms-2012	Nr. Species at each site-2003	Nr. Species at each site-2012	Morisita-Horn Dissimilarity 2003 vs 2012
8	10	19	12	39	13	41	226	712	3.34	12.07	0.26	0.29	0	0	4	5	0.066
67	10	19	4	33	4	33	69	573	0.68	7.95	0.17	0.24	0	0	3	4	0.290
68	10	19	1	17	1	17	17	295	0.14	3.75	0.14	0.22	0	0	1	5	0.348
26	20	29	33	35	41	40	712	694	25.41	30.69	0.62	0.77	2	5	7	8	0.009
78	20	29	40	51	46	56	799	972	28.68	34.89	0.62	0.63	0	0	9	10	0.026
79	20	29	55	75	59	80	1024	1389	16.97	25.44	0.29	0.32	0	0	2	2	0.000
7	30	cleared	45	cleared	48	cleared	833	cleared	14.64	cleared	0.31	cleared	0	cleared	9	cleared	NA
50	30	39	66	102	70	109	1215	1892	18.56	34.72	0.27	0.32	0	0	3	3	0.000
77	30	39	63	87	63	87	1094	1510	17.48	27.75	0.28	0.32	0	8	3	4	0.007
32	60	69	50	62	59	70	1024	1215	35.91	43.87	0.61	0.63	39	54	12	11	0.052
33	60	69	61	92	67	98	1163	1701	32.16	44.77	0.48	0.46	19	40	12	11	0.205
38	60	69	47	60	60	64	1042	1111	29.42	31.82	0.49	0.50	3	22	12	9	0.363
5	80	89	59	73	71	85	1233	1476	32.65	41.30	0.46	0.49	1	7	16	17	0.099
23	80	89	60	68	64	71	1111	1233	53.77	53.51	0.84	0.75	23	44	13	9	0.201
28	80	89	65	72	66	74	1146	1285	54.35	60.39	0.82	0.82	41	49	13	11	0.024
88	Reference	Reference	53	66	53	67	920	1163	30.44	40.97	0.57	0.61	30	30	13	10	0.028
89	Reference	Reference	63	68	63	68	1094	1181	30.35	28.85	0.48	0.42	83	81	7	9	0.002
90	Reference	Reference	44	44	44	44	764	764	25.93	28.67	0.59	0.65	36	36	13	12	0.074

Table 3. Deviations in observed importance value (IV) changes from expectations based on 2003 across-age data in 13 most important species

CLAM classification-based on distributions of species in secondary forests vs reference forests in 2003	CLAM classification-based on distributions of species in early vs late secondary forests in 2003	2003 rank in overall IV	Species	10 to 19 years	20 to 29 years	30 to 39 years	60 to 69 years	80 to 89 years	Reference 2003 to Reference 2012
Secondary	Early Secondary	1	*Tabebuia heterophylla*	✓	✓	+	-	✓	NP
Reference	Late Secondary	2	*Prestoea acuminata*	-	+	✓	+	✓	-0.038814557
Generalist	Generalist	3	*Cecropia schreberiana*	-	+	-	-	✓	-0.00987397
Generalist	Late Secondary	4	*Syzygium jambos*	✓	✓	-	-	✓	-0.012117652
Secondary	Generalist	5	*Schefflera morototoni*	+	✓	-	✓	✓	0.071739262
Secondary	Late Secondary	6	*Inga laurina*	+	-	-	✓	✓	-0.002209056
Generalist	Late Secondary	7	*Casearia arborea*	NP	-	-	✓	✓	0.008992644
R	Late Secondary	8	*Alchornea latifolia*	-	+	-	✓	✓	-0.004209882
Secondary	Late Secondary	9	*Ocotea leucoxylon*	✓	✓	-	✓	✓	-0.009158369
Reference	R	10	*Dacryodes excelsa*	NP	NP	NP	NP	✓	0.042826154
R	R	11	*Buchenavia tetraphylla*	NP	NP	-	-	+	-0.040011548
Reference	R	12	*Micropholis guyanensis*	NP	NP	NP	-	✓	-0.034833813
R	Generalist	13	*Cyathea arborea*	✓	+	✓	-	✓	NP

✓ indicates that observed direction of change (i.e., positive or negative) in IV within age class from 2003 to 2012 matched expected change based on comparison with next-oldest age class in 2003 chronosequence

– indicates that observed change in IV within age class from 2003 to 2012 was negative when expected change based on comparison with next-oldest age class in 2003

+ indicates that observed change in IV within age class from 2003 to 2012 was positive when expected change based on comparison with next-oldest age class in 2003

R=too rare to classify

NP=not present at either survey

*PRAC,CESC,ALLA not present in 10/19 yr class

*INLA,CAAR not present in 20/29 yr class

*CESC,SYJA,ALLA,BUTE not present in 30/39 yr class

*MIGU,CYAR not present in 60/69 yr class

Values in Ref 2003 to Ref 2012 column are actual changes in IV

Table 4. Total aboveground biomass by site in 2003 and 2012 (Mg/ha)

Site	Age in 2003	Age in 2012	2003 WGFL estimate	2003 VBFL estimate	2012 WGFL estimate	2012 VBFL estimate
8	10	19	17.20	15.15	64.10	54.18
67	10	19	3.16	3.39	40.74	39.36
68	10	19	0.61	0.57	18.73	14.81
26	20	29	150.50	136.30	185.03	165.41
78	20	29	173.58	122.23	209.05	111.63
79	20	29	90.13	79.04	137.31	120.42
7	30	cleared	78.71	71.14	cleared	cleared
50	30	39	96.80	85.23	187.90	164.69
77	30	39	91.85	80.70	135.11	118.63
32	60	69	160.75	131.72	183.39	157.66
33	60	69	152.53	113.78	190.10	143.42
38	60	69	167.41	152.20	160.13	143.58
5	80	89	186.75	187.41	233.91	236.51
23	80	89	292.10	247.35	270.19	230.25
28	80	89	284.05	275.16	323.09	313.65
88	Ref	Ref	156.07	128.49	215.58	173.27
89	Ref	Ref	78.42	74.25	78.39	73.14
90	Ref	Ref	133.14	131.05	151.34	148.14

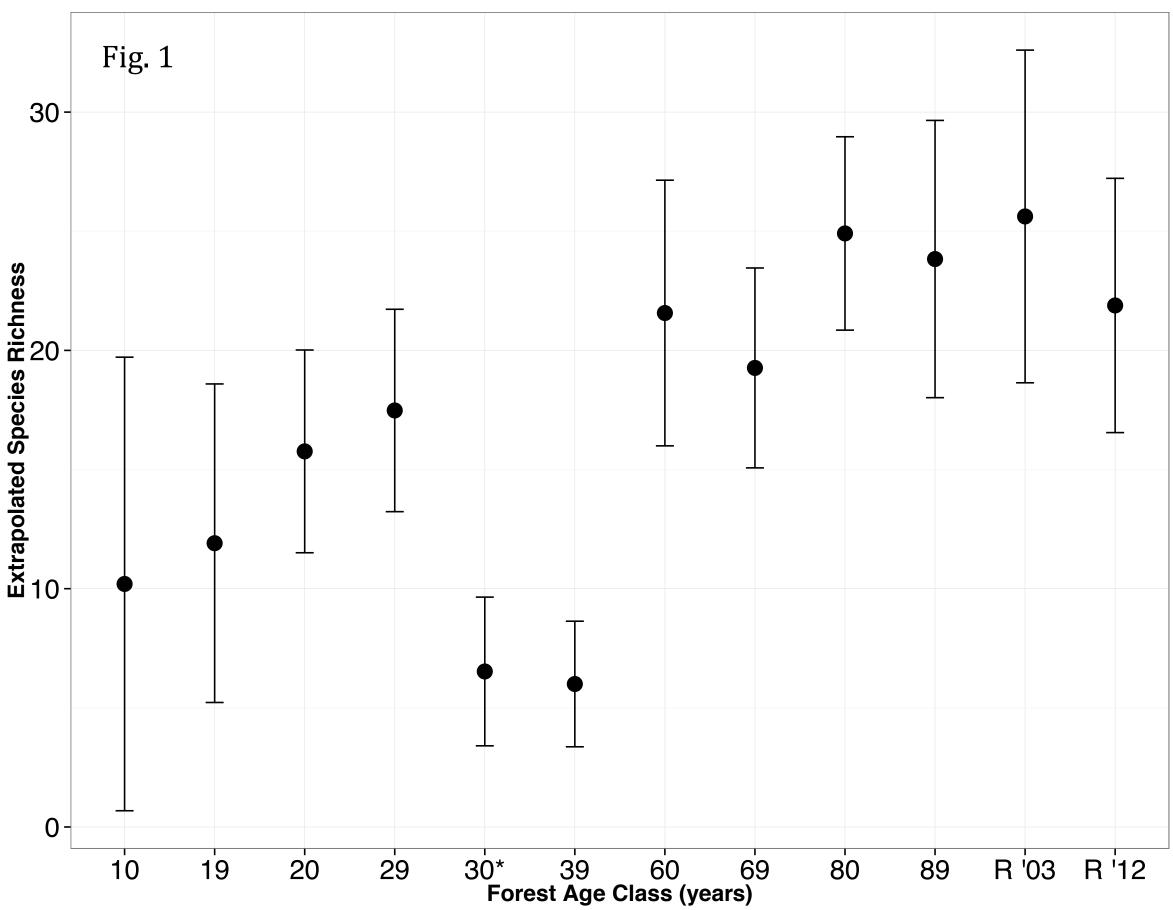

Fig. 1: Extrapolated species richness values (sample size 186). Dots are means and bars are 95% confidence intervals. *The lost site (site 7) was excluded from this class for comparison.

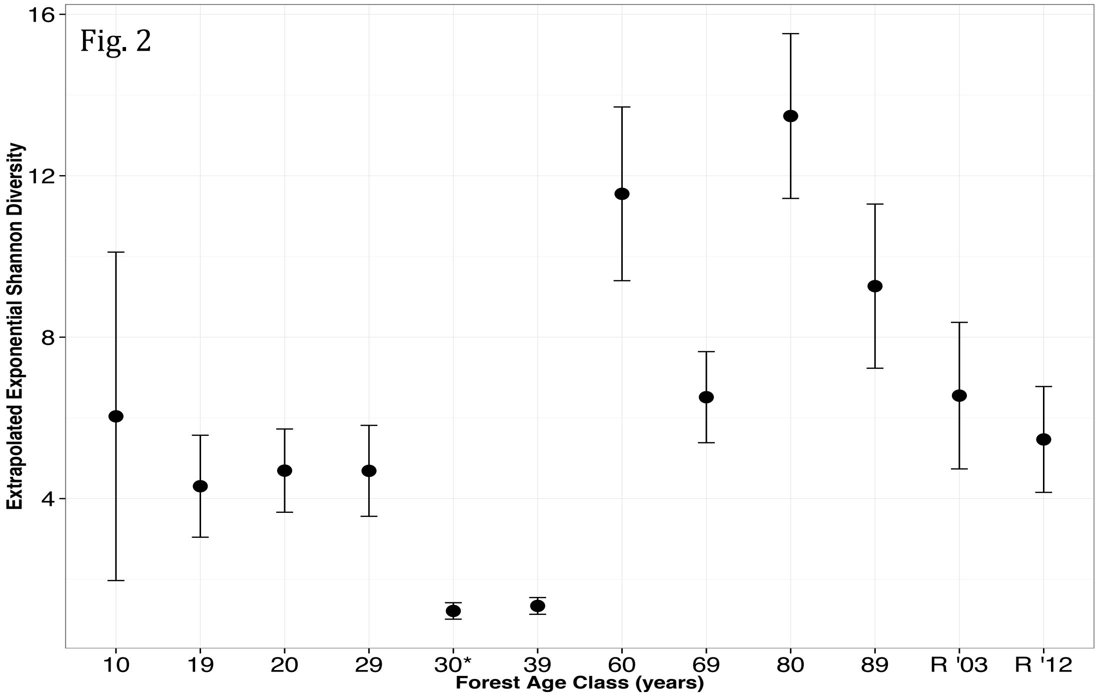

Fig. 2: Extrapolated exponential Shannon's diversity values (sample size 186). Dots are means and bars are 95% confidence intervals. *The lost site (site 7) was excluded from this class for comparison.

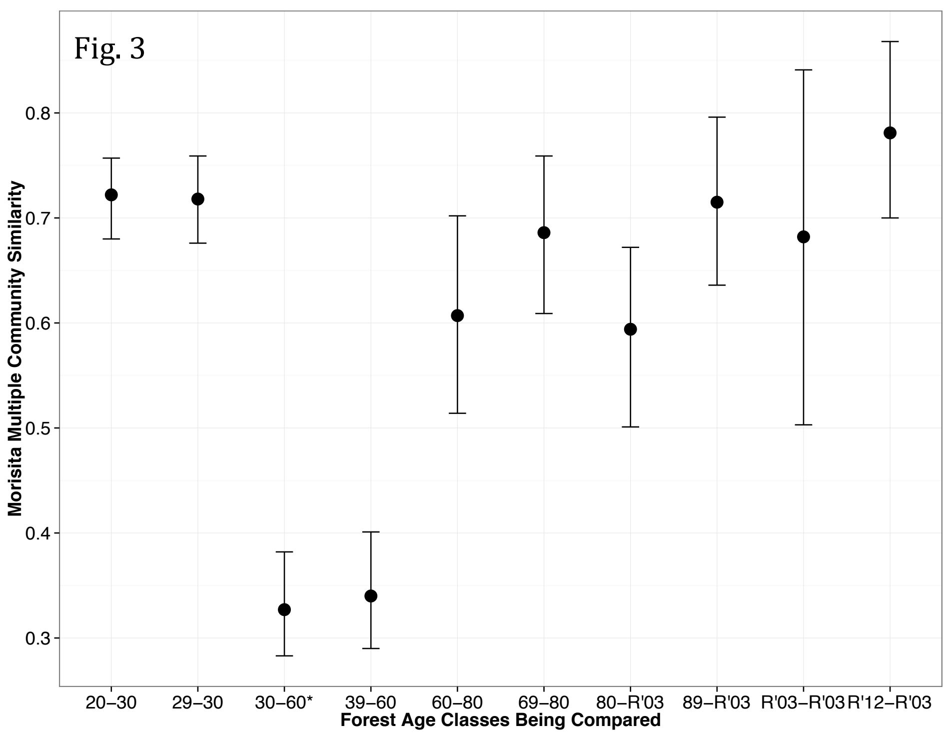

Fig. 3: Cross-age comparisons in Multiple Morisita Community Similarity (MMCS) showing how age classes change in similarity relative to the next-oldest class in 2003. *The lost site (site 7) was excluded from this class for comparison.

Fig. 4

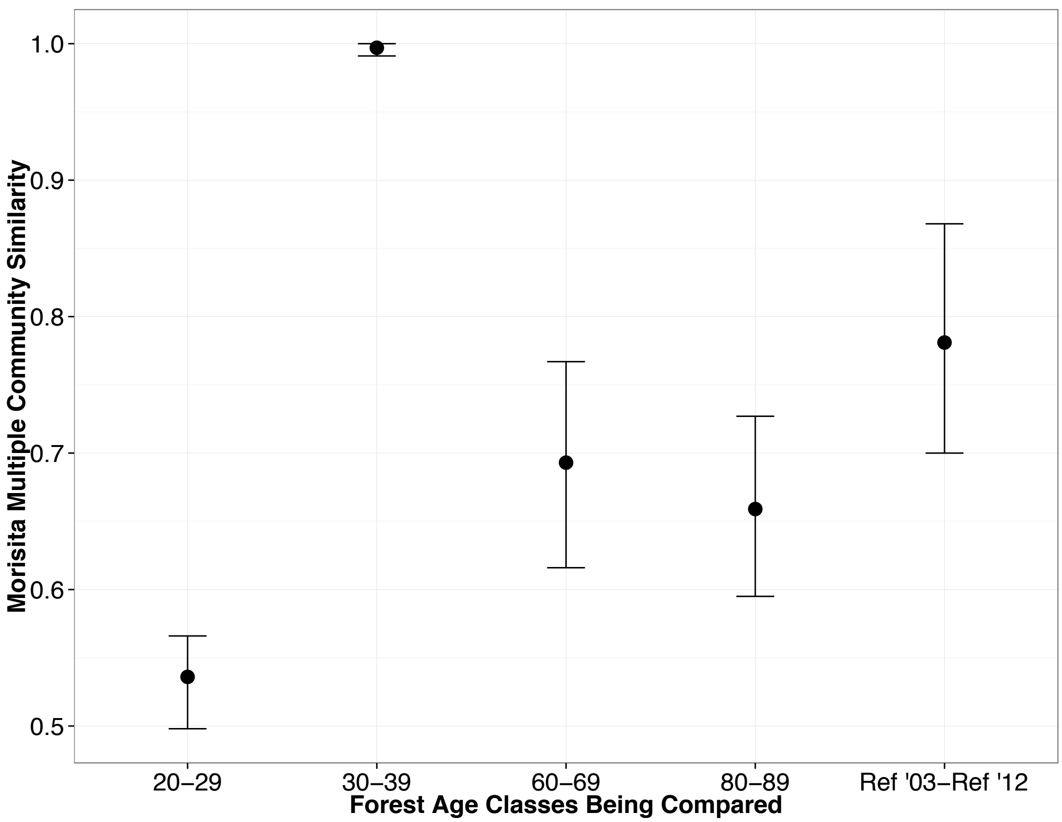

Fig. 4: Within-age comparisons in Multiple Morisita Community Similarity (MMCS) showing relative change in communities. *The lost site (site 7) was excluded from this class for comparison.

Fig. 5a

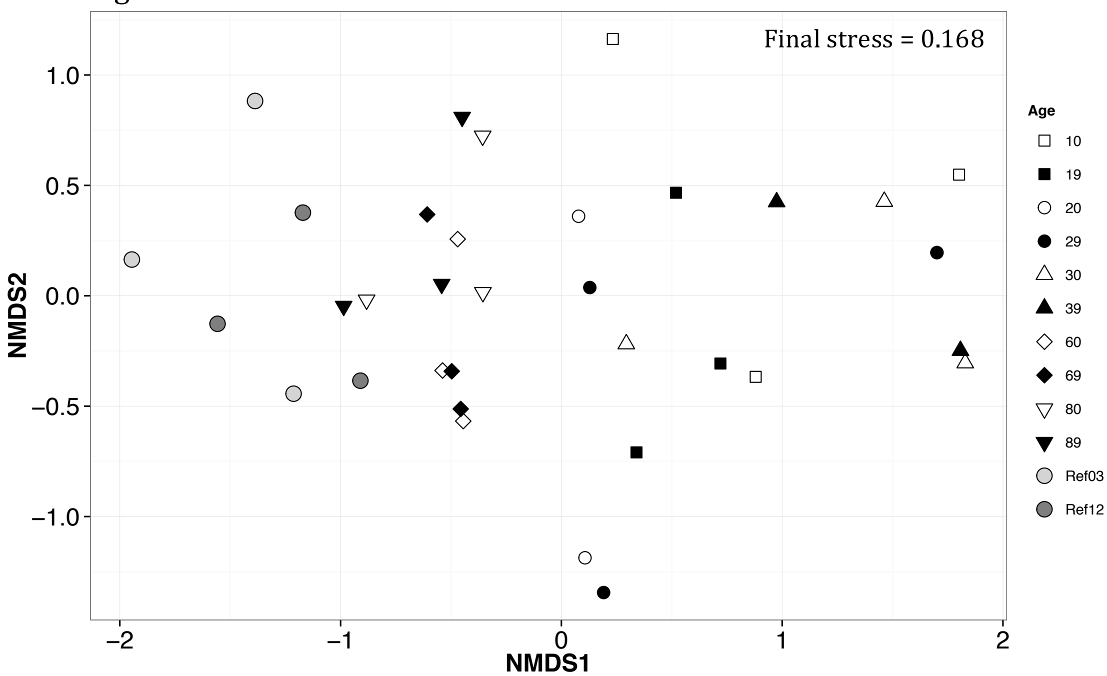

Fig. 5b

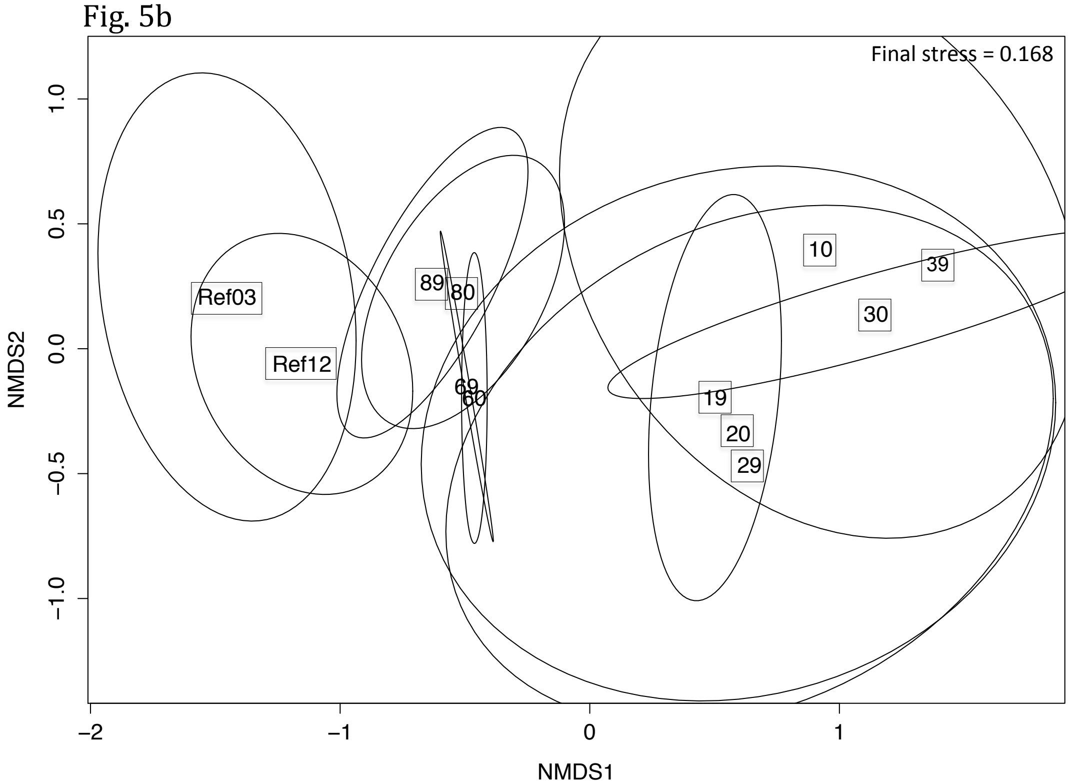

Fig. 5a: NMDS analysis of species abundances in each site in 2003 and 2012 based on Chao-Jaccard dissimilarity measure scores. **Fig. 5b:** same NMDS plot but with 95% confidence interval ellipses and centroids included to aid in interpretation. The 39-year-old class doesn't have an ellipse because there were only 2 sites in this class. Centroid boxes purposefully excluded for the 60- and 69-year-old classes.

General Conclusion

For this project, I collected data in 2012 from a well-replicated chronosequence of naturally-regenerated tropical forests on abandoned pastureland in Puerto Rico to characterize changes in species composition, structure and aboveground biomass accumulation over 89 years of succession. Based on comparisons with reference forest plots, I determined approximate ages by which these important forest components returned to pre-disturbance conditions. Then, to test whether or not my data supported the predictions based on chronosequence data from 2003, I compared my observations from 2012 with predicted changes based on patterns of changes seen across age classes at the same sites in 2003.

I showed that tropical forests rapidly recover structural characteristics of pre-disturbance forests. In general, total aboveground biomass also showed rapid recovery, though different methods for estimating biomass stocks affected how biomass changed with age. Though species diversity also exhibited rapid recovery to pre-disturbance levels with age, species assemblages remained distinct from communities in reference forests after 89 years. These findings support the results of other studies of tropical forest succession.

Comparisons of changes observed from 2003 to 2012 with changes predicted from the chronosequence in 2003 yielded mixed results. Though the 2003 chronosequence correctly predicted changes in some forest age classes, it failed to correctly predict many of the observed changes in forest structure, biomass and species composition within age classes. Cross-age-class changes in species communities seen in 2012 suggested a deterministic model of community changes with age in older secondary forests. Patterns across younger classes revealed more stochastic trajectories. Comparison of 2012 and 2003 data provided support for the interpretation that deterministic processes were more important in older secondary forests, with stochasticity playing a stronger role in the successional trajectories of younger forests. This implies that chronosequence-based predictions may be more applicable to some age classes or to some communities exhibiting equilibrium dynamics.

While chronosequence studies can successfully indicate future changes in secondary forests, they should ideally be combined with repeated visits to capture unpredictable effects of random factors that can shape successional pathways.

With continued changes in land use across the globe, the importance of tropical secondary forests for conservation and provision of ecosystem services and functioning will only increase. This study sheds light on how we can expect these forests to change and function with age, and it provides insights for researchers who depend on chronosequences to study these increasingly important ecosystems.

Appendix

Table A1: Species list and wood specific gravity values

Plant Status	Family	Species	Wood specific gravity (g cm^{-3})	Source
N	Euphorbiaceae	*Alchornea latifolia* Sw.	0.427	1
N	Leguminosae	*Andira inermis* (Wright) DC.	0.643	1
N	Combretaceae	*Buchenavia tetraphylla* (Aubl.) R.A. Howard	0.619	1; Reyes, et al. 1992
N	Salicaceae	*Casearia arborea* (Rich.) Urb.	0.574	1
N	Rhizophoraceae	*Cassipourea guianensis* Aubl.	0.820	1
N	Salicaceae	*Casearia sylvestris* Sw.	0.705	1
N	Urticaceae	*Cecropia schreberiana* Miq.	0.290	Little & Wadsworth, 1964
N	Sapotaceae	*Chrysophyllum argenteum* Jacq.	0.784	1
N	Verbenaceae	*Citharexylum spinosum* L.	0.757	1
I	Rutaceae	*Citrus paradisi* Macfad.	0.708	Turrell, et al. 1967
I	Rutaceae	*Citrus* spp.	0.746	Turrell, et al. 1967 (mean of 4 commercial spp.)
N	Clusiaceae	*Clusia* spp.	0.668	1
N	Boraginaceae	*Cordia alliodora* (Ruiz & Pav.) Oken	0.520	1
EN	Boraginaceae	*Cordia borinquensis* Urb.	0.700	1
N	Boraginaceae	*Cordia collococca* L.	0.420	1
N	Polygonaceae	*Coccoloba diversifolia* Jacq.	0.800	1
N	Boraginaceae	*Cordia* spp.	0.510	1
N	Boraginaceae	*Cordia sulcata* A. DC.	0.600	1
N	Polygonaceae	*Coccoloba swartzii* Meisn.	0.700	1
N	Cyatheaceae	*Cyathea arborea* (L.) Sm.	N/A	N/A
N	Burseraceae	*Dacryodes excelsa* Vahl	0.480	1
N	Araliaceae	*Dendropanax arboreus* (L.) Decne. & Planch.	0.420	1
N	Myrtaceae	*Eugenia confusa* DC.	0.810	1
EN	Myrtaceae	*Eugenia stahlii* (Kiaersk.) Krug & Urb.	0.730	1
N	Moraceae	*Ficus citrifolia* Mill.	0.440	1; Longwood, 1961
N	Moraceae	*Ficus* spp.	0.412	1
N	Meliaceae	*Guarea guidonia* (L.) Sleumer	0.565	1
N	Euphorbiaceae	*Gymnanthes lucida* Sw.	1.100	1
EN	Chrysobalanaceae	*Hirtella rugosa* Thuill. Ex Pers.	0.900	1
N	Salicaceae	*Homalium racemosum* Jacq.	0.795	1
N	Leguminosae	*Inga laurina* (Sw.) Willd.	0.665	1
N	Leguminosae	*Inga vera* Willd.	0.575	1
N	Sabiaceae	*Meliosma herbertii* Rolfe	0.420	1
N	Sapotaceae	*Micropholis guyanensis* (A. DC.) Pierre	0.669	1; Weaver, 1993
N	Melastomataceae	*Miconia* spp.	0.623	1
N	Melastomataceae	*Miconia tetrandra* (Sw.) D. Don ex G. Don	0.700	1
N	Myrtaceae	*Myrcia deflexa* (Poir.) DC.	0.800	1
N	Myrtaceae	*Myrcia amazonica* DC.	0.820	1
N	Myrtaceae	*Myrcia splendens* (Sw.) DC.	0.800	1
N	Myrtaceae	*Myrcia* spp	0.811	1
N	Lauraceae	*Ocotea floribunda* (Sw.) Mez	0.395	1
N	Lauraceae	*Ocotea leucoxylon* (Sw.) Laness.	0.462	1
N	Leguminosae	*Ormosia krugii* Urb.	0.500	1
N	Ochnaceae	*Ouratea striata* (Tiegh.) Urb.	0.727	1
N	Myrtaceae	*Pimenta racemosa* (Mill.) J.W. Moore	0.900	1
N	Arecaceae	*Prestoea acuminata* var. *montana* (Graham) A.J. Hend. & Galeano	N/A	N/A
EN	Euphorbiaceae	*Sapium laurocerasus* Desf.	0.380	1
N	Araliaceae	*Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin	0.456	1
N	Elaeocarpaceae	*Sloanea berteroana* Choisy ex DC.	0.800	1
I	Bignoniaceae	*Spathodea campanulata* P. Beauv.	0.351	1
I	Myrtaceae	*Syzygium jambos* (L.) Alston	0.700	1
N	Bignoniaceae	*Tabebuia heterophylla* (DC.) Britton	0.566	1
N	Staphyleaceae	*Turpinia occidentalis* (Sw.) G. Don	0.335	1
N	Lamiaceae	*Vitex divaricata* Sw.	0.620	1
N	Rutaceae	*Zanthoxylum martinicense* (Lam.) DC.	0.602	1

Plant status key: EN = endemic, N = native, I = naturalized

1 = Zanne, et al. Global wood density database. Dryad. Identifier: http://hdl.handle.net/10255/dryad.235

Species names based on Little and Wadsworth, 1964 & Little et al., 1974 with updated names from *The Plant List* (2013). http://www.theplantlist.org

Where multiple wood specific gravity values were reported, average values were used. Genus-level averages were used if species-specific values were unavailable.